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An Evaluation of Freshwater Mussels in the Lower Ohio River in Relation to the Olmsted Locks and Dam Project: 1998 Studies

by *Barry S. Payne, Andrew C. Miller*

Prepared for U.S. Army Engineer District, Louisville

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Preface

The study herein was conducted by the U.S. Army Engineer Research and Development Center (ERDC) Environmental Laboratory (EL), Vicksburg, MS, in 1998 for the U.S. Army Engineer District, Louisville, Louisville, KY. The purpose was to analyze spatial distribution, density, recruitment, and community composition of mussels in prominent beds in the lower Ohio River in relation to construction and operation of the Olmsted Locks and Dam Project.

Divers for this study were from the Tennessee Valley Authority and included Messrs. Larry Neill, Robert James, Dennis Baxter, and William Fraley. Assistance in the field was provided by Mr. Will Green, University of Southern Mississippi. Dr. Andrew C. Miller was the diving inspector for this work. Assistance in the laboratory was provided by Ms. Katheryn Barko, University of Wisconsin at Stevens Point.

During the conduct of this study, Drs. John W. Keeley and John Harrison were Director, EL; Dr. Conrad J. Kirby was Chief, Ecological Resources Division (ERD), EL; and Drs. Alfred F. Cofrancesco and Edwin A. Theriot were Chief, Aquatic Ecology Branch (AEB), ERD. Authors of this report were Drs. Barry S. Payne and Andrew C. Miller, AEB.

At the time of publication of this report, Dr. Lewis E. Link was Acting Director of ERDC, and COL Robin R. Cababa, EN, was Commander.

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1 Introduction

Background

The U.S. Army Engineer District, Louisville, is replacing Locks and Dams 52 and 53 in the lower Ohio River (LOR) with a new structure located slightly downstream of Lock and Dam 53 (U.S. Army Corps of Engineers 1991) near Olmsted, Illinois. The structure being built will consist of two 110-ft[1] by 1,200-ft locks, a 2,200-ft-wide navigable pass controlled by remotely operated hydraulic wickets, and a short section of fixed weir connecting the project to the Kentucky shore. The new locks will be on the right-descending bank (RDB) on the Illinois side of the river. During periods of normal and low flow, navigation will pass through the locks. During high flow, vessels will use the navigable pass near the center of the channel. The new project, now being constructed, is at River Mile (RM) 964.4. Existing Lock and Dam 53 is at RM 962.8, and existing Lock and Dam 52 is at RM 938.9.

Once completed, the Olmsted project will increase water levels by a maximum of 10 ft in the pool above the dam for approximately 42 percent of the year. This increased stage will occur only during normal and low flow. During high-water periods (58 percent of the year), dam sections will be lowered to a horizontal position on the river bottom. Upriver stage will be similar to preproject conditions when these dam sections are down. In addition to upstream changes, the hydraulic regimen immediately downstream of the new structure will be altered, as will navigation traffic patterns. Commercial vessels will have to pass close to the RDB when entering or exiting the lock. During high water, commercial vessels will operate in the thalweg at RM 964.4, as they have always done.

Potential changes in hydraulics and traffic patterns immediately downriver of the new project are of special interest with respect to a dense and diverse bed of mussels that begins at approximately RM 966 and extends several miles downstream (Payne, Miller, and Shafer 1994; Payne and Miller 1997). This bed includes the endangered species *Plethobasus cooperianus* (U.S. Fish and Wildlife Service 1991) and is heavily dominated by a single species, *Fusconaia ebena*. In addition, the bed and other species have economic, ecological, and cultural value deserving protection. Results of previous studies of this prominent mussel bed are included in publications by Williams (1969), Williams and Schuster (1982), Taylor (1989), Neff, Pearson, and Holdren (1981), Miller,

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[1] To convert feet to meters, multiply by 0.3048.

Payne, and Siemsen (1986), Miller and Payne (1988), Miller and Payne (1991), Payne and Miller (1989), Payne, Miller, and Shafer (1994), and Payne and Miller (1997).

River hydraulics determine sedimentation, substratum type, bed stability, and, therefore, where a mussel bed can exist in a large river (Coker et al. 1921). Long-term stability of a mussel bed depends on clay, silt, and sand deposited during seasonal low flows being removed by subsequent high flows without eroding underlying gravel and cobble. Reproduction and recruitment of *Fusconaia ebena* (Lea) potentially relates to hydraulic conditions in several ways. Sperm released by males must be entrained in water currents drawn through the mantle cavities of nearby females. Low-water velocity associated with low discharge might enhance fertilization success (Yokely 1972). In contrast, high discharge in spring attracts spawning aggregations of *Alosa chyrsochloris*, the only host fish of *F. ebena* glochidia (Coker et al. 1921; Surber 1913), to swiftly flowing water over gravelly shoals (Wallus, Yeager, and Simon 1990). In turn, depositional conditions probably benefit settlement of juvenile mussels after the 1- to 3-week period typically required for metamorphosis (Coker et al. 1921; Howard 1914). Juvenile *F. ebena* probably settle at a length of approximately 0.15 mm (Howard 1914) and are thus susceptible to being swept downstream during high discharge.

Planning and construction of the Olmsted Locks and Dam Project have been the basis of regular quantitative sampling of a prominent mussel bed in a mainstream shoal since 1983. *Fusconaia ebena* heavily dominates the LOR mussel community (Miller, Payne, and Siemsen 1986); relative abundance of the dominant typically varies from 70 to 90 percent. The dominant population is characterized by extreme annual variation in recruitment success; approximately a decade ago, growth and survival of a cohort of 1981 recruits that dominated the population during the 1980s were described (Payne and Miller 1989). Continued monitoring has yielded additional information on growth and survival of that important cohort and a much longer record of annual variation in recruitment.

Purpose and Scope

The objective of the present study is to evaluate the spatial distribution of mussels in the bed downstream of the Olmsted project as well as selected locations in the upriver pool. In addition, recruitment patterns, community composition, and density of nonindigenous species, including the Asian clam, *Corbicula fluminea*, and the zebra mussel, *Dreissena polymorpha,* are characterized. Special emphasis is given to an evaluation of annual variation in recruitment of the dominant unionid, *F. ebena,* in relation to river hydraulic conditions. These quantitative data can be used to assess environmental effects of alterations of hydraulic regimen, commercial navigation traffic patterns, and benthic scour and deposition associated with construction and operation of the Olmsted project. It is anticipated that studies will continue until the project has operated for at least several years.

2 1998 Studies

Sites and Methods

Sampling was conducted 8-11 August 1998 at a major mussel bed (OLM bed) downriver of the Olmsted Locks and Dam Project between RM 967 and 969 and another bed (PC bed) upriver of the project near Post Creek (RM 956.5 and 957.6). At the OLM bed, four sites were quantitatively sampled 10 times each using 0.25-m^2 quadrats (Table 1). These sites were within a central portion of the bed between RM 967.3 and 967.5 and were spaced at approximately 100-m intervals along a line essentially parallel to the Illinois shoreline. Sites occurred within the elevation range of 274.4 to 276.8 ft. Thus, all were in the nearshore half of the bed, which ranges from approximately 266 ft farshore to 280 ft nearshore (Payne and Miller 1998). River stage (Cairo gauge) was 26.1 ft during quantitative sampling; at this stage, divers worked at depths of approximately 20 to 23 ft while sampling these sites on 8 August 1998. Sampling was conducted at these locations based on expectation of high mussel density given their proximity to Quantitative Sites I and II of July 1995 studies (Payne and Miller 1998). Those sites in 1995 had yielded unionid densities greater than 100 individuals per square meter.

Table 1
Position of Quantitative Sampling Sites in the Lower Ohio River at Olmsted, 8 August 1998

Site	Latitude	Longitude	Depth, ft	Elevation, ft	Number of Quadrats
I	3708.882	8905.769	20.3	276.8	10
II	3708.970	8905.734	22.7	274.4	11
III	3708.959	8905.778	21.0	276.1	10
IV	3708.924	8905.753	21.2	275.9	10

In addition, five sites were sampled semiquantitatively for unionids and quantitatively for zebra mussels (Table 2). Sites 1 and 2 were at intermediate elevations within the bed at RM 968.13 and 968.10, respectively. Site 3 was at RM 967.53 and within the bed, although near the farshore limit. Site 4 was at RM 967.48 and very near Quantitative Site I. Site 5 was at RM 967.29, within the bed, but date, depths, and elevations in Table 2 correspond to the position of the dive boat. At each site, one diver moved approximately 100 ft nearshore, and a second diver moved approximately 100 ft farshore, describing substratum and

Table 2
Site Positions for Semiquantitative Unionid and Quantitative Zebra Mussel Samples in the Lower Ohio River at Olmsted, 9 August 1998

Site	Latitude	Longitude	Depth, ft	Elevation ft	Unionid Samples (n)	Zebra Mussel Samples (n)
1	3708.291	8905.901	27.7	269.6	Nearshore (4) Farshore (4)	Nearshore (2) Farshore (2)
2	3708.341	8905.917	26.2	271.1	Nearshore (4) Farshore (4)	Nearshore (2) Farshore (2)
3	3708.798	8905.723	29.4	267.9	Nearshore (4) Farshore (4)	Nearshore (2) Farshore (2)
4	3708.860	8905.769	21.8	275.5	Nearshore (4) Farshore (4)	Nearshore (2) Farshore (2)
5	3709.034	8905.742	21.4	275.9	Nearshore (4) Farshore (4)	Nearshore (2) Farshore (2)

mussel density. At their final position, each diver removed all unionids (by feel) from substratum within four placements of a 0.25-m^2 quadrat. In addition, each diver obtained two samples of substratum using a 0.0625-m^2 quadrat for determinations of zebra mussel density.

Lastly, a single set of qualitative samples was collected for native mussels, followed by a 30-min search by each of two divers to collect all "non-*Fusconaia ebena*." Both efforts enhanced community composition data. Because *Fusconaia ebena* heavily dominates the OLM bed, collections of mussels that specifically exclude this species enhance the likelihood of obtaining locally rare species, including *Plethobasus cooperianus*.

At the PC bed, three sites were quantitatively sampled for native unionids by removing substratum with mussels from replicate (n = 10) 0.25-m^2 quadrats. These three sites were located nearshore, midshore, and farshore (Table 3). At both the nearshore and farshore locations, 10 substratum samples were removed from 0.0625-m^2 quadrats for determinations of zebra mussel density. Also at these two sites, a set of qualitative samples of native unionids were collected to more fully evaluate community composition. Qualitative sampling consisted of divers collecting, first in three sets of five mussels each and then in nine sets of 20 mussels each, all individuals encountered by touch.

Table 3
Site Positions for Samples of Unionids and Zebra Mussels in the Lower Ohio River at Post Creek, 10 August 1998

Site	Latitude	Longitude	Depth, ft	Elevation, ft	Samples
I	3713.840	8857.237	12.2		Unionid quantitative (10) Unionid qualitative ZM quantitative (10)
II	3713.839	8857.188	16.5		Unionid quantitative (10) Unionid qualitative ZM quantitative (10)
III	3713.806	8857.209	19.3		Unionid quantitative (10) Unionid qualitative ZM quantitative (10)

Results

Olmsted

Quantitative studies. The four sites quantitatively sampled at Olmsted in 1998 were heavily dominated by *F. ebena* (Tables 4 and 5). This species accounted for 95.9 percent of all unionids obtained. Recently recruited mussels (individuals less than 30 mm long) comprised only 1.8 percent of the community; however, half of the species collected were represented by at least one such recent recruit.

Table 4
Percent Abundance for Freshwater Mussels Collected at Four Sites at the Olmsted, IL, Bed, 1998

Species	Subsite 1	Subsite 2	Subsite 3	Subsite 4	Total
F. ebena	90.24	95.96	97.73	95.83	95.86
E. lineolata	1.63	1.08	0.28	1.60	1.04
Q. metanevra	0.00	0.27	0.85	0.64	0.52
Q. pustulosa	2.44	0.54	0.00	0.32	0.52
O. reflexa	0.81	0.81	0.28	0.00	0.43
A. plicata	2.44	0.00	0.28	0.32	0.43
Q. quadrula	1.63	0.00	0.28	0.00	0.26
O. olivaria	0.00	0.27	0.00	0.64	0.26
E. dilatata	0.00	0.00	0.00	0.64	0.17
Q. nodulata	0.00	0.54	0.00	0.00	0.17
M. nervosa	0.00	0.27	0.00	0.00	0.09
A. ligamentina	0.00	0.27	0.00	0.00	0.09
L. recta	0.81	0.00	0.00	0.00	0.09
C. tuberculata	0.00	0.00	0.28	0.00	0.09
Total individuals	123	371	353	312	1,159
Total species	7	9	7	7	14
% Individuals <30 mm	5.69	3.23	0	0.64	1.81
% Species <30 mm	28.57	66.67	0	28.57	50
Menhinick's index	0.63	0.47	0.37	0.4	0.41
Species diversity (H')	0.49	0.25	0.15	0.24	0.27
Evenness	0.25	0.11	0.07	0.12	0.1

Table 5
Frequency of Occurrence of Freshwater Mussels Collected at Four Sites at the Olmsted, IL, Bed, 1998

	Subsite 1	Subsite 2	Subsite 3	Subsite 4	Total
F. ebena	100.00	100.00	100.00	100.00	100.00
E. lineolata	20.00	40.00	10.00	50.00	30.00
Q. metanevra	0.00	10.00	20.00	20.00	12.50
Q. pustulosa	20.00	20.00	0.00	10.00	12.50
O. reflexa	10.00	30.00	10.00	0.00	12.50
A. plicata	20.00	0.00	10.00	10.00	10.00
Q. quadrula	20.00	0.00	10.00	0.00	7.50
O. olivaria	0.00	10.00	0.00	20.00	7.50
E. dilatata	0.00	0.00	0.00	10.00	2.50
Q. nodulata	0.00	20.00	0.00	0.00	5.00
M. nervosa	0.00	10.00	0.00	0.00	2.50
A. ligamentina	0.00	10.00	0.00	0.00	2.50
L. recta	10.00	0.00	0.00	0.00	2.50
C. tuberculata	0.00	0.00	10.00	0.00	2.50
Total samples	10	10	10	10	40

Because of the heavy dominance of *F. ebena*, diversity was extremely low, measuring just 0.27 (Shannon's index) and 0.41 (Menhinick's index). A total of 14 species were included among the 1,159 individuals collected. Evenness expresses Shannon's index as a fraction of maximum possible diversity, which corresponds to equal abundance of all species (Pileou 1969). In the case of 14 species, maximum diversity equals 2.64 (i.e, the natural logarithm of 14). Thus, eveness was only 0.10. By any measure, the community at Olmsted, although rich in species, is low in diversity because of the extreme dominance of *F. ebena*.

