Hydrobiologia (2021) 848:311–320
https://doi.org/10.1007/s10750-020-04436-2

PRIMARY RESEARCH PAPER

Demographic characteristics of young-of-year freshwater mussel populations in ponds

Wendell R. Haag · James A. Stoeckel

Received: 26 May 2020 / Revised: 22 September 2020 / Accepted: 8 October 2020 / Published online: 27 October 2020

Abstract We describe demographics of young-of-year (YOY) Pondmussels (*Ligumia subrostrata*) and Giant Floaters (*Pyganodon grandis*) in ponds during 2009 and 2011. YOY attained large size by approximately 6 months (Pondmussel, mean = 48.5 mm; Floater = 57.5), most individuals were sexually mature, and most females were gravid. Size and sex ratios varied among ponds. Pondmussel size was negatively related to mussel density, suggesting food competition; Floater size was not related to density. Size was not related to glochidial infestation pressure on fishes, suggesting that acquired immunity did not affect YOY performance. The percentage of gravid female Pondmussels varied between years from 27 to 100%, and 91% of female Floaters were gravid in 2011. Mean fecundity was high (Pondmussel = 34,311; Floater = 38,873). The proportion of gravid females and mean fecundity were not related to male density, showing that fertilization was efficient. Variation in size, sex ratios, and gravidity among ponds suggests that small differences in environmental conditions or demographic stochasticity can have large effects on populations. Rapid growth, early maturity, efficient fertilization, and high fecundity of YOY are contrary to traditional views of mussel life history, but these traits may allow Pondmussels and Floaters to rapidly colonize disturbed, unstable habitats.

Keywords Unionidae · Life history · Juveniles · Recruitment · Growth

Introduction

Factors affecting animals early in their life can have lasting effects on individual performance and population structure. Competition for food among filter-feeding bivalves can result in reduced growth (Eldridge et al., 1979), which in turn may delay sexual maturity or growth beyond a size vulnerable to predation. Female freshwater mussels (order Unionoida) fertilize eggs by filtering sperm from the water, and low male density or removal of sperm by other filter feeders both are proposed to influence fertilization and fecundity (Downing et al., 1993; Strayer, 1999). Freshwater mussels are unique among bivalves in having larvae (glochidia) that require a period as parasites on fishes, and host-parasite interactions also may influence subsequent juvenile performance. For

---

Handling editor: Manuel Lopes Lima

W. R. Haag (✉)
US Forest Service, Center for Bottomland Hardwoods Research, Frankfort, KY 40601, USA
e-mail: wendell.haag@usda.gov

J. A. Stoeckel
School of Fisheries, Aquaculture, and Aquatic Science, Auburn University, Auburn, AL 36849, USA

example, fishes exposed to high glochidial burdens can acquire partial immunity to subsequent glochidial infestation, which may influence juvenile mussel fitness after the parasitic stage (Dodd et al., 2006).

Virtually nothing is known about factors that affect mussels in their first year of life or the demographics of those populations in the wild. Juvenile mussels are rare in many wild populations, they are difficult to collect in large numbers and without size bias, and it can be difficult to determine their true age. Consequently, most information about juvenile growth or other traits is from a laboratory or hatchery environment (e.g., Carey et al., 2013). Information about juvenile demographics is important for understanding mussel life history and for conservation. Mussels are traditionally characterized as slow-growing, late-maturing organisms, but this generalization does not capture the breadth of life history diversity in the group (Haag, 2012). Similarly, mussel populations are assumed to recover slowly from anthropogenic or natural disturbance due to small post-disturbance population size, low levels of recruitment, and delayed juvenile maturity (Neves, 1993; Shea et al., 2013). Observations of juvenile demographics in the wild are necessary to evaluate these assumptions.

We previously conducted an experiment in ponds to evaluate the effect of host fish abundance on mussel recruitment (Haag & Stoeckel, 2015). That study produced large numbers of young-of-year (YOY) mussels of two species in a natural context in a series of ponds, and the experimental design allowed us to examine virtually the entire YOY populations. Here, we take advantage of this unique opportunity and report on the demographics of YOY mussel populations produced in that study. We examine variation in size, sex ratios, sexual maturity, and fecundity among species and ponds and how these traits were related to mussel density and glochidial infestation pressure on fishes.

