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Growth and Survival of Recent Recruits to a Population of Fusconaia ebena (Bivalvia: Unionidae) in the Lower Ohio River

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ABSTRACT.—Demographically complete sampling of a large population of *Fusconaia ebena* (Lea) in a mainstream shoal in the lower Ohio River from 1983 through 1987 revealed extensive annual variation in recruitment. Survival and early growth rate were assessed by monitoring size increase and relative abundance of an exceptionally abundant, and therefore distinct, cohort of recent recruits. Individuals recruited to the population in 1981 comprised approximately 70% of the entire population throughout the study period, indicating both negligible mortality of this successfully settled cohort as well as lack of subsequent strong recruitment. Shell length of *F. ebena* increased at a linear rate throughout the 1st 6 years of life. The annual growth increment was approximately 8 mm. Biomass increased exponentially over the same age range. Longevity of *F. ebena* at this location was estimated to range from 11 to 18 years. First reproduction was estimated to occur at an age of 6 years and at a tissue mass equal to only 14% of that of the oldest adults in the population. A long reproductive lifespan is required to maintain this population, which is characterized by extensive annual variation in recruitment success.

INTRODUCTION

Recruitment, growth and survival of freshwater bivalves is often assessed by monitoring changes in density and size demography of natural populations (*e.g.*, Aldridge and McMahon, 1978; Burky *et al.*, 1981). However, demographically complete censuses have rarely been made of unionid populations in mainstream river shoals (Miller and Payne, 1988), although this is the principal habitat of most species (Stansbery, 1970). Unique among freshwater bivalves, large, thick-shelled unionids adapted to life in river shoals combine a long reproductive life with high reproductive output each year (Coker *et al.*, 1921; Chamberlain, 1931; Burky, 1983). Almost nothing is known of recruitment, early growth and survival of individuals in natural populations of riverine unionids (Surber, 1913; Coker *et al.*, 1921). We report observations of early growth and survival of recent recruits to a large population of *Fusconaia ebena* (Lea) in a mainstream shoal in the lower Ohio River.

MATERIALS AND METHODS

The population sampled dominates a rich unionid community (Miller *et al.*, 1986) in a gravelly shoal in the free-flowing portion of the Ohio River below Lock and Dam 53. The 5-km-long bed is approximately 125 m wide, and spans a depth range of approximately 5 m from the inner to outer margin. A total of 24, 17 and 20 quantitative substrate samples were collected in 1983, 1985 and 1987, respectively, by divers equipped with SCUBA, within the central portion of the bed. Sampling was conducted in the autumn near the end of the growing season (Chamberlain, 1931); dates of sampling were 28–29 September in 1983, 31 October–1 November in 1985, and 29–30 September in 1987. Each sample was collected by removing all substrate to a depth of 10–15 cm from a 0.25-m^2 sampling frame. Each sediment sample was washed through a series of sieves (smallest mesh aperture of 4 mm), and all living *Fusconaia ebena* were picked from the sorted sediment samples. A total

of 256, 269 and 219 *F. ebena* were collected in 1983, 1985 and 1987, respectively. A detailed description of the sampling procedure is given elsewhere (Miller and Payne, 1988).

Shell length (SL, the greatest anterior-posterior dimension across the valves) of living individuals was measured to the nearest 0.1 mm using a dial caliper. Total mass (TM) of each individual was measured to the nearest 0.1 g using a top-loading electronic balance. Prior to weighing, mussels were kept submerged, forced to close their shell valves prior to emergence, and blotted dry. This procedure minimized inter-individual variation in loss of mantle cavity water (regression of the logarithm of TM on the logarithm of SL yielded an r^2 of 0.97). Distinct cohorts of small mussels were identified in SL frequency histograms prepared from each of the three surveys. Growth and age estimates were based on the growth rate of a dominant recruitment class apparent in the 1983, 1985 and 1987 histograms as well as within histogram comparisons of the average size of the dominant and other distinct cohorts. Age estimates are often based on counts of shell annuli formed during overwinter cessation or marked reduction of growth (Chamberlain, 1931; Coon *et al.*, 1977; Strayer *et al.*, 1981). Winter annuli are difficult to distinguish from other environmental and physiological interruptions of bivalve shell growth (Rhoads and Lutz, 1980). The massiveness of shells of most riverine unionids makes identification of winter annuli especially difficult (Chamberlain, 1931; Strayer *et al.*, 1981). Age-to-size estimates are not provided for large mussels. Distinct cohorts of large mussels could not be discerned and winter annuli on shells could not be objectively distinguished from additional rings caused by other interruptions of shell growth (on the exterior surface or in microscopical examination of thin cross sections).

Each year a group of approximately 40 *Fusconaia ebena* spanning the size range of individuals in the natural population were fixed in 12% neutral formalin and used for determinations of tissue and shell growth components. Tissues were removed from shell valves, tissues and valves were dried at 60 C to constant weight, and tissue dry mass (TDM) and shell dry mass (SDM) determinations were made using a top-loading electronic balance. The 1987 subsample of *F. ebena* was inspected for the presence of gonadal tissue to estimate the average size at first reproduction (gametes were not evident in male or female gonads and embryos were not present in gill marsupia of the autumn-collected mussels).

RESULTS

The number of *Fusconaia ebena* per square meter averaged (±SD) 43 ± 21, 63 ± 26, and 43 ± 19 in 1983, 1985 and 1987, respectively. Seventy-one percent of all *F. ebena* collected in 1983 belonged to a single cohort of individuals with an average SL of 15.8 mm (range = 12.8 to 19.5 mm) (Fig. 1). Minor cohorts centered at 7.4 and 28.1 mm SL comprised 3 and 6% of the population, respectively. The cohorts centered at 7.4, 15.8 and 28.1 mm SL in 1983 appear to represent 1982, 1981 and 1979 recruitment, respectively. The remaining 19% of the total population was made up of indistinguishable cohorts greater than 40 mm SL whose subsequent growth rates could not be estimated from SL frequency histograms based on the 1985 and 1987 surveys.

The average SL of the dominant 1981 cohort increased to 29.5 mm (ranging from 23.0 to 38.4 mm) by autumn 1985 (Fig. 1). The 1981 cohort comprised 71% of total sample of *Fusconaia ebena* in 1985, due to low mortality of this dominant cohort combined with lack of strong recruitment since 1981. The average SL of the 1981 cohort increased to 47.3 mm (range = 35.5 to 56.0 mm) by late September 1987. The relative abundance of this cohort remained undiminished at 74%. The 1987 survey provided evidence of additional but minor recruitment since 1981. Individuals between 14 and 26 mm SL comprised 11% of the 1987 sample, and probably represented 1985 recruitment.

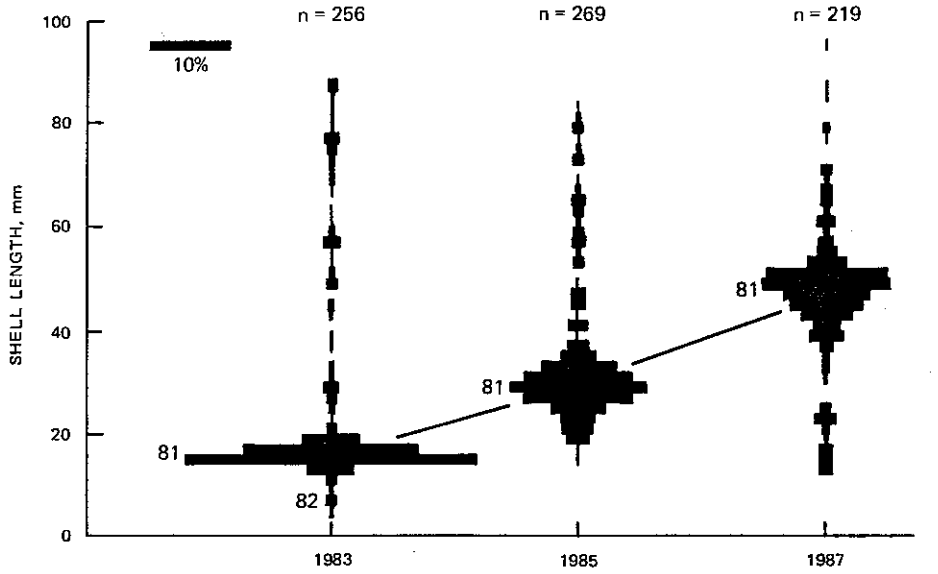

FIG. 1.—Shell length frequency histograms of *Fusconaia ebena* in the lower Ohio River on 28–29 September 1983, 31 October–1 November 1985 and 29–30 September 1987. Numbers next to cohorts identify probable year of recruitment; total sample size is indicated above each histogram

Shell length growth of *Fusconaia ebena* over the 1st 6 full growth seasons was linear; TM growth rate exponentially increased with increasing age (Fig. 2). Corresponding rates of TDM and SDM growth were computed from the following regressions based on subsamples used each year for tissue and shell component analyses:

$$\log \text{TDM (g)} = 2.997 \log \text{SL (mm)} - 5.016; \quad P < 0.001;\ r^2 = 0.995;\ n = 113$$
$$\log \text{SDM (g)} = 2.740 \log \text{SL (mm)} - 3.054; \quad P < 0.001;\ r^2 = 0.996;\ n = 113$$

The rate of SDM increase is slightly lower than that of TDM increase. Consequently, tissue-to-shell mass ratios were observed to increase as a linear function of SL according to the following regression equation:

$$\text{TDM/SDM} = 0.000163\text{SL} + 0.0214; \quad P < 0.001;\ r^2 = 0.366;\ n = 113$$

This trend is not due to increased shell erosion with age, because TDM and SDM measurements were made only on mussels that did not exhibit much shell erosion. Sexual maturity (as indicated by the presence of gonadal tissue) was noted in all mussels greater than 39 mm SL and in no mussels below 32 mm SL. Therefore, sexual maturity appears to be achieved during the 5th full season of growth, and first reproduction probably occurs the next summer at an average age, SL, and TDM of 6 yr, 45 mm, and 0.9 g, respectively. The maximum length of *Fusconaia ebena,* averaged from 1983, 1985 and 1987 SL distributions, is approximately 88 mm (Fig. 1). This length corresponds to a TDM of 6.5 g. Thus, individuals increase seven-fold in TDM during their reproductive lifespans.

DISCUSSION

Age estimates of juvenile cohorts identified in Figure 1 are concordant with the observed growth of the dominant cohort and the few published reports of recruitment and early

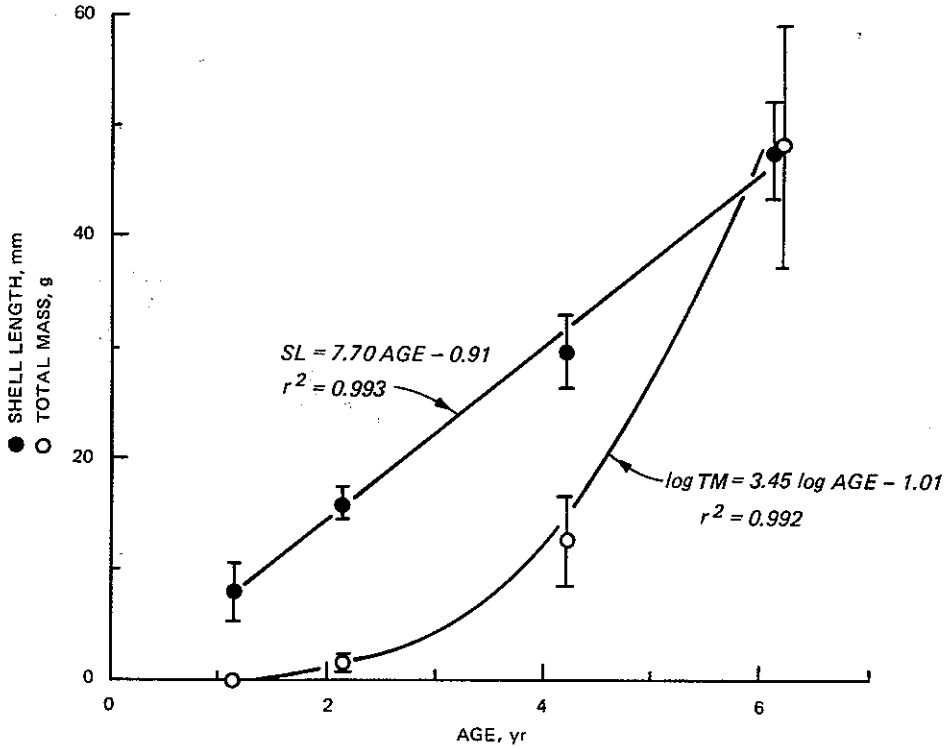

FIG. 2.—Models of early growth of *Fusconaia ebena* in the lower Ohio River. Error bars represent ±1 SD about the mean; if not shown, ±1 SD is within the plotted point. Size estimates are based on the 1982 cohort in 1983 and the 1981 cohort in 1983, 1985 and 1987 (*see* Fig. 1)

