1995

Distribution, Age Structure, and Movements of the Freshwater Mussel *Elliptio complanata* (Mollusca: Unionidae) in a Headwater Stream

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ABSTRACT

The distribution, age structure, and movements of the unionid mussel *Elliptio complanata* (Lightfoot) were studied in a first-order stream in Virginia, USA. Mean density of the mussel in this low-gradient, sand-bottomed stream was 2.5 individuals/m^2 and biomass was 3.4 g dry mass/m^2. About 87% of the population had a shell length of 6-9 cm, or age of 4-6 years. Only 11% of the population was less than four years old; the age of the oldest individuals encountered was only eight years. Distribution of the mussels was highly clumped, but no physical, chemical, or hydrologic factors examined were significantly correlated with mussel abundance. All young mussels (age < three years) were burrowed into the sediment, whereas older individuals occurred both below and at the sediment surface, depending on time of year. About 90% of the population was burrowed below the surface during the winter, but a high of 80% of the mussels moved to the surface in March and April, the time of peak reproductive activity. Tagged mussels moved an average of 2.9 m during one year. Although the direction of those movements was erratic, the overall movement of the population was a net 27 cm downstream, indicating no directed upstream movement to compensate for downstream displacement during storms.

INTRODUCTION

The unionid mussel *Elliptio complanata* (Lightfoot) is widespread and abundant in the lotic and lentic systems of most of North America. Because of its size and abundance, this species may comprise a large proportion of the invertebrate biomass in lakes or streams (Amyot and Downing 1991). Many studies have focused on the geographic distribution, life history, and ecological importance of *E. complanata* (Clarke 1981, Strayer et al. 1981, Ayers 1984, Downing et al. 1993). However, several facets of the ecology of this mussel are still unresolved, particularly for populations in small streams.

A primary question concerns the factors affecting the distribution of individuals within a stream (Amyot and Downing 1991). The distribution of reproductively mature *E.*

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complanata is often highly clumped, but the factors determining habitat suitability and hence the clumped distribution pattern are not well known (Strayer and Ralley 1993). Investigators have suggested the potential role of a variety of physical, chemical, and hydrologic factors including sediment particle size and water velocity, both of which are important in determining the distribution of many aquatic invertebrates (Minshall 1984). Preference for specific particle sizes by *E. complanata*, however, has not been well documented, and most studies suggest that this species may be a habitat generalist (e.g. Clarke 1981). More data are needed to determine the various factors that govern habitat suitability for *E. complanata*.

There is also an indication of a non-random vertical distribution of this mussel within sediments. Amyot and Downing (1991), studying *E. complanata* in a Quebec lake, noted seasonal movements of most of the population between the sediment surface and subsurface. Individuals were primarily epibenthic during the warmer months, but the majority burrowed deep into the sediments during the colder winter months. Young members of the population remained endobenthic even during the warmer months when larger individuals migrated to the surface. An endobenthic existence may be beneficial, especially for juveniles, as a mechanism to avoid predation (Negus 1966) or to avoid being displaced downstream during periods of high flow (Hinch et al. 1989). The existence of seasonally-timed vertical movements of mussel populations or of an endobenthic existence for juveniles has not been well documented at warmer latitudes or in lotic systems.

The distribution of *E. complanata* in streams is also influenced by dispersal ability. Although generally considered sessile organisms, post-glochidial stage mussels undergo both passive and active movements (Kat 1982). In low order lotic environments, passive downstream movements are primarily caused by the effects of flow, especially during storms. Mussels also have a limited ability to actively move about the sediment (McMahon 1991). Movements directed upstream, a re-colonization mechanism for some aquatic invertebrates (Söderstrom 1987), have not been documented for post-glochidial mussels, but active movements by the mussels could be directed upstream to offset potential downstream displacement.

We studied a population of *E. complanata* in a sandy-bottomed, headwater stream, to determine the abundance and age structure of the mussels and to determine aspects of their distribution in the stream. A sampling program was designed to elucidate the factors that affected *E. complanata* distribution, while additional studies focused on quantifying the extent of both horizontal and vertical movements over a year. Horizontal movements were examined to determine distances travelled by the mussels and to determine if movements were directed up or downstream. Sampling was also conducted to determine whether vertical movements occurred and if those movements differed with season or age of the mussels.

