

## ***Influence of life-history variation on demographic responses of three freshwater mussel species (Bivalvia: Unionidae) in the Clinch River, USA<sup>†</sup>***

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### ABSTRACT

1. Variation in age, shell growth, and demographic responses of two endangered mussel species, *Epioblasma brevidens* and *Epioblasma capsaeformis*, and a third non-listed species, *Lampsilis fasciola*, were studied from 2004–2008 in a 32-km reach of the Clinch River, TN.

2. Observed maximum age and length of *E. brevidens* was 28 yr and 71.5 mm for males and 15 yr and 56.6 mm for females; of *E. capsaeformis*, 12 yr and 54.6 mm for males and 9 yr and 48.6 mm for females; and of *L. fasciola*, 45 yr and 91.3 mm for males and 24 yr and 79.8 mm for females.

3. Estimated population size was ~46 000 individuals for *E. brevidens*, ~862 000 individuals for *E. capsaeformis*, and ~33 000 individuals for *L. fasciola*.

4. Mean recruitment per year of 1 yr-olds ranged from 12.0% to 24.0% for *E. brevidens*, 4.2% to 56.6% for *E. capsaeformis*, and 10.0% to 38.5% for *L. fasciola*, and mean annual population growth rate was 21.0%, 31.3%, and –24.3%, respectively.

5. Juveniles were detectable but temporally and spatially variable in occurrence, and a significant proportion of the age-class structure of each species. Recruitment was exceptionally high for *E. capsaeformis* during years when discharge was low in spring and summer.

6. Population size, growth, recruitment, and mortality rates of the shorter-lived *E. capsaeformis* were correspondingly higher than those of *E. brevidens* and *L. fasciola*.

7. The federal recovery plan for *E. brevidens* and *E. capsaeformis* identifies quantification of demographic variables as a critical step toward meeting the recovery needs of each species. The data collected in this study begin to meet these needs and can be used to monitor and evaluate population performance of each species. Published in 2011 by John Wiley & Sons, Ltd.

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KEY WORDS: Clinch River; freshwater mussels; *Epioblasma brevidens*; *Epioblasma capsaeformis*; *Lampsilis fasciola*; life history and demographic variation; age; shell growth; population size; recruitment

### INTRODUCTION

The decline of freshwater mussels in the USA is a national issue stemming from factors related to habitat loss and degradation of river and lake ecosystems (Neves *et al.*, 1997; Lydeard *et al.*, 2004). Management and restoration of native mussels will require a thorough understanding of species life history and population biology (National Native Mussel

Conservation Committee, 1998). The larvae (glochidia) of most mussel species require fish hosts in order to transform into juveniles and disperse to new habitats. Vital rates such as population growth, recruitment, and mortality are poorly understood for most species, but the studies that have been conducted have shown a wide range of population responses under various ecological conditions (Negus, 1966; Neves and Widlak, 1987; Hastie *et al.*, 2000b; Payne and Miller, 2000;

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Haag, 2002; Vilella *et al.*, 2004; Howard and Cuffey, 2006). Most species are characterized by sporadic recruitment, high longevity (lifespan >20 years), and complex life histories. The lack of data on mussel populations hinders the ability of managers to implement effectively the recovery plans of numerous endangered mussel species (US Fish and Wildlife Service (USFWS), 2004). Demographic data serve critical management needs, including: (1) risk assessment of site-specific and ecosystem impacts; (2) identifying natural (biotic and abiotic) and human factors influencing population trends; (3) setting priorities for imperiled species for recovery; and (4) identifying actions to restore and maintain populations. Demographic responses of mussel populations vary considerably over space and time, and are influenced by life-history traits such as longevity, somatic growth and abundance and dispersal ability of host fishes. Quantification of population size, growth rates, mortality rates and age-class structure is essential to monitoring programmes intended to measure effects of stream discharge, water temperature, habitat quality, water quality and other environmental variables influencing mussel population responses. Hence, a major challenge for biologists is to distinguish and quantify natural population fluctuations from changes caused by human disturbances. Demographic responses of undisturbed populations can serve as a baseline to judge the performance of populations in need of restoration and management.

The Clinch River in Hancock County, Tennessee contains a diverse mussel assemblage of >40 species (Ahlstedt, 1991). Because of its high species richness, the river is of national significance to conservation of mussel resources in the USA (Ahlstedt, 1991; Neves *et al.*, 1997). Although this assemblage has been monitored for density and richness for 30 years from 1979–2009 (Ahlstedt *et al.*, 2005; J. Jones, USFWS unpublished data), demographic rates of these populations have not been assessed, and only a few studies have characterized age-class structure (Scott, 1994; Rogers *et al.*, 2001; Jones and Neves, 2002; Jones *et al.*, 2004). Populations of most mussel species occurring in this river reach have been recruiting regularly and are considered stable. This reach provides an opportunity to collect demographic data to establish species-level baselines. Three species were selected to study shell growth, cohort structure and demographic trends and rates, to include two endangered species *Epioblasma brevidens* and *Epioblasma capsaeformis* and a third non-listed species *Lampsilis fasciola*. These species were selected because they exhibit contrasting variation in their life history traits and demographic rates; namely, in the abundance and dispersal ability of their host fishes, and in their population growth rate, abundance and longevity. For example, *E. capsaeformis* can achieve large local population sizes, but it is a relatively short-lived species (typically <10 years) with presumably lower dispersal capabilities. It utilizes small, abundant darter species in the subgenus *Nothonotus* as its primary fish host; e.g. redline darter *Etheostoma rufilineatum*. By comparison, *E. brevidens* is longer-lived, characterized by smaller population sizes and higher dispersal capabilities, utilizing a relatively mobile, large darter as its primary fish host; the logperch *Percina caprodes*. Similarly, *L. fasciola* rarely achieves large local population sizes but has even greater dispersal capability than the two endangered species because it uses black bass *Micropterus* spp. as its primary fish hosts. These different life-history traits presumably influence the ability of these mussel species to maintain abundance and colonize habitats.

The purpose of this study was to investigate the demographic responses of *E. brevidens*, *E. capsaeformis* and *L. fasciola* within the context of variation in their life-history traits. The objectives were to estimate and compare: (1) their shell growth and longevity; (2) their population growth and mortality rates; (3) their age-class structure, recruitment and population size; and (4) the spatial and temporal variation of these variables. These data are necessary to evaluate management actions, such as translocation of adults and release of propagated juveniles intended to restore mussel populations in rivers targeted for population restoration.

## MATERIALS AND METHODS

### Study area and site selection

The study area is a 32-km reach of the Clinch River from river kilometres (RKM) 277.1 to 309.6, Hancock County, Tennessee. The reach is located in north-eastern Tennessee just south of the Virginia border, in the Valley and Ridge physiographic province of the southern Appalachian Mountains. Mussel habitat (gravel shoals) is abundant in the river, but interspersed with longer, slower-flowing pools (>1 RKM) containing poorer quality habitat. Typical lengths of gravel shoals in this reach are 100–200 m but occasionally are longer. The river is fourth-order throughout Hancock County and features moderate gradient, riffle-run fluvial morphology. Most mussel species currently exhibit recruitment of juveniles in this reach, presumably indicative of a viable, minimally impaired assemblage. Freshwater mussels were sampled at 13 sites, selected from those previously surveyed by Ahlstedt (1991). These sites represent all major shoals in the study reach and are summarized by location, dimensional characteristics and sampling information (Table 1). A few small sites <1000 m<sup>2</sup> were not sampled because of difficult access, but the contribution of these localized mussel assemblages to total population abundance is considered insignificant. Data from two sites sampled in 2004 were obtained from Ahlstedt *et al.* (2005) and Ostby (2005) (Table 1).

### Age and growth

Shells of *E. brevidens*, *E. capsaeformis*, and *L. fasciola* were collected from the study area at various site locations from 2004 to 2006. In addition, length and age data from older shells of *L. fasciola* (13 males (14–45 yr) and 5 females (17–24 yr)) were obtained from Scott (1994) and Henley *et al.* (2001). These studies were conducted in the Clinch River at several sites in Virginia and at one site in Tennessee (Kyles Ford) over the last 10–20 yr. Shells of various lengths were collected to represent the population size- and age-class structure of each species in the river. Thin sections of shells were prepared following procedures described by Clark (1980) and Neves and Moyer (1988), using a Buehler Isomet low-speed saw unit with a diamond-impregnated blade (Buehler, Evanston, Illinois). Shells were cut from the centre of the umbo to the ventral margin. Cut valves were glued (2-Ton Clear Epoxy, Illinois Tool Works, Devcon, Massachusetts) to petrographic microslides (27 × 46 mm), vacuum-sealed into a petrographic chuck, attached to the cutting arm of the saw, and sectioned at a thickness of 280 µm

Table 1. Location, dimensions, and sampling information for sampled sites in the Clinch River, TN

Site location name	River kilometre (river mile)	Latitude	Longitude	Site dimensions				
				Length (m)	Width (m)	Area (m <sup>2</sup> )	No. (n) 0.25m <sup>2</sup> quadrats yr <sup>-1</sup>	Year (s) sampled
Wallen Bend (upper)	309.6 (192.4)	36° 34' 44.85"	83° 00' 10.59"	43	74	3182	60	2004-2008
Wallen Bend (lower)	309.5 (192.3)	36° 34' 50.24"	83° 00' 20.82"	410	41.3	16933	120	2007
Kyles Ford*	305.1 (189.6)	36° 33' 43.54"	83° 02' 23.48"	200	75	15000	146	2004
Webb Island	301.7 (187.5)	36° 33' 04.22"	83° 03' 49.14"	143	32	4576	60	2006
Brooks Island (upper)*	295.6 (183.7)	36° 32' 12.23"	83° 07' 19.19"	80	45	3600	26	2004
Brooks Island (lower)	295.3 (183.5)	36° 32' 12.50"	83° 07' 34.88"	120	50	6000	60	2005
Little E. Island	293.7 (182.5)	36° 32' 27.77"	83° 08' 47.92"	160	70	11200	60	2005
Frost Ford (upper)	291.8 (181.3)	36° 31' 56.20"	83° 09' 2.41"	215	70	15050	60	2004-2008
Frost Ford (lower)	291.3 (181.0)	36° 31' 48.88"	83° 09' 3.13"	172	50	8600	72	2007
Falls Branch Shoal	288.7 (179.4)	36° 31' 18.68"	83° 11' 39.6"	127	42	5334	40	2006
Sneedville	287.6 (178.7)	36° 31' 11.06"	83° 11' 25.07"	56	36	2016	40	2006
Briery Creek Shoal	280.8 (174.5)	36° 29' 53.62"	83° 15' 26.52"	150	44	6600	40	2006
Swan Island	277.1 (172.2)	36° 28' 23.84"	83° 17' 23.71"	128	45	5760	60	2004-2008

\*Data sampled in 2004 for these sites were obtained from Ostby (2005) and Ahlstedt *et al.* (2005), respectively.