Native mussel density estimates at quantitative Sites II, III, and IV were very high; median values ranged from 125 to 130 individuals per square meter (Figure 1). Density at Site I was moderately high (44 individuals per square meter). The number of individuals obtained in a single 0.25-m^2 quadrat ranged from 0 (at Site I) to 75 (at Site II); however, that high value was an outlier at Site II.

Dominance of a single cohort was indicated in the size structure of the *F. ebena* population (Figure 2). The 1990 cohort ranged almost entirely from 36 to 64 mm and had an average length of approximately 52 mm. This single cohort comprised approximately 95 percent of the population. Total length range was 8 to 100 mm. Because of the extreme dominance of *F. ebena* in quantitative samples, no other native mussel was collected in sufficient numbers to warrant analysis of population-size demography.

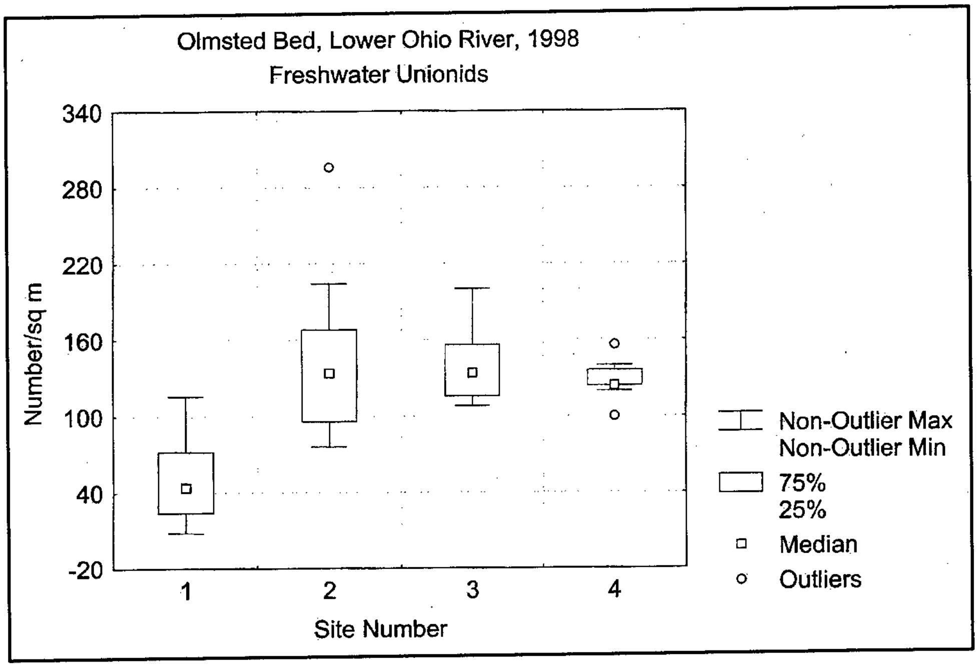

Figure 1. Native mussel density at the Olmsted mussel bed in the lower Ohio River, August 1998

Semiquantitative mapping. Sites 1 and 2 were located approximately at RM 968.1, and Sites 3, 4, and 5 ranged from approximately RM 967.6 to 967.2. Sites spanned an elevation range of 278.3 ft in the nearshore direction to approximately 268.8 ft in the farshore direction. Thus, all sites were within the mussel bed that spans from approximately 280 to 265 ft (Payne and Miller 1998). Average density per site ranged from only 4.0 mussels per square meter at the farshore location at Site 3 to 129.0 mussels per square meter at the farshore location at Site 4 (Table 6). Three of the ten sites had low density (<20 individuals per square meter). Five sites had moderate density (20-50 individuals per square meter). Two sites had high density (>50 individuals per square meter).

Substratum at Sites 1 and 2, both at nearshore and farshore dive locations, was coarse sand with some cobble. Site 3 at both dive positions was described as a relatively equal mix of coarse sand and gravel. Site 4 was similar to Site 3 but with slightly more gravel. Substratum at Site 4 was also similar to Sites 3 and 4, but had more cobble.

When combined with the results of recent surveys (Payne and Miller 1998), semiquantitative sampling indicated that the farshore and nearshore limits of the mussel bed at OLM were at approximately the 265- and 280-ft elevation contours, respectively (Figure 3). However, even within the central portion of the bed, spatial variation in density is considerable. Between elevations 268 and 276 ft, a total of 15 sites sampled semiquantitatively since 1995 have supported low density (<20 individuals per square meter). Sixteen sites between elevations 268 and 276 ft have supported moderate density (20-50 individuals per square meter); twenty sites have supported high density (>50 individuals per square meter). High mussel density has never been observed farshore of the 266-ft elevation contour or nearshore of the 277-ft contour.

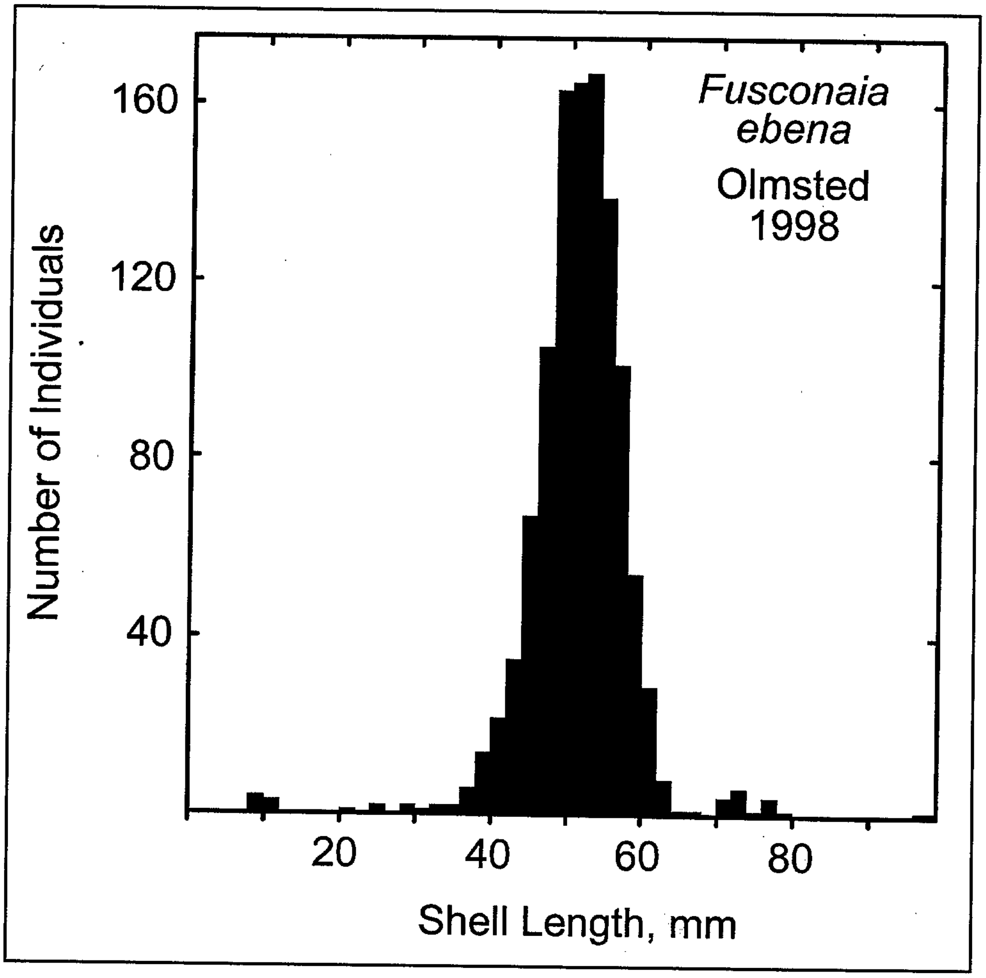

Figure 2. Length-frequency histogram for *Fusconaia ebena* in quantitative samples at Olmsted, August 1998

Fusconaia ebena heavily dominated semiquantitative samples, with relative abundance ranging from 75.8 percent at the nearshore location at Site 5 to 100.0 percent at the nearshore location at Site 3 (Table 6). A total of nine species were represented among 415 mussels collected by semiquantitative sampling; no species were obtained that were not represented among quantitative samples. Approximately 89 percent of all *F. ebena* ranged from 34 to 61 mm and were members of the heavily dominant 1990 cohort. The average length of mussels of the 1990-year class was approximately 50 mm, based on the length-frequency histogram of individuals obtained by semiquantitative sampling (Figure 4). The total length range was 30 to 90 mm.

Qualitative studies. A total of 12 species of native mussels were represented among 180 individuals collected qualitatively (Table 7). Although *F. ebena* heavily dominated (73 percent), dominance was less than indicated by more objective quantitative or semiquantitative methods. *Quadrula pustulosa* was moderately abundant, comprising 7.8 percent of the qualitative sample of the unionid community. *Plethobasus cyphyus* was obtained in qualitative but not quantitative samples. Thus, a total of 15 species were represented among 1,754 individuals collected by all methods in 1998.

Table 6
Native Mussels from Semiquantitative Samples, Olmsted, August 1998

Species	Nearshore			Farshore		
	Percent Abundance	Percent Frequency	Mean Density	Percent Abundance	Percent Frequency	Mean Density
Site 1						
A. p. plicata	0.0	0.0	21.0	5.6	25.0	18.0
F. ebena	95.2	100.0		88.9	100.0	
Q. metanevra	4.8	50.0		5.6	25.0	
Site 2						
F. ebena	93.5	100.0	31.0	100.0	75.0	19.0
Q. pustulosa	6.5	25.0		0.0	0.0	
Site 3						
F. ebena	100.0	100.0	44.0	75.0	75.0	4.0
O. olivaria	0.0	0.0		25.0	25.0	
Site 4						
F. ebena	98.0	100.0	50.0	96.9	100.0	129.0
Q. pustulosa	0.0	0.0		0.8	25.0	
E. crassidens	0.0	0.0		1.6	25.0	
E. lineolata	2.0	25.0		0.0	0.0	
O. reflexa	0.0	0.0		0.8	25.0	
Site 5						
A. p. plicata	3.0	25.0	33.0	0.0	0.0	52.8
F. ebena	75.8	100.0		86.4	100.0	
Q. metanevra	6.1	25.0		0.0	0.0	
Q. pustulosa	3.0	25.0		10.6	100.0	
Q. quadrula	3.0	25.0		1.5	20.0	
E. lineolata	9.1	50.0		1.5	20.0	
Total individuals	179			236		

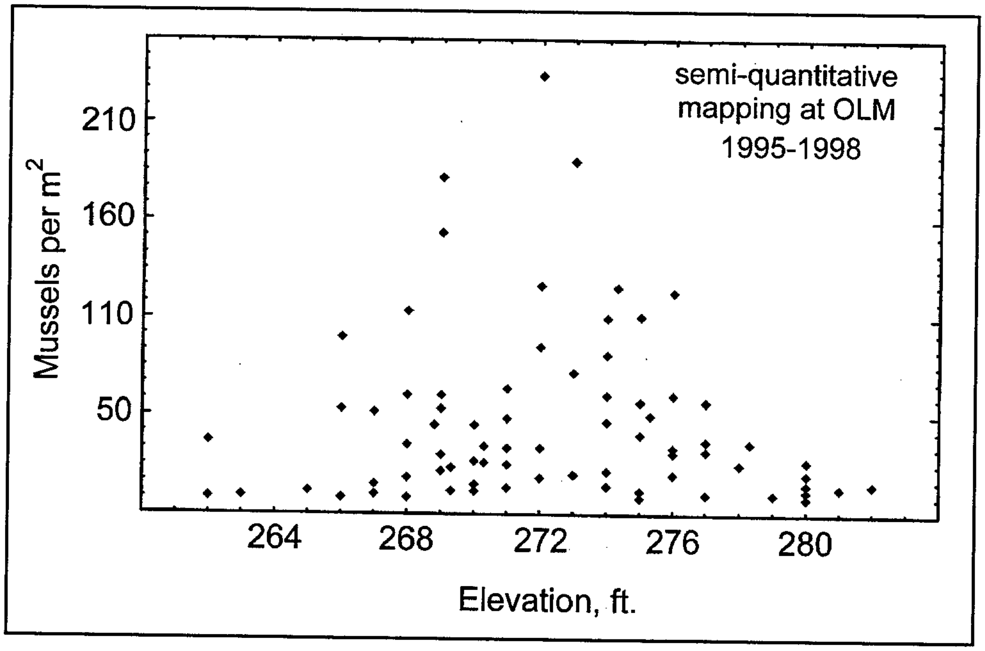

Figure 3. Mussel density in relation to elevation at Olmsted, 1995-1998

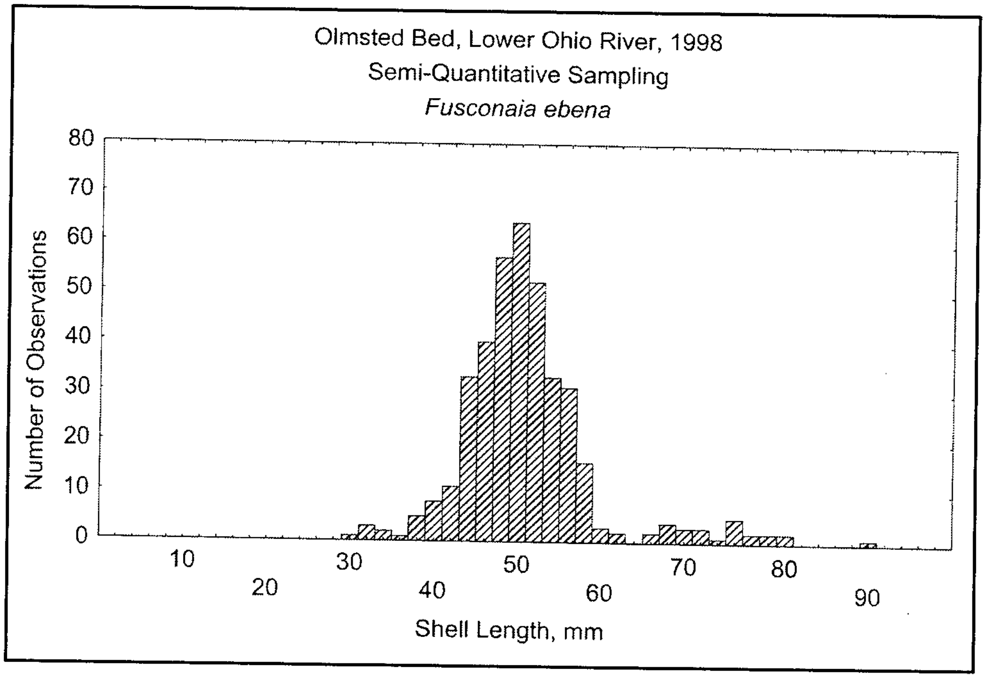

Figure 4. Length-frequency histogram for *Fusconaia ebena* in semiquantitative samples at Olmsted, August 1998

Table 7
Mussels Collected in Qualitative Samples at Olmsted, August 1998

Species	Number of Individuals	Percent Abundance
Amblema p. plicata	6	3.33
Elliptio crassidens	5	2.78
Ellipsaria lineolata	7	3.89
Fusconaia ebena	131	72.78
Ligumia recta	2	1.11
Megalonaias nervosa	2	1.11
Obovaria olivaria	1	0.56
Plethobasus cyphyus	1	0.56
Quadrula nodulata	1	0.56
Quadrula pustulosa	14	7.78
Quadrula metanevra	2	1.11
Quadrula quadrula	8	4.44
Total individuals	180	
Total species		12

Nonindigenous species. Median density of the Asiatic clam, *Corbicula fluminea,* ranged from approximately 15 individuals per square meter at Quantitative Site I to 8 individuals per square meter at Quantitative Site IV (Figure 5). The highest density recorded at any quadrat was only 36 individuals per square meter—a low value for this species that grows to a maximum size of approximately 35 mm and for which high-density populations measure more than 1,000 individuals per square meter.