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METHODS AND MATERIALS

The study was conducted from August 1993 to August 1994 in Buzzards Branch, a first-order blackwater stream located in Surry County, in southeastern Virginia. The stream is part of the Blackwater River drainage in the Coastal Plain physiographic province. Stream gradient at the study site is low (0.1%), resulting in a sediment primarily of sand. However, the stream also includes reaches of sand-silt in the lower section of the stream and embedded gravel in the upper sections. The sediment typically extends 15-40 cm down to underlying clay (Strommer and Smock 1989). Annual mean discharge over seven years was 0.04-0.08 m^3/s. Details concerning organic matter storage and macroinvertebrate production in Buzzards Branch are published elsewhere (Metzler and Smock 1990, Smock 1990, Smock et al. 1992).

Sampling was conducted over a 950-m stretch of stream that was divided into four sections based on the predominant sediment particle size: silt/sand, sand, sand/gravel, gravel. The lengths of the sections, which graded into one another moving upstream, were silt/sand=175 m; sand=350 m; sand/gravel=275 m; and gravel=150 m. An estimate of mussel abundance was made in each section to provide an estimate of overall abundance in the stream. Replicate plots 1 m in length and extending across the wetted stream channel were sampled in each of the four sections ($n_{sand/silt}=20$, $n_{sand}=32$, $n_{sand/gravel}=27$, $n_{gravel}=20$). Approximately 30% of each section, or a total of 150 m^2 of the stream, was sampled during August 1994 using a hard-pronged rake to remove the sediment and expose mussels down to a depth of about 8 cm. Abundance within each sediment section was expressed as the number of mussels per streambed area. These numbers were weighted according to the proportion of the total streambed area that each sediment section comprised and summed to give an estimate of the overall abundance of *E. complanata* in the stream. A Kruskal-Wallis analysis of variance was used to determine if abundance differed among the four sections.

Mussels were collected in August 1994 to determine biomass. Biomass of mussels per unit streambed area was determined by estimating the biomass of individuals using a regression equation relating size to mass. The regression equation was developed from 67 individuals whose shell lengths were measured with calipers and the soft tissue dried at 60°C and weighed. The mussels ranged in length from 2.2 cm to 10.4 cm, encompassing the size range of mussels collected in the stream.

The shells of the mussels used for the biomass estimate were aged using the modified method of Neves and Moyer (1988). The right valves of 38 shells were sectioned using a variable-speed dremel tool. Valves were polished using a vertical belt sander with 120 and 320 grit sizes. A thin section of the shell was then sliced and glued to a glass slide using thermoplastic cement. The exposed side of the section was polished and viewed under a stereoscope. Ages were determined by counting internal annuli (Negus 1966). Pseudoannuli were easily identified and so were not included in the age estimate. The software package FISHPARM™ (Prager et al. 1989) was used to determine age-growth parameters based on the length and age data. The age structure of the population was then estimated using the generated parameters and the von Bertalanffy asymptotic growth equation, which provides the best model for estimating growth of freshwater mussels (Moyer 1984):

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

where L_t = shell length at time t
L_∞ = theoretical maximum shell length
k = growth constant
t_o = hypothetical age when shell length = 0
t = age of the mussel.

The vertical distribution of mussels in the sediment was determined monthly at 15 1-m^2 plots randomly located in the stream. A hard-pronged rake was used to remove layers of sediment in each plot until a mussel was exposed. The depth from the original top of the streambed down to the mussel was recorded. Raking continued down to near the underlying clay. It was assumed no mussels burrowed into the clay. All mussels were measured and returned to the sediment. The mussels were pooled into nine length categories and a Mann-Whitney U test was used to determine whether the depth distribution of the mussels (which ranged from 0-10 cm) varied significantly with mussel length. A Mann-Whitney U test was also used to determine if significant differences in depth distribution existed with time of year.

A variety of physical, chemical, and hydrologic parameters were measured to characterize the stream environment and to determine if relationships existed between those variables and the distribution and number of mussels on the sediment surface. Sampling was conducted at 76 plots located every 12.5 m along the 950-m stretch of the stream. Each plot consisted of a 1-m^2 quadrat located at midchannel. The number of mussels on the surface and the environmental characteristics were determined every other month at each plot. Water depth and velocity are reported as the mean of three measurements at each plot. Velocity was measured at the sediment surface with a Marsh-McBirney impulse flow meter. Channel width was determined as width of the wetted channel. Conductivity and pH were monitored because localized ground water inputs caused these variables to fluctuate over the length of the study site. Monthly mean water temperature in the stream was determined using a Hydrolab Datasonde continuous recorder.