(Neves and Moyer, 1988). Thin sections of shells were examined using 40 × magnification. Internal growth lines were considered true annuli if they were continuous from the umbonal region to the outer surface of the shell. It was assumed, based on previous shell-ageing in the rivers of south-west Virginia (Neves and Moyer, 1988), that one annulus was formed each year. This assumption of annual shell ring deposition in freshwater mussels has been further validated in more than 12 species in North America (Veinott and Cornett, 1996; Haag and Commens, 2008). Lengths for 0 to 3 yr old individuals were obtained by back-calculating length-at-age based on internal annuli of 5–10 older shells because shells ≤ 3 yr old were difficult to collect from the river. Juveniles were considered age 0 if no external annulus was observed on the shell, which typically were individuals 5–12 mm long when measured near the end of the growing season. Therefore, on adult mussels the first external annulus was considered the age 0 annulus.

Live mussels collected from 2004 to 2008 were aged using predicted length-at-age as computed by a von Bertalanffy growth curve (VBGC) (von Bertalanffy, 1938). The VBGC is written as:

$$L_t = L_\infty [1 - e^{-k(t-t_0)}]$$

where  $L_\infty$  ( $L$ -infinity) is a theoretical maximum (asymptotic) length,  $k$  is a growth coefficient indicating how quickly  $L_\infty$  is approached,  $t$  is time or age in years,  $t_0$  is the time in years when length would theoretically be equal to zero, and  $e$  is the natural log exponent. All three species are sexually dimorphic; thus, age and growth analyses were conducted separately for males and females. Sex ratio was determined using frequency of ≥ 2 yr old individuals because 1 yr olds are not clearly dimorphic. The 1 yr olds were randomly split using a 50:50 ratio unless the sex was clearly discernable.

### Population demographics

Population demographic characteristics, such as population density and abundance, and age-class frequency, were estimated at various sites in the river from 2004 to 2008. All sampling was conducted in late summer or early autumn when water levels were low, and juvenile mussels had reached sizes suitable for collection (e.g. ~ 10 mm). Three sites, upper Wallen Bend (WB), upper Frost Ford (FF) and Swan Island (SI), were sampled consecutively each year to examine population change over time. These sites were selected because they represent the upper (RKM 309.6), middle (RKM 291.8) and lower (RKM 277.1) boundaries of the study reach, and each has different location and habitat characteristics that are suitable for long-term monitoring. Data were collected by systematic, 0.25 m<sup>2</sup> quadrat samples placed along transect lines. Both quadrats and transects were evenly spaced throughout the entire shoal area. Total area (m<sup>2</sup>) of mussel beds was determined by multiplying mean river width, measured at 10 m intervals, by total length of the reach (Table 1). Small, exposed gravel bars and islands not containing mussels but within the immediate shoal area were measured and removed from analysis. Site dimensions (length and width) were measured using a standard 100 m measuring tape. Upstream and downstream limits of the bed were determined by visually inspecting substrate composition (e.g. an abrupt change from suitable gravel substrate to

unsuitable bedrock or soft sediments), water depth, flow velocity, and absence of mussels. All 0.25 m<sup>2</sup> quadrats were excavated to approximately 20 cm in depth. Mussels were measured for length (nearest 0.1 mm) using digital calipers and returned to their approximate position of collection. Mean population size at each site was estimated by multiplying mussel density (m<sup>-2</sup>) by total site area.

Age frequencies of live mussels were determined using predicted length-at-age from the VBGC. Since the number of individuals collected was greater for *E. capsaeformis* and to maintain sampling consistency among sites each year, age frequencies for this species were estimated only from data collected at WB, FF and SI. However, because the number of individuals collected was lower for *E. brevidens* and *L. fasciola*, mean age frequencies were estimated from all sites sampled from 2004 to 2008, and total age frequencies per year from all sites sampled in a single year.

Population growth rate and mortality rate were estimated using standard demographic procedures described in Morris and Doak (2002) and Miranda and Bettoli (2007), respectively. For samples collected at yearly intervals during the current study, growth rate was computed at each time step using a discrete time population growth equation:

$$\lambda_t = (N_{t+1}/N_t)$$

where  $\lambda_t$  is the annual population growth rate,  $N_t$  is the number of individuals (or density) in the population at year  $t$ , and  $N_{t+1}$  is number of individuals in the next year. The natural log ( $\log_e$ ) of  $\lambda$  values was used to compute the arithmetic mean, standard error, and associated 95% confidence intervals (CI), and then transformed back using inverse  $\log_e$ . A time series of mussel density data (1979 to 2004) from the Clinch River, Hancock County, TN, was obtained from Ahlstedt *et al.* (2005). These data were collected by random 0.25 m<sup>2</sup> quadrat sampling at three sites (RKM 305.1 (Kyles Ford), RKM 295.6 (Brooks Island), and SI) in shoal areas containing high mussel densities to facilitate long-term monitoring. Although collection of these data differed in sample design, they were collected using a consistent procedure and hence were suitable to provide estimates of annual population growth rate over a longer 25 yr time period. Since these sites were sampled about every 5 yr and occasionally at unequal intervals, the linear regression method proposed by Dennis *et al.* (1991) was used to estimate mean  $\lambda$  and associated 95% CIs; see Morris and Doak (2002) for a description of the method. The linear regression method assumes that censuses are uncorrelated from one interval to the next. The Durbin–Watson  $d$  statistic was used to test for strength of temporal autocorrelation in the data.

A catch-curve regression analysis of number-at-age was conducted to estimate total mortality for each species:

$$\ln(N_t) = \ln(N_0) - Z(t)$$

where  $N_t$  is the number in a year class at time  $t$ ,  $N_0$  is the original number in a year class, and  $Z$  is the instantaneous rate of mortality (Miranda and Bettoli, 2007). This procedure is computationally analogous to simple linear regression [ $y = a - b(x)$ ], where the slope ( $b$ ) is equivalent to  $Z$ . The instantaneous rate ( $Z$ ) was converted to an interval or annual ( $\text{yr}^{-1}$ ) mortality rate ( $A$ ), where  $A = 1 - e^{-Z}$ . Because the catch-curve procedure requires a large sample size encompassing a range of age and size classes to obtain a reliable estimate of mortality, estimates were obtained with

both sexes combined. The assumptions of catch-curve regression to estimate mortality are: (1) constant recruitment; (2) equal survival among year classes (3) constant survival from year to year; (4) constant natural mortality each year and among all year classes; and (5) catch-curves are fitted to samples representative of the true age structure of the population (Miranda and Bettoli, 2007). In addition, an independent estimate of mortality was obtained by comparing density of dead shells to live individuals collected in quadrat samples. All empty shells were assumed to have died within a 1-yr time period unless exhibiting signs of long-term erosion and dissolution; i.e. chalky and brittle nacre.

Since females of each species display a highly visible mantle-lure when releasing glochidia, the density (m<sup>-2</sup>) of displaying females was quantified using quadrat sampling from 2004 to 2006. A quadrat ( $N = 12$  per site) consisted of two 15.24 m-long weighted lines evenly spaced 1.52 m wide, and systematically positioned along transect lines to provide even coverage of the site area. The long axis of the quadrat was oriented in the direction of flow, allowing a biologist to snorkel upstream between the lines to count displaying female mussels.

Recruitment was defined in this study as the percentage of 1 yr old individuals relative to the census size per site. Age-0 individuals typically are too small (<10 mm) to be reliably sampled. For *E. brevidens* and *L. fasciola*, mean recruitment was calculated using data from all sites sampled in a year, but for *E. capsaeformis* only from WB, FF, and SI. Recruitment was calculated by pooling data from respective sites and dividing number of 1 yr old individuals by total number of individuals  $\geq 2$  yr old. The approximate smallest (lower bound) observed size of 1 yr old individuals, which was set at  $\geq 15$  mm for both *Epioblasma* spp. and  $\geq 20$  mm for *L. fasciola*, and the predicted age-at-length boundary between 1 and 2 yr olds (upper bound of 1 yr olds and lower bound of 2 yr olds) was used to categorize 1 yr olds of each species. Correlation analyses were conducted to test for stock-recruitment relationships between number of displaying female mussels (stock) from 2004 to 2006 and number of 1 yr old mussels (recruits) and population size in subsequent years from 2005 to 2007. Correlation analyses were conducted only using data from WB, FF, and SI where both data types were available.

## Data analyses

A generalized linear model (GLM) was used to test for significance of trends in the time series data collected from 2004–2008 at WB, FF, SI, and a generalized linear mixed model (GLMM) was used to test the long-term trend data collected from 1979–2004 at Kyles Ford, Brooks Island and SI. Both models were implemented using a Poisson distribution and the log link function. The Pearson correlation coefficient was used to test for positive or negative correlation between random variables. Descriptive statistical analyses were conducted using MINITAB Statistical Software (Minitab, Inc., State College, Pennsylvania). Parameters of the von Bertalanffy growth equations, catch-curve mortality analyses and associated significance tests were estimated using the Fisheries Stock Assessment program (FSA-package) developed by Dr Derek Ogle at Northland College, Wisconsin. The GLM, GLMM and FSA-package were implemented in the program R (R Development Core Team 2006).

RESULTS

Age and growth

Observed maximum age and length of *E. brevidens* was 28 yr and 71.5 mm for males, and 15 yr and 56.6 mm for females. Predicted asymptotic length ( $L_{\infty}$ ) was 59.2 mm (95% CI = 52.8 mm and 63.3 mm) for males and 52.4 mm (95% CI = 50.6 mm and 54.0 mm) for females, the growth coefficient ( $k$ ) for each sex was  $0.159 \text{ yr}^{-1}$  (95% CI =  $0.116 \text{ yr}^{-1}$  and  $0.199 \text{ yr}^{-1}$ ) and  $0.255 \text{ yr}^{-1}$  (95% CI =  $0.224 \text{ yr}^{-1}$  and  $0.282 \text{ yr}^{-1}$ ) and  $t_0$  for each sex was  $-1.39$  (95% CI =  $-1.74$  and  $-1.3$ ) and  $-0.77$  (95% CI =  $-0.87$  and  $-0.7$ ), respectively (Figure 1).

Observed maximum age and length of *E. capsaeformis* was 12 yr and 54.6 mm for males, and 9 yr and 48.6 mm for females. Predicted asymptotic length was 39.9 mm (95% CI = 33.8 mm and 42.6 mm) for males and 49.8 mm (95% CI = 47.0 mm and 52.2 mm) for females, the growth coefficient for each was  $0.420 \text{ yr}^{-1}$  (95% CI =  $0.310 \text{ yr}^{-1}$  and  $0.582 \text{ yr}^{-1}$ ) and  $0.271 \text{ yr}^{-1}$  (95% CI =  $0.228 \text{ yr}^{-1}$  and  $0.310 \text{ yr}^{-1}$ ), and  $t_0$  for each sex was  $-0.72$  (95% CI =  $-0.93$  and  $-0.6$ ) and  $-0.81$  (95% CI =  $-0.94$  and  $-0.73$ ), respectively. The oldest male (12 yr) of *E. capsaeformis* was not included in computing the growth curve for males because the length of this individual upwardly biased the predicted length.