The length-frequency histogram of the *C. fluminea* populations at Olmsted indicated simple age and size structure (Figure 6). Individuals ranged from only 8 to 18 mm, and all individuals appeared to be members of a single cohort (probably 1997 recruits, assuming any 1998 recruits were too small to be retained on a 6.4-mm sieve). The average length of *C. fluminea* at Olmsted was 15 mm.

Dreissena polymorpha density was moderately high at Olmsted. Average density (S.D.) equaled 6,716 (420) individuals per square meter. Individuals ranged in length from 4 to 28 mm (Figure 7). Individuals less than 8 mm probably were 1998 recruits. Mussels ranging from 10 to 20 mm represented 1997 recruitment. A few individuals greater than 22 mm long probably represented 1996 recruitment. The 1997 cohort (1-year-old animals) comprised almost all of the population.

Post Creek

Quantitative sampling. *Fusconaia ebena* was much lower in relative abundance at Post Creek than Olmsted. Among 281 unionids obtained from

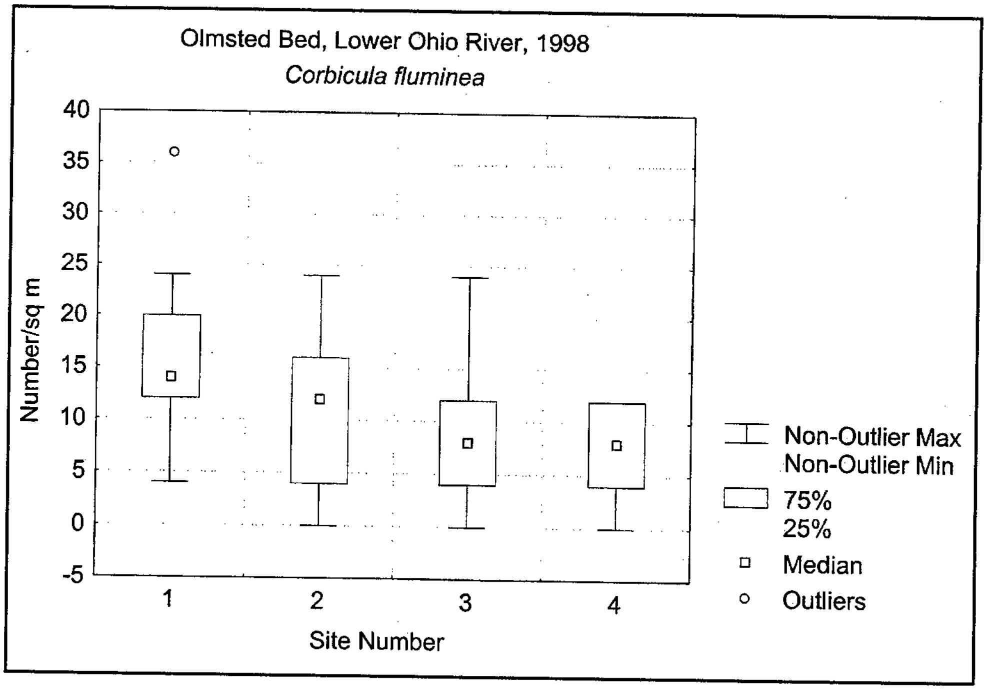

Figure 5. *Corbicula fluminea* density at Olmsted, August 1998

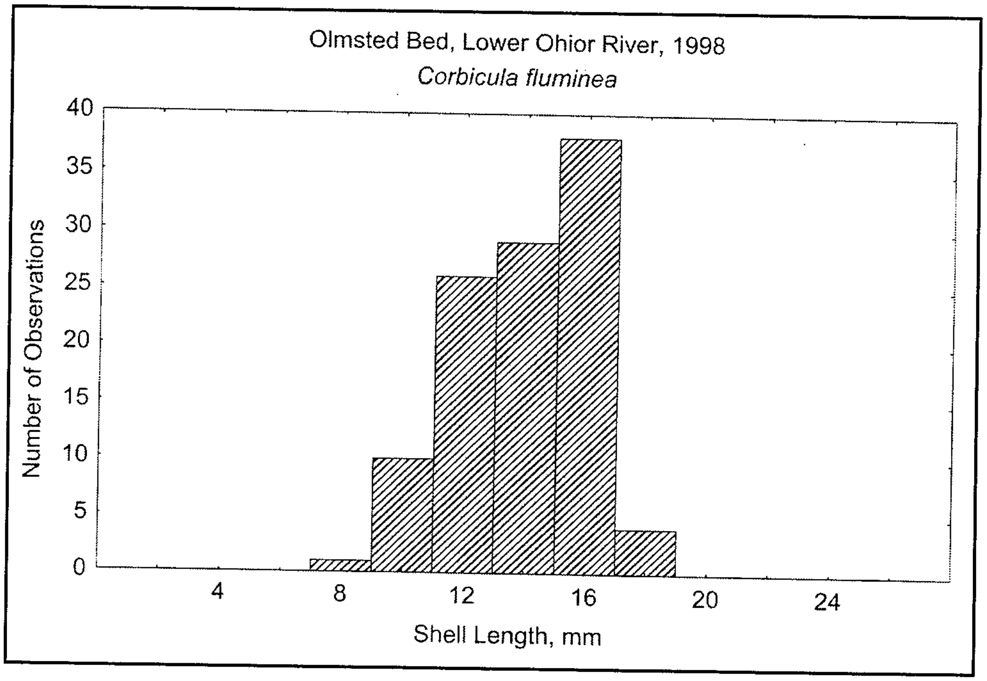

Figure 6. Length-frequency histograms for *Corbicula fluminea* at Olmsted, August 1998

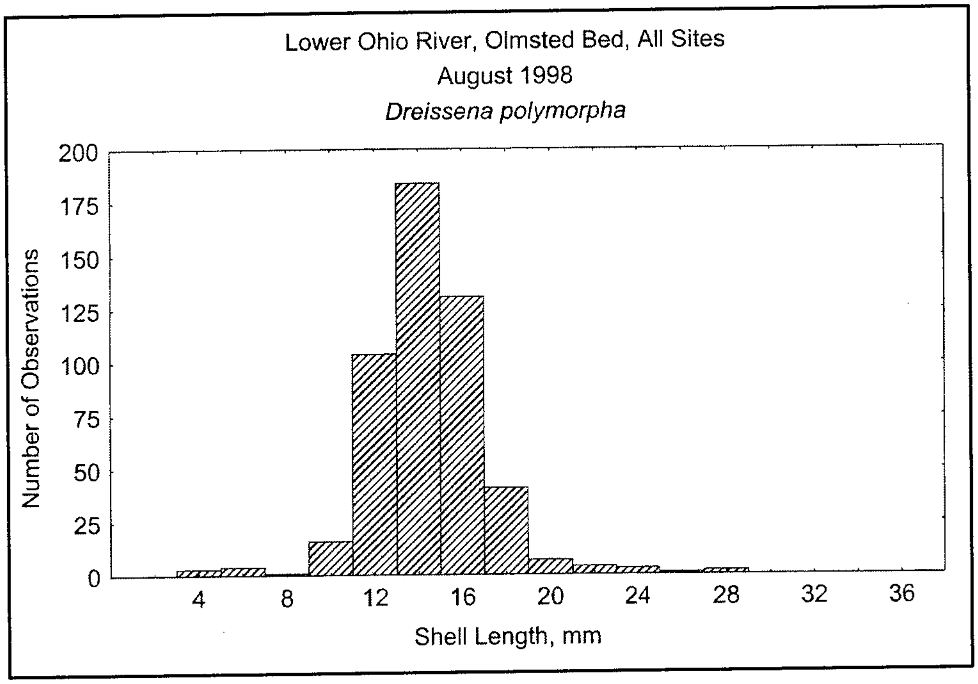

Figure 7. Length-frequency histogram for *Dreissena polymorpha* at Olmsted, August 1998

30 quantitative samples at Post Creek, 137 were *F. ebena* (48.8 percent) (Tables 8 and 9). Relative abundance of *Quadrula pustulosa* (25.1 percent) was approximately half that of *F. ebena. Obliquaria reflexa* (7.5 percent), *Amblema plicata* (6.0 percent), *Ellipsaria lineolata* (4.6 percent), and *Q. quadrula* (2.1 percent) were common. A total of 18 species were represented in quantitative samples at Post Creek. Recent recruits (<30 mm long) comprised 7.8 percent of the community, with approximately half of all species showing some evidence of recent recruitment. Diversity and evenness were moderate. The Shannon-Weaver index equaled 1.67 and Menhinick's index equaled 1.07. Evenness equaled 0.58.

Although mussel diversity was greater at Post Creek than Olmsted, density was lower. Median mussel density ranged from 53 individuals per square meter at Site I to 20 individuals per square meter at Site II (Figure 8). The number of mussels collected at Post Creek per 0.25-m^2 quadrat ranged from 2 to 21. Overall, density of native mussels at Post Creek was less than one-third the density observed at Olmsted.

Size structure of the dominant *F. ebena* population at Post Creek (Figure 9) was similar to the structure at Olmsted. At Post Creek, virtually all of the population was greater than 32 mm but less than 61 mm. Mussels in this range represented the 1990 cohort. However, the 1990 cohort at Post Creek had an average length of 45 mm—approximately 7 mm less than at Olmsted. The total length range of *F. ebena* was 10 to 80 mm.

Table 8
Percent Abundance of Freshwater Mussels Collected at the Post Creek Site in the Lower Ohio River, 1998

Species	Subsite 1	Subsite 2	Subsite 3	Total
F. ebena	50.60	45.76	47.37	48.75
Q. pustulosa	22.60	22.03	25.00	25.13
O. reflexa	3.42	18.64	6.58	7.47
A. plicata	7.53	5.08	2.63	5.96
E. lineolata	4.79	1.69	6.58	4.63
Q. quadrula	1.37	1.69	3.95	2.14
M. nervosa	2.74	0.00	0.00	1.42
P. alatus	0.68	0.00	2.63	1.07
Q. nodulata	1.37	0.00	1.32	1.07
C. tuberculata	0.00	1.69	1.32	0.71
E. dilatata	0.68	1.69	0.00	0.71
O. olivaria	1.37	0.00	0.00	0.71
Q. metanevra	0.00	0.00	2.63	0.71
T. truncata	0.68	0.00	0.00	0.36
T. verrucosa	0.00	1.69	0.00	0.36
L. fragilis	0.68	0.00	0.00	0.36
L. recta	0.68	0.00	0.00	0.36
L. teres	0.68	0.00	0.00	0.36
Total individuals	146	59	76	281
Total species	15	9	10	18
% Individuals <30 mm	7.53	6.77	9.21	7.82
% Species <30 mm	46.67	33.3	40	50
Menhinick's index	1.24	1.17	1.15	1.07
Species diversity	1.62	1.5	1.59	1.67
Evenness	0.6	0.68	0.69	0.58

In addition to *F. ebena*, *Quadrula pustulosa* was obtained at Post Creek in sufficient numbers to allow inspection of population-size demography (Figure 10). *Quadrula pustulosa* ranged from 16 to 68 mm long. The length range of 32 to 50 mm included approximately two-thirds of the population.

Qualitative sampling. A total of 357 individuals and 13 species were collected by qualitative methods at Post Creek (Table 10). *Fusconaia ebena* comprised 47 percent of the community sample. *Quadrula p. pustulosa* (22 percent) was also abundant. *Amblema p. plicata* (6.4 percent), *Ellipsaria lineolata* (7.8 percent), and *Q. quadrula* (5.0 percent) were common.