Sediment particle size was characterized at every other site (n=38) by collecting sediments with a polyethylene corer (inner diameter=4.2 cm), air drying the sediments and passing the sample through a series of sieves (16 mm, 1 mm, 0.5 mm, 0.25 mm, 0.15 mm, 0.053 mm). The percentage composition by mass of each size fraction was then calculated. The median phi value, calculated following Cummins (1962), was used to describe the overall particle size distribution of the sediment in the plots. Organic matter content of the sediment was determined from cores collected from each plot. Sediments were oven dried at 50°C, weighed, combusted in a muffle furnace for four hours at 550°C, and re-weighed.

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The movements of mussels were followed by permanently marking mussels and determining the distance each moved over one year. Mussels were marked following Amyot and Downing's (1991) use of Devcon™ Wet Surface Repair Putty to glue numbered Dymo™ plastic labels to the mussels. All mussels found within the 76 1-m^2 plots in August-September 1993 were tagged (n=160), measured, and placed back in their original positions in the sediment. The exact location of each mussel within a plot was determined by subdividing the quadrat into 100 10x10 cm subquadrats. During each subsequent month a search was conducted to locate the marked mussels and determine the distance from their previous location.

After one year, the entire 950-m study section of the stream was raked to locate as many of the marked mussels as possible. The total distance traveled by each mussel over the year was calculated as the sum of the straight-line distances travelled during each time period. The net upstream or downstream distance traveled was determined as the distance between each mussel's first and last observed location.

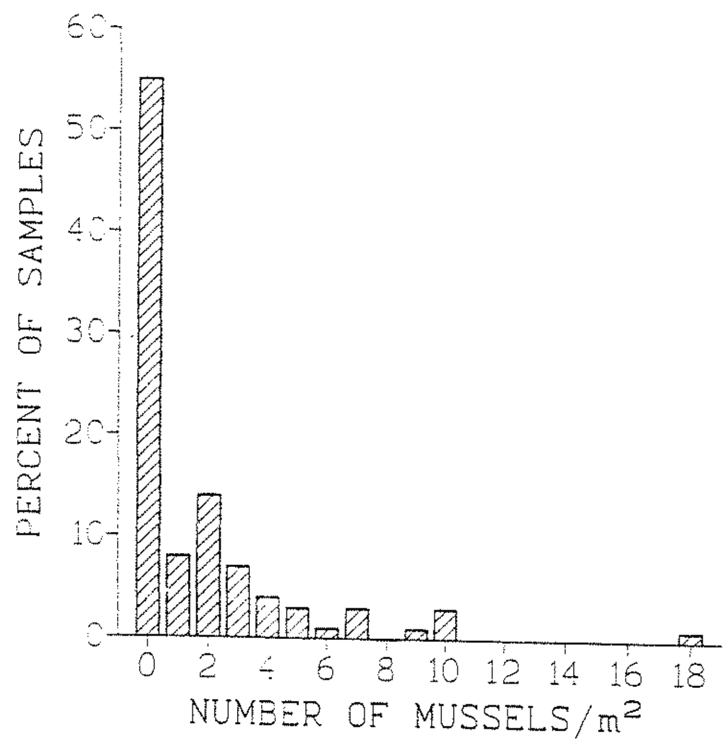

Figure 1. The density distribution of mussels in 1-m^2 plots in Buzzards Branch (n=76).

RESULTS

The distribution of *E. complanata* in Buzzards Branch was apparently clumped. Of the 76 plots sampled in August 1994, 55% contained no *E. complanata* and about 20% contained 90% of the observed mussels (Fig. 1). The maximum density of mussels during the study was 28 individuals/m^2. Mean density throughout the stream was 2.5 individuals/m^2, or 3428 mussels over the 950-m-long study area.

There was a strong relationship between mussel biomass and shell length and between mussel age and shell length (Fig. 2). The shell length-body mass regression equation for this mussel population was:

$$\ln(\text{mass}) = -6.056 + 3.156(\ln(\text{length})) \quad r^2=0.97$$

The von Bertalanffy growth equation, rearranged to solve for age and using the parameter estimates $L_\infty=12.15$, $k=0.2137$, and $t_0=0.3759$ derived from a subset of the *E. complanata* population was:

$$t = (\ln((12.15 - L_t)/12.15)/-0.2137) + 0.3759 \quad r^2=0.80$$

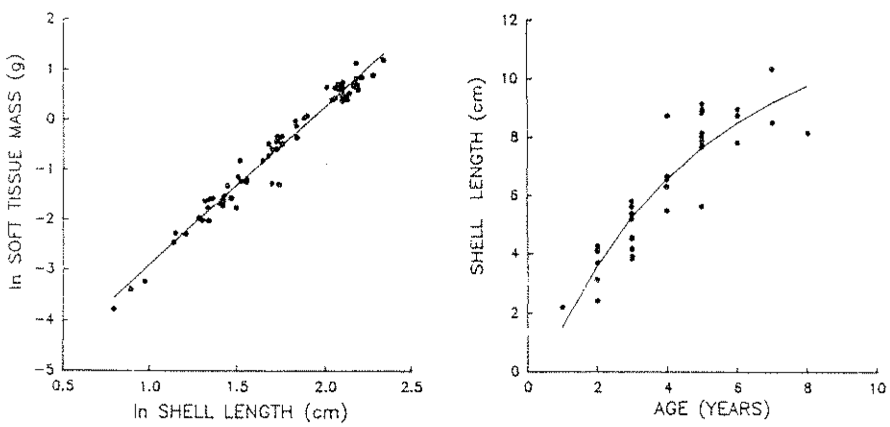

Figure 2. Length-mass and length-age relationships for *E. complanata*.

About 90% of the population had a shell length of 6-9 cm (Fig. 3), corresponding to an approximate age of 4-6 years. Over 90% of the biomass was also found in the 6-9 cm length categories (Fig. 3). The oldest individual encountered was eight years old. The biomass attributable to these mussels in the stream was 3.4 g dry mass/m^2.

Mussels burrowed into the sediment to a maximum depth of 10 cm (Fig. 4). The depth distribution of the population varied both seasonally and with the age of the mussels. Mussel length varied significantly with depth of burrowing (Mann-Whitney U test, $p<0.05$). Whereas no small mussels (< 5 cm in length, age < three years) were found at the sediment surface, large mussels were present throughout the sediment (Fig. 4).

The percentage of mussels on the surface varied through the seasons (Fig. 5). At least 90% of the population occurred below the surface during December and January when

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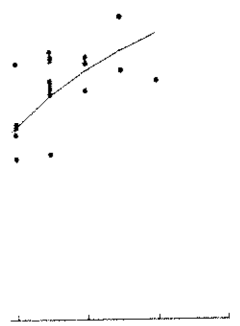

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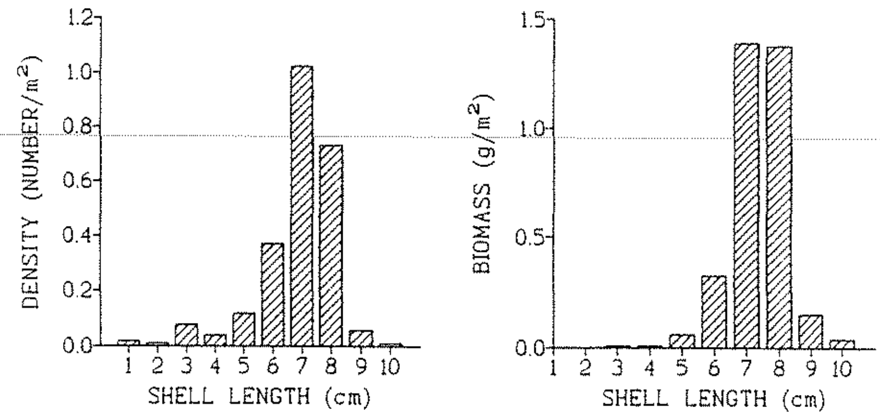


Figure 3. Density and biomass of *E. complanata* by shell length.

Annual mean values of the physical, chemical and hydrologic parameters measured in Buzzards Branch over the year are provided in Table 1. No parameter was strongly correlated with the surface abundance of mussels. The highest coefficient of determination (r^2) was only -0.24 for the percent occurrence of 0.053-0.15 mm sediment particles. The August 1994 sampling that focused on determining the potential effect of sediment particle size on mussel abundance showed a mean density in the sand/silt area of 1.5 mussels/m^2 compared to 3.2-3.3 individuals/m^2 in the other three sediment areas (Fig. 6). A Kruskal-Wallis analysis of variance, however, found no significant difference in mussel abundance among the different sediments.

The movements of 84 tagged mussels were successfully followed throughout the year. Mussels moved an average distance of 2.9 m during the study. Movements were erratic, a mussel's path often crossing back upon itself as it moved short distances both longitudinally and laterally within the channel (Fig. 7). Significantly more tagged mussels moved downstream than moved upstream over the year (Chi-Square Test, $p<0.05$). The mean net distance traveled by all of the tagged mussels was 27 cm downstream. The total and net distances travelled include the movements of three mussels that far out-distanced the others. Two individuals moved a net 12.5 m and 25.5 m upstream, and a third moved 46.2 m downstream. No other mussels moved more than 6 m total over the year (Fig. 8).