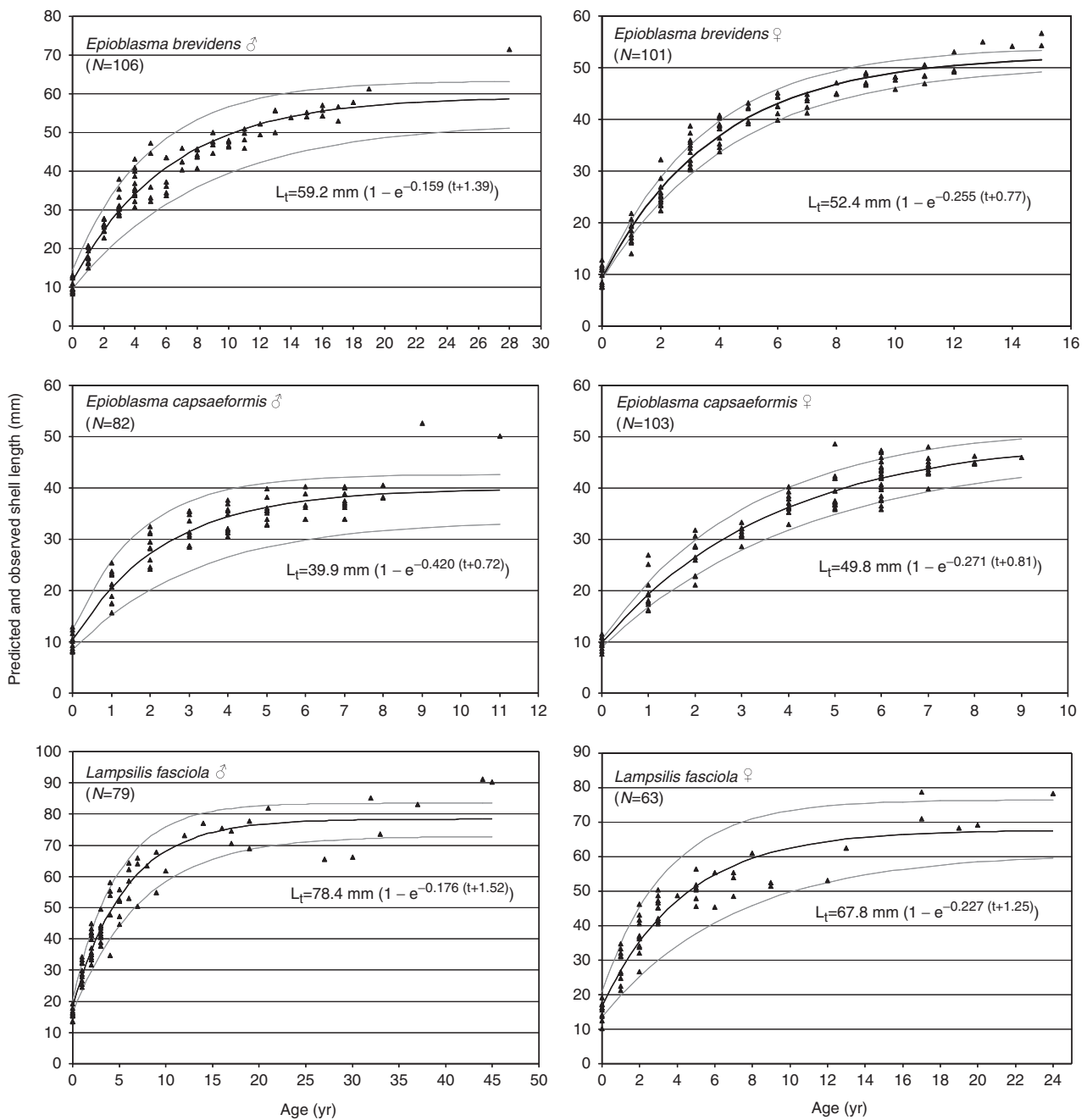


Figure 1. Estimated von Bertalanffy growth curves of predicted length-at-age (thick black line) with 95% confidence intervals (thin grey lines) for three species in the Clinch River. Observed length-at-age is shown by triangles.

Observed maximum age and length of *L. fasciola* was 45 yr and 91.3 mm for males, and 24 yr and 79.8 mm for females. Predicted asymptotic length was 78.4 mm (95% CI = 72.9 mm and 83.5 mm) for males and 67.8 mm (95% CI = 61.2 mm and 76.5 mm) for females, and the growth coefficient for each was  $0.176 \text{ yr}^{-1}$  (95% CI =  $0.136 \text{ yr}^{-1}$  and  $0.213 \text{ yr}^{-1}$ ) and  $0.227 \text{ yr}^{-1}$  (95% CI =  $0.142 \text{ yr}^{-1}$  and  $0.290 \text{ yr}^{-1}$ ), and  $t_0$  for each sex was  $-1.52$  (95% CI =  $-1.86$  and  $-1.30$ ) and  $-1.25$  (95% CI =  $-1.75$  and  $-1.1$ ), respectively.

For all three species, observed maximum age and shell length was greater in males than females. However, based on lengths of live individuals in the river, average length of adult female *E. capsaeformis* was greater than that of males. Predicted and observed shell growth for all three species and both sexes was highest from ages 0–5 yr and then decreased thereafter (Figure 1). Differences in growth among species were reflected in VBGC parameter estimates of  $k$  and  $L_\infty$ , which were highest in *E. capsaeformis*. Bauer (1992) and Hastie *et al.* (2000a) showed that these parameters were inversely correlated among European populations of the freshwater pearl mussel *Margaritifera margaritifera*, where populations comprising mainly small, short-lived adults displayed higher  $k$  compared with populations comprised of larger, older individuals. A similar growth pattern generally held between species in this study, with the shorter-lived, smaller-sized *E. capsaeformis* exhibiting higher  $k$  and lower  $L_\infty$ .

### Population size and density

Estimates of total population size for all three species should be viewed as conservative, as marginal habitat areas were not surveyed. Individuals of each species occur in such habitats but at very low density. Total population size of *E. brevidens* at

investigated sites was estimated at 46 436 individuals, with moderate to large differences observed among sites (Table 2). Local population size ranged from a minimum of 660 individuals at Briery Creek (RKM 280.8) to a maximum of 12 900 individuals at FF (RKM 291.8), with 95% CI greater than  $\pm 50\%$  of the means. At sites monitored consecutively from 2004 to 2008, population sizes were stable from 2004 to 2006, with moderate increases detected from 2006 to 2008 at WB and FF, although trends were not significant (Figure 2). Density was consistent among sites and sample years, ranging between  $0.2$  and  $0.86 \text{ m}^{-2}$  and always  $< 1 \text{ m}^{-2}$ . Likewise, the species occurred at densities ranging from  $0.1$ – $1.1 \text{ m}^{-2}$  at 12 long-term monitoring sites sampled from 1979 to 2004 in Tennessee and Virginia (Ahlstedt *et al.*, 2005). During this 25-yr period, most estimates of density were below  $1 \text{ m}^{-2}$  (Figure 3).

Total population size of *E. capsaeformis* was estimated at 862 426 individuals, with large differences observed among sites (Table 2). Local population size ranged from a minimum of 4637 individuals at Sneedville (RKM 287.6) to a maximum of 604 150 individuals at FF, with 95% CIs typically less than  $\pm 50\%$  of the means. At sites monitored consecutively, population sizes appeared stable from 2004 to 2006, and then increased greatly from 2006 to 2008 owing to high juvenile recruitment (Figure 2). During this period, population density more than tripled at FF and reached a remarkable  $40.1 \text{ m}^{-2}$  in 2008. Similarly, while density increased at WB, absolute density was much less than FF, and at SI density appeared to increase but the trend was not significant.

Total population size of *L. fasciola* was estimated at 32 840 individuals, with modest differences observed among sites (Table 2). Local population size ranged from a minimum of 384 individuals at SI to a maximum of 6450 individuals at FF,

Table 2. Estimates of site and total population size for three mussel species in the Clinch River, TN; only data from 2008 were used to calculate population sizes for sites sampled in multiple years

Site	Year (s) sampled	Number of individuals ( $\pm 95\%$ CI)		
		<i>Epioblasma capsaeformis</i>	<i>Epioblasma brevidens</i>	<i>Lampsilis fasciola</i>
Wallen Bend (upper)	2004	5940 $\pm$ 2254	636 $\pm$ 707	1697 $\pm$ 1103
	2005	4455 $\pm$ 2123	636 $\pm$ 707	1273 $\pm$ 974
	2006	4243 $\pm$ 2025	212 $\pm$ 415	636 $\pm$ 707
	2007	16122 $\pm$ 4143	1061 $\pm$ 897	849 $\pm$ 810
	2008	28426 $\pm$ 7458	2121 $\pm$ 1471	1485 $\pm$ 1042
Wallen Bend (lower)	2007	38946 $\pm$ 14841	3951 $\pm$ 4032	5644 $\pm$ 4755
Kyles Ford	2004	35400 $\pm$ 8232	7800 $\pm$ 3822	5700 $\pm$ 3528
Webb Island	2006	6711 $\pm$ 3069	1220 $\pm$ 1165	1525 $\pm$ 1291
Brooks Island (upper)	2004	9415 $\pm$ 4681	3877 $\pm$ 3342	1108 $\pm$ 1504
Brooks Island (lower)	2005	13600 $\pm$ 7527	1200 $\pm$ 1334	1600 $\pm$ 1527
Little E Island	2005	59901 $\pm$ 13893	1007 $\pm$ 1388	3523 $\pm$ 2521
Frost Ford (upper)	2004	112373 $\pm$ 22853	3010 $\pm$ 3346	7023 $\pm$ 4928
	2005	81270 $\pm$ 22041	5017 $\pm$ 4244	2007 $\pm$ 3931
	2006	111370 $\pm$ 31318	5017 $\pm$ 4244	5017 $\pm$ 4244
	2007	330097 $\pm$ 75188	9030 $\pm$ 5482	3010 $\pm$ 3346
	2008	604150 $\pm$ 104850	12900 $\pm$ 8355	6450 $\pm$ 4923
Frost Ford (lower)	2007	32967 $\pm$ 8155	3822 $\pm$ 2514	956 $\pm$ 1314
Falls Branch	2006	15469 $\pm$ 7026	5334 $\pm$ 2902	3200 $\pm$ 2393
Sneedville	2006	4637 $\pm$ 1781	1008 $\pm$ 838	605 $\pm$ 875
Briery Creek	2006	8580 $\pm$ 5039	660 $\pm$ 1295	660 $\pm$ 1295
Swan Island	2004	3840 $\pm$ 2439	2304 $\pm$ 1763	2304 $\pm$ 1763
	2005	3456 $\pm$ 2357	768 $\pm$ 1055	0 $\pm$ 0
	2006	768 $\pm$ 1055	1152 $\pm$ 1281	1536 $\pm$ 1466
	2007	7296 $\pm$ 3305	3456 $\pm$ 2357	1152 $\pm$ 1281
	2008	4224 $\pm$ 2733	1536 $\pm$ 1816	384 $\pm$ 752
Total		862426 $\pm$ 189285	46436 $\pm$ 34274	32840 $\pm$ 27720

