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American Midland Naturalist is currently published by The University of Notre Dame.

Recruitment of Fusconaia ebena (Bivalvia: Unionidae) in Relation to Discharge of the Lower Ohio River

BARRY S. PAYNE AND ANDREW C. MILLER

Environmental Laboratory, U.S. Army Engineer, Research and Development Center, Vicksburg, Mississippi 39180

ABSTRACT.—Demographically complete sampling of a large population of *Fusconaia ebena* (Lea) in a mainstream shoal in the lower Ohio River (LOR) from 1983 through 1998 revealed two extremely successful recruitment years—1981 and 1990. 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 y. The first model applied to ages 2 through 10 y when annual growth averaged 6.1mm. The second model applied to ages 10 through 17 y when annual growth averaged only 1.1 mm. A survivorship curve was based on density of the 1981 cohort from age 2 through 17 y. During that period a constant proportion (17%) of the cohort died each year. Only 9% of the 1981 cohort alive in 1983 were still alive in 1998. In both 1981 and 1990 rapid and large spring rises in LOR discharge were immediately followed by rapid and large declines. These rises coincided with the expected spawning peak of *Alosa chrysochloris*, the only known 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.

INTRODUCTION

River hydraulics determine sedimentation, substratum type, bed stability and, therefore, where a mussel bed can exist in a large river (Coker *et al.*, 1921). Longterm 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 chrysochloris*, the only known host fish of *F. ebena* glochidia (Surber, 1913; Coker *et al.*, 1921), to swiftly flowing water over gravelly shoals (Wallus *et al.*, 1990). In turn, depositional conditions probably benefit settlement of juvenile mussels after the 1–3 wk period typically required for metamorphosis (Howard, 1914; Coker *et al.*, 1921). 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 a major locks and dam project in the lower Ohio River (LOR) near Olmsted, Illinois, has been the reason for regular quantitative sampling of a prominent mussel bed in a mainstream shoal since 1983. *Fusconaia ebena* heavily dominates the LOR mussel community (Miller *et al.*, 1986); relative abundance of *F. ebena* typically varies from 70 to 90%. The population is characterized by extreme annual variation in recruitment success; approximately a decade ago we described growth and survival of a cohort of 1981 recruits that dominated the population during the 1980s (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. Our purpose herein is to update that earlier record and evaluate annual variation in recruitment in relation to river hydraulic conditions and host availability.

STUDY AREA AND METHODS

The mussel bed extends from approximately elevation 85 m nearshore to 81 m farshore and River Kilometer (RK) 1555 upstream to 1559 downstream along the Illinois side of the lower Ohio River (LOR) (Payne and Miller, 1997). The bed is in a gravelly shoal of the free-flowing portion of the LOR downstream of both existing Lock and Dam 53 (RK 1549) and the replacement Olmsted Locks and Dam Project now under construction (RK 1552). Substratum D_{50} (50% of sample weight is smaller than this particle diameter) ranges from 7 to 20 mm nearshore and from 0.5 to 3 mm farshore (data collected in 1993 and 1994 by the St. Louis District, USACE). The confluence of the LOR and the upper Mississippi River (UMR) at Cairo, Illinois is only 23 km downstream of the mussel bed.

Demographically complete samples of *Fusconaia ebena* were obtained in summer or fall of 1983 through 1998 by having divers excavate the substratum to a depth of 15 cm from 0.25 m² quadrats. Replicate samples (usually ten) were always taken from multiple sites (usually two to four) in a central portion of the mussel bed, 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 to 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 UMR affect hydraulic conditions at the study site, 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.

RESULTS

Demography of the LOR population of *Fusconaia ebena* over the past 15 y has been characterized by extreme dominance of only 2 y classes—1981 and 1990 (Fig. 1). Seventy one percent of the population in 1983 was comprised of a single cohort (1981) of recent recruits. In 1992 the 1990 y class comprised 85% of the population. Recruitment in years other than 1981 and 1990 was minor or not evident. Population density ranged from 6.8 to 29.9 individuals per m² from 1983 to 1998 (Table 1).

In 1983 individuals of the 1981 cohort averaged 15.8 mm long and ranged from 11.8 to 20.6 mm (Fig. 1). 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.
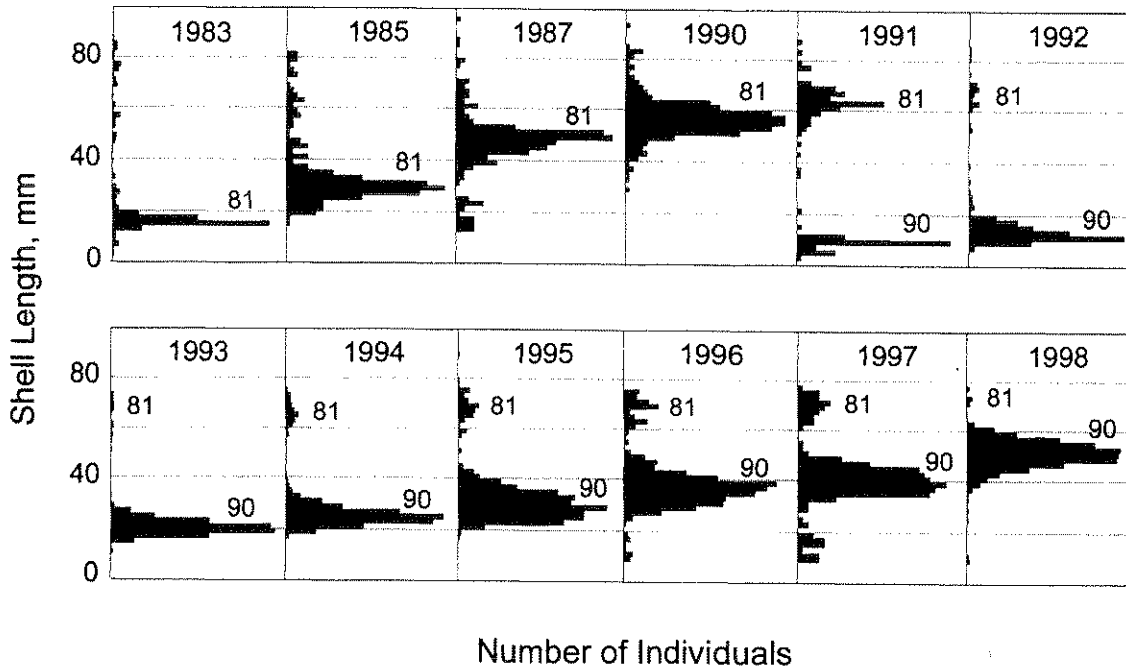
FIG. 1.—Length-frequency histograms of *Fusconaia ebena* from 1983 through 1998. Numbers identify the 1981 and 1990 cohorts

Thus, with reasonable certainty, all individuals visible without aid of magnification were sorted from substratum.

The small cohort centered at 7.4 mm in 1983 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,

TABLE 1.—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 m²	
			Mean	SD
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	1194	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	1072	26.8	11.8

* Study design was not appropriate for comparison to other years

quickly eroded and was not consistently evident in individuals of the still young 1981 cohort in 1983. Second, juvenile *Fusconaia 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 (Coker *et al.*, 1921; Yokely, 1972) and the spring portion of the growth season has passed. Annual growth of the 1981 cohort from 1983 to 1985 averaged slightly less than 7 mm per y (Fig. 1). Thus, it is unlikely that juveniles starting benthic life at less than 0.2 mm in early-to-midsummer attained an average length of 7.4 mm by early fall.

The 1990 cohort was first evident in 1991 when it was approximately equal in abundance to the 1981 cohort (Fig. 1). The latter had grown to an average length of 63.4 mm (Fig. 1). 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 y in juvenile *Fusconaia ebena* and several other unionids (Coker *et al.*, 1921). The smallest individuals of the 1990 cohort were not retained on the finest sieve until 1992 (Fig. 1). Once fully represented in 1992 relative abundance of the 1990 cohort (85%) greatly exceeded that of the formerly dominant 1981 cohort (10%).

Minor recruitment was evident in several years other than 1981 and 1990 (Fig. 1). 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 (Fig. 1). 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 (Fig. 1).

Thus, 16 y of monitoring provided evidence of two extremely large year classes (1981 and 1990) and several minor year classes (possibly 1979, 1982, 1984, 1985, 1993, 1994, 1995 and 1996) of the *Fusconaia ebena* population in the LOR. The nine-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.

In any population of long-lived individuals, decreased growth rate with increased age and size causes overlap of individuals of adjacent cohorts, obscuring upper and lower size limits of a particular year class. For example, 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 (Fig. 1). Regardless of such difficulties, central tendency in size distribution of the two dominant year classes usually was apparent (Fig. 1).

Growth rates were estimated using average lengths estimated for the 1981 and 1990 cohorts. Inspection of the histograms in Figure 1 was used with normal probability plots to identify the length range that included nearly all individuals of the 1981 and 1990 cohorts in a particular year. Mean lengths were computed for all individuals falling within those length ranges (Table 2). The best representation of *Fusconaia ebena* growth through age 17 was provided by two linear regressions of mean shell length (SL, mm) on age (A, years) (Fig. 2). The first model, applicable to ages 2 through 10 y, was SL = 2.50 + 6.06 A; $r^2 = 0.96$; P < 0.0001. Despite some intercohort differences, this model fit both the 1981 and 1990 cohorts. The 1990 cohort was smaller than the 1981 cohort from age 4 through 7 y. However, above average growth of the 1990 cohort was evident from age 7 through 8 y and the 1981 cohort showed below average growth from age 6 through 9 y.

TABLE 2.—Minimum, maximum and mean shell length (SL in mm) estimates for 1981 and 1990 cohorts of *Fusconaia ebena* from the LOR mussel bed. See text for further discussion

Year	1981 Cohort SL			1990 Cohort SL		
	Min.	Max.	Mean	Min.	Max.	Mean
1983	11.8	20.6	15.8			
1985	24.1	35.4	29.5			
1987	36.2	55.7	47.4			
1990	47.0	67.7	56.5			
1991	52.0	72.0	63.4	3.9	14.5	8.9
1992	55.6	74.6	66.5	7.2	20.1	12.8
1993	54.3	73.8	65.9	11.4	29.8	20.4
1994	56.0	74.5	65.9	15.4	35.1	25.1
1995	56.0	79.2	67.8	19.7	45.2	30.2
1996	58.3	76.4	68.1	23.4	51.6	36.7
1997	61.7	77.5	69.5	28.5	55.0	40.7
1998	65.8	78.3	73.0	36.1	64.0	51.4

Overall, the single linear regression indicating annual growth of 6.1 mm provided an excellent fit for both cohorts from age 2 through 10 y.

Growth from age 10 through 17 y was much slower, with data available only for the 1981 cohort. The linear model applied to these ages was SL = 52.9 + 1.08 A; r^2 = 0.85; $P < 0.002$.

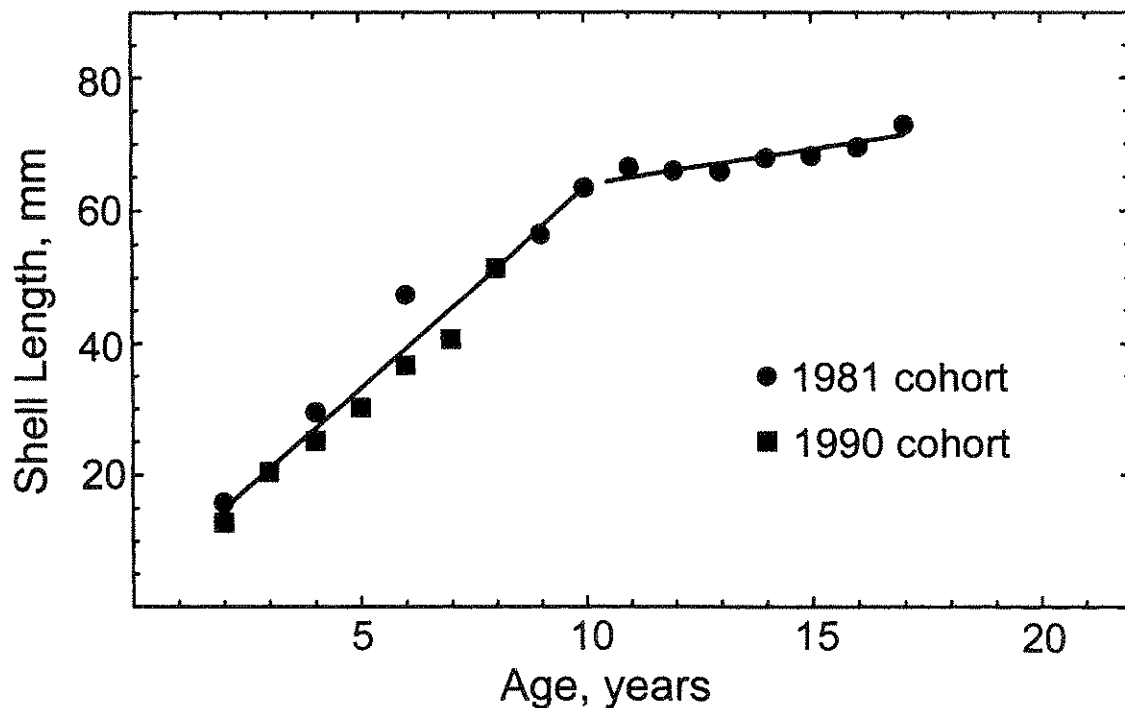A survivorship curve was based on the declining density of the 1981 cohort from 1983

FIG. 2.—Linear growth of the 1981 and 1990 cohorts of *Fusconaia ebena* from age 2 through 10 y and of the 1981 cohort from age 10 through 17 y

The figure shows a plot with y-axis "Individuals per 0.25 m^2" (logarithmic scale from 0.1 to above 10) and x-axis "Age, years" (5 to 20). Data points with a declining fitted line are shown. Annotations: $\log_{10}y = 1.298 - 0.0816x$, $r^2 = 0.83$, $p < 0.0002$.
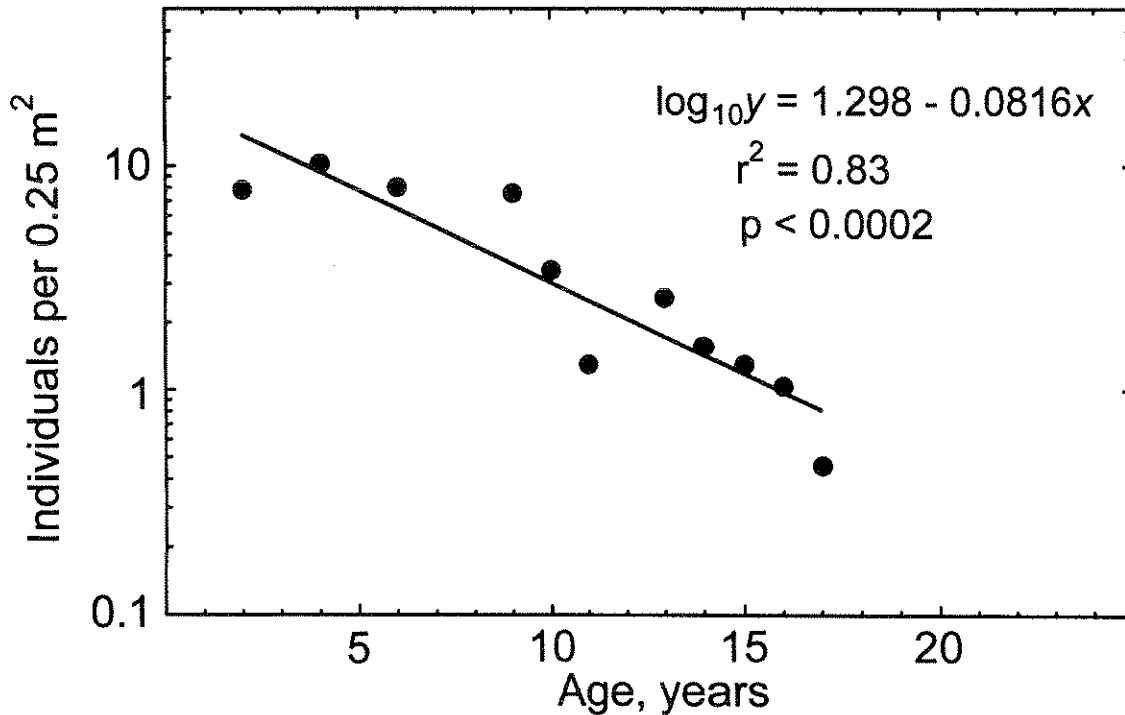
FIG. 3.—A survivorship curve based on declining density of the 1981 cohort of *Fusconaia ebena* from age 2 through 17 y

through 1998 (Fig. 3). This curve indicates a constant proportion (17%) of the cohort died each year from age 2 through 17 y. Cumulative mortality from 1983 to 1998 was 94%, as density declined from 13.7 to 1.2 individuals per 0.25 m². Extension of the model predicts mortality over 96% at age 20 y.

Average discharges of the LOR and UMR near their confluence are 7646 and 5522 m³·s⁻¹ with considerable seasonal variation (Fig. 4). In the LOR depositional conditions and low discharge (<5000 m³·s⁻¹) tend to occur from July through October whereas erosional conditions and high discharge (>10,000 m³·s⁻¹) occur from December through April (Fig. 4). Due to a backwater effect near the confluence of the LOR and UMR, depositional conditions are greater if UMR discharge is simultaneously and substantially higher.

Discharge from April through July was of special interest with respect to *Fusconaia ebena* recruitment. Water temperature in the LOR typically rises from 10 C to the average seasonal maximum of 28 C from April through July (Fig. 5). 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 *Alosa chrysochloris* (Wallus *et al.*, 1990). Discharge records from 1977 through 1996 were analyzed for two reasons. First, initial sampling in 1983 indicated that exceptional recruitment of *F. ebena* probably had not occurred for several years before the recruitment in 1981. Second, the youngest recruitment cohort certain to be fully included in 1998 samples, if present, would be 1996 recruits.

Hydraulic conditions in the LOR were unusual, complex and remarkably similar from April through July of 1981 and 1990 (Fig. 6). In both years LOR discharge was approximately 6000 m³·s⁻¹ in early April, rose rapidly to 11,000 m³·s⁻¹ by late April and dropped
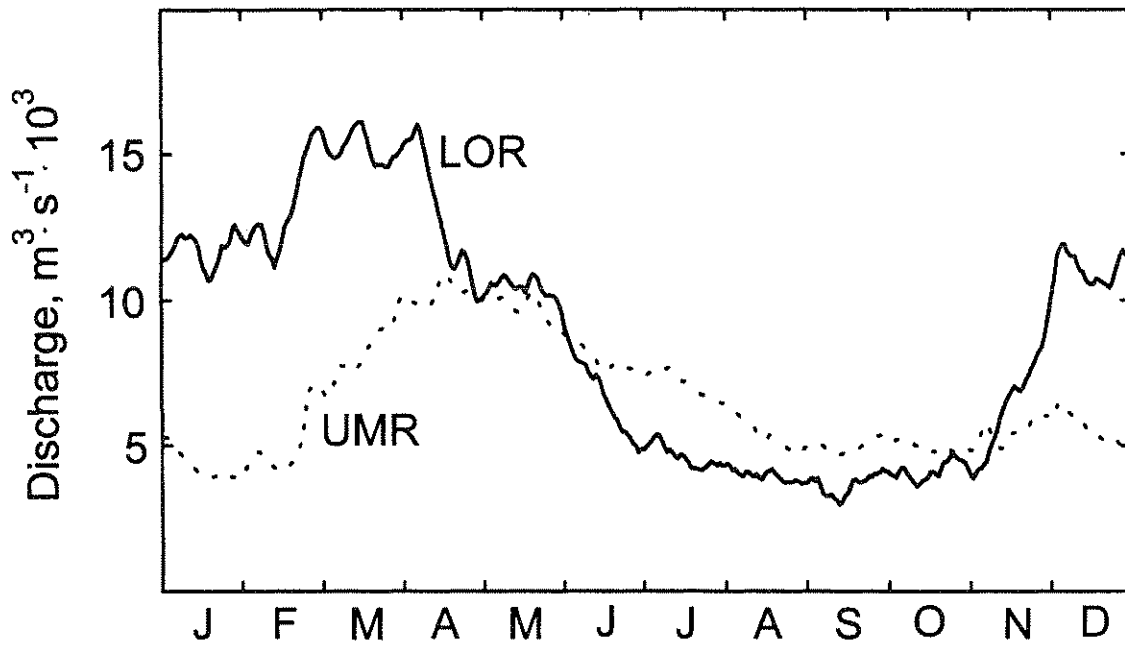
FIG. 4.—Average discharge (20-y record) of the lower Ohio River (LOR) at Metropolis, Illinois, and upper Mississippi River (UMR) at Thebes, Illinois
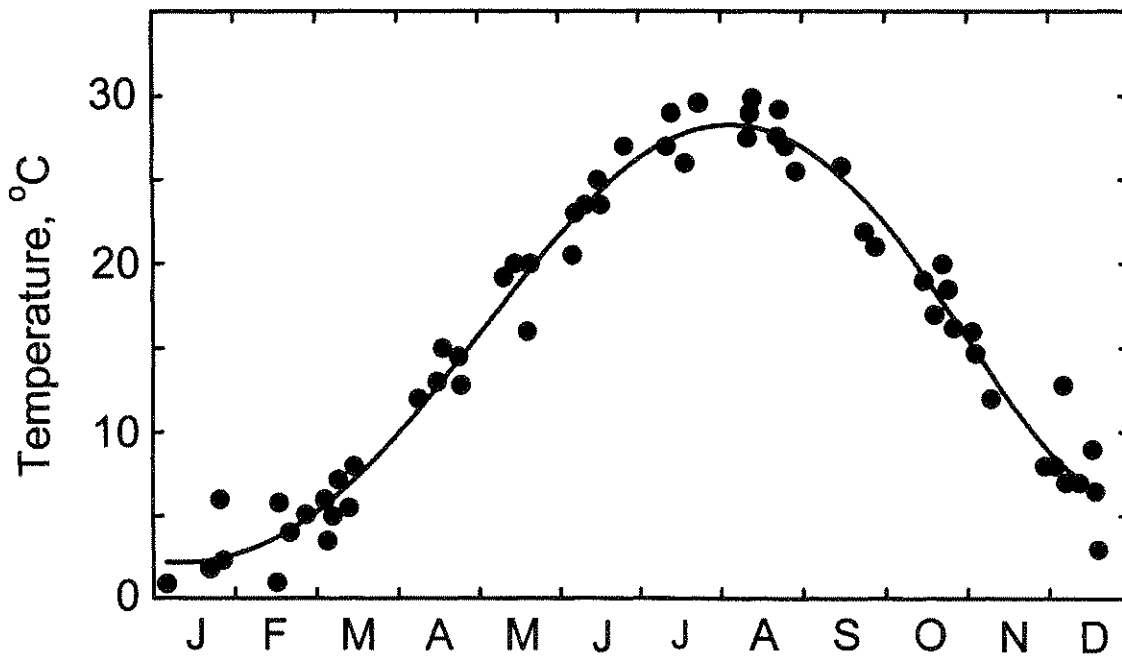

FIG. 5.—Surface temperature of the lower Ohio River at Lock and Dam 53. Data were compiled for a 10-y period from annual records of the U.S. Geological Survey
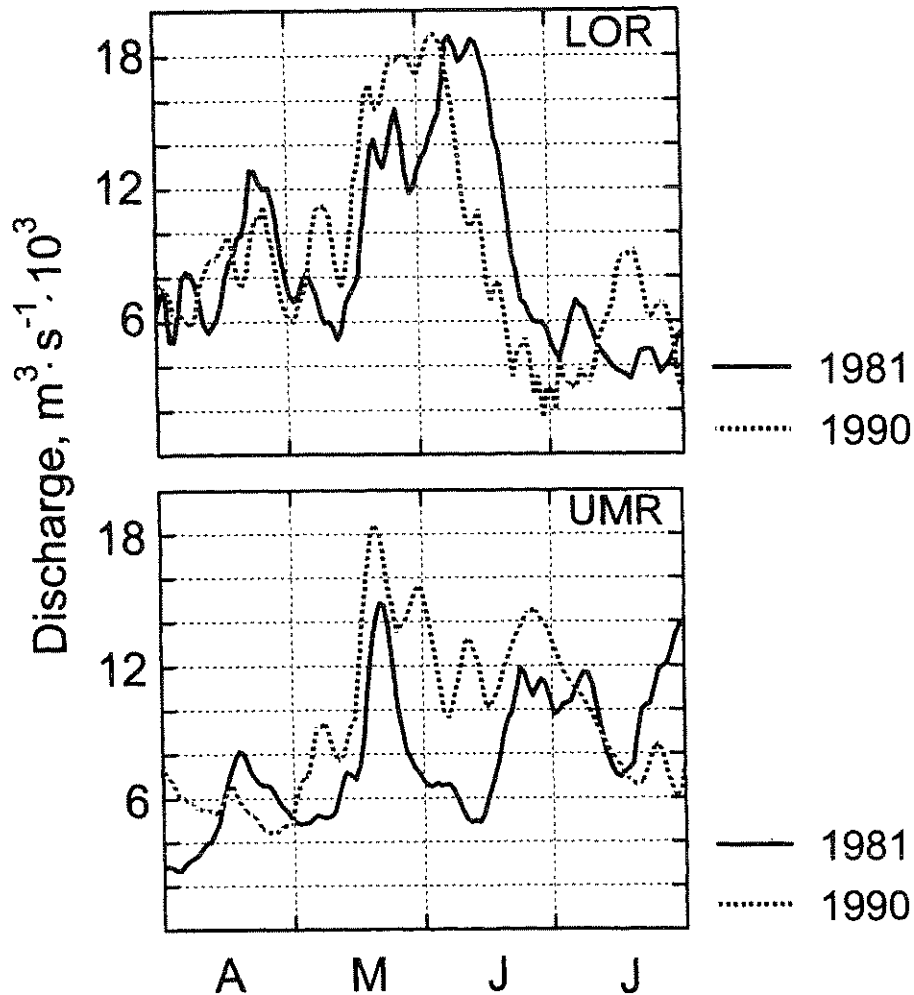
FIG. 6.—Comparision of April through July discharge, 1981 and 1990, of the lower Ohio River (LOR) at Metropolis, Illinois, and upper Mississippi River (UMR) at Thebes, Illinois

rapidly to 6000 $m^3 \cdot s^{-1}$in early May. Then, LOR discharge rose rapidly to 14,000 $m^3 \cdot s^{-1}$ by mid May and 19,000 $m^3 \cdot s^{-1}$ by mid June, but plummeted to 2000 $m^3 \cdot s^{-1}$ by late June (1990) or 4000 $m^3 \cdot s^{-1}$ by early July (1981). In both years UMR discharge greatly exceeded LOR discharge for extended periods from late June through July (Fig. 6). In 1981 UMR discharge was more than twice that of the LOR for most of late June through July. In 1990 UMR discharge was 2–8 times greater than LOR discharge from late June through July.