DISCUSSION

Elliptio complanata contributed a large proportion of the invertebrate biomass within Buzzards Branch. Total invertebrate biomass in this stream was reported as 1.9 g dry mass/m^2 by Smock et al. (1992), 0.3 g/m^2 of that total being attributed to *E. complanata*. Smock et al. (1992) estimated *E. complanata* density at 0.5 individuals/m^2, but that study did not adequately quantify mussel abundance because of their patchy distribution in the stream and the small area of the sampling device. The present study, based on sampling a greater area of the stream, found 2.5 individuals/m^2 and a biomass of 3.4 g/m^2. When added to the biomass of the other invertebrates (Smock et al. 1992), *E. complanata* comprised about 68% of the total invertebrate biomass.

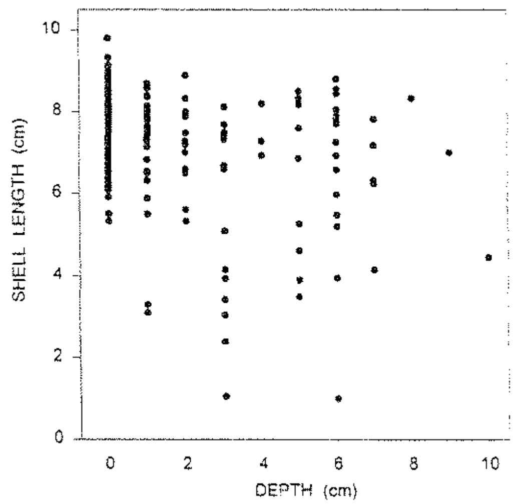
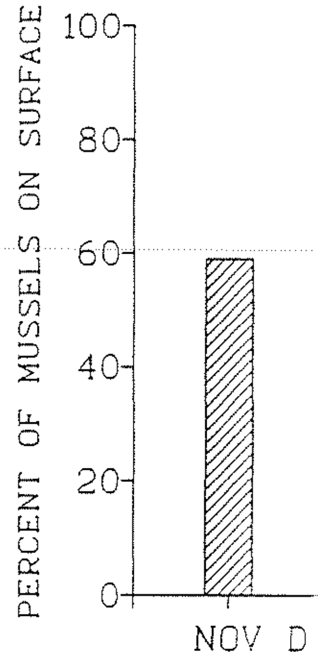


Figure 4. Depth distribution of *E. complanata* according to shell length. Distance was measured from the sediment surface to the middle of each shell; each shell actually extended deeper into the sediment.

This percentage is not extraordinarily high compared to that reported for unionids in other studies. Ökland (1963) and Mann (1964), for example, found unionids may comprise up to 90% of the benthic macrofauna biomass in lakes and streams. Also, the density of *E. complanata* in Buzzards Branch was not particularly high compared to that in other aquatic systems (Kat 1982, Amyot and Downing 1991), where densities 10-30 times higher than in Buzzards Branch suggest that mussels dominate the benthic macrofaunal biomass of those systems.

Although comprising a high proportion of the biomass, *E. complanata* contributed only a small fraction of the annual invertebrate production in the stream. Strayer et al. (1981) reported a mean production to biomass (P/B) ratio of about 0.15 for several northern populations of this mussel. Using this value, which may be conservative given the warmer waters of Buzzards Branch, the estimated annual production of the Buzzards Branch population is 0.5 g/m^2. Since production by the remainder of the invertebrate community in Buzzards Branch was 15.8 g/m^2 (Smock et al. 1992), *E. complanata* probably contributed less than 3% of the total invertebrate production.



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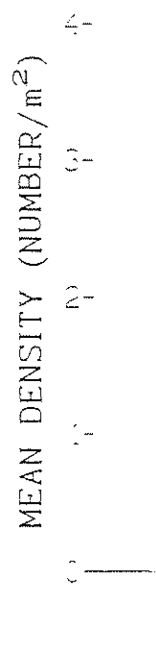

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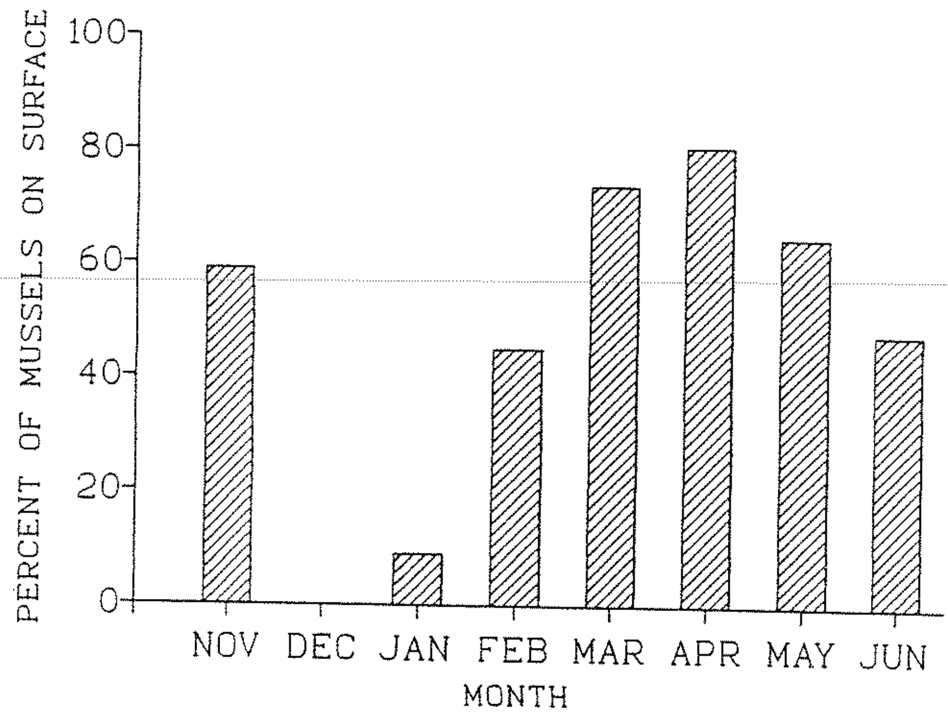


Figure 5. The percentage of the *E. complanata* population occurring at the sediment surface according to the time of the year.

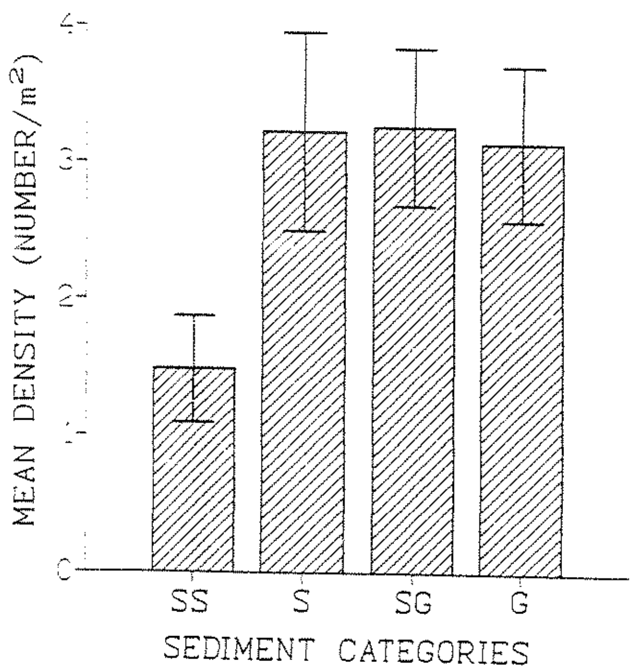


Figure 6. Density of *E. complanata* according to the predominant sediment particle sizes in sections of the stream. SS=silt/sand; S=sand; SG=sand/gravel; G=gravel. Error bar=1 SE.