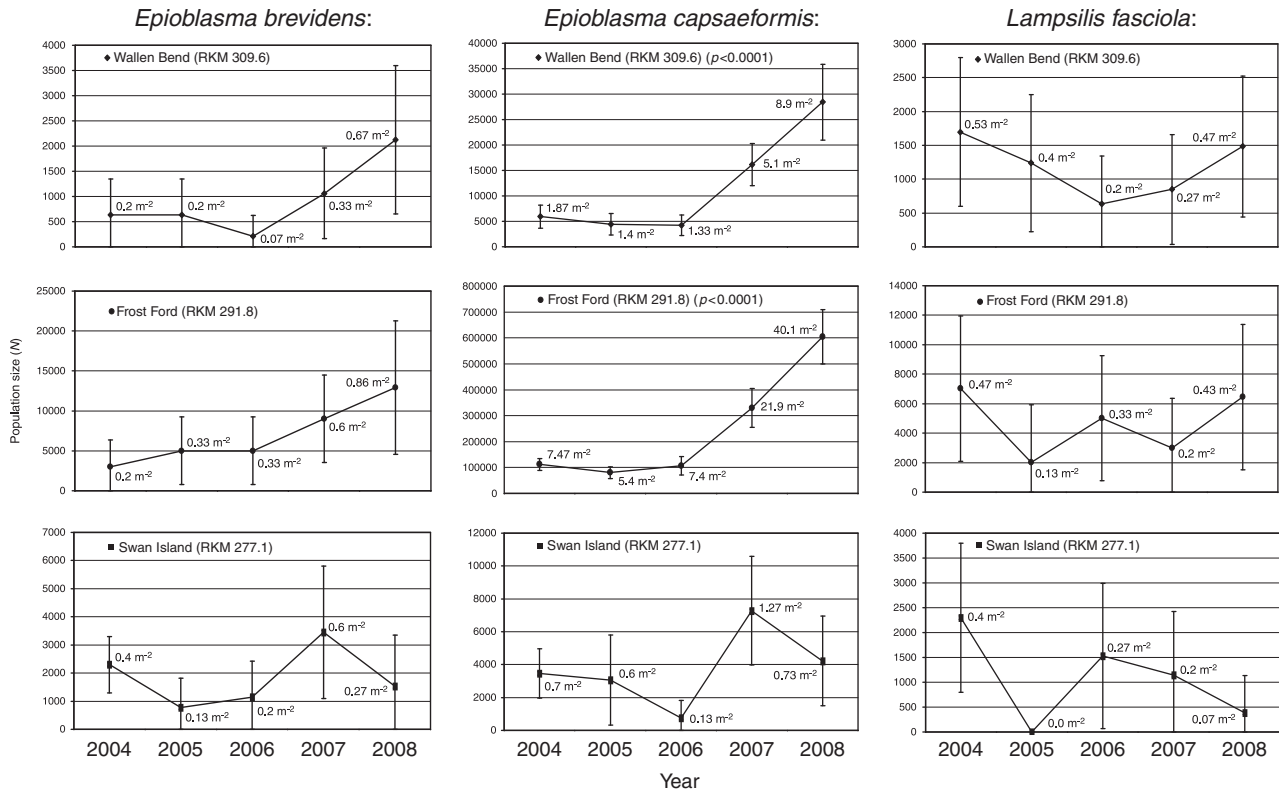


Figure 2. Estimates of population size for three species at three sites in the Clinch River, TN, sampled consecutively from 2004–2008. Error bars are 95% confidence intervals. The corresponding site density is shown next to population size. Reported *P*-values indicate a significant increasing trend in population size for *Epioblasma capsaeformis*.

with 95% CIs typically ±60–100% of the means. At sites monitored consecutively, population sizes appeared stable from 2004 to 2008, with seemingly slight but insignificant decreases over time (Figure 2). Density of this species also was consistent among sites and sample years, ranging between 0.07 and 0.53 m<sup>-2</sup> but always <1 m<sup>-2</sup>. In 2005 at SI, no individuals of this species were collected in quadrat samples; thus, the estimate of 0 m<sup>-2</sup> shown in Figure 2. The species was present at the site but was just not detected in quadrat samples. It was found at densities <0.75 m<sup>-2</sup> at monitoring sites sampled from 1979–2004 by Ahlstedt *et al.* (2005) and exhibited a significant upward trend over this period (Figure 3).

**Population age structure**

Both mean frequency (two-dimensional histograms) and total frequency per year (three-dimensional histograms) of sampled individuals by age-class are shown in Figure 4. Mean age-class frequencies from 2004 to 2008 of males and females are given separately and were positively biased toward males for all three species. Total age-class frequencies per year are displayed with sexes combined. Trends for each species during this period were for higher frequency of younger individuals and lower frequency of older individuals — the expected pattern for populations that are regularly recruiting at high levels. Frequencies ranged from 15 to 33 individuals for *E. brevidens*, 105 to 611 for *E. capsaeformis*, and 13 to 26 for *L. fasciola*. Middle-aged (4–8 yr) and older individuals (>9 yr) dominated the samples taken from 2004 to 2006, whereas sub-adults

(1–3 yr) were more prevalent in 2007–2008, especially for *E. capsaeformis*. This species exhibited strong recruitment of 1 yr old individuals beginning in 2006, with a very large increase observed from 2007–2008. Older individuals (> 10 yr) of *L. fasciola* were not observed, despite the high maximum ages of males and females based on shell ageing. Older individuals undoubtedly exist in the population, but their occurrence was uncommon and not detected based on the sampling effort. In this reach, the population of this species currently appears to contain mostly younger to middle-aged individuals. However, caution is warranted when ageing live mussels by the VBGC method, because predicted ages of larger and older individuals are less accurate as the slope of the curve reaches its asymptote. Thus, some of the middle-aged individuals may be older than predicted.

**Number of displaying female mussels**

Estimated number of displaying females of *E. brevidens* ranged from zero at WB in 2005 to a maximum of 818 at FF in 2004 (Figure 5). Among-site variation was high but similar in magnitude, with estimates typically in the hundreds of individuals. No significant trends over time were detected. The number of displaying females relative to total sexually mature females per site (≥5 yr) ranged from 0–100% per year (Table 3). No correlation (*P* = 0.148) was observed between number displaying and site population size.

Estimated number of displaying females of *E. capsaeformis* ranged from a minimum of 165 at SI in 2006 to a maximum of

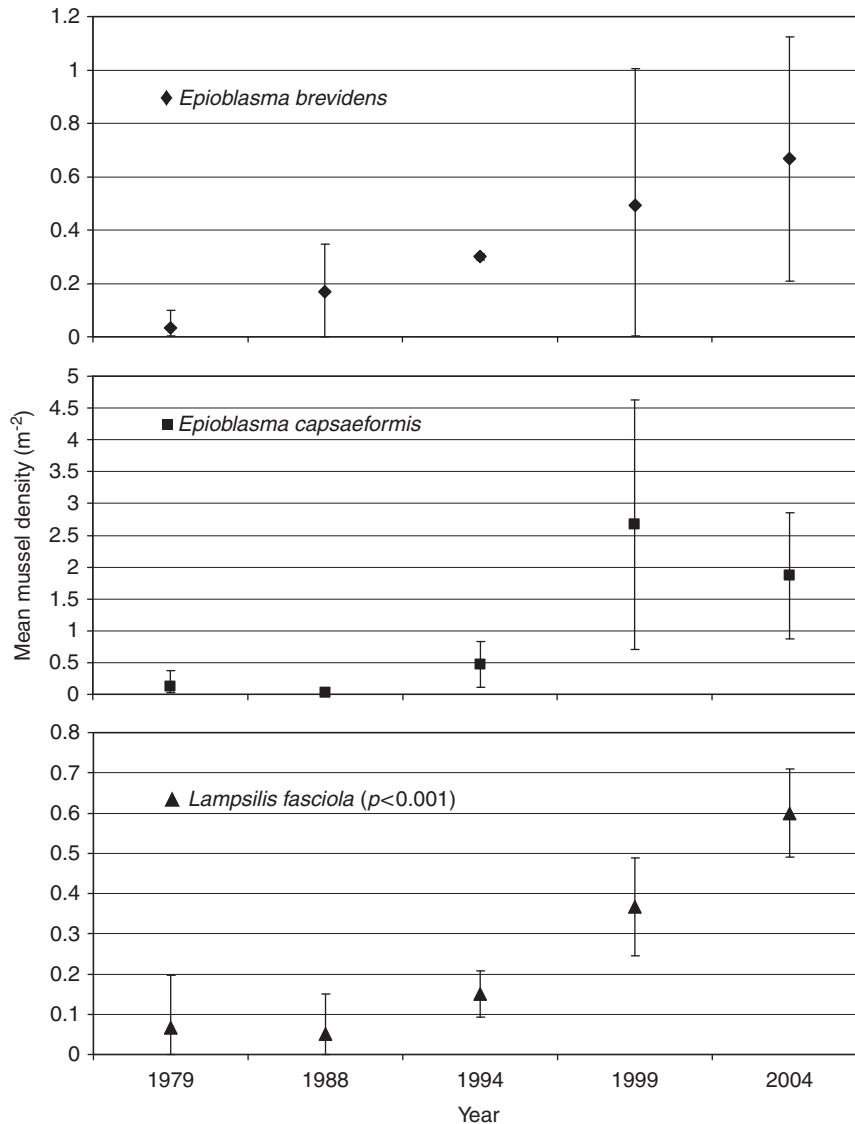


Figure 3. Mean density for three species over a 25 yr period (1979–2004) estimated from three sites: Swan Island (RKM 277.1), Brooks Island (RKM 295.6); and Kyles Ford (RKM 305.1) in the Clinch River, TN. Data are from Ahlstedt *et al.* (2005). Error bars are 95% confidence intervals.

19958 at FF in 2005. Among-site variation was high and dissimilar in magnitude, with estimates ranging from hundreds to many thousands of individuals. For example, the number of displaying females was much higher at FF, ranging from ~10 000–20 000 per year. Significant differences between some sample years were observed at WB and FF (Figure 5). The number of displaying females relative to total sexually mature specimens per site<sup>-1</sup> ( $\geq 5$  yr) ranged from 27–100% per year. A significant positive correlation (Pearson correlation = 0.864,  $P = 0.003$ ) was observed between number displaying and site population size.

Estimated number of displaying females of *L. fasciola* ranged from zero at WB in 2005 to a maximum of 214 at FF in 2005. Among-site variation was high but similar in magnitude, with estimates ranging from dozens to about 200 female mussels. No significant trends were detected. Number of displaying females relative to total sexually mature females per site ( $\geq 4$  yr) ranged from 0–8% per year, and there was no

correlation ( $P = 0.407$ ) between number displaying and site population size.