Materials and methods

Experimental design

Our experimental design is summarized as follows; for additional details, see Haag & Stoeckel (2015). We conducted the study in twelve, 0.1-ha earthen ponds at the South Auburn Fisheries Research Station (SAFRS) near Auburn, Alabama, USA. All ponds were 56 × 18 m with average depth of about 1 m (maximum 2 m). Ponds were fed from a reservoir that lacks mussels, and water exited the ponds through a screened outlet. Prior to the experiments, we drained all ponds and allowed them to dry to reduce existing populations of aquatic organisms. We used 19 mm-mesh plastic netting and steel fence posts to cordon off a 12 × 18 m section at the end of each pond opposite the outflow, and experiments were conducted within this 216 m^2 area. We buried the netting about 0.15 m in the pond bottom to prevent escapement of fishes or mussels. This smaller enclosure allowed us to create desired conditions of fish and mussel density using fewer animals and facilitated greater sampling efficiency, but it also ensured high water quality because of circulation with the entire pond volume.

We used two mussel species in the experiments, the Pondmussel, *Ligumia subrostrata* (Say, 1831), and the Giant Floater, *Pyganodon grandis* (Say, 1829). Both species are characteristic members of mussel assemblages in lentic or lowland habitats in the southcentral U.S. We collected gravid females of both species in Lafayette County, Mississippi, in November and December to ensure that they were gravid but had not yet released glochidia. Mussels were held in ponds at SAFRS until initiation of the experiments; holding ponds were not used in the experiments. We used Bluegill (*Lepomis macrochirus* Rafinesque, 1810) as a host for mussels. Bluegill is a suitable host for both species and is easily maintained in ponds. We purchased Bluegills 8–15 cm total length (American Sportfish Hatchery, Montgomery, AL) to minimize variation in glochidial infection due to fish size.

Haag & Stoeckel (2015) evaluated how mussel recruitment and population growth were related to three factors: host abundance, mussel species identity, and interactions between mussel species. Four ponds were randomly assigned as “Pondmussel only”, four as “Floater only”, and four ponds as “Pondmussel + Floater”. In each pond were stocked 9–10 randomly selected gravid females of the indicated species; Pondmussel + Floater ponds received 9–10 individuals of each species. Within each set of four ponds, ponds were randomly assigned to one of four host abundances: 10, 50, 200, and 500 fish. These abundances corresponded to about 1, 5, 20, and 50 host fishes/female mussel, respectively, and fish densities ranging from 463 (10 fish) to 23,148 (500 fish) fish/ha.

Haag & Stoeckel (2015) evaluated relationships between mussel recruitment, host abundance, and species identify with a full factorial experimental design. In this study, we were interested in more general characteristics of YOY populations unrelated to the factors evaluated by Haag & Stoeckel (2015) (see "Data analysis" section).

We conducted the experiment in 2009 and repeated it in 2011. In both years, we stocked Bluegill from mid-December to early January and we stocked mussels about 2 weeks later. We supplemented the natural forage base for Bluegill with commercial fish food, fed three times weekly throughout the experiment. We terminated experiments in November so that YOY mussels were near maximum size for the year. Because we did not initially know the size range of YOY individuals, in 2009 we sampled up to 20 randomly selected 0.25-m^2 quadrats with a suction dredge from the first few ponds and processed all material across a graduated series of sieves (minimum mesh size = 2.5 mm). We found no individuals < 28 mm length, a size that is easily detected by hand sampling, and we sampled all remaining ponds in 2009 and all ponds in 2011 by feeling through the substrate with our hands. We found few dead YOY mussels by hand sampling ($< 1\%$). In both years, we drained the ponds after the initial November sampling to retrieve remaining mussels. We allowed ponds to remain dry until July of the following year and searched the pond bottoms approximately monthly during this time. Most remaining mussels were recovered by the end of January, but living individuals were found in dewatered pond sediment as late as March, and dead shells were recovered until June. We observed minimal evidence of predation on mussels (e.g., shells broken or placed on shore by muskrats, otters, or other predators) during or after the experiment, and because of the lengthy period of sampling after draining the ponds, we assumed that total counts of YOY mussels recovered from ponds (live and dead individuals combined) represented absolute levels of recruitment during the experiment.