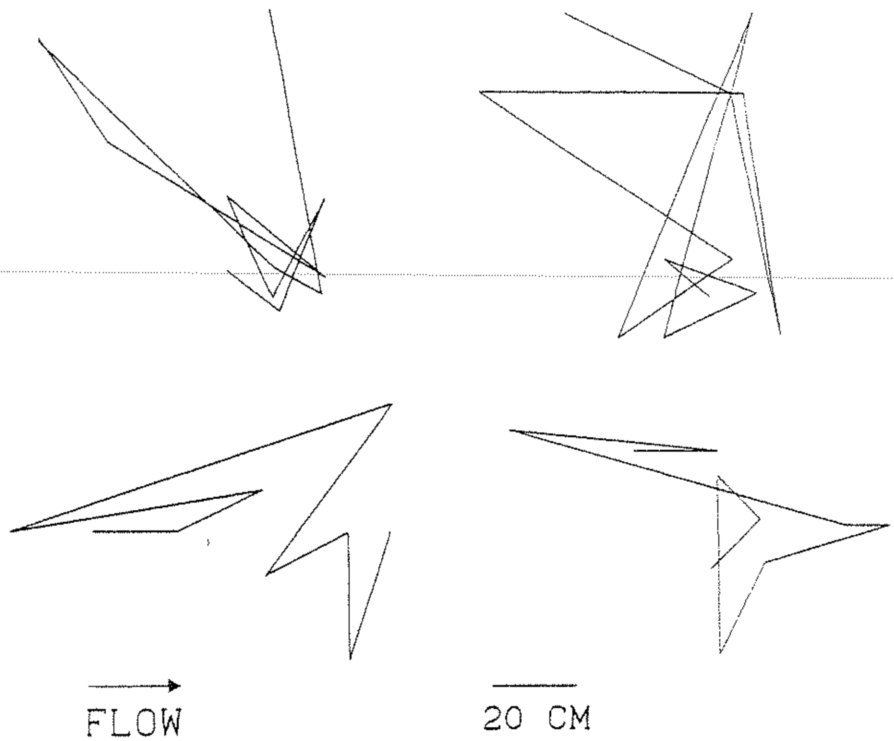
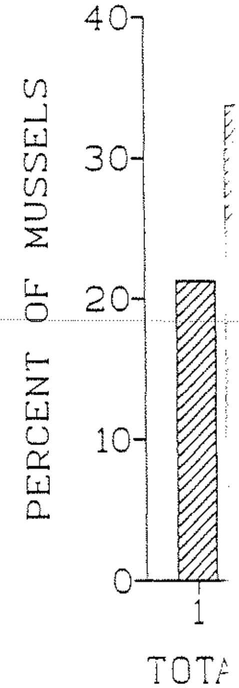


Figure 7. Plots of the movements on the streambed of four *E. complanata* over one year. The movements shown are typical of those of most tracked individuals.

The age structure of the population was similar to that reported for other unionid mussels (Magnin and Stanczykowska 1971, Strayer et al. 1981). Other studies have shown young individuals comprise a small proportion of *E. complanata* populations (Lewandoski and Stanczykowska 1975, Green 1980). This could arise from inadequate sampling of the subsurface sediments to which young mussels migrate. This study, however, showed that young mussels were rare even when the entire habitable sediment column was sampled. Young mussels in Buzzards Branch and elsewhere (Strayer et al. 1981) therefore apparently contribute little to stream biomass.

The maximum age of individuals in the population (8 years) was considerably less than that reported for other populations. Individuals in northern lakes attain ages ranging from 13-30 years (Magnin and Stanczykowska 1971, Kesler and Bailey 1993), and several species of unionids have lifetimes that extend over a century (McMahon 1991). An *E. complanata* population in the nearby Pamunkey River contained individuals that had reached a maximum age of 17 years (Ayers 1984). It is unknown if eight years is the potential maximum age of the mussels in Buzzards Branch or if individuals will continue to grow older. A short-life span may be a function of mussel mortality due to shell erosion. Extensive erosion was observed on many of the shells, the rate of which is probably enhanced by the predominately sand substrate found in Buzzards Branch.



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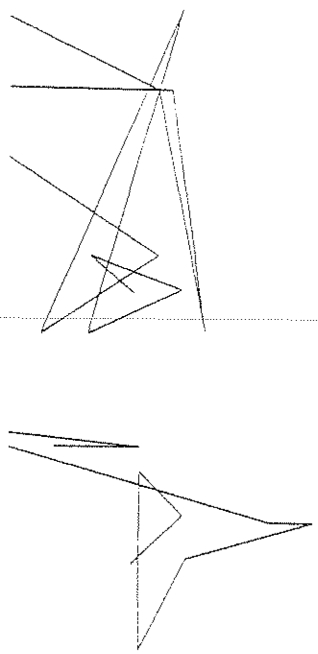

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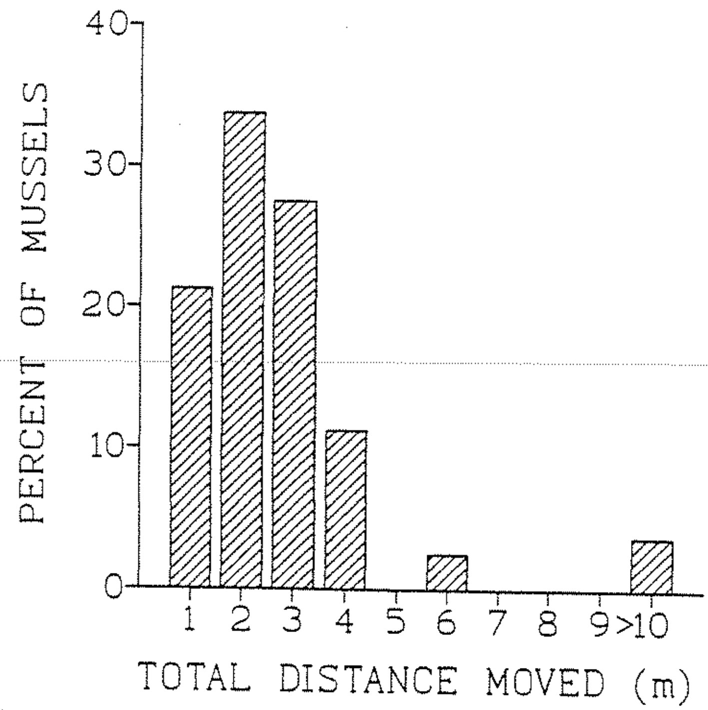

Figure 8. Percent of mussels that moved given distances over one year.

None of the physical, chemical, or hydrologic parameters examined in this study was highly correlated with mussel abundance. Other investigators (Horne and McIntosh 1979, Huehner 1987, Strayer and Ralley 1993) have noted the difficulty in determining factors affecting mussel distribution within streams and lakes. Although sediment particle size affects abundance of many aquatic invertebrates (Minshall 1984), *E. complanata* abundance was not related to this factor, thus supporting Clarke's (1981) description of this mussel as a habitat generalist. The apparently clumped distribution of this species appears to be the result of as yet unidentified factors.

Not only did the mussels appear to have a clumped distribution longitudinally along the channel, but their distribution pattern also showed a distinct vertical component. Burrowing into the sediment may be a behavioral adaptation to decrease exposure to disturbances such as shell abrasion and downstream dislocation during spates or to predation. The extent of movement by mussels between the surface and subsurface sediments was influenced by the age of the mussels and time of year. Young mussels, which are most susceptible to disturbances, occurred exclusively in the subsurface sediments and remained there until about three years of age (five cm shell length). After reaching age three, most mussels displayed seasonal movements to and from the sediment surface, similar to the observations of Amyot and Downing (1991).

The percent of mussels on the sediment surface varied greatly over the year. Mussels displayed vertical movement with changing seasons, similar to the findings of Amyot and

Downing's (1991) study of a lake-dwelling *E. complanata* population. Movement of the majority of older mussels to the surface during the spring corresponded to the period of reproductive activity in this geographic area, glochidia being released to the water column from March to mid-May (Ayers 1984). Reproductively active individuals would have to be at or near the surface for the successful release of glochidia. Beginning in May, an increasing proportion of the population moved back into the sediment until the winter months when nearly all individuals were buried. Burial at this time would be advantageous because the winter is the period of highest discharge and therefore the time of greatest likelihood for a mussel to be swept downstream or subjected to high shell erosion rates.

In addition to their vertical movements, the mussels moved longitudinally both up and downstream. The nearly 3 m of longitudinal movement over the year appeared erratic in direction, although the net direction of movement was slightly downstream. The net downstream movement by adult *E. complanata* was probably a result of passive displacement during high flow rather than being due to active, directed movement. The few individuals that moved long distances (e.g. 12-47 m) may have been transported during spates or, especially for those that moved upstream, may have been carried by raccoons in aborted attempts at predation. Although the mussels presumably depend on the glochidial stage and fish hosts for the majority of their upstream recolonization, long distance movements by only a few reproductively active adults could also contribute to recolonization of upstream areas.

Although considered sessile organisms, *E. complanata* showed both vertical and horizontal movements within the streambed. The vertical movements suggest a migration of the organisms in response to changing season and a positioning of the individuals according to age. This migration has implications for the accuracy of studies designed to determine mussel abundance and for the mussels' availability as prey. The longitudinal movements suggest that the mussels are capable of affecting their distribution within a stream. The movements however, are erratic in direction and the mussels do not appear drawn to an area based on any known factors. Further studies are warranted to clarify the causes of the clumped distribution demonstrated by *E. complanata*.

Table 1. Physical, chemical, and hydrologic data for Buzzards Branch. Values are annual means from monthly sampling from August 1993 to August 1994 at 76 sites along the stream.

Mean water temp.	14.7 °C	Mean depth	0.15 m
Mean pH	6.78	Mean width (wetted channel)	1.9 m
Mean flow	8.8 cm/s	Mean conductivity	126 μS/cm
Mean discharge	0.04 m^3/s	Mean organic matter content	1.5 %

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