Table 9
Frequence of Occurrence of Freshwater Mussels Collected at the Post Creek Site in the Lower Ohio River, 1998

Species	Subsite 1	Subsite 2	Subsite 3	Total
F. ebena	100.00	90.00	100.00	96.67
Q. pustulosa	100.00	70.00	70.00	80.00
O. reflexa	50.00	70.00	40.00	53.33
A. plicata	80.00	30.00	20.00	43.33
E. lineolata	50.00	10.00	30.00	30.00
Q. quadrula	10.00	10.00	30.00	16.67
M. nervosa	30.00	0.00	0.00	10.00
P. alatus	10.00	0.00	20.00	10.00
Q. nodulata	20.00	0.00	10.00	10.00
C. tuberculata	0.00	10.00	10.00	6.67
E. dilatata	10.00	10.00	0.00	6.67
O. olivaria	10.00	0.00	0.00	3.33
Q. metanevra	0.00	0.00	20.00	6.67
T. truncata	10.00	0.00	0.00	3.33
T. verrucosa	0.00	10.00	0.00	3.33
L. fragilis	10.00	0.00	0.00	3.33
L. recta	10.00	0.00	0.00	3.33
L. teres	10.00	0.00	0.00	3.33
Total sites	10	10	10	30.00

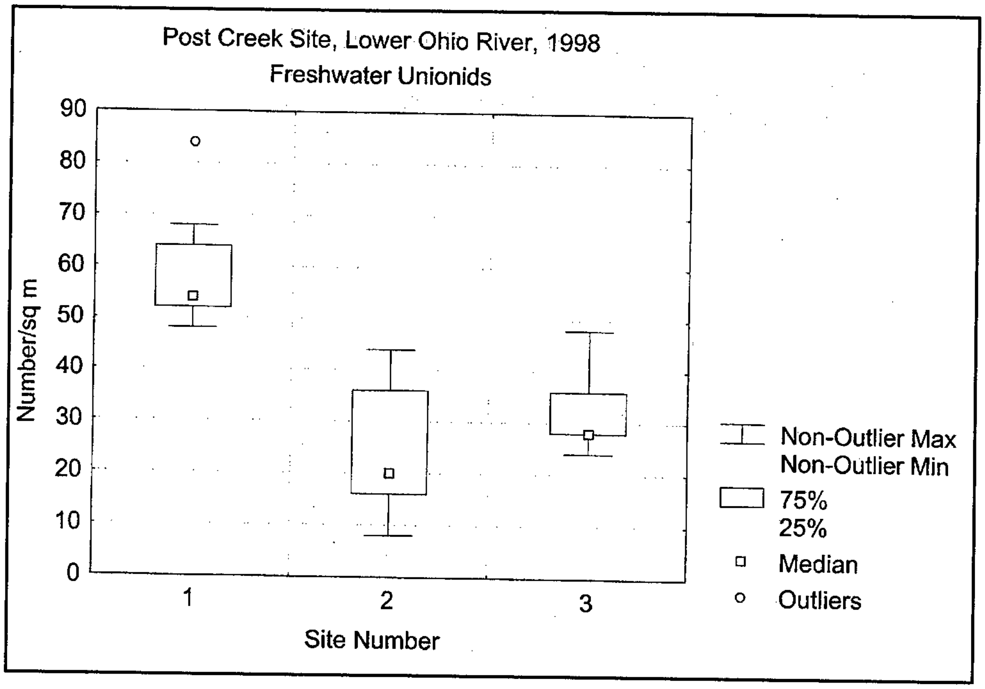

Figure 8. Native mussel density at the Post Creek mussel bed in the lower Ohio River, August 1998

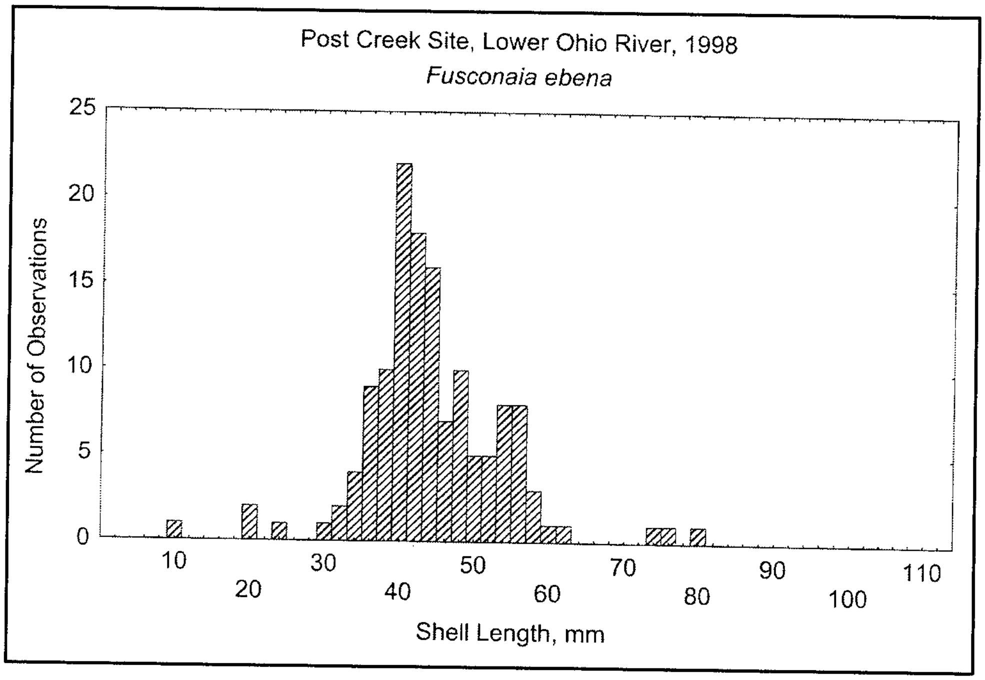

Figure 9. Length-frequency histogram for *Fusconaia ebena* in quantitative samples at Post Creek, August 1998

Elliptio crassidens was obtained in qualitative but not quantitative samples. Qualitative plus quantitative sampling yielded a total of 638 individuals and 19 species.

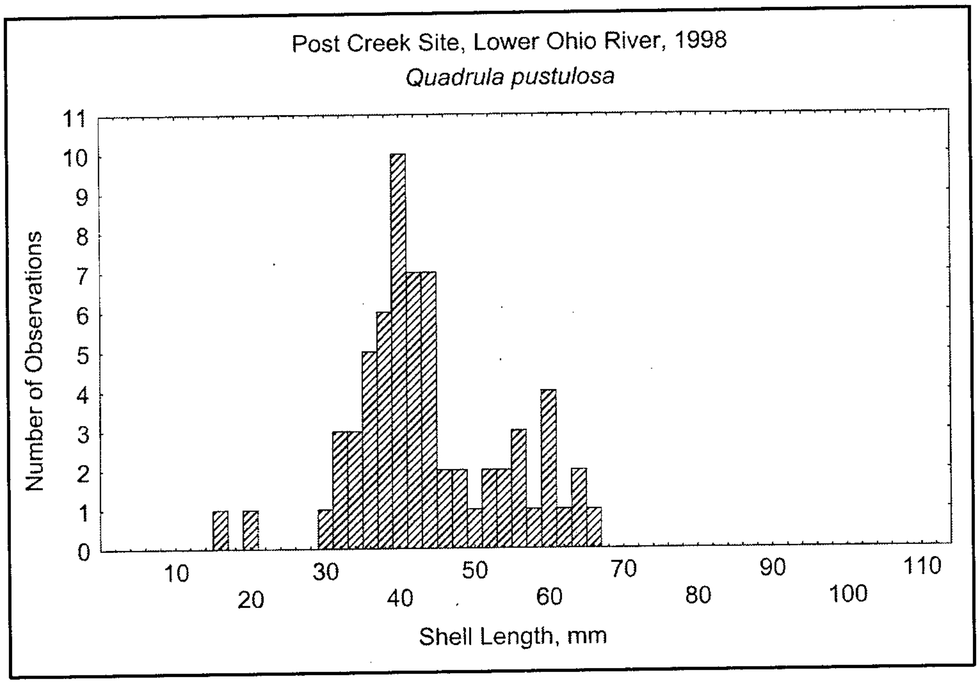

Figure 10. Length-frequency histogram for *Quadrula pustulosa* in quantitative samples at Post Creek, August 1998

Table 10
Mussels Collected in Qualitative Samples at Post Creek, August 1998

Species	Number of Individuals	Percent Abundance
Amblema p. plicata	23	6.44
Cyclonaias tuberculata	7	1.96
Elliptio crassidens	4	1.12
Ellipsaria lineolata	28	7.84
Fusconaia ebena	168	47.06
Megalonaias nervosa	8	2.24
Obliquaria reflexa	12	3.36
Potamilus alatus	3	0.84
Quadrula nodulata	1	0.28
Quadrula postulosa	77	21.57
Quadrula metanevra	6	1.68
Quadrula quadrula	18	5.04
Tritigonia verrucosa	2	0.56
Total individuals	357	
Total species		13

Nonindigenous species. *Corbicula fluminea* density at Post Creek ranged from a median value of 53 individuals per square meter at Site I to 20 individuals per square meter at Site II (Figure 11). These values were only slightly higher than at Olmsted and indicative of a relatively low population density for this species. Size demography of the *C. fluminea* population at Post Creek (Figure 12) was virtually identical to that at Olmsted. All individuals measured between 8 and 18 mm and had an average length of 14 mm. Only a single cohort (probably a 1997 year class) was evident.

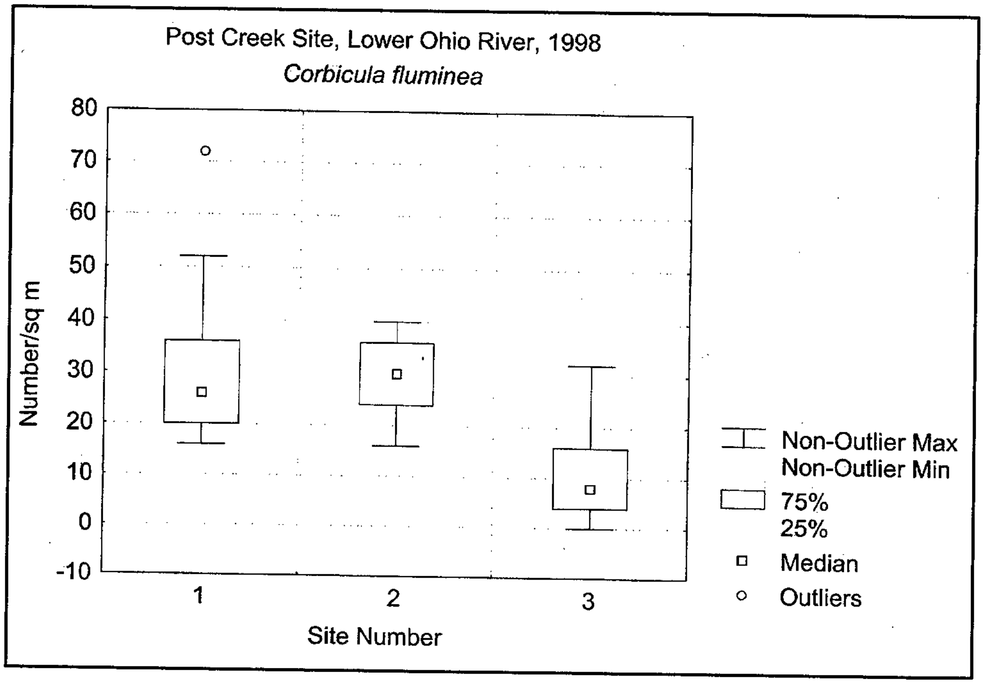

Figure 11. Density of *Corbicula fluminea* at Post Creek, August 1998

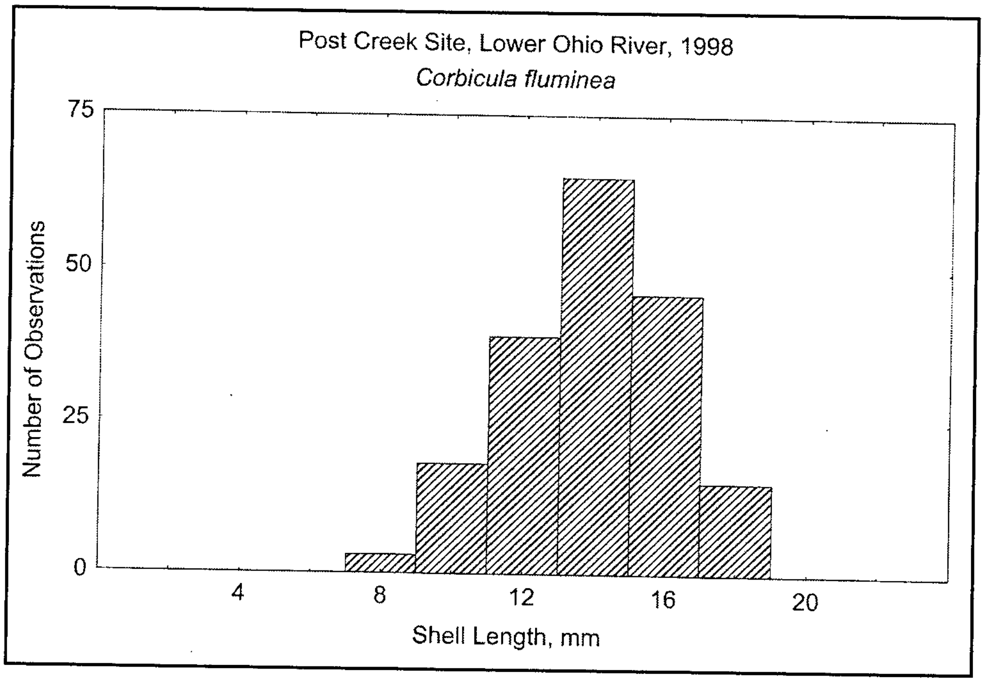

Figure 12. Length-frequency histogram for *Corbicula fluminea* at Post Creek, August 1998

Discussion

The nearshore limit of the Olmsted mussel bed occurs at approximately 278 to 280 ft elevation (Payne and Miller 1997) and reflects historical patterns of extremely low river stage. During the winter of 1980/1981 and the summer and fall of 1988, the 279-ft elevation contour of the shoal was exposed to air for at least 14 consecutive days—enough to kill many unionids. The 281-ft elevation was exposed for maximum periods of 25, 35, and 59 consecutive days in the fall of 1976, winter of 1980/1981, and summer of 1988—enough to kill most unionids. Thus, it is not surprising that native mussel density is quite low nearshore of the 279-ft elevation contour.

The farshore limit of the mussel bed occurs at approximately elevation 267 ft. This limit is less distinct than the nearshore boundary and reflects lack of suitably stable sand and gravel. Increasingly erosional conditions cause scoured sand and bedrock to be the predominant substratum farshore of elevation 267. However, isolated patches of somewhat more stable substratum (sand or sand and gravel) are occasionally encountered farshore of elevation 267 that support dense assemblages of mussels. In addition, patches of sand that may not be stable for more than a few years temporarily can provide suitable substratum for recent recruits. A lack of large, old mussels in such patches suggests that such substratum and mussels are eventually swept away by scouring flows, preventing the establishment of a complex age structure in mussel assemblages encountered much farshore of elevation 267 (Payne and Miller 1998).

Within the mussel bed, there is a high degree of variability in mussel density. In general, substratum type is not clearly correlated with mussel density between the 279 and 267 elevation contours (Payne and Miller 1998) except that erosional patches of sand or bedrock obviously do not support mussels. Patchiness of mussel density is apparent among quadrats within sites as well as among sites. Both a high degree of sample replication (i.e., at least 10 quadrats per site) and some degree of site replication (at least two closely adjacent subsites per site) are required to establish if location-specific estimates of density are to be confidently compared to establish spatial patterns of density distribution. Although densities of 200-300 individuals per square meter are occasionally encountered, these are outlier data and always are due to extremely dense clusters of recent recruits (especially *F. ebena*). A density range of 50 to 100 individuals per square meter is more likely to correspond to "local carrying capacity" with respect to a complex, age-structured assemblage.

Fusconaia ebena heavily dominates mussels in the stable shoals of the lower Ohio River. Despite being a species-rich community (with 32 species, Payne and Miller 1997), the mussel bed at Olmsted has low diversity in terms of the Shannon's or Menhinick's indices. This is a mathematical consequence of the high relative abundance of the dominant species. The community at Post Creek is similarly rich in species, but *F. ebena* is much less heavily dominant than at Olmsted. Thus, diversity indices for the Post Creek community indicate moderate diversity. In a broad sense, in which diversity simply equals richness, the lower Ohio River community is indeed diverse at both Olmsted and Post Creek.

Good recruitment appears to be a communitywide phenomenon at Post Creek and Olmsted. The 1990 cohort of *F. ebena* is exceptionally abundant at both locations. However, one or a few individuals of less than 30-mm length have been recovered of nearly all species present on the bed. Obviously, the rarest species yield so few individuals that it is possible to miss recent recruits of those taxa even if they exist.

Native mussels in the lower Ohio River, including *F. ebena*, have been resilient to high-density populations of nonindigenous bivalves. The first such species invasion was by the Asian clam, *C. fluminea*. A dense population of this species in the lower Ohio River was first observed in 1957 (Sinclair and Isom 1961; McMahon 1983). The sampling by these authors at Olmsted began in 1983. From 1983 to 1993, *C. fluminea* was very dense (typically 1,000 to 3,000 individuals per square meter), and populations were characterized by complex age and size structure (typically three to five cohorts) with the oldest and largest individuals being 2 to 3 years old and 30 to 40 mm long. Despite sustained high density and complex demography of *C. fluminea*, no correlation was found between native mussel and *C. fluminea* density within the Olmsted bed (Miller and Payne 1988). A negative relationship would have been evidence of competition between these taxa. Since 1993, *C. fluminea* density has greatly declined, and the population now has simple age structure (typically one cohort) and includes few individuals greater than 15 mm long.

Dreissena polymorpha first appeared in the lower Ohio River in 1991 (Payne, Miller, and Shafer 1994) and has replaced *C. fluminea* as the dense nonindigenous bivalve existing with native mussels. However, only the 1994 generation of *D. polymorpha* has been extremely dense (49,000 individuals per square meter in September 1994 to 5,000 individuals per square meter in July 1995). This dense cohort heavily infested native mussels in 1994 and early 1995, resulting in reduced unionid growth (Payne and Miller 1998), but has not caused major declines in density such as have been reported in the Great Lakes. High density of *D. polymorpha* has not been sustained in the lower Ohio River. Cohorts since the 1994-year class have not been especially dense. It remains to be seen if *D. polymorpha* can occur in sustained abundance in the lower Ohio River at a density sufficiently high to have drastic effects on native bivalves.

3 Population Dynamics of *Fusconia ebena*

Site and Methods

Demographically complete samples of *F. ebena* were obtained at Olmsted in the summer or fall of 1983 through 1998 by having divers excavate substratum from 0.25-m^2 quadrats. Replicate samples (usually 10) were always taken from multiple sites (usually two to four) in a central portion of the mussel bed (Table 11) except in 1993 when the objective was to map the bed's boundaries and there was no concentration of sampling in a central location (Payne and Miller 1997). Thus, 1993 results are compared with other years with respect to demography but not density. Mussels were sorted in the field after sampled substratum was taken to shore and washed through a series of sieve screens except in 1983 when mussels were sorted from unsieved substratum in white enamel pans. The square mesh of the smallest sieve screen had a diagonal aperture of 6.4 mm. The greatest anterior-posterior dimension across the valves (shell length) of each *F. ebena* was measured to the nearest 0.1 mm using calipers. Length-frequency histograms were constructed for composites of each year's sample of *F. ebena*, using 2-mm class intervals over a length range typically from 10 to 90 mm. Mussels were returned to the shoal after measurement except for a few specimens kept as voucher material for dry mass measurements (Payne and Miller 1989) or for use in laboratory studies (Payne and Miller 1987).

Daily estimates of river discharge (United States Geological Survey annual records) from April through July were compiled for 1977 through 1996 and evaluated with respect to annual variation in mussel recruitment. Discharge of both the LOR and upper Mississippi River (UMR) affect hydraulic conditions at the LOR mussel bed, as the confluence of these two large rivers is only 23 km downstream of the bed. Thus, discharge records were analyzed for both the LOR and UMR.

Mussel and Fish Relationship

Both *F. ebena* and *A. chrysochloris* inhabit large rivers and prefer moderately swift water and stable sandy or gravelly shoals (Cummings and Mayer 1992; Wallus, Yeager, and Simon 1990; Surber 1913). Glochidia of *F. ebena* must

Table 11
Summary Information on Demographically Complete Quantitative Samples of *Fusconaia ebena* from the LOR Mussel Bed

Date	Number of Quadrats	Number of *F. ebena*	Individuals per 0.25 m^2	
			Mean	S.D.
29 Sep 1983	24	256	10.7	5.3
31 Oct 1985	17	269	15.8	6.5
29 Sep 1987	20	219	11.0	4.8
23 Sep 1990	30	267	8.9	4.6
1 Oct 1991	20	136	6.8	3.4
26 Aug 1992	40	628	15.7	8.3
2 Sep 1993	46	973	*	*
31 Aug 1994	40	1,194	29.9	12.5
20 Jul 1995	40	632	15.8	15.9
12 Aug 1996	50	504	10.1	10.2
8 Aug 1997	30	237	7.9	5.2
9 Aug 1998	40	1,072	26.8	11.8

Note: * Study design was not appropriate for comparison to other years.

attach to gills of *A. chrysochloris* for successful transformation to the benthic juvenile stage (Coker et al. 1921; Surber 1913). Not surprisingly, therefore, the mussel's geographic distribution is entirely within the fish's distribution. Both are common in large rivers draining into the lower and middle Mississippi River system, including the Ohio and many of its principal tributaries (Etnier and Starnes 1993; Cummings and Mayer 1992; Miller and Payne 1992; Wallus, Yeager, and Simon 1990; Payne and Miller 1989; Robinson and Buchanan 1988). Although highly migratory and occasionally found in brackish water in rivers draining into the Gulf of Mexico, *A. chrysochloris* is not anadramous (Lee et al. 1980). Resident populations occur upstream of high lift dams on the Ohio, Tennessee, Cumberland, and Arkansas rivers (Wallus, Yeager, and Simon 1990; Robinson and Buchanan 1988). Indeed, locks and dams in the Arkansas River, although imposing to fish migration, deepened the river channel, reduced suspended solids, and apparently improved habitat for *A. chrysochloris* (Robinson and Buchanan 1988).

Adult *A. chrysochloris* make prominent upstream runs to spawn over rocky or gravelly shoals in spring or early summer (Wallus, Yeager, and Simon 1990). Release of glochidia conglutinates by *F. ebena* during such spawning aggregations of *A. chrysochloris* is likely to enhance successful parasitism of fish (Kat 1984). *Alosa chrysochloris* used to be common in the UMR, where *F. ebena* once dominated native unionids in main channel shoals (Theler 1987). A hydroelectric dam built at Keokuk, Iowa, in 1913 prevented upstream migration and led to extirpation first of *A. chrysochloris* and more gradually of *F. ebena* (Theler 1987; Lee et al. 1980; Coker 1914). Spring and summer migrations must have been required for *A. chrysochloris* to spawn in the UMR; in this northernmost extension of the species' range, overwintering was apparently not possible. Both *A. chyrsochloris* and *F. ebena* remain common, with the latter often dominant among mussels, in run-of-river reservoirs in more southerly portions of the fish's range.

Annual Variation in Recruitment

Average density of *F. ebena* at Olmsted has ranged from 7 to 30 individuals per 0.25 square meter from 1983 to 1998 (Figure 13). Demography of the LOR population of *F. ebena* has been characterized by extreme dominance of only two year classes—1981 and 1990 (Figures 14 and 15). Seventy-one percent of the population in 1983 was comprised of a single cohort (1981) of recent recruits. In 1992, the 1990-year class comprised 85 percent of the population. Recruitment in years other than 1981 and 1990 was minor or not evident.

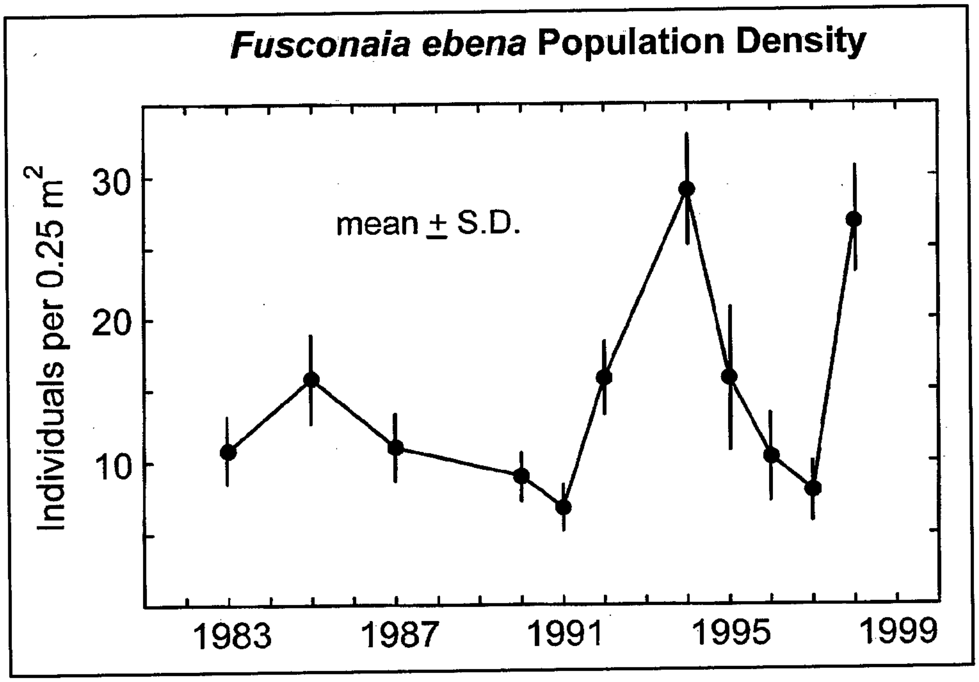

Figure 13. Density of *Fusconaia ebena* at Olmsted, 1983-1998

In 1983, individuals of the 1981 cohort averaged 15.8 mm long and ranged from 11.8 to 20.6 mm (Figure 14). Evidence that this cohort settled in 1981 included presence of a very minor cohort of even more recent recruits. The latter cohort had an average length of 7.4 mm and ranged from 3.9 to 10.3 mm. In that first year of sampling, mussels were sorted from each quantitative sample of substratum in the field using white enamel pans. Thus, with reasonable certainty all individuals visible without aid of magnification were sorted from substratum.

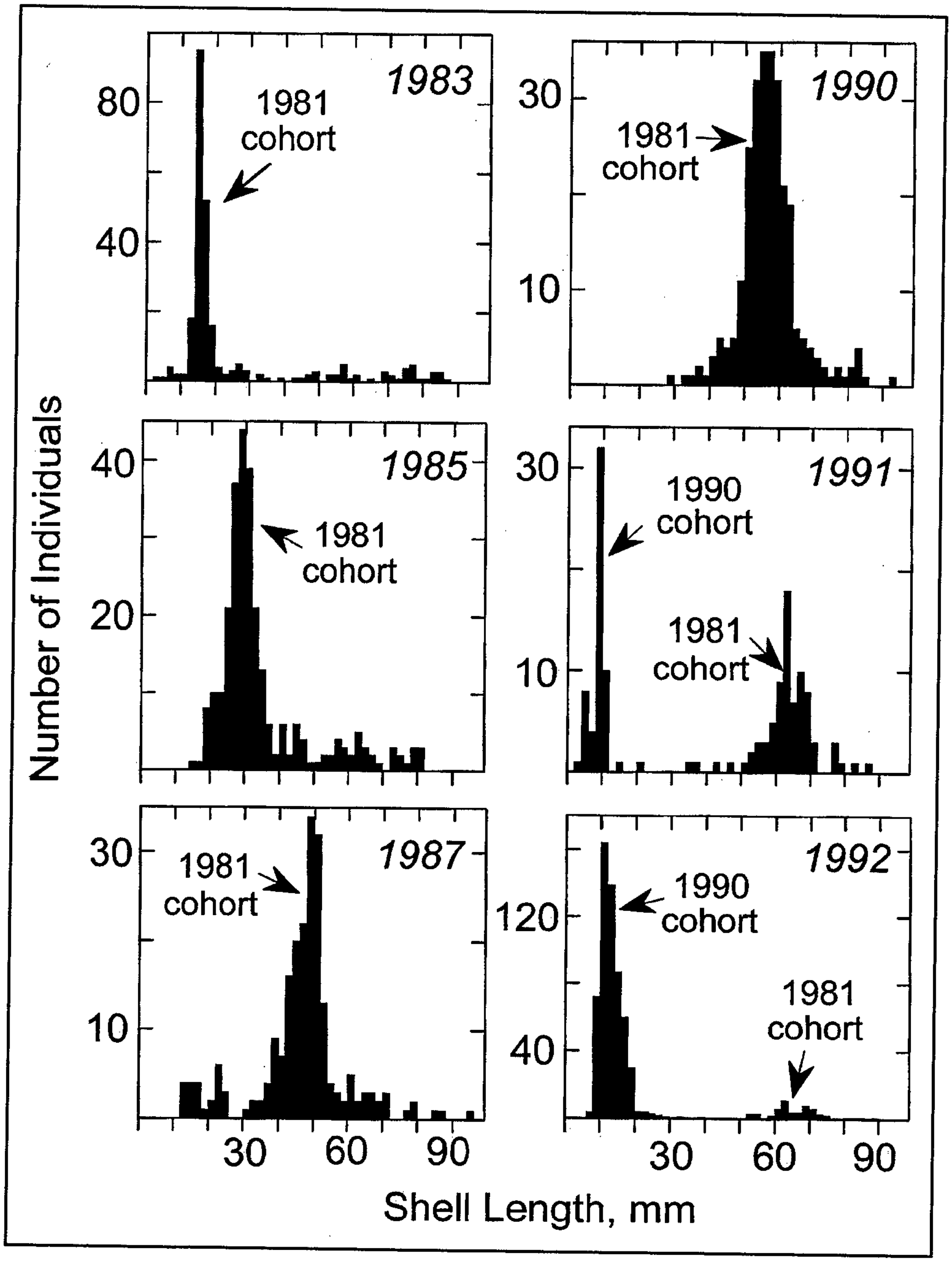

Figure 14. Length-frequency histograms for *Fusconaia ebena* at Olmsted, 1983-1992

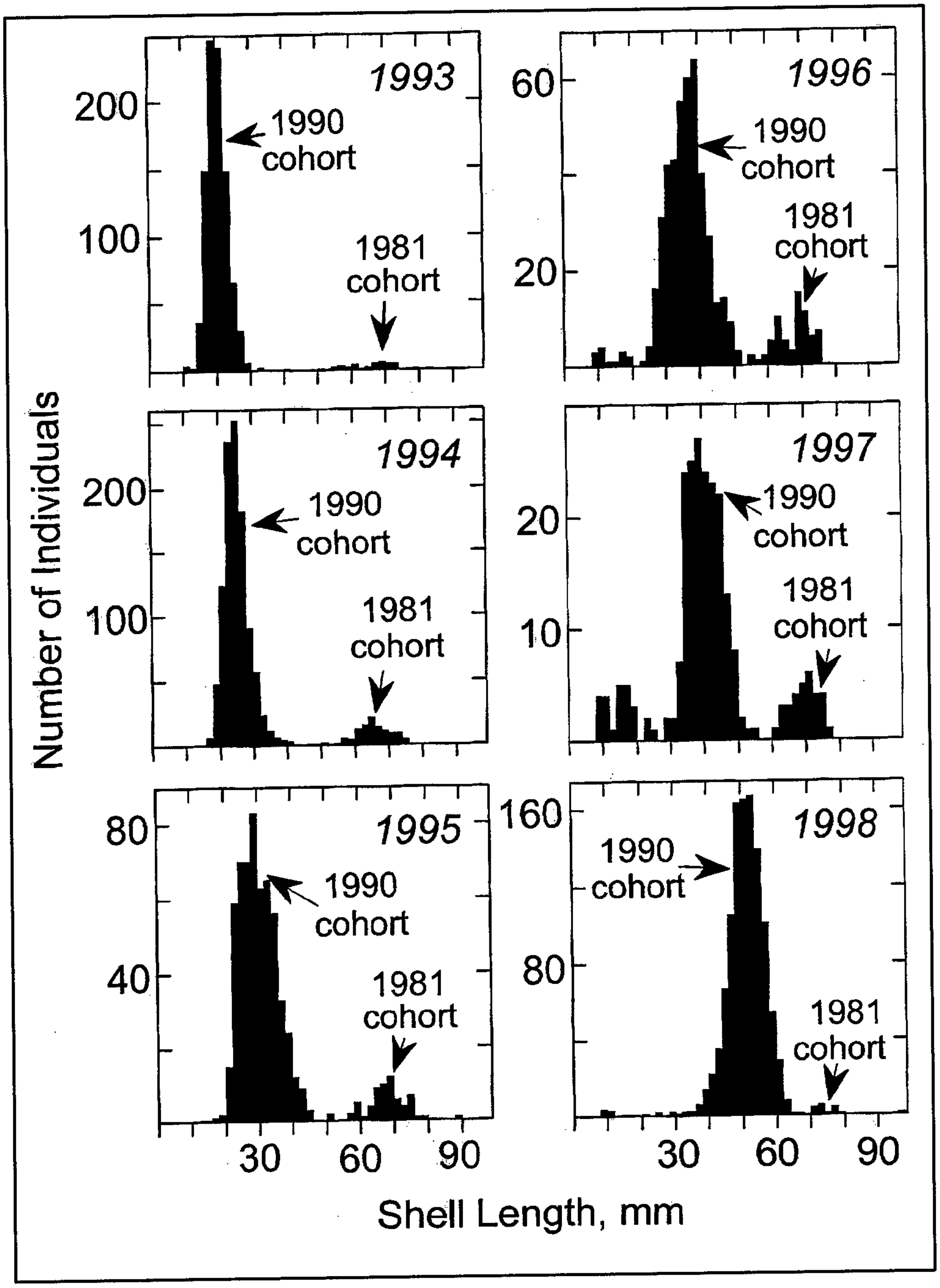

Figure 15. Length-frequency histograms for *Fusconaia ebena* at Olmsted, 1993-1998

The small cohort centered at 7.4 mm probably represented 1982 (rather than 1983) recruitment for several reasons. First, these individuals did not yet show much umbonal erosion, allowing a distinct shell "annulus" to be discerned that suggested first overwintering at less than 2 mm. This shell annulus, located very high on the shell umbo, quickly eroded and was not consistently evident in individuals of the still young 1981 cohort in 1983. Second, juvenile *F. ebena* probably settle from their host fish mainly in early summer at a length of less than 0.2 mm (Howard 1914). Major structural changes unrelated to length increase must occur before newly settled juveniles become a miniature form of an adult bivalve (Yokely 1972; Coker et al. 1921) and the spring portion growth season has passed. Annual growth of the 1981 cohort from 1983 to 1985 averaged slightly less than 7 mm per year (Figure 14). Thus, it is unlikely that juveniles starting benthic life at less than 0.2 mm in early summer to midsummer attained an average length of 7.4 mm by early fall.

The 1990 cohort had average length of 12.8 mm in 1992 and was approximately equal in abundance to the 1981 cohort (Figure 14). The latter had grown to an average length of 66.6 mm (Figure 14). Many mussels less than 10 mm in 1991 were found hanging from the underside of the sieve by a sticky hyaline thread. A byssal gland to secrete such threads is retained for as much as 2 years in juvenile *F. ebena* and several other unionids (Coker et al. 1921). Thus, although first evident in 1991, the 1990 cohort was not fully represented in samples until 1992 (Figure 14). Once fully represented, relative abundance of the 1990 cohort (85 percent) greatly exceeded that of the formerly dominant 1981 cohort (10 percent).

Minor recruitment was evident in several years other than 1981 and 1990 (Figures 14 and 15). However, low abundance of minor cohorts adds uncertainty to year class assignments. In addition to the 1982 year class, a minor cohort probably representing 1979 recruitment (average length of approximately 28 mm) was evident in 1983. Minor recruitment in 1984 and 1985 was suggested by small peaks centered at approximately 23 and 15 mm, respectively, in the 1987 length-frequency histogram. Minor peaks centered at 10 and 18 mm in 1996 probably represented 1994 and 1993 recruitment, respectively. In 1997, minor cohorts centered at 10, 18, and 24 mm probably represented 1995, 1994, and 1993 recruitment. A minor cohort centered at 10 mm in 1998 probably represented 1996 recruitment.

Thus, 16 years of monitoring provided evidence of two extremely strong year classes (1981 and 1990) and several minor year classes (possibly 1979, 1982, 1984, 1985, 1993, 1994, 1995, and 1996) of *F. ebena* population in the lower Ohio River. The 9-year separation and extremely high relative abundance of the 1981 and 1990 cohorts allowed estimation of *F. ebena* growth rate directly from the series of length-frequency histograms.

Growth and Survival

In any population of long-lived individuals, decreased growth rate with increased age and size causes overlap of individuals of adjacent cohorts, tending to obscure upper and lower size limits of a particular year class. For example, the recent recruits ranging from 12 to 26 mm in 1987 were difficult to discern in the lower tail of the length distribution of the dominant 1981 cohort in 1990 (Figure14). Regardless of such difficulties, central tendency in size distribution of the two dominant year classes usually was apparent (Figures 14 and 15).

Growth rates were estimated using average lengths estimated for the 1981 and 1990 cohorts. Averages were based on size-class intervals near the modal length of individuals per cohort. Mussels falling in class intervals near the upper and lower size limits of each cohort were omitted. These omissions had virtually no effect on averages because of low relative abundance of mussels in near-boundary size classes. The best representation of *F. ebena* growth through age 17 was provided by two linear regressions of shell length (SL, mm) on age (A, years) (Figure 16). The first model, applicable to ages 2 through 10 years, was SL = 2.79 + 5.90 A; $r^2 = 0.98$; $p < 0.0001$). Despite minor intercohort differences, this model fit both the 1981 and 1990 cohorts. The 1990 cohort was slightly smaller than the 1981 cohort from ages 4 to 7 years, probably because of a temporarily severe infestation of *Dreissena polymorpha* from 1994 through 1995 (Payne and Miller 1998). However, above average growth of the 1990 cohort was evident from age 7 through 8 years. Furthermore, the 1981 cohort showed below average growth from age 6 through 9 years. Overall, the single linear regression indicating annual growth of 5.9 mm provided an excellent fit for both cohorts from ages 2 through 10 years.

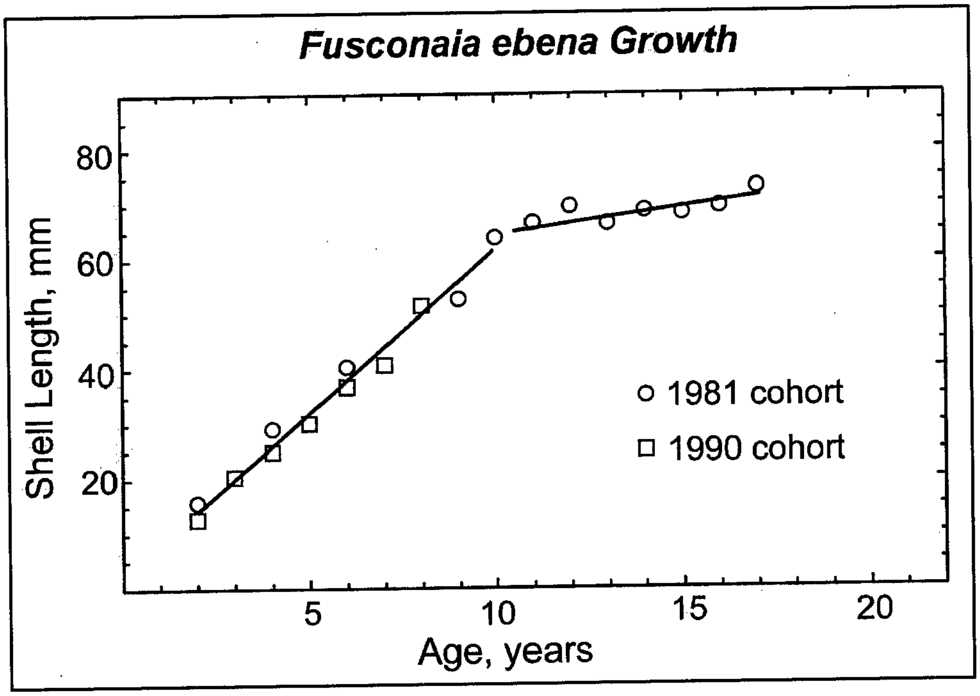

Figure 16. Length-to-age relationships for *Fusconaia ebena* at Olmsted

Growth from ages 10 through 17 years was much slower, with data available only for the 1981 cohort. The linear model applied to these ages was SL = 55.9 + 0.91 A; $r^2 = 0.68$; $p < 0.02$). The poorer fit of this model relative to that for early growth reflected both slow growth and low relative abundance of the 1981 cohort from 1993 through 1998.

A survivorship curve was based on the declining density of the 1981 cohort from 1983 through 1998 (Figure 17). This curve indicates a constant proportion (16.8 percent) of the cohort died each year from age 2 through 17 years. Cumulative mortality from 1983 to 1998 was 94 percent, as density declined from 14.0 to 0.9 individuals per 0.25 m^2. Extension of the model predicts mortality greater than 96 percent at age 20 years.

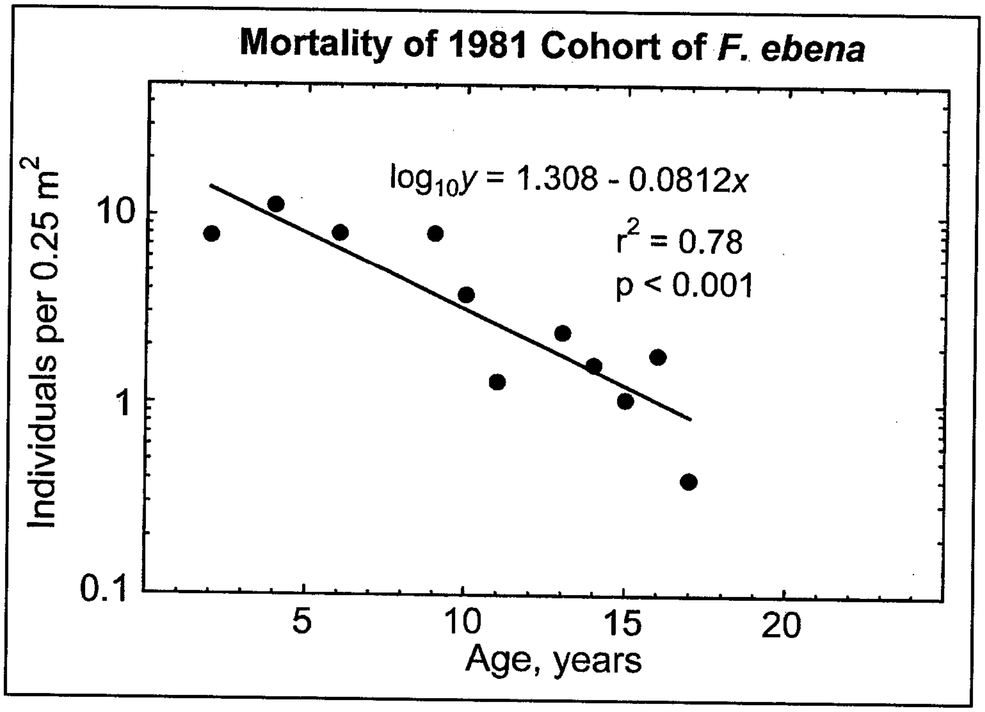

Figure 17. Density decline of the 1981 cohort of *Fusconaia ebena* at Olmsted, 1983-1998

Annual Variation in Hydraulic Conditions

Average discharges of the LOR and UMR near their confluence are 7,646 and 5,522 $m^3 s^{-1}$ with considerable seasonal variation (Figure 18). In the LOR, depositional conditions and low discharge (<5,000 $m^3 s^{-1}$) tend to occur from July through October, while erosional conditions and high discharge (>10,000 $m^3 s^{-1}$) occur from December through April (Figure 18). Because of a backwater effect near the confluence of the LOR and UMR, depositional conditions are greater than those because of low LOR discharge alone if UMR discharge is simultaneously and substantially higher.

Discharge from April through July was of special interest with respect to *F. ebena* recruitment. Water temperature in the LOR typically rises from 10 °C to the average seasonal maximum of 28 °C from April through July (Figure 19). This period of rapid water temperature rise to the summer maximum almost certainly includes *F. ebena* population peaks in fertilization, glochidia release, and juvenile settlement (Coker et al. 1921) as well as the peak spawning period of *A. chrysochloris* (Wallus, Yeager, and Simon 1990). Discharge records from 1977 through 1996 were analyzed for two reasons. First, initial sampling in 1983 indicated that exceptionally strong recruitment of *F. ebena* probably had not occurred for several years prior to the strong recruitment in 1981. Second, the youngest recruitment cohort certain to be fully included, if present, in 1998 samples would be 1996 recruits.