Characterization of YOY mussel populations

We measured the size of all YOY mussels retrieved from each pond (total length, nearest 0.1 mm). In both years, we returned to the laboratory a subsample of up to 60 live individuals retrieved during initial pond sampling in November. In 2009, we examined subsamples of both species for gravidity, and we determined the sex of all subsampled Pondmussels based on shell and gill morphology; we did not sex Floaters because the shell and gills are not obviously sexually dimorphic. In 2011, we examined gonadal tissue of all subsampled individuals and the gills of mature females. From this, we estimated in each pond the percentage of sexually mature individuals, sex ratios of mature individuals, the percentage of females that were gravid, and mean fecundity of gravid females in each pond. We recognized sexually mature individuals by the presence of large gonads organized in distinct lobes; immature individuals had clear, granular, and undifferentiated gonadal tissue. We identified females by the presence of oocytes and males by the presence of creamy-white, fine-textured testes (Haag & Staton, 2003; Saha & Layzer, 2008). Gravid females had glochidia or embryos in the gills, which were distended to various degrees; non-gravid females had empty, flaccid gills. We report data on maturity, sex ratios, gravidity, and fecundity only from ponds with ≥ 10 individuals.

Data analysis

We combined results of the 2009 and 2011 experiments for analysis of YOY size because size did not differ according to year for either species (see "Results" section). We omitted ponds with ≤ 5 individuals (8 out of 24 ponds) from analyses involving size because we could not obtain meaningful estimates of mean size in those ponds. We examined differences in YOY size between species and years using a two-factor analysis of variance with log-transformed mean length in each pond as the response variable and species and year as fixed class variables ($N = 20$ observations from 16 ponds; Pondmussel + Floater ponds had observations for both species). We tested sex ratios in each pond for deviations from 1:1 using G-tests with Williams's correction and the Benjamini–Hochberg procedure for multiple testing.

We examined potential effects of glochidial infestation pressure on fishes and overall mussel density on YOY size. We were not able to directly measure glochidial burdens on fishes during the experiment. Instead, we used the estimated total number of glochidia produced by adult mussels stocked in a particular pond/the number of fish in that pond as a measure of the infestation pressure on fishes. Our assumption was that higher infestation pressure represents greater potential for acquired immunity or other effects of high glochidial burdens on host fishes. For mixed-species ponds, we used the total number of glochidia produced by both species. We estimated glochidial production based on the mean size of adult mussels stocked in each pond and existing length-fecundity relationships for each species (Haag, 2013; Haag & Stoeckel, 2015). For mussel density, we used the number of YOY mussels in each pond, and we summed the numbers of YOY for both species in mixed-species ponds to reflect total bivalve density. We examined potential effects of infestation pressure and mussel density on YOY size with a two-factor general linear model, with mean YOY size in each pond as the dependent variable and infestation pressure and mussel density as continuous independent variables (all three variables log-transformed). We performed a separate model for each species because an initial ANCOVA model of the effect of YOY density on size while accounting for differences in mean size between the two species had a marginally significant interaction term (density × species, $F_{1,16} = 3.19$, $P = 0.093$), suggesting that the slopes of the relationships for the two species differed.

Fig. 1 Young-of-year Pondmussels and Giant Floaters retrieved from experimental ponds in November, 2009. Note calipers for scale

Results

YOY individuals reached a large size by the end of their first growing season (Fig. 1). Across all individuals (both years and all ponds), Pondmussels averaged 48.5 mm (± 6.7 SD, range = 28.1–69.5 mm) and Floaters averaged 57.5 mm (± 9.0, range = 35.1–87.5; Fig. 2). Assuming a growing season of 184 days (see "Discussion" section), instantaneous growth was 0.028/day (as mm) for Pondmussels and 0.027/day for Floaters (based on initial glochidial lengths of 0.270 and 0.375 mm, respectively, Barnhart et al., 2008; Pondmussel and Floater glochidia do not grow on fishes, so glochidial size closely approximates the size of newly metamorphosