

## Competitive interactions between early life stages of *Villosa iris* (Bivalvia: Unionidae) and adult Asian clams (*Corbicula fluminea*)

Mindy M. Yeager<sup>1</sup> Richard J. Neves<sup>2,4</sup>, and Donald S. Cherry<sup>3</sup>

<sup>1</sup>Potesta and Associates, 2300 MacCorkle Avenue, S. E., Charleston, WV 25304; <sup>2</sup>Virginia Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, Virginia Tech, Blacksburg, VA 24061; <sup>3</sup>Biology Department, Virginia Tech, Blacksburg, VA 24061

**ABSTRACT:** The behavioral effects of adult Asian clams (15-25 mm) on glochidia and newly metamorphosed unionids were evaluated for 4 h in static containers with dyed glochidia and juvenile mussels, using a dissecting microscope and attached video recorder. Ten day flow-through tests in sediment with juvenile mussels and Asian clams at five densities were conducted to test a density-dependent response in mortality of juveniles. Seven day flow-through tests with juvenile mussels and three densities of Asian clams evaluated whether juveniles were displaced by Asian clams. Adult Asian clams readily ingested glochidia, as evidenced by dyed valve fragments in feces. Similarly, dead glochidia and young juveniles were contained within the pseudofeces of clams. There was a positive correlation between clam density and mortality of juvenile mussels; treatments containing 8 - 32 Asian clams per container experienced 100% mortality of unionids. Growth rates of juveniles in the containers with clams were significantly lower than those in control containers without Asian clams ( $P < 0.05$ ). Similarly, juvenile unionids were displaced downstream in greater numbers in chambers with Asian clams than in chambers without clams. These preliminary experiments demonstrate that Asian clams at high densities can affect the survival and growth of newly metamorphosed juvenile freshwater mussels.

**Keywords:** *Corbicula*, Unionidae, competition, survivorship, growth, *Villosa*, juvenile

The decline of native freshwater mussels in the river systems of North America during this century has been well documented (Neves 1987). Prior to the 1940's, this decline and extirpation of mussel populations were attributed to degraded habitats and water quality from industrial and agricultural pollution, sedimentation, and dam construction (van der Schalie 1938). Since then, the decline of unionids has continued, principally from the same causes but additionally from a suite of non-point source pollution effects (Neves *et al.* 1997). Sediment and contaminants in runoff are causing immeasurable damage to stream faunas, and the physical and chemical degradation of substratum and water quality continues to create adverse conditions for both survival and recovery of mussel populations in many waterways.

Since the discovery of the Asian clam (*Corbicula fluminea* (Müller, 1774)) in the US in 1938 (Burch 1944), the species quickly flourished and expanded its range along the Pacific Coast (Counts 1986). In the late 1950's, it reached the Gulf Coast and then rapidly spread into Interior Basin rivers that contained the most diverse unionid fauna on the continent. The clam's prolific reproductive capabilities, high densities,

and ecological role as a filter feeder are traits conducive to competition with native bivalves. It often becomes the dominant benthic species within a few years of invasion, capable of achieving densities of thousands per square meter (Eng 1979; Sickle 1979, 1986).

Evidence to document competitive interactions between Asian clams and native bivalves has been principally anecdotal and inconclusive (Sickel 1986). Substratum space and food availability are two requisite resources that could be limiting in rivers with high densities of Asian clams and natural or depleted densities of freshwater mussels. Gardner *et al.* (1976) reported declines in unionid populations upon invasion of the Asian clam in the Altamaha River, Georgia. Fuller and Richardson (1977) observed physical displacement of unionids by Asian clams in the Savannah River, Georgia and South Carolina, and labeled this non-indigenous clam an amensalistic competitor. With respect to juvenile unionids, Sickle (1976) found fewer juvenile mussels on sandbars where Asian clams were abundant and concluded that *C. fluminea* might interfere with recruitment of native unionids. Thus, the extent and competitive impact of Asian clams on native mussel populations is speculative and uncorroborated. The purpose of this study was to examine the interactions

<sup>4</sup> For correspondence contact R.J. Neves  
(Email: mussel@vt.edu)

between the early life stages of a unionid mussel and adult Asian clams, to determine whether the potential exists for negative effects on mussel recruitment. Interactions between the two bivalves were examined by observing their contact behaviors and testing them together in flow-through chambers to determine whether mortality and displacement were related to clam densities.

## Methods

Adult Asian clams, ranging from 15 - 25 mm in length, were collected from the Clinch River, Virginia. Clams were held in river sediment and dechlorinated tap water in a flow-through fiberglass Living Stream and fed a live tri-algal suspension containing *Chlamydomonas* sp., *Ankistrodesmus* sp., and *Chlorella* sp. (Foe and Knight 1986) until used in experiments. Gravid *Villosa iris* (I. Lea, 1829) also were collected from the Clinch River and returned to the laboratory in water-filled coolers. The glochidia were removed from the gravid female by gently prying the valves apart, inserting a water-filled syringe into the marsupial gill, and flushing out the glochidia. The glochidia then were quickly checked for viability using a saturated salt solution (Zale and Neves 1982). Encystment of glochidia on 12-18 cm largemouth bass (*Micropterus salmoides*) was accomplished by placing the fish in a well aerated, 19 L aquarium for at least 30 min, with the extracted glochidia of the gravid female. When several fish were exposed together, they were left in the encystment aquarium for up to 2 hr depending on glochidial density. The bass were kept in 500 L fiberglass tanks that were siphoned daily, once the juveniles began excystment from the hosts.

### Videotaping of juvenile mussels

The interactions between the two bivalve species were observed to examine the outcomes of encounters between them. Both glochidia and juveniles of *V. iris* were videotaped in the presence of adult *C. fluminea*. Adult clams, placed in 250 ml beakers with Clinch River water and in 400 ml bioassay dishes with Clinch River sediments and water, were filmed with the juveniles and glochidia. The glochidia were dyed with methylene blue so that they could be more easily seen, but the juveniles were not dyed because the effect of methylene blue on the mussels is unknown. The previously described tri-algal suspension was added to induce filter-feeding by the clams. The interactions between bivalves were viewed using a Zeiss dissecting microscope, connected to an RCA videorecorder, and television for recording activity. A total of 240 min of videotape was used to

characterize the interactions. During this time, one large clam ( $\approx 25$  mm) was observed in water with the approximately 30 glochidia. Three clams and juvenile mussels were added to the bioassay dishes in increments of approximately 30 individuals. When the mussels could no longer be observed interacting with the clam, more mussels were added to the test chambers. Sediment was prepared for use in this experiment and subsequent testing by sieving Clinch River sediments to remove the size fraction from 1-53  $\mu\text{m}$ . Removal of the silt fraction, which is within the size range of the glochidia and juveniles, allowed for easier retrieval of the mussels.

### Flow-through tests

Flow-through tests were conducted for 10 d with 1 - 3 d old juvenile *V. iris* and adult *C. fluminea*, to determine whether juvenile survival was negatively affected by increasing densities of adult Asian clams. Our test chambers were assembled from 600 ml plexi-glass beakers, and a single inlet was placed on the side of the container, 2.5 cm from the bottom. The inlet was positioned approximately 1.5 cm above the sediment. Water flowed out of the chamber through a nitex mesh fitted over a 1 cm x 4 cm rectangular hole positioned on the front of the beaker, so that total volume was 550 mL. This volume allowed a sediment to water ratio of approximately 1:4. A series of five treatments, each with 2 replicates, containing 32, 16, 8, 4, and 2 *C. fluminea*, along with a control containing no clams, were tested. Eight juvenile mussels were placed in each of the replicate beakers. Flow was created by siphoning dechlorinated tap water from a 500 L fiberglass head box positioned above the water bath, where a  $25 \pm 2$  °C temperature was maintained for the test beakers. Ambient laboratory lighting was used on a 16:8 light to dark photoperiod. Addition of the tri-algal suspension to the headbox provided a uniform food supply to all test chambers. Flow into the test chambers averaged  $63 \text{ ml min}^{-1}$  (range 54 - 71  $\text{ml min}^{-1}$ ). Mortality, growth, and shell recovery data were analyzed using an ANOVA procedure followed by a Dunnett's test.

### Displacement experiment

Experiments were conducted to determine whether the presence of adult *C. fluminea* resulted in the displacement of early juvenile *V. iris*. Flow-through troughs were created using plastic gutters 40.5 cm in length, fitted on one end with an inlet hose. A 10 cm head space was created by cutting 1.8 cm off the top of a plastic gutter end and inserting it into the trough, which allowed a more laminar flow into and through the trough. The trough was filled with 1050 g of Clinch River sediment, and water flowed out of the chamber over another plastic gutter end cut 1.8 cm

below the trough height. The water flowing out of a chamber was collected in a funnel and passed through a 105  $\mu\text{m}$  mesh container. The experiment was run for 7 d on two separate occasions. In the first experiment, 20 older juvenile *V. iris* (14 - 21 d old) were placed in the troughs with 0, 10, or 20 adult clams. During the second experiment, each trough contained 75 younger juvenile mussels (2-4 days old) and either 0, 6, or 12 adult clams. The screen-mesh containers were rinsed daily, and the numbers of juvenile mussels washing out of the chambers were recorded.

## Results

### Behavioral observations

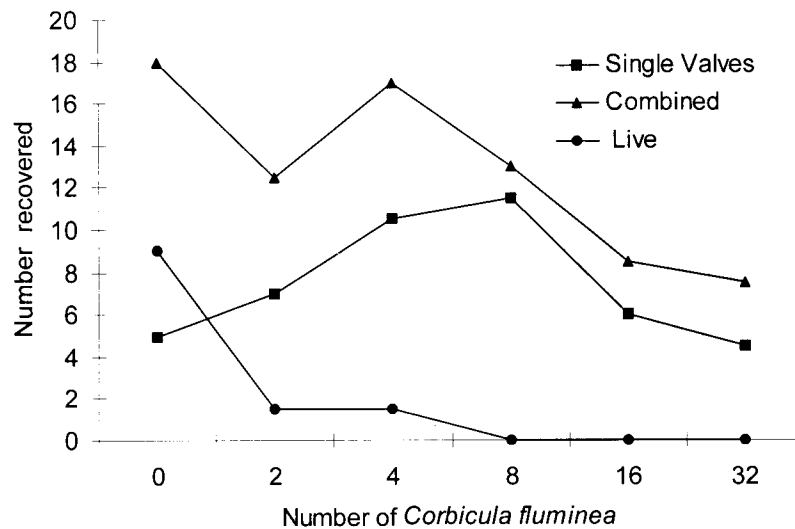
Review of the videotape with adult Asian clams in confinement with dyed glochidia revealed that glochidia were affected in two ways. It was readily apparent that glochidia were ingested by the clams through their incurrent siphon. Glochidia, some retaining the color of methylene blue and some clear, were present in the feces of clams observed to siphon in the glochidia. The second means by which glochidia were affected by clams was by being entangled in the mucous of pseudofeces which formed along the pedal gape of the clams. Similar results were seen when the adult clams were videotaped with juvenile *V. iris*. The juvenile mussels were within the size range of particles that could be siphoned by the clams. While some shell fragments were found within the feces of adult clams, many juveniles were rejected by being expelled from the excurrent siphon. Juvenile

mussels were observed being transported up the foot of the clam during pedal feeding and became bound in the mucous at the pedal gape. These juvenile mussels were not observed to be ingested, and their fate was undetermined.

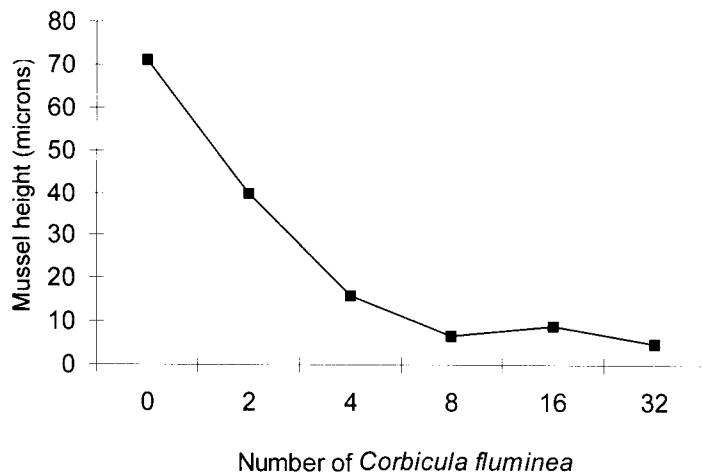
### Flow-through tests

Mortality of juvenile mussels in the 10-day test exhibited a clam density-dependent response, with mortality generally increasing as the number of clams in the test chambers increased (Fig. 1). The treatments containing 8, 16, and 32 clams all had 100% mortality of juvenile mussels, while the treatments with 2 and 4 clams each had 92.5% mortality. Mortality in one of the control replicates was 30%. However, the other control replicate had 80% mortality, due to the interruption of flow through a clogged hose which resulted in a low dissolved oxygen level. Similar interruption of flow occurred in one of the 32-clam treatment replicates. Both of these replicates were included in the analysis. The effect of adult clams on juvenile *V. iris* mortality was apparent, as was the case in the additional test endpoints, but the high variability in survival of controls and the low number of replicates resulted in differences in mortality not being statistically significant ( $F=2.68, N=2, P=0.131$ ). If the two anomalous replicates are excluded, the differences in mortality are highly significant.

Recovery of combined valves decreased with increasing clam number (Fig. 1), except for the 2-clam treatment. In the controls, 90% of the mussel valves were recovered. The 2, 4, 8, 16, and 32-clam



**Figure 1.** Number of live juvenile mussels and valves recovered in flow-through experiments with six densities of *Corbicula fluminea*.



**Figure 2.** Growth of juvenile mussels recorded at 6 densities of *Corbicula fluminea* over a 10-day period.

treatments had 62.5%, 85.0%, 62.5%, 42.5% and 37.5% recovery, respectively. All treatments except the four-clam treatment had significantly lower recovery than in the control ( $F=19.1$ ,  $N=2$ ,  $P=0.0013$ ).

As previously described, higher clam densities were correlated with greater fragmentation of mussel valves. For this reason, the number of retrieved single valves was calculated. This number increased with increasing clam number in the 0, 2, 4, and 8-clam treatments (Fig. 1). However, the number of single shells then declined. The mean percent of valves recovered as single valves was only 13.8% in the control and 28.0%, 30.9%, 44.2%, 32.3%, and 26.5% in the 2, 4, 8, 16, and 32-clam treatments, respectively.

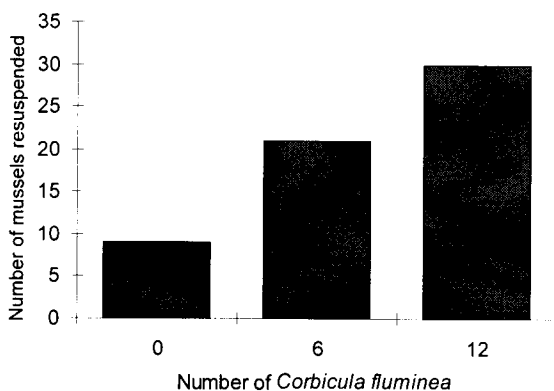
Although it was not specifically monitored as part of the experiment, growth increments on the

juvenile mussel valves seemed to indicate the length of time that mussels coexisted with clams prior to death. Growth of the mussels, measured as valve height, was greatest in the controls; a mean height of 71.3  $\mu\text{m}$  over the 10 d period (Fig. 2). The second highest growth (40.0  $\mu\text{m}$ ) was recorded in the 2-clam treatment, which was not significantly different from mean size of control clams. Growth in the 4, 8, 16, and 32-clam treatments was significantly lower than that in the control, with means of 15.9, 6.7, 8.8, and 5.0  $\mu\text{m}$ , respectively ( $F=8.20$ ,  $N=2$ ,  $P=0.0117$ ).

#### Displacement experiment

In the first displacement experiment, using 14 – 21 d juveniles, no trend was evident in displacement of juveniles. During the 7 d test period, one mussel washed out of the 10-clam treatment and one half-valve was recovered from the 20-clam treatment. No mussels were washed out of the control tank.

In the second experiment, using 2– 4 d old juveniles, mussels were displaced in all 3 treatments, with more juveniles recovered at the higher densities of adult clams (Fig. 3). At the end of seven days, nine juvenile mussels (12%) had been displaced in the 0-clam treatment. During the same time period, 21 mussels (28%) and 30 mussels (40%) had been displaced in the 6 and 12-clam treatments, respectively.



**Figure 3.** Displacement of juvenile mussels at 3 densities of *Corbicula fluminea* over a 10-day period.

#### Discussion

One of the most vulnerable periods in the life history of young mussels is when the juvenile drops from the fish host and seeks a suitable habitat to survive (Neves

and Widlak 1987). While the explicit factors that define suitable habitat are unknown, it has been reported that they inhabit depositional areas (Neves and Widlak 1987) with low flow, where they can feed pedally and siphon interstitial water (Yeager *et al.* 1994). While Asian clams occur in the gravel and cobble substrata occupied by adult unionids, they often preferentially inhabit sand and detrital areas (Gardner *et al.* 1976), more characteristic of the depositional areas in lotic systems. The presence of adult *C. fluminea*, which are filter-feeders and deposit feeders (Reid *et al.* 1992), may impair recruitment of unionids by disturbance and displacement of young juveniles and through incidental siphoning of newly metamorphosed individuals. Although juvenile *V. iris* and glochidia are slightly larger than the reported size range of particles ingested by *C. fluminea* (McMahon 1991, Reid *et al.* 1992), it was observed that they could be ingested and passed through the gut or bound in clam mucus and rejected as pseudofeces. Clams foraging in depositional areas could therefore cause mortality in newly transformed juveniles. In the flow-through test, the presence of *C. fluminea* in the sediment was shown to impair survival and growth of juvenile mussels. Also, the presence of valve fragments from juveniles indicates one possible outcome of cohabitation with the larger Asian clams. Due to the persistence of mussel valves in sediments, it was possible to recover valves of dead mussels to confirm that juveniles died and were simply not recovered. This allowed us to determine approximately how long mussels coexisted with the clam by measuring the growth increment that occurred prior to mortality. Some valves were obviously fragmented in passing through the gut of the clams, as determined by videotape analysis in containers with no substratum. The decreased recovery of shells in the higher clam concentrations is attributed to the difficulty in collecting valve fragments from a mixed substratum. Some valves were destroyed undoubtedly from passing through the gut of the clams, possibly on more than one occasion. This conclusion is supported by the greater number of half shells retrieved from the higher clam concentrations, up to the 16-clam treatment. At the highest clam densities, the decline in single valve numbers most likely resulted from the overall decline in mussel valve recovery (greater fragmentation).

The first displacement test with 14-21 d juvenile mussels failed to produce any downstream displacement of juveniles, regardless of the density of clams. This is probably due to the size of 2-3 wk juveniles which were 400-600  $\mu\text{m}$ , as opposed to the 220-250  $\mu\text{m}$  juveniles used in the second experiment. The lack of

response indicates that mussels of this size may be more resistant to the disturbance by the clams than the smaller juveniles. Results of the second resuspension chamber experiments with 2 - 4 d juveniles, showed that adult *C. fluminea* can displace juvenile *V. iris* perhaps into lower quality habitats. While the data demonstrate obvious negative effects, our conclusions are tentative for lack of replication resulting from the seasonal availability of juvenile mussels.

The adult-larval interaction hypothesis (Woodin 1976) predicts that discrete assemblages of deposit feeders can be maintained through adult-juvenile interactions. According to Hines *et al.* (1989), deposit feeders can ingest larvae in surface sediments and disrupt juveniles while searching for food. In riffle areas where depositional habitat is scarce, this may be an effective mechanism to impair recruitment of young, juvenile mussels

The effects of adult *C. fluminea* on juvenile mussels, suspected but overlooked in previous studies, merits further investigation. However, previous studies of adults of both taxa to detect competitive interactions between species have produced mixed conclusions. For example, Kraemer (1979) states that Asian clams have been present in the Buffalo River, Arkansas, for 10 y and that they inhabit only localized sandy patches of river bottom where indigenous mussels are rare. It is unknown whether unionid recruitment is occurring in these populations. Similarly, Leff *et al.* (1990) investigated competitive interactions between *Elliptio complanata* and *C. fluminea* by examining seston removal rates and spatial distribution. While no competitive effect was shown, they reported a slightly greater shell length in mussels in stream reaches with Asian clams as opposed to those in an upstream reach without clams. These data may indicate no impairment to *E. complanata* growth by *C. fluminea*, or they may indicate an age class shift toward larger individuals resulting from decreased recruitment in the stream reach with clams present. In light of our laboratory experiments, our tentative conclusion is that rivers with a high abundance of Asian clams are subject to impairment of juvenile mussel recruitment. Certainly, ingestion and displacement of juveniles by Asian clams would result in some mortality and a subsequent decrease in recruitment for unionid populations.

After eons of speciation and adaptation by native unionids in US waterways, particularly in the Southeast, it is highly improbable that all available niches for bivalve filter-feeders were not filled by the native assemblage. There was no grand niche left

vacant, such that the non-indigenous Asian clam could invade, achieve high densities, dominate in benthic biomass, and yet have no significant adverse effect on native unionids. Ecological principles and our laboratory experiments strongly suggest that unionids in rivers with an abundance of Asian clams are subject to competitive interactions with this non-indigenous species. From our preliminary laboratory results, we provide evidence that recruitment of newly metamorphosed juvenile mussels in a river is impeded by the presence of a dense Asian clam population. Proscribed research is needed to both qualify and quantify the significance of this mobile, filter-feeding competitor to unionid populations, particularly in rivers experiencing reduced recruitment and low standing stocks of native mussels. The chronic decline in recruitment within unionid populations in many streams and rivers of the eastern US, and the continued proliferation of Asian clam populations in many of the same waterways, may not be coincidental.

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