Daily discharge of the LOR during April through July was averaged for 1981 and 1990 and then compared to discharge during the same period for 1977 through 1996 (Fig. 7). The unusual discharge patterns of 1981 and 1990 were somewhat similar to those in four other years—1983, 1984, 1995 and 1996 (Fig. 7). Minor recruitment was evident for all of these years except 1983. In all 4 y 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 2–4 wk earlier (mid 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
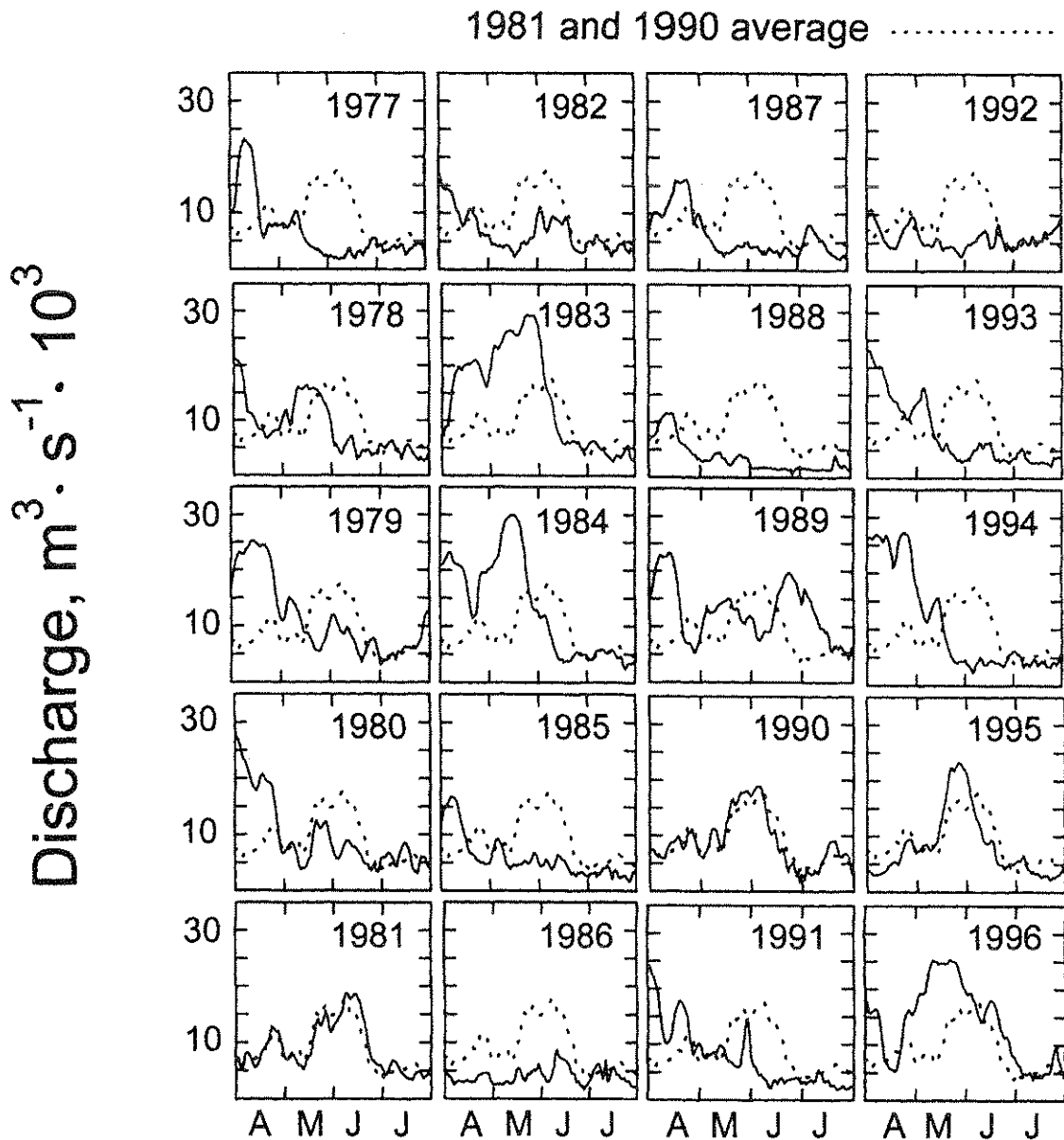
Fig. 7.—April through July discharge, 1977–1996, of the lower Ohio River (LOR) at Metropolis, Illinois. Dashed line shows discharge during this period averaged for 1981 and 1990

July. In addition, at least moderately 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

Both *Fusconaia ebena* and *Alosa chrysochloris* inhabit large rivers and prefer moderately swift water and stable sandy or gravelly shoals (Surber, 1913; Smith, 1979; Wallus *et al.*, 1990; Cummings and Mayer, 1992). Glochidia of *F. ebena* must attach to gills of *A. chrysochloris* for successful transformation to the benthic juvenile stage (Surber, 1913; Coker *et al.*, 1921). 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 (Robinson and Buchanan, 1988; Payne and Miller, 1989; Wallus *et al.*, 1990; Cummings and Mayer, 1992; Miller and Payne, 1992; Etnier and Starnes, 1993). 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 (Robinson and Buchanan, 1988; Wallus *et al.*, 1990). Indeed, locks and dams in the Arkansas River, although impeding to fish migration, deepened the river channel, reduced suspended solids and apparently improved habitat for *A. chrysochloris* (Robinson and Buchanan, 1988).

Adult *Alosa chrysochloris* make prominent upstream runs to spawn over rocky or gravelly shoals in spring or early summer (Wallus *et al.*, 1990). Release of glochidia conglutinates by *Fusconaia 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* (Coker *et al.*, 1914; Lee *et al.*, 1980; Theler, 1987). Spring migration must have been required for *A. chrysochloris* to spawn in the UMR; overwintering was apparently not possible in this northernmost extension of the species' range. Both *A. chrysochloris* 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.