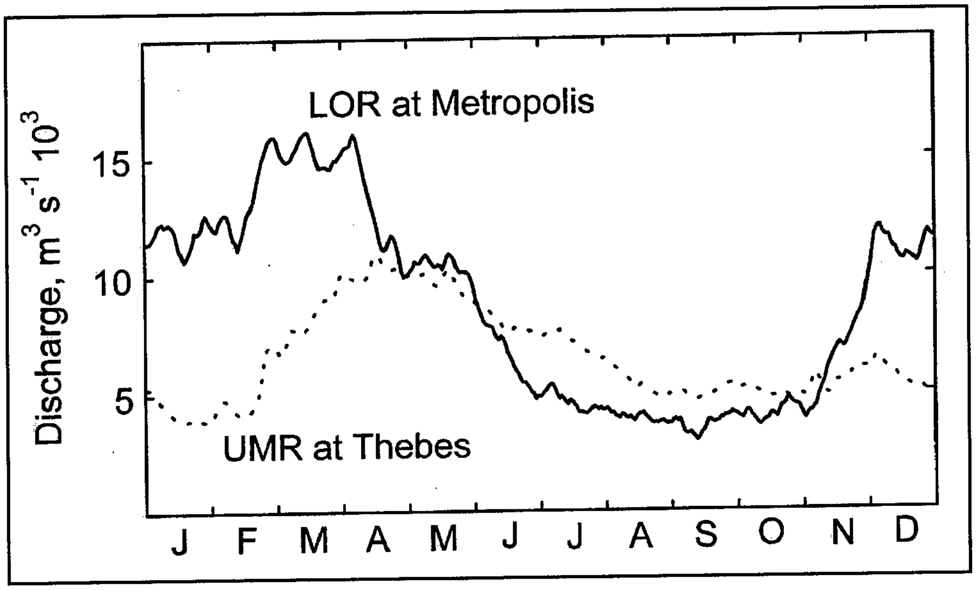

Figure 18. Seasonal pattern of discharge (20-year record) of the lower Ohio and upper Mississippi rivers near their confluence

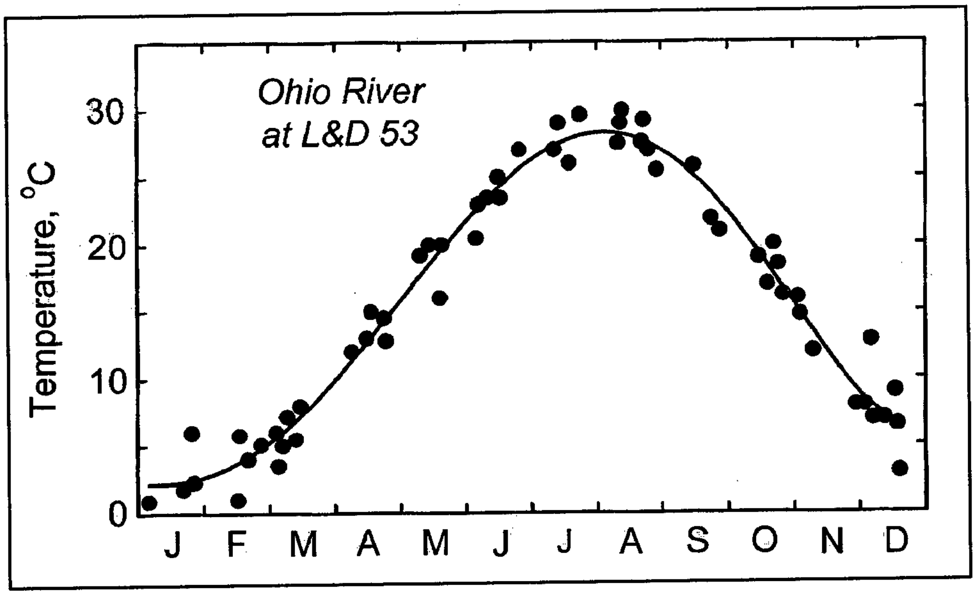

Figure 19. Seasonal pattern of surface water temperature (10-year composite record) of the lower Ohio River at Lock and Dam 53

Hydraulic conditions in the LOR were unusual, complex, and remarkably similar from April through July of 1981 and 1990 (Figure 20). In both years, LOR discharge was approximately 6,000 $m^3 s^{-1}$ in early April, rose rapidly to 11,000 $m^3 s^{-1}$ by late April, and dropped rapidly to 6,000 $m^3 s^{-1}$in early May. Then, LOR discharge rose rapidly to 14,000 $m^3 s^{-1}$ by mid-May and 19,000 $m^3 s^{-1}$ by mid-June, but plummeted to 2,000 $m^3 s^{-1}$ by late June (1990) or 4,000 $m^3 s^{-1}$ by early July (1981). In both years, UMR discharge greatly exceeded LOR discharge for extended periods from late June through July (Figure 20). In 1981, UMR discharge was more than twice that of the LOR for most of late June

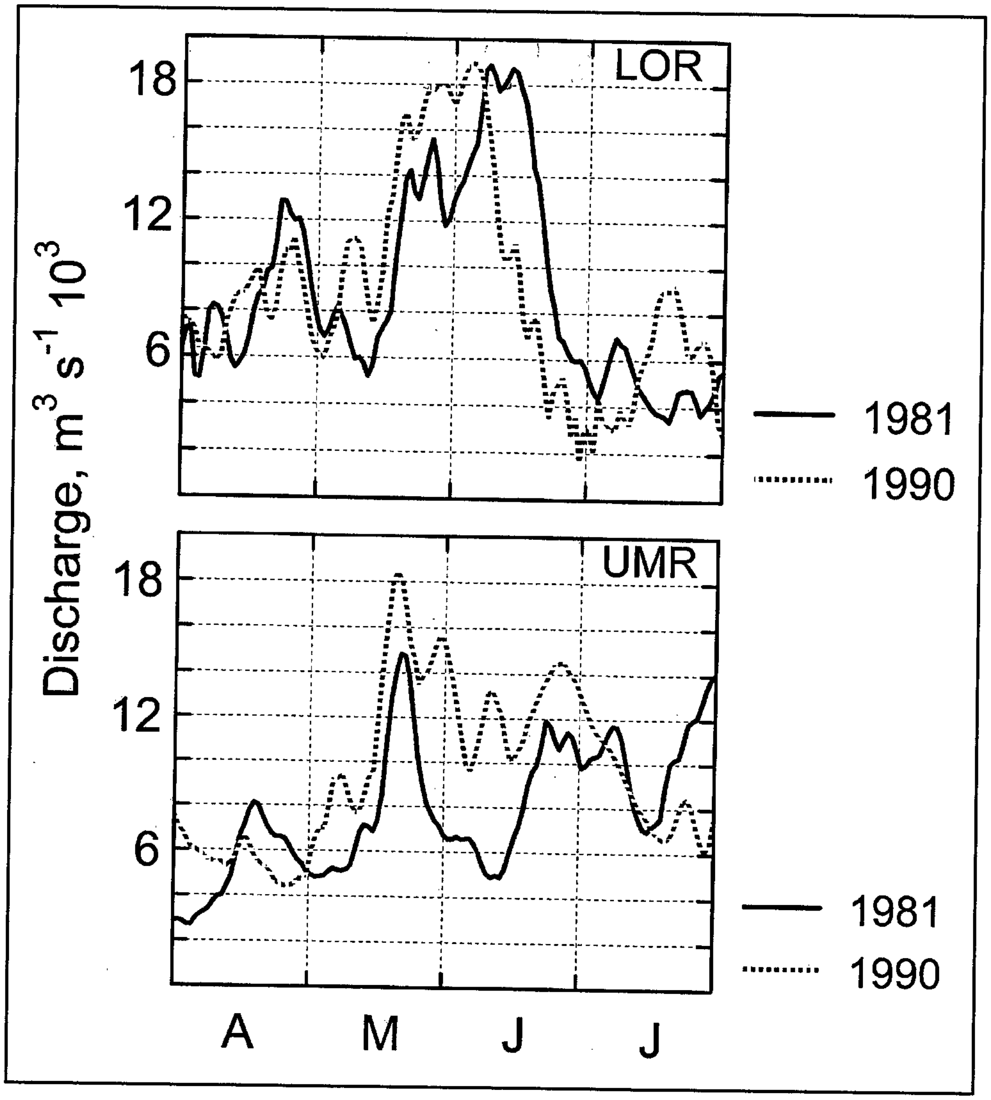

Figure 20. April through July discharge of the lower Ohio and upper Mississippi rivers in 1981 and 1990

through July. In 1990, UMR discharge was 2-8 times greater than LOR discharge from late June through July.

The uniqueness of these conditions in 1981 and 1990 was evaluated by reviewing April through July discharge records for 1977 to 1996 (Figure 21). Inspection of Figure 21 suggests that the almost identical discharge patterns in 1981 and 1990 were somewhat similar to those in four other years—1983, 1984, 1995, and 1996. Minor recruitment was evident for all of these years except 1983. In all 4 years, large April and May rises in LOR discharge occurred that were quickly followed by rapid and large June declines. However, the spring discharge peaks ended 2 to 4 weeks earlier (mid-May to late May) and were not as precisely matched in magnitude as in 1981 and 1990. Minor recruitment in 1979, 1982, 1985, 1993, 1994, 1995, and 1996 occurred in years with relatively depositional conditions in late June or early July. In addition, at least moderately

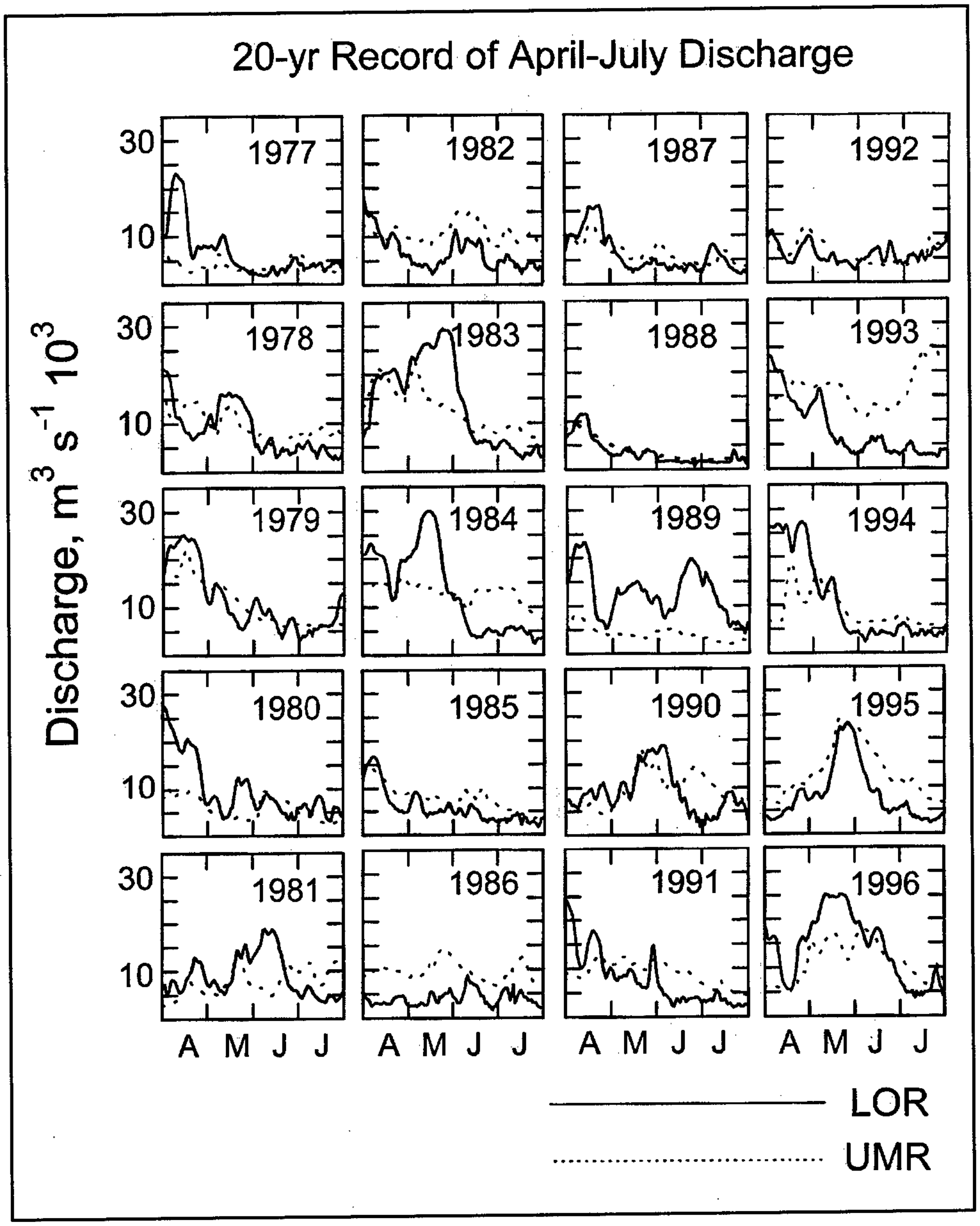

Figure 21. April through July discharge of the lower Ohio and upper Mississippi rivers, 1977 to 1996

high discharge occurred in April or May of all of these years, although only in 1995 and 1996 was there a major peak in discharge in May.

Discussion

A combination of four hydraulic conditions, remarkably similar in spring and early summer of 1981 and 1990, were potentially beneficial to recruitment of *F. ebena* in those years. First, despite a rapid April and May rise in LOR discharge in both years, there were brief periods of below average discharge (<7,000 $m^3 s^{-1}$) in both early April and early May. Low discharge and associated low-water velocity may enhance fertilization success by allowing sperm released into the water by males to be drawn into the mantle cavities of nearby females instead of being carried rapidly downstream (Downing and Downing 1992).