#### Juvenile recruitment

Recruitment of 1 yr old *E. brevidens* ranged from a minimum of 12.0% in 2006 to a maximum of 24.0% in 2007 (Figure 6). Mean recruitment of 1 yr olds estimated across sample years (2004–2008) was 16.4% ( $\pm 4.3$ ). During this period, recruitment appeared stable, with no significant trends detected. There was no significant correlation ( $P = 0.968$ ) between number of displaying females and number of recruits.

Recruitment of 1 yr old *E. capsaeformis* ranged from a minimum of 4.2% in 2004 to a maximum of 56.6% in 2008. Mean recruitment of 1 yr olds measured across all sample years was 28.9% ( $\pm 20.5$ ), with a significant ( $P < 0.0001$ ) increase detected from 2004 to 2008. No significant correlation ( $P = 0.067$ ) was observed between number of displaying



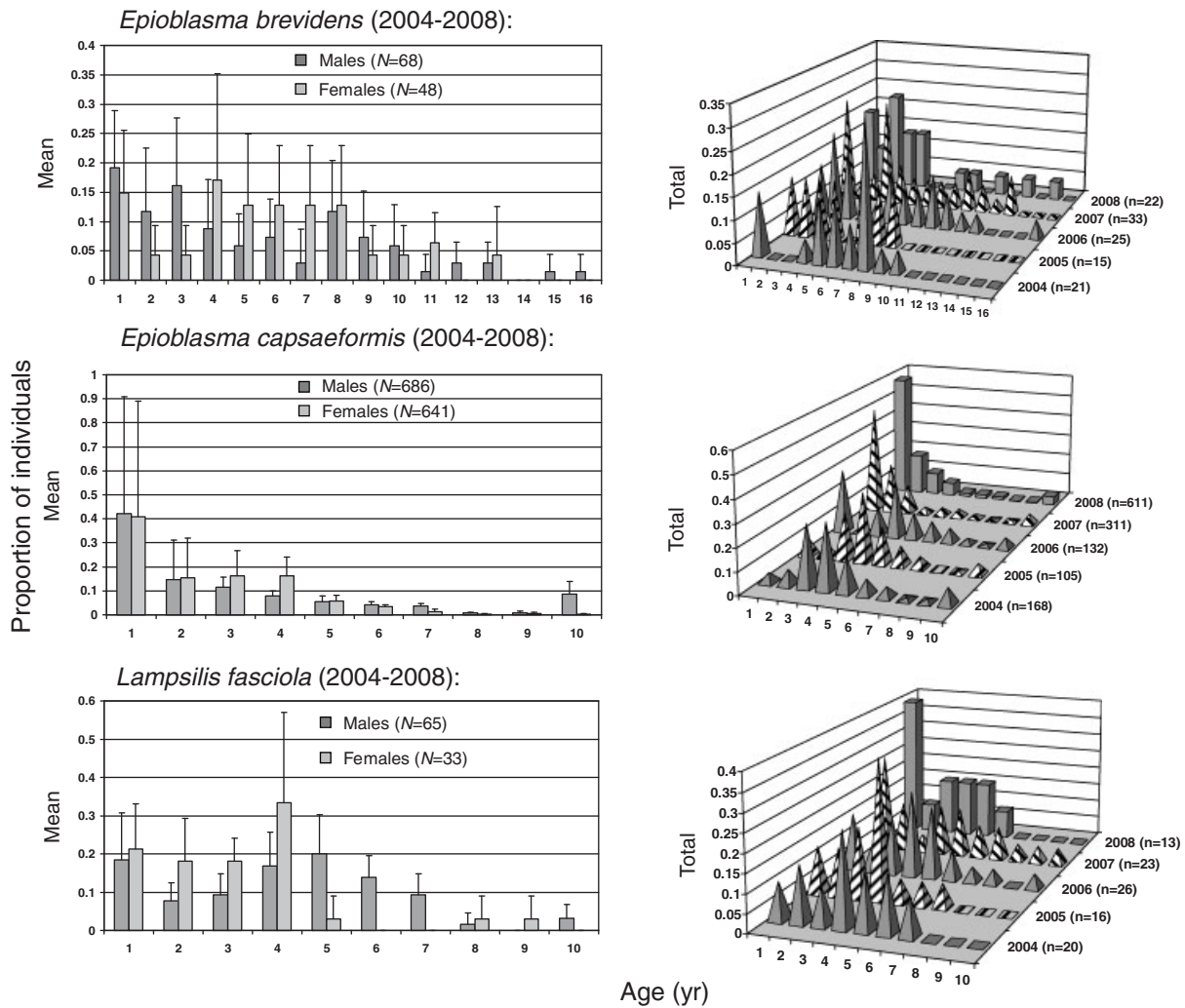


Figure 4. Population age histograms for three species in the Clinch River, TN show (1) mean frequencies for males and females, where error bars represent 95% confidence intervals, and (2) total frequencies for each year sampled. Because sample sizes were small for *Epioblasma brevidens* and *Lampsilis fasciola*, mean frequencies were estimated from all sites sampled from 2004–2008 and total frequencies per year from all sites sampled in a single year. In contrast, sample sizes were much larger for *E. capsaeformis*; therefore, to maintain sampling consistency among sites per year, age frequencies were estimated only from data collected at WB, FF and SI (RKM 309.6, 291.8 and 277.1, respectively). No quantitative differences exist between differently shaped and coloured frequency bars in three-dimensional histograms, which were used to help visualize cohort structure among sample years.

females and number of recruits at the 0.05  $\alpha$ -level, but at a slightly higher  $\alpha$ -level (e.g. 0.075) the relationship would be significant.

Recruitment of 1 yr old *L. fasciola* ranged from a minimum of 10.0% in 2004 to a maximum of 38.5% in 2008. Mean recruitment of 1 yr olds measured across all sample years was 20.5% ( $\pm 10.3$ ), with no significant trends detected. There was no significant correlation ( $P = 0.339$ ) between number of displaying females and number of recruits.

**Population growth and mortality rates**

Mean annual population growth rate of *E. brevidens* was 6.3% from 1979 to 2004, based on data collected by Ahlstedt *et al.* (2005), and 21.0% from 2004 to 2008 based on data obtained in the current study (Table 4). For all three species, no temporal auto-correlation was detected among censuses. Mean annual mortality rate was 16.7% based on catch-curve

regression analysis, and 6.2% based on dead shells obtained from quadrats (Table 4; Figure 6). Mean annual population growth rate of *E. capsaeformis* was 12.5% from 1979 to 2004 and 31.3% from 2004 to 2008. Mean annual mortality rate was 32.0% based on catch-curve analysis and 7.5% based on dead shells. Mean annual population growth rate of *L. fasciola* was 14.3% from 1979 to 2004 and -24.3% from 2004 to 2008. Mean annual mortality rate was 26.3% based on catch-curve analysis, and 6.0% based on dead shells.

**DISCUSSION**

**Influence of life history variation on demographic responses**

Life-history traits such as body size and lifespan are intrinsic to individuals within species and populations, and their expression imposes constraints on the structure of

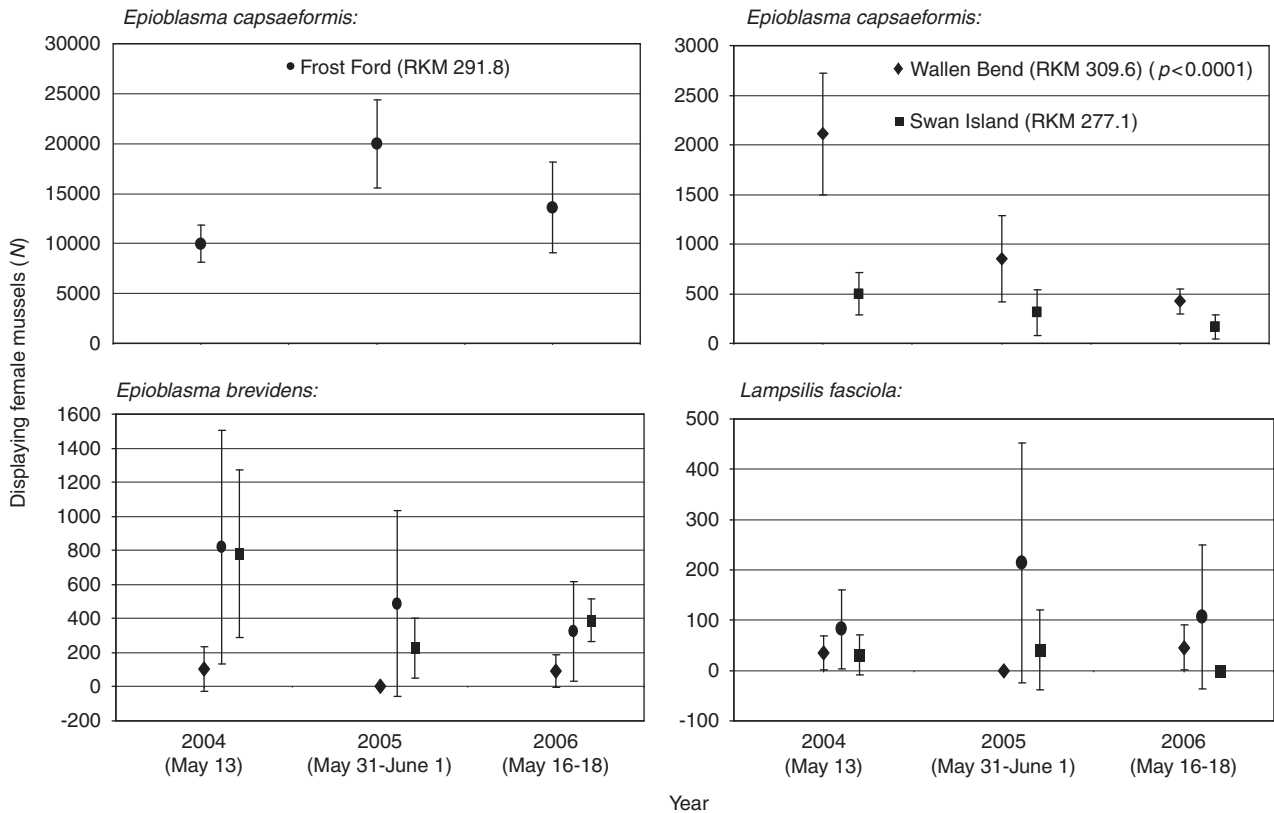


Figure 5. Estimated number of displaying female mussels for each species at three sites in the Clinch River, TN, sampled consecutively from 2004–2006. Error bars represent 95% confidence intervals. Reported  $P$ -value indicates significant decrease in number of displaying females of *Epioblasma capsaeformis* at WB. Sample dates are when data were collected, but also represent the approximate peak of the display period for female *E. capsaeformis* (Jones *et al.*, 2005), which typically coincided with receding water level ( $< 31 \text{ m}^3 \text{ s}^{-1}$  (1100 cfs)) in late spring (mid-May to early June).

Table 3. Percentage of displaying female mussels relative to the total number of sexually mature females per site (in parentheses) for each species. Percentages given should be considered rough approximations, as the 95% CIs (not shown) are large ( $> 50$ – $100\%$  of mean values) for both sexually mature females and displaying females (see Figure 5 for CIs). Females of *Epioblasma brevidens* and *E. capsaeformis* were considered mature at  $\geq 5$  yr and *Lamprolaima fasciola* at  $\geq 4$  yr

Species	Sample year	Sites		
		Wallen Bend	Frost Ford	Swan Island
<i>Epioblasma brevidens</i>	2004	ND (104)	82% (818)	100% (781)
	2005	0% (0)	12% (486)	ND (227)
	2006	43% (91)	32% (324)	100% (391)
<i>Epioblasma capsaeformis</i>	2004	100% (2111)	66% (9980)	100% (500)
	2005	100% (850)	59% (19958)	27% (309)
	2006	100% (422)	65% (13608)	ND (165)
<i>Lamprolaima fasciola</i>	2004	8% (35)	4% (82)	4% (31)
	2005	0% (0)	ND (214)	ND (41)
	2006	ND (46)	ND (107)	ND (0)

ND Not enough data to make a calculation because no mature females were collected in the quadrat samples.

populations, resulting in shifts in life-history strategies. As shown in this study, the shorter-lived *E. capsaeformis* must compensate for its shorter lifespan with higher population growth rate and abundance. Longevity data are limited for most mussel populations, but available studies on fishes can provide insights. Beverton and Holt (1959) showed that populations of marine fishes comprising smaller-sized, shorter-lived adults typically exhibited accelerated body growth (= higher  $k$ ) and a compensative increase in  $r$ ; those that contained larger-sized, longer-lived adults have lower  $k$

and  $r$ . Further, as  $k$  increased, the instantaneous mortality rate ( $Z$ ) increased (Beverton and Holt, 1959). Therefore, to a certain extent, population-level performance, as measured by body growth and mortality, is bounded by factors intrinsic to individual-level performance, such as maximum age and size, age-at-maturity and fecundity. Life-history traits in fishes have been fundamental determinants of population performance, and their investigation has been central to understanding species biology and resource management (Winemiller and Rose, 1992).

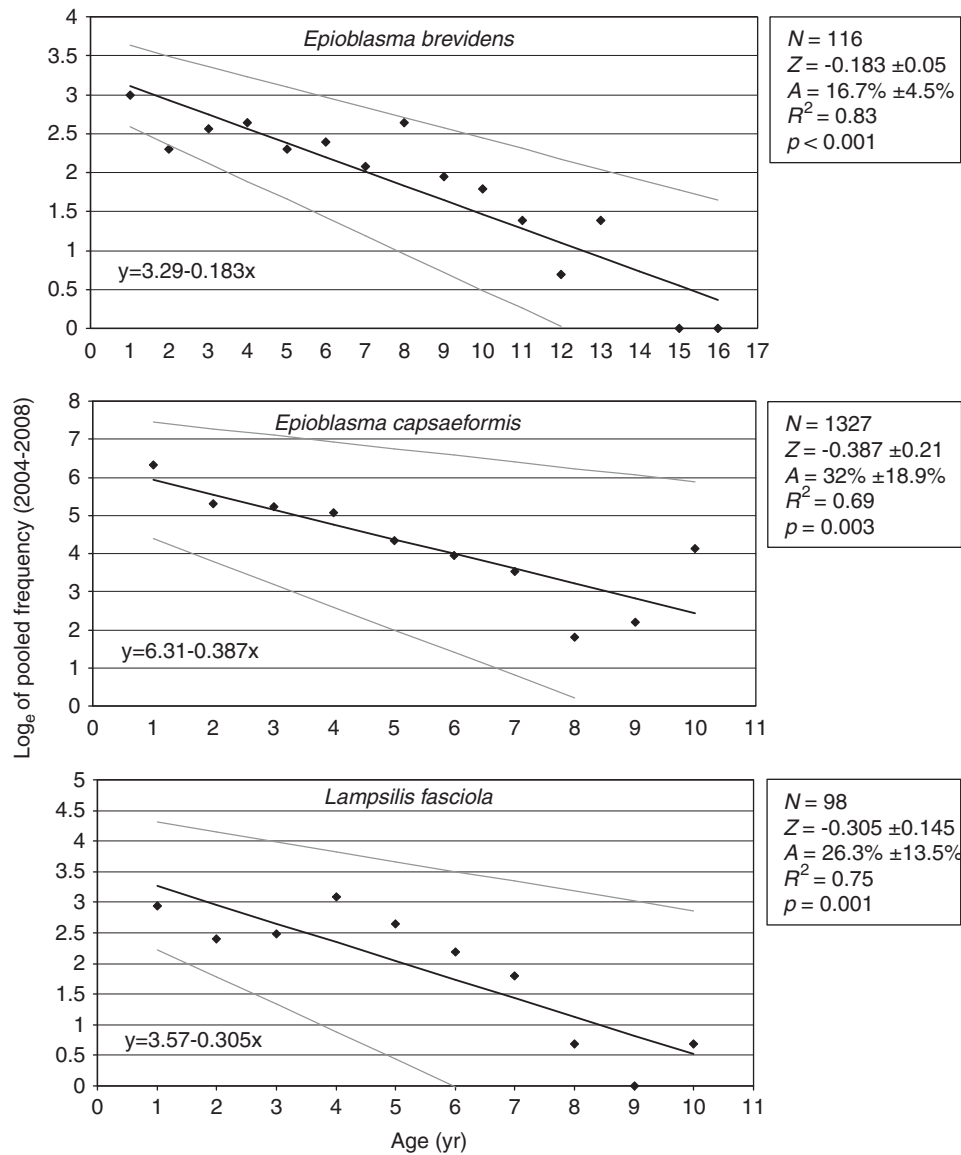


Figure 6. Mortality rates of each species were estimated from catch-curve linear regression analyses, where  $N$  is sample size,  $Z$  = instantaneous mortality rate, and  $A$  = annual mortality rate. Thin grey lines are 95% confidence intervals. Frequency data are pooled across years and sites; data for *E. capsaeformis* are pooled from WB, FF, and SI.

Table 4. Summary of population growth rates and mortality rates for three mussel species in the Clinch River, TN. Estimates were obtained by combining data from investigated sites. Data are from the current study from 2004–2008 and from 1979–2004 Ahlstedt *et al.* (2005). Mortality rates were calculated by combining data from both sexes and using two independent methods: (1) dead shells collected from quadrats, and (2) catch-curve regression analysis (see Figure 6)

Species	Growth rate $\lambda$ ( $\pm 95\%$ CI) expressed as annual net growth		Mortality rate ( $\pm 95\%$ CI)	
	1979–2004	2004–2008	Dead shells	Catch-curve
<i>Epioblasma brevidens</i>	6.3% ( $\pm 11.3\%$ )	21.0% ( $\pm 60.0\%$ )	6.2% ( $\pm 10.3\%$ )	16.7% ( $\pm 4.5\%$ )
<i>Epioblasma capsaeformis</i>	12.5% ( $\pm 22.5\%$ )	31.3% ( $\pm 75.8\%$ )	7.5% ( $\pm 5.2\%$ )	32.0% ( $\pm 18.9\%$ )
<i>Lampsilis fasciola</i>	14.3% ( $\pm 26.0\%$ )	-24.3% ( $\pm 51.5\%$ )	6.0% ( $\pm 6.2\%$ )	26.3% ( $\pm 13.5\%$ )

The influence of age and growth on population dynamics of the European pearl mussel *Margaritifera margaritifera* was described in a series of papers by Bauer (1992 and references

therein); as lifespan and maximum size increased,  $k$  declined. Generally, an increase in  $k$  was correlated with a reduction in lifespan, maximum size, and lower latitude populations

(Bauer, 1991). Somatic growth was positively influenced by extrinsic factors such as increased temperature and habitat productivity, such that maximum size and age correspondingly declined (Bauer, 1992). In the early 20th century, some Bavarian populations had reached extremely high densities, where hundreds per square metre were known to have occurred over 20–30 km of stream length (Bauer, 1991). However, as individual lifespan was very high (50–100 yr), the inherent capacity of these populations to recruit and rebound from declines due to habitat degradation probably was limited and slow. Hence, the pattern and rate of decline for many *M. margaritifera* populations was gradual and extended over a long time trajectory, but one that ultimately led to extirpation of some populations. This fate is shared with many long-lived species of North American mussels, where populations have become trapped in reservoir environments or other altered lotic conditions and are cut off from their hosts, ultimately becoming non-reproducing — such populations can persist for a few decades before extirpation.

The relationship between individual performance and population performance has been largely unexplored for North American freshwater mussels. The handful of studies reporting von Bertalanffy growth parameters loosely support the above hypotheses (Table 5), but lack corroborative population-level data to draw inferences between individual-level and population-level performance. For example, species belonging to the subfamily Ambleminae usually are longer-lived (16–61 yr) and exhibit reduced  $k$  (0.01–0.19) when compared with species belonging to the subfamily Lampsilinae, which usually are shorter-lived (11–32 yr), exhibit higher  $k$  (0.07–0.40), but these parameters vary widely among species. Further, most lampsilines are sexually dimorphic and can exhibit differences in age and growth between sexes; e.g. females of *L. fasciola* and *Lemiox*

*rimosus* have reduced age and size but higher  $k$  compared with males (Table 5), and similarly in this study, for females of *E. brevidens* and *L. fasciola* (Figure 1).

The results of this study and others illustrate the interconnectedness between maximum age and size with  $k$ ; namely, that as the former two increase, the latter will decrease. These studies further suggest that mussel species expressing life-history traits of short lifespan and high somatic growth may warrant special conservation consideration. They are likely to have higher natural mortality and a reduced capacity to withstand long-term impacts, despite the possible advantages of having a higher population growth rate. Many of the shorter-lived lampsiline species, such as those in the genera *Epioblasma*, *Lemiox*, and *Villosa*, express these traits and therefore may be more vulnerable to local extirpation and ultimately extinction. In fact, in the Clinch River upstream of Norris Reservoir, three species of *Epioblasma* and two species of *Villosa* are now extinct or extirpated from the river, respectively, and several species belonging to these genera are locally extirpated from impaired reaches in the upper river in Virginia.