growth of *Fusconaia ebena* and similar thick-shelled species (Surber, 1913; Coker *et al.*, 1921). The single natural host of *F. ebena* glochidia appears to be the skipjack herring *Alosa chrysochloris* (Surber, 1913). *Fusconaia ebena* is the dominant species in mussel communities in mainstream shoals of the lower Ohio and Tennessee Rivers (Williams, 1969; Miller *et al.*, 1986) and was also a common mussel in the upper Mississippi River prior to construction of a hydroelectric dam at Keokuk, Iowa that prevents upstream migration of *A. chrysochloris* (Coker, 1914; Theler, 1987). The high host specificity of *F. ebena* is unusual among unionaceans (Kat, 1984). Juvenile *F. ebena* leave this host fish within a narrow time period near mid-August (Surber, 1913). Juvenile length at settlement is almost certain to be less than 1 mm (Kat, 1984). It is unlikely that a new cohort of recruits achieves an average SL of 8.2 mm in only 6 wk. Thus, the minor cohort centered at 8.2 mm SL in late September of 1983 probably settled in mid-August of 1982. Juveniles of thick-shelled species of the genera *Quadrula* and *Obovaria,* whose initial growth rates are likely to be similar to that of *F. ebena,* do not reach lengths of 11–16 mm until their 2nd year of growth (Coker *et al.*, 1921). The annual growth increment of just less than 8 mm observed for the dominant cohort from 1983 to 1987 was consistent with the year class assignments indicated in Figure 1.

Young *Fusconaia ebena* in the lower Ohio River clearly maintain linear rates of growth in length and increasing rates of growth in mass over the 1st 6 yr of life. Furthermore, the sustained relative abundance of the 1981 cohort from 1983 to 1987 demonstrates that

mortality of successfully settled mussels is negligible between the ages of 2 and 6 yr. Newly settled juveniles quickly transform their lightweight shell into a structure massive enough to allow survival in gravelly riverine shoals (Coker *et al.*, 1921). The initial premium placed on shell mass increase is soon followed by proportionately greater allocation of energy to tissue vs. shell, resulting in increased TDM/SDM with increasing age.

The longevity of *Fusconaia ebena* remains uncertain based on our observations restricted to early growth. However, at least 11 but not as many as 18 years appear to be required for *F. ebena* to attain its average maximum SL of 88 mm in the lower Ohio River. Eleven to 12 years are required for a cohort to achieve the average maximum SL of 88 mm based on a continued linear rate of SL growth observed for mussels 7–50 mm long (Fig. 2). An age of 18 for 85 mm SL mussels is suggested by Williams' (1969) estimates of size-to-age relationships of *F. ebena* in the lower Ohio River. Williams' estimates were based solely on major growth lines on shells, a method we found to be too subjective and prone to error by overestimating age (*also see* Rhoads and Lutz, 1980). The majority of older mussels in his collection from the same bed we sampled had 17–19 major growth lines and an average maximum SL of approximately 85 mm. Similarly, 88 mm SL was the average maximum size of *F. ebena* during this study. Williams counted 9–11 winter annuli in individuals 55–60 mm SL. In contrast, our observations of early growth suggest that SLs of 55–60 mm are likely to be attained during the 7th yr of life (Fig. 2). Thus, Williams' age estimate of approximately 18 years for individuals 85 mm long is probably too high. Continued monitoring of growth of the 1981 cohort will allow verification of average longevity of *F. ebena* in the lower Ohio River. Average longevity of *F. ebena* of at least 11 but not as much as 18 years is at the low end of the range of published estimates of longevity of riverine unionids (Coon *et al.*, 1977). However, like Williams, these investigators relied on counts of shell growth lines to estimate ages of 11–25 years for the largest specimens of nine thick-shelled species they collected from the upper Mississippi River.

Our results demonstrate the importance of demographically complete sampling of riverine mussel populations and for the first time have allowed quantification of recruitment plus early growth and survivorship of a distinct cohort in a natural population. The population of *Fusconaia ebena* in the mainstream shoal we studied in the lower Ohio River is characterized by extreme annual variation in recruitment plus linear SL growth and negligible mortality of successfully settled recruits during the first few years of life. Mainstream river shoals are an endangered but principal habitat of most species of North American unionids (Stansbery, 1970). Detailed ecological studies are needed of recruitment patterns of mussels in such habitats to elucidate basic but largely unknown aspects of unionid population dynamics.

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