Second, the rapid and large rise in LOR discharge from early May to early (1990) or mid- (1981) June may have attracted spawning aggregations of *A. chrysochloris* to the gravelly shoal. In both years, this LOR rise was accompanied by a similar but earlier ending (mid-May to late May) rise in UMR discharge; thus, there was no backwater effect of the UMR on the LOR during this period. Based on water temperature, the early May to June rise in LOR discharge in 1981 and 1990 precisely coincided with the period during which *A. chyrsochloris* were likely to have made spawning runs. In the Tennessee River, Wallus, Yeager, and Simon (1990) netted *A. chrysochloris* with flowing gametes over gravelly shoals in 16 °C water. Yolk-sac larvae of *A. chrysochloris* were collected at 21 °C in Alabama; peak densities of post yolk-sac larvae of *A. chrysochloris* occur in the Tennessee River usually in late May or early June (Wallus, Yeager, and Simon 1990 and references within). The LOR typically attains a temperature of 16 °C near the first of May and 21 °C by late May (Figure 19). During the spring temperature rise of 1981, 16 °C was attained by mid-April and 24 °C by early June. In 1990, temperature rose rapidly from 12 °C in mid-April to 24 °C in mid-June. In addition to temperature requirements, spawning aggregations of *A. chrysochloris* are associated with high-water velocity (Wallus, Yeager, and Simon 1990). Both water temperature and velocity were probably favorable for fish-spawning aggregations during the rapid and large rise in LOR discharge in May to early June or mid-June. Wallus, Yeager, and Simon (1990) observed spawning of *A. chrysochloris* over deeply submersed gravel (7.3 m) in the Tennessee River. Average depth over the LOR mussel bed was 6.4 to 7.0 m at the onset and 11.9 to 13.4 m at the end of the midspring to late spring rise in discharge 1981 and 1990.

Third, the extremely rapid and great decline in LOR discharge from mid-June to late June and early July in 1981 and 1990 created depositional conditions favorable to juvenile mussel settlement. It is also possible that depositional conditions allowed spent adult fish or recently hatched young-of-the-year *A. chrysochloris* to remain over the mussel bed, enhancing opportunities both for glochidia attachment and local settlement of metamorphosed juveniles. The short duration of the transition from erosional to depositional conditions in June of both 1981 and 1990 resembles the average parasitic lifespan of *F. ebena* glochidia. The timing was coincident with the probable seasonal peak of glochidia release and juvenile settlement. Howard (1914), based on limited data, estimated a 23-day parasitic period for *F. ebena* glochidia. A 2-week period is more likely based on studies of other tachytictic amblemines (Yeager and Neves 1986; Yokely 1972; Coker et al. 1921). With respect to timing of glochidia release, Yokely (1972) observed that a very similar species in a nearby geographic location, *Pleurobema cordatum* in the Tennessee River near Florence, Alabama, begins to release glochidia in late April, with peak release in June. He estimated that temperatures greater than 21 °C were required for glochidia to mature in the mussel gill marsupia. In general, peak population release of glochidia by tachytictic amblemines tends to occur soon after temperature rise above 20 °C—typically in late spring to early summer (Yeager and Neves 1986; Yokely 1972; Coker et al. 1921).

Thus, the successive rise and decline in LOR discharge in late spring and early summer was rapid enough to enhance both aggregation of spawning fish via high-water velocity and juvenile mussel settlement via low-water velocity. Furthermore, seasonal timing was appropriately coincident with probable peaks in both *A. chrysochloris* spawning and release of *F. ebena* glochidia. The much greater discharge of the UMR relative to the LOR in late June and early July further enhanced depositional conditions in the LOR. The backwater effect of the UMR on the LOR during this period may have further enhanced successful settlement of juvenile *F. ebena.*

Hydraulic conditions do not have to benefit *F. ebena* fertilization, aggregation of host fish, and successful settlement of juvenile to benefit recruitment of juveniles in a particular year. Some benefit may accrue if any one of these three processes is enhanced. Probably of greatest importance are host-fish aggregation and juvenile settlement; fertilization tends to be successful even when recruitment is not (Bauer 1988). Fertilization probably benefits from both reduced water velocity in the boundary layer, regardless of general hydraulic conditions, and mussel population density. Nonetheless, hydraulic conditions of April through July of both 1981 and 1990 were appropriate in nature and timing to have conceivably benefited every aspect of *F. ebena* reproduction. Considered in light of the extraordinarily successful recruitment of 1981 and 1990, the complex and precisely matched hydraulic conditions of those two years seem more than circumstantial.

Specific hydraulic conditions benefiting early survival were associated with the highly successful recruitment of *F. ebena* in the hydraulically dynamic LOR. However, other factors must play a role as well, especially relative mussel and fish density (Kat 1984). Abundance of adult mussels has been positively correlated with successful parasitism of host fish based on interpopulation comparisons of *Margaritifera margaritifera* in several central European rivers (Bauer 1988). However, the extraordinary annual variation in recruitment success observed was within a single population. Such temporal variation within a population of long-lived individuals suggests a primary cause other than an effect of adult mussel density on successful parasitism. Local abundance of glochidia hosts can be affected not only by aggregated spawning of *A. chrysochloris* but also by annual variation in this fish's abundance in the LOR. However, with a lifespan of approximately 5 years (Wallus, Yeager, and Simon 1990), the strength of a particular year class of *A. chrysochloris* is not likely to account for exceptionally strong *F. ebena* recruitment in 1981 and 1990. Such an effect of a single fish year class would be more likely if young fish rapidly acquired and maintained immunity to glochidia infestation, thus making young fish the principal glochidia host (Bauer and Vogel 1987). However, adult *A. chyrsochloris* are known to host *F. ebena* glochidia (Surber 1913).

The survivorship curve developed for the 1981 cohort indicates that only 23 and 4 percent of 2-year old mussels survive to age 10 and 20 years, respectively. Extension of the growth model predicts that an individual surviving 20 years is approximately 74 mm long. The largest individuals collected averaged 85 mm from 1983 to 1998. These individuals represent the minute fraction of the population that have extraordinary longevity, above-average growth, or a combination of these traits. If the growth rate of 0.91 mm per year observed for ages 10 through 17 years is extended, 36 years are needed for an average individual to attain the length of 85 mm. Typically, growth rate decreases with increasing age; thus, 36 years may underestimate maximum longevity. However, maximum longevity must be distinguished from average longevity. Certainly, survival beyond 20 years is uncommon.

The dominance of the 1981 and 1990 cohorts of *F. ebena* in the LOR offered a rare opportunity to directly assess length-to-age relationships in a long-lived unionid species residing in a mainstream shoal of a large river. Not surprisingly, age-to-size relationships for long-lived species of freshwater mussels are based mainly on short-term studies that rely on the distance between annual growth rings in the shell (e.g., Coon, Eckblad, and Trygstad 1977; Chamberlain 1931). However, distinguishing annual from other significant interruptions of shell growth is somewhat subjective, difficult, and prone to error (Rhoads and Lutz 1980), especially in species such as *F. ebena* with slow adult growth, massive shells, and a dark periostracum (Coker et al. 1921). Mark and recapture as well as cage studies have been used to assess growth in such species (Coker et al. 1921) but are difficult to successfully complete in open channels of large rivers.

The survivorship model for the 1981-year class of *F. ebena* from age 2 through 17 years is the first such model based on long-term monitoring of a single cohort of a long-lived riverine unionid. According to this model, a constant proportion (16.8 percent) of the cohort survived from year x to year x + 1. Thus, the probability of dying was independent of age within this portion of the lifespan. Bauer (1988) compared ages of living and dead *M. margaritifera* using annual growth lines in the hinge ligament and derived survivorship curves for mussel populations from central European rivers ranging from eutrophic to oligotrophic. Cultural eutrophy was correlated with mortality rate. Survivorship curves ranged from one similar in shape to that of *F. ebena* in the LOR (at eutrophic sites) to a convex curve (at oligotrophic sites) in which nearly all adults survived to very old age and then died within a few years. The former curve is common in animal populations, falling between the extremes of heavy concentration of death at the onset or end of the lifespan (McNaughton and Wolf 1973). Indeed, survivorship of *F. ebena* in the LOR from age 2 through 17 years is remarkably similar, both qualitatively and quantitatively, to survivorship of herring gulls on an island in Maine (McNaughton and Wolf 1973 and references within). A constant proportion (approximately 20 percent) of gulls died each year from age 2 to 17 years, and like *F. ebena*, only a small fraction survived beyond age 17 years.

Like most survivorship curves, the one for this study was not based on the entire lifespan—owing to the extreme difficulty of assessing larval and early juvenile mortality. A single adult female, depending on species and size, releases approximately 75,000 to 5 million glochidia in a reproductive season (Bauer 1988; Neves and Widlak 1988; Yeager and Neves 1986; Kat 1984; Young and Williams 1984; Coker et al. 1921). Nearly all mortality occurs very early in the lifespan; extremely high fecundity is required to balance high mortality of glochidia and settling juveniles. Thus, even a small increase in percent survival in the very early life stages can translate into long-term dominance of a particular year class.

Extraordinary recruitment success of *F. ebena* in only 2 years during a period of approximately two decades is remarkably similar to results of a classic study of the age composition of herring (*Clupea harengus*) catches in the Atlantic off Norway from 1907 through 1926 (Russell and Yonge 1975; Hardy 1965). Norwegian herring were dominated by just two year classes (1904 and 1914) during 20 years of monitoring. The life history of Norwegian herring and *F. ebena* in the lower Ohio River are basically similar in several respects. Longevity is similar. The 1904-year class of herring died out by 1924; the 1981-year class of *F. ebena* was mostly dead by 1998. Sexual maturity is reached early such that individuals reproduce for many years. Finally, both populations are characterized by extremely high mortality in their early life history. Early life in both cases involves little protection from harsh physical and biological forces in open aquatic environments. Loss of eggs, yolk-sac larvae, and early juvenile stages are undoubtedly the greatest source of mortality to herring, a species that broadcasts eggs over spawning grounds in the open sea. Presumably, biological predation and shortage of the right planktonic food pose great risk to eggs and young herring (Hardy 1965). Glochidia and early juvenile *F. ebena* are susceptible to similarly high mortality from physical forces in hydraulically dynamic main channels of large rivers in addition to predation and other biological factors.

In populations of long-lived and highly iteroparous animals, such as *C. harengus* or *F. ebena*, favorable conditions for early survival can cause a few year classes to heavily dominate for many years. Much like the 1904- and 1914-year classes of *C. harengus* in the Atlantic off Norway from 1907 through 1928, the 1981- and 1990-year classes dominated the LOR population of *F. ebena* from 1983 through 1998. Hydraulic conditions in the LOR from April through July of both years were remarkably similar and appropriate for enhanced recruitment. Infrequent but occasionally very strong recruitment may be characteristic of unionid populations in relatively unregulated reaches of large rivers—once a common but now rare habitat of mussels in North America.

4 Summary

Personnel of the U.S. Army Engineer Research and Development Center have used qualitative and quantitative methods to collect bivalves in the lower Ohio River since 1983. Results indicate that mussel beds of the lower Ohio River remain characterized by high richness, heavy dominance of *F.ebena*, good recruitment rates of juveniles (albeit annually quite variable), and resilience to nonindigenous species invasions. This resilience may be a consequence of the inability, thus far, of zebra mussels to establish sustained high-density populations. However, the mussel bed clearly was resilient to long-term high density of *C. fluminea* (from approximately 1958 to the late 1980s). *Fusconaia ebena* was once the dominant thick-shelled unionid of stable river shoals throughout the lower Ohio River and the upper Mississippi River. In the lower Ohio River, its dominance has corresponded with other indicators of a healthy community, including high richness, resilience, recruitment, and presence of an endangered species. These traits all suggest that mussel beds of the lower Ohio River remain among the most ecologically valuable and interesting in the nation.

River hydraulic conditions are important with respect to the location of mussel beds and patterns of annual recruitment in the lower Ohio River. The nearshore limit of the mussel bed at Olmsted closely coincides with sustained periods of low water. Because most unionids are long lived, river stage must be considered over a few decades rather than just a few years to reveal this relationship. Similarly, long-term analysis of data revealed an apparent relationship between river discharge pattern from April through July and recruitment of *F. ebena*. Two years with exceptionally strong recruitment, 1981 and 1990, were remarkably closely matched with respect to hydraulic conditions that may have benefited both the probability of successful attachment of glochidia to fish gills and subsequent settlement of juveniles from fish.

Continued monitoring using qualitative and quantitative methods will provide data that can be used to determine if construction and operation of the Olmsted Locks and Dam project have negative effects on the mussels of the lower Ohio River. Long-term data have proven invaluable for interpreting causes and significance of fluctuations in physical and biological parameters, including population and community demographics and abundance of nonindigenous species.

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13. ABSTRACT ***(Maximum 200 words)***

Surveys were conducted in August 1998 to assess community characteristics, population demography of dominant species, status of endangered species, and characteristics of nonindigenous populations of freshwater bivalves in the lower Ohio River (LOR). Data will be used to analyze ecological effects of construction and operation of a new lock and dam at River Mile (RM) 964.4. Primary focus has been on a prominent mussel bed just downstream of the project at Olmsted, Illinois. Studies have shown that this mussel bed extends approximately from elevation 278 ft nearshore to 267 ft farshore. Moderate (20-50 individuals per square meter) or high density (>50 individuals per square meter) assemblages of mussels tend to be at more central elevations on the bed from approximately RM 966.4 to 968.3. The downstream and farshore limits of the mussel bed tend to be less distinct than the nearshore and upstream limits.

The community downstream of the project is extremely dominated by *Fusconaia ebena.* A mussel bed being monitored upstream of the project at RM 957 near Post Creek is clearly dominated by this species, but much less heavily than at Olmsted. Both communities have been resilient to long-term occurrence (since approximately 1960) of the Asiatic clam, *Corbicula fluminea,* and more recent occurrence of the zebra mussel, *Dreissena polymorpha.*
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Both mussel beds are characterized by extreme dominance of just two year classes, 1981 and 1990, of the dominant species.

Demographically complete sampling of *F. ebena* (Lea) at Olmsted has been conducted from 1983 through 1998. Dominance of the 1981 and 1990 cohorts allowed length-to-age relationships to be estimated directly from length-frequency histograms. Two linear relationships adequately described growth rates from age 2 through 17 years. The first applied to ages 2 through 10 years when annual growth averaged 5.9 mm per year. The second model applied to ages 10 through 17 years when annual growth averaged only 0.9 mm per year. A survivorship curve was based on density of the 1981 cohort from age 2 through 17 years. During that period, a constant proportion (17 percent) of the cohort died each year. Only 6 percent of the 1981 cohort in 1983 was still alive in 1998. Annual variation in hydraulic conditions related to recruitment success. In both 1981 and 1990, rapid and large spring rises in LOR discharge were immediately followed by similarly rapid and large declines. The rise coincided with the expected spawning peak of *Alosa chrysochloris,* the only fish host for *F. ebena* glochidia. The rapid return to low-flow and depositional conditions was appropriately timed to enhance successful settlement of juvenile *F. ebena* after their parasitic stage on *A. chrysochloris* gills.