Understanding a species' life history and demographic characteristics provides the basis for effective management. While recent life-history theory has placed less emphasis on categorizing species as purely  $r$ - and  $K$ -strategists, dominant themes of the theory such as density-dependent regulation, resource availability, and environmental variability are still prominent considerations in current demographic and system modelling (Reznick *et al.*, 2002). Although freshwater mussels exhibit traits of both  $r$ -strategists (high fecundity, low survival of newly metamorphosed juveniles, and no parental care) and  $K$ -strategists (increased longevity and high adult survival) (Villemela *et al.*, 2004), a range of traits are expressed among species. Relative to other mussel species, *E. capsaeformis* expresses traits more characteristic of an  $r$ -strategist as

Table 5. Observed maximum age ( $A_{max}$ ) and the estimated von Bertalanffy growth parameters of asymptotic length ( $L_{\infty}$ ) and growth constant ( $k$ ) of North American (U.S.A.) mussel species reported from other studies

Subfamily and species	Location	$A_{max}$	$L_{\infty}$	$k$	Study
<b>Ambleminae</b>					
<i>Amblema plicata</i>	Ouachita River, AR	25 yr	87 mm	0.13	Christian <i>et al.</i> , 2000
	White River, AR	25 yr	58 mm	0.19	
<i>Elliptio dilatata</i>	Clinch River, VA	61 yr	98 mm	0.10	Scott 1994*
<i>Fusconaia cor</i>	Clinch River, VA	20 yr	65 mm	0.12	Kitchel 1985
<i>Fusconaia cuneolus</i>	Clinch River, VA	32 yr	82.4 mm	0.13	Bruenderman and Neves 1993
<i>Fusconaia ebena</i>	White River, AR	27 yr	116 mm	0.13	
	Black River, AR	51 yr	58 mm	0.18	Christian <i>et al.</i> , 2000
<i>Megaloniais nervosa</i>	St. Francis River, AR	41 yr	218 mm	0.04	
	Cache River, AR	42 yr	185 mm	0.01	
<i>Quadrula quadrula</i>	Ozark Reservoir, AR	16 yr	20 mm	0.10	
	Dardanelle Reservoir, AR	24 yr	49 mm	0.13	
<b>Lampsilinae</b>					
<i>Actinonaias pectorosa</i>	Clinch River, VA	21 yr	146 mm	0.08	Scott 1994
<i>Cyprogenia stegaria</i>	Clinch River, TN	26 yr	53 mm	0.15	Jones and Neves 2002
<i>Dromus dromas</i>	Clinch River, TN	25 yr	70 mm	0.12	Jones <i>et al.</i> , 2004
<i>Lampsilis fasciola</i> (♂)	Clinch River, VA	32 yr	87 mm	0.13	Scott 1994
<i>Lampsilis fasciola</i> (♀)		24 yr	78 mm	0.16	
<i>Lemiox rimosus</i> (♂)	Clinch River, TN	15 yr	78 mm	0.07	Jones <i>et al.</i> , 2010
<i>Lemiox rimosus</i> (♀)		11 yr	35 mm	0.31	
<i>Lemiox rimosus</i> (♂)	Duck River, TN	15 yr	56 mm	0.24	
<i>Lemiox rimosus</i> (♀)		11 yr	38 mm	0.40	
<i>Medionidus conradicus</i>	Clinch River, VA	24 yr	61 mm	0.19	Scott 1994
<i>Villosa iris</i>		25 yr	79 mm	0.09	

\*The study by Scott (1994) includes additional estimates of  $A_{max}$  and  $L_{\infty}$ , but only maximum values are reported here; thus, associated  $k$  values are at the lower end but probably are more representative estimates.

described by MacArthur and Wilson (1967) and Pianka (1970), such as shorter lifespan, higher instantaneous growth rate ( $r_{max}$ ), smaller body size, and a population size that is more variable and non-equilibrium over time.

**Influence of ecological processes on demographic responses**

Observed variation in population size and density among the three species was striking. The shorter-lived *E. capsaeformis* achieved a much greater population size and density in a short 5 yr time period, being 10- to 20-fold greater in abundance than *E. brevidens* and *L. fasciola*, and it was the only investigated species to significantly increase in population size from 2004 to 2008. Density of this species was high but locally quite variable, especially at FF where density and population size more than tripled, suggesting that the population dynamics of this species is governed at finer

spatial scales and more influenced by local habitat features, fish fauna or other ecological variables. In contrast, populations of the longer-lived *E. brevidens* and *L. fasciola* have remained stable over time, showing slight increases or decreases, respectively. The density of these two species was lower, less variable, and similar among sites, suggesting that their dynamics are governed over larger spatial scales. These results demonstrate that population change for some mussel species can be extremely rapid under certain environmental conditions, whereas the pace of population growth for others can be insignificant under the same conditions. Perhaps *E. capsaeformis* is an outlier in this regard, but the paradigm of mussels being predominantly long-lived and with slow to moderate population growth rates needs to be reconsidered, with careful attention given to longevity and somatic growth.

The high recruitment and large increases in population size of *E. capsaeformis* from 2006 to 2008 are probably due in part to moderate to low discharge that occurred in the spring–summer of 2005, 2006 and 2007 (Figure 7). First, it is

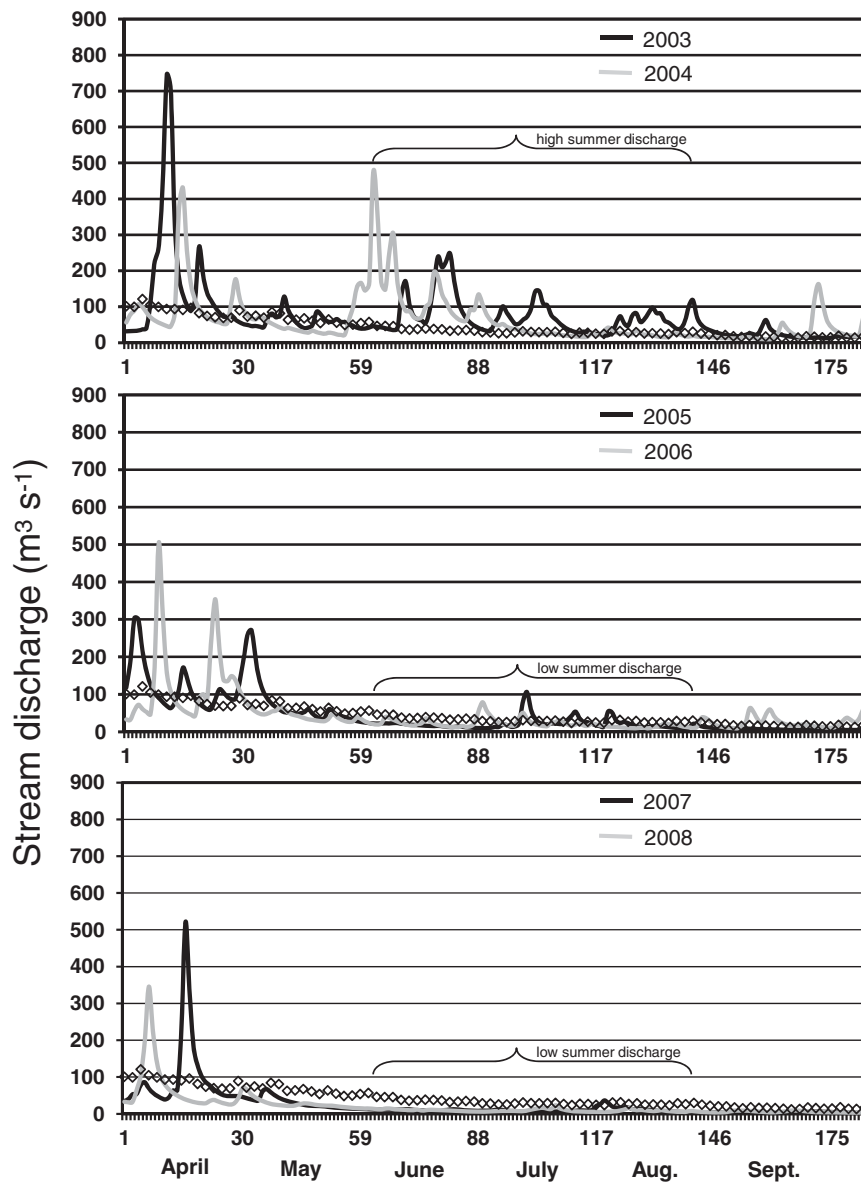


Figure 7. Daily stream discharge in the Clinch River (~RKM 244.4) taken at USGS stream gauge #0352800 located upstream of Tazewell, Claiborne Co., TN. The diamond-shaped symbol represents mean daily stream discharge from 1919–2008.

possible that low discharge in the river during this critical reproductive period facilitated mussel–host interactions and therefore increased infestation of glochidia onto the host. The broad homogeneous shoal at FF provides ideal flow conditions for females to display and release their glochidia, being more laminar and less turbulent, and hence conducive to its small body size and weight while displaying in the hyporheic zone. During these conditions, water clarity is improved and the small darter hosts of *E. capsaeformis* are likely to be dispersed on shoals to feed, reproduce and interact with mussels rather than seeking refugia due to high, turbulent flow. Discharge was  $57 \text{ m}^3 \text{ s}^{-1}$  (<2000 cubic feet per second (cfs)) in late May and June in each of these years, followed in the summer months by low discharge and only a few minor spates of  $57\text{--}113 \text{ m}^3 \text{ s}^{-1}$  (2000–4000 cfs). Most females of *E. capsaeformis* will display their mantle-lure to attract fish hosts typically from spring to early summer (April–June) (Jones *et al.*, 2005). While a few may display through July and into early August, the bulk and peak of the event occurs in this narrow time-frame. The host fish presumably is attracted initially to the colour of the whitish-blue mantle-pad, and then to the micro-lures that mimic cerata of larval-stage aquatic insects (Jones *et al.*, 2006). Thus, moderate to low discharge conditions are probably important in aiding this complex interaction between the female mussel and fish host. Second, low discharge and reduced spates during the summer period may facilitate the settlement, byssal-thread attachment, feeding, and growth of young juveniles, thus increasing their survival. Once glochidia have attached and encysted on a host, they usually take 2–4 weeks to transform and excyst at water temperatures of 21–24°C (Jones *et al.*, 2005). In contrast, discharge was much higher in 2003–2004, with major spates occurring throughout the spring and summer; recruitment of 1 yr old juveniles was low in each following year. Low-flow discharge dynamics are likely to be favourable to *E. brevidens*, *L. fasciola* and other species as well, but the females of these two species display their mantle lures over a wider time-frame, to include the autumn. Thus, infestation of glochidia on hosts and juvenile recruitment of these species may not be as affected by high spring–summer discharges.