A combination of four hydraulic conditions in the LOR, remarkably similar in spring and early summer of 1981 and 1990, was potentially beneficial to recruitment of *Fusconaia 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 (<7000 m^3·s^{-1}) in both early April and early May (Fig. 6). 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 *Alosa chrysochloris* to the gravelly shoal. In both years this LOR rise was accompanied by a similar but earlier ending (mid 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 temperatures, the early May to June rise in LOR discharge in 1981 and 1990 coincided with the period during which *A. chrysochloris* were likely to have made spawning runs. In the Tennessee River Wallus *et al.* (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 *et al.*, 1990 and references within). The LOR typically attains a temperature of 16 C near the first of May and 21 C by late May (Fig. 5). Limited USGS temperature data for the LOR during the spring temperature rise of 1981 indicated that 16 C was attained by mid April and 24 C by early June. Temperature records for 1990 indicated a rapid rise 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 *et al.*, 1990). Both water temperature and velocity were probably favorable for *A. chrysochloris* spawning aggregations during the rapid and large rise in LOR discharge in May to early or mid June. Wallus *et al.* (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 mid 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 that may favor juvenile mussel settlement. It is also possible that depositional conditions allowed spent adult fish or recently hatched young-of-the-year *Alosa 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 *Fusconaia ebena* glochidia. The timing was coincident with the probable seasonal peak of glochidia release and juvenile settlement. Howard *et al.* (1914), based on limited data, estimated a 23-d parasitic period for *F. ebena* glochidia. A 2 wk period is more likely based on studies of other tachytictic amblemines (Coker *et al.*, 1921; Yokely, 1972; Yeager and Neves, 1986). Surber's (1913) limited observations of *F. ebena* glochidia on *A. chrysochloris* in the upper Mississippi River, more northerly and slightly cooler than the LOR, indicated completion of the parasitic period by mid-August. With respect to timing of glochidia release, Yokely (1972) observed that a similar species in a nearby 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 (Coker *et al.*, 1921; Yokely, 1972; Yeager and Neves, 1986). Our sampling of the LOR *F. ebena* population spanned the period 20 July to 31 October (Table 1). Gravid *F. ebena* have not been obtained during that period, indicating glochidia release before midsummer. Surber's (1913) study in the upper Mississippi River indicated that juvenile *F. ebena* leave *A. chrysochloris* in mid-August.

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 by high water velocity and juvenile mussel settlement by low water velocity. Furthermore, seasonal timing was approximately coincident with probable peaks in both *Alosa chrysochloris* spawning and release of *Fusconaia 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 *Fusconaia ebena* fertilization, aggregation of host fish and successful settlement of juveniles to benefit recruitment in a particular year. Some benefits may accrue if any one of these three processes is enhanced. Probably most important 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 matched hydraulic conditions of those two years seems more than circumstantial.

Specific hydraulic conditions benefiting early survival were associated with the highly successful recruitment of *Fusconaia ebena* in the hydraulically dynamic LOR. However, other factors must be important 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 we 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 *Alosa chrysochloris* but also by annual variation in its abundance in the LOR. However, with an individual lifespan of approximately 5 y (Wallus *et al.*, 1990), the strength of a particular year class of *A. chrysochloris* is not likely to account for exceptional *Fusconaia 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. chrysochloris* are known to host *F. ebena* glochidia (Surber, 1913).

The dominance of the 1981 and 1990 cohorts of *Fusconaia ebena* in the LOR offered a rare opportunity to directly assess survivorship and length-to-age relationships in a long-lived unionid species residing in a mainstream shoal of a large river. These assessments did not have to rely on subjective counts of annual growth rings in the shell (Rhoads and Lutz, 1980) which are especially difficult in species such as *F. ebena* with slow adult growth, massive shells and a dark periostracum (Coker *et al.*, 1921). The survivorship curve developed for the 1981 cohort indicates that only 23 and 4% of 2-y-old mussels survive to age 10 and 20 y, respectively. The growth model predicts that an average individual surviving 20 y is approximately 74 mm long. The largest individuals collected averaged 85 mm from 1983 to 1998. These large individuals represent a minute fraction of the population that have extraordinary longevity, above-average growth or a combination of these traits.

Our survivorship model for the 1981 year class of *Fusconaia ebena* from age 2 through 17 y 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%) 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. This pattern 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). Like most survivorship curves, ours 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 (Coker *et al.*, 1921; Kat, 1984; Young and Williams, 1984; Yeager and Neves, 1986; Bauer, 1988; Neves and Widlak, 1988). 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 *Fusconaia ebena* in only 2 y 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 (Hardy, 1965; Russell and Yonge, 1975). Norwegian herring were dominated by just two year classes (1904 and 1914) during 20 y 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. Individuals reproduce for many years. Substantially slowed growth of mussels greater than 60 mm long and 10-y old (Fig. 3) possibly indicates the size and age at which reproductive allocation substantially competes with so-

matic and shell growth. Payne and Miller (1989) observed that gonadal tissue was consistently evident in *F. ebena* larger than 39 mm. Finally, both *C. harengus* and *F. ebena* 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, 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 *Clupea harengus* or *Fusconaia 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 have 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.

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