The effect of discharge on recruitment and settlement of juveniles has been hypothesized for some time (Coker *et al.*, 1921; Neves and Widlak, 1987). Recent studies have shown that high and low discharge can strongly influence survival of both adults and juveniles. Recruitment of juvenile *Margaritifera falcata* in a California stream was more successful during low discharge years, with a 60% decline in recruitment observed during high discharge years (Howard and Cuffey, 2006). In the summer of 2000, a severe drought in the south-eastern USA caused record low flows in the Flint River basin (Golladay *et al.*, 2004). These authors observed population increases of common mussel species and no change in the imperiled species at stream sites that maintained flow. Payne and Miller (2000) documented two very successful recruitment years in 1981 and 1990 for *Fusconaia ebena* in the lower Ohio River. These cohorts dominated the age-class structure for a decade or longer. They attributed this success to a rapid water rise in spring that aggregated spawning *Alosa chrysochloris* – the only known host – over mussel beds, which presumably enhanced glochidial infestation, and also to a quick return to normal flow conditions that allowed successful settlement of juveniles. Of course, record low discharge

( $2.8\text{--}4.2 \text{ m}^3 \text{ s}^{-1}$  (100–150 cfs)) was observed for several months in the Clinch River during the summers of 2005 and 2007, and as shown, recruitment of *E. capsaeformis* and other species was strong during these historic drought events. Field studies therefore show that recruitment can be surprisingly robust under low discharge conditions. Some mortality of adults of this and other species was observed in the de-watered margins of shoals during this period, but high recruitment more than offset the losses. However, Haag and Warren (2008) caution that the effects of drought and low discharge can be context-specific, with high mortality occurring for mussel populations occupying small streams where desiccation can be more severe.

Flood conditions seem to have the opposite effect, inhibiting recruitment and inducing mortality in adults. In February 1998, a major flood occurred in the River Kerry in north-western Scotland, killing an estimated 50 000 *M. margaritifera* or 4–8% of the total population (Hastie *et al.*, 2001). Large-scale channel destruction resulted in severe scouring and loss of mussel beds. Gangloff and Feminella (2007) assessed mussel abundance and richness in relation to stream geomorphology at 24 sites in eight southern Appalachian streams and concluded that habitat conditions during floods, rather than during summer base-flow, was the limiting factor. Other ecological factors such as seasonal temperatures also may influence mussel population dynamics, especially as they relate to the brooding and release of glochidia (Jones *et al.*, 2005).

Thus, various ecological processes probably play a role in regulating mussel populations, including drought, flood, seasonal stream temperatures, predation, host fish availability, and habitat quality. The degree of influence these extrinsic ecological factors play in regulating populations is in need of further study, but clearly many negative effects have been documented (Neves and Odom, 1989; Neves *et al.*, 1997; Hastie *et al.*, 2001). For example, losses from muskrat predation can be severe, exceeding 20% of population size in just a few years and hindering recovery of endangered mussels (Neves and Odom, 1989). The positive influences on mussel populations are less understood; certainly clean water is a basic requirement, but given a healthy environment, what natural ecological processes are most responsible for their regulation? Are the main factors more abiotic (e.g. temperature, stream discharge) or biotic (e.g. inter-specific competition, disease) in nature? Further, how can one distinguish fluctuations due to natural vs human factors? As these questions are answered, ecological and anthropogenic correlates can be sought.

### Demographic rates and age structure of healthy mussel populations

The Clinch River contains one of the best examples of a diverse mussel assemblage in North America, with multiple cohorts and yearly recruitment for most species. This assemblage offers the opportunity to establish long-term monitoring in order to understand typical demographic rates of numerous species. This knowledge is critical for establishing species-level baselines to gauge restoration efforts. So then, what should the recruitment rate, mortality rate and age structure of a healthy population look like? For a population to grow, average recruitment rate must exceed average mortality rate over a given time period, but the intervening

distribution of age-classes can accommodate a variety of population structures, especially for long-lived species. The mean age structure of *E. capsaeformis* was dominated by younger age classes, and mean annual recruitment (28.9%) was high over the study period. In fact, this high recruitment allowed for a significant increase in abundance and thus population growth. However, annual mortality rate (32%) estimated by the catch-curve exceeded this recruitment rate. Obviously, the assumption of constant recruitment for the catch-curve analysis was violated over the sample period. The high recruitment from 2006 to 2008 increased the slope of the regression equation, leading to an overestimate of the mortality rate. Furthermore, the catch-curve method does not account for age-specific mortality, which is probably lower for ages 1–5 compared with ages 6–10 for this species. Recent field and laboratory studies have documented high yearly survival (>90%) of sub-adult mussels (ages 1–4) of *E. capsaeformis*, *E. brevidens*, *Lampsilis fasciola*, and *Villosa iris* (N. Eckert, Virginia Department of Game and Inland Fisheries, unpublished data). Therefore, we hypothesize that expected survivorship of this species in the study reach is probably bimodal or perhaps curvilinear, with higher survival for ages 1–5 ( $\geq 90\%$ ) and lower survival for ages 6–10 ( $\geq 70\%$ ). Based on such a hypothesized bimodal survivorship curve and a stable age distribution (SAD), mean annual recruitment of 1 yr-olds would be about 15% (Figure 8). Recruitment of *E. capsaeformis* was irregular and pulsed, characterized by boom and bust years. The high recruitment recorded from 2006 to 2008 was perhaps atypical and related to historically low discharge conditions. However, these results show that the age structure of this species can vary quickly over short time periods and that for short-lived species like *E. capsaeformis*, recruitment will on average need to be  $\geq 15\%$  to maintain population stability and growth. No individuals >10 yr of *L. fasciola* were collected; therefore, the catch-curve mortality estimates of this species are unrealistically high and hence unreliable. However, given the longer lifespan of this species, average annual mortality is  $\sim 10\%$  or less based on a SAD, suggesting that similar recruitment rates are needed to maintain homeostasis. While the catch-curve regression method can provide rough estimates of mortality, it needs to be used with caution. The assumptions of the method will

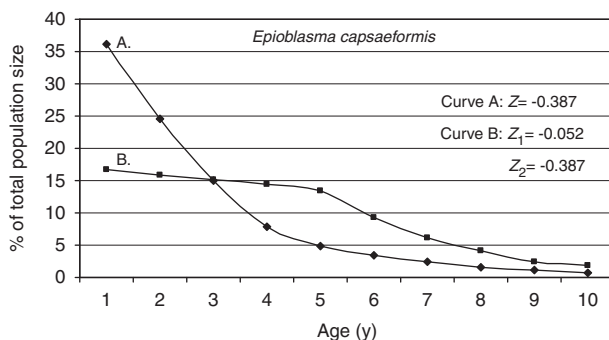


Figure 8. Hypothesized survivorship curves were computed using  $N_t = N_0 e^{-Zt}$ , where  $N_t$  is the number in an age-class at time  $t$ ,  $N_0$  the original number in an age-class, and  $Z$  is the instantaneous mortality rate. Curve A was computed for ages 1–10 using  $Z$  reported in Figure 6, and curve B was computed using two (bimodal) age-specific rates,  $Z_1$  for ages 1–5 and  $Z_2$  for ages 6–10.

often be violated for mussels and lead to erroneous estimates. Specifically, recruitment is unlikely to be constant for most populations, and for longer-lived species, old individuals will be under-sampled.

Mortality rates estimated from collected shells were <10% for all three species. This method provided estimates independent of the rates derived from catch-curves, and supports our claim that rates derived from the catch-curve method for *L. fasciola* were too high. However the mean mortality estimate for *E. capsaeformis*, based on the shell method, is probably too low for two reasons. First, the shell of this species is small, thin, light-weight and susceptible to being washed away into pool areas during high flow events. In the spring, hundreds of freshly dead female shells can be seen lying on the large shoals (e.g. FF) shortly after the peak of the display period, and they are nearly all dispersed 2–3 months later. This mortality may be related to physiological stress involved with displaying for an extended time period (>2 weeks). Second, the thin shell erodes and breaks down quickly, perhaps <1 yr based on field observations, and hence its detection in quadrat samples would be under-represented.

Strayer *et al.* (2004) posed the following question; if mussel species are reproductively viable for decades; does their recruitment occur during most years or only rarely and under just the right combination of conditions? The results of this study and others of presumably healthy mussel populations can begin to answer this question. As shown here, short-lived (<15–20 yr) species will need to sustain higher levels of recruitment or their populations will decline and die out. Despite its capacity for fast population growth and to achieve high abundance, the short-lived *E. capsaeformis* is more susceptible to extirpation, whereas longer-lived (>20–30 yr) species can afford to recruit less frequently and at lower levels in order to maintain their populations. Recruitment success will be driven by ecological conditions such as discharge; under the right conditions, recruitment can be very high and under the wrong conditions, very low. Therefore, patterns of recruitment success for many species will be characterized by both good and bad years. Some populations may recruit at low levels (e.g. <5%) for years and then occasionally under favourable conditions be punctuated with a large cohort, such as seen in *F. ebena* in the lower Ohio River (Payne and Miller, 2000). Vilella *et al.* (2004) studied the population dynamics of three Atlantic slope mussel species from 1996–2000 in the Cacapon River, West Virginia, a tributary of the Potomac River, and showed that recruitment rates for *Elliptio complanata* and *Lampsilis cariosa* were low (1–4%), while those of *E. fisheriana* were periodically high (15–23%). Haag (2002) studied the population dynamics of numerous Gulf slope mussel species from 1999–2001 (this study is ongoing – W.R. Haag, US Forest Service pers. commun.) in the Sipsey River, AL, a tributary of the Tombigbee River, and showed that recruitment rates of *Elliptio arca*, *Fusconaia cerina*, *Pleurobema decisum*, *Quadrula asperata*, and other species were highly variable along taxonomic, spatial and temporal scales, ranging from nearly 0 to 60%. Thus, highly variable recruitment probably is a normal pattern for most riverine species, which inevitably will lead to unequal and disparate age-class structures. However, recent studies conducted on healthy populations have shown that while juvenile mussels can be temporally and spatially

variable in occurrence, they are a detectable and significant feature of the age-class structure.

### Conservation implications

This study provides quantitative data to evaluate population performance of two endangered mussel species and a third non-listed mussel species. The recovery plan for *E. brevidens* and *E. capsaeformis* identifies collection of demographic data as a critical step in monitoring recovery of each species (USFWS, 2004). The data collected in this study can be used to judge their future performance in the Clinch River and other ecologically similar rivers targeted for population re-introduction and augmentation to meet recovery plan goals. Because of the current abundance and stable or positive growth rates of *E. brevidens* and *E. capsaeformis* at investigated sites, conducting translocations of these two species is a feasible recovery option. However, to safeguard against overharvest, the number of adult mussels to be removed per site per year for translocation should be  $\leq 1\%$  of local population size (Jones and Neves, 2008). Characterization of life history and demographic variation, especially longevity and recruitment, will be critical in determining population fluctuations due to natural versus anthropogenic factors.

Density and size-class data of mussels have been collected in the Clinch River for nearly 30 years. Populations of some species have remained stable or even increased in abundance during this period. However, many species in the river occur at a density of  $< 1 \text{ m}^{-2}$  and thus are difficult to assess accurately for recruitment and age-class structure. Understanding how these myriad species persist in the river will require more research, but it is becoming clear that they can exhibit a wide range of demographic responses over time, which are undoubtedly driven by key life-history traits such as longevity, the host fishes they parasitize and various environmental variables. Nonetheless, they have persisted for decades, emphasizing the need for long-term monitoring and adequate time series data to understand their demographic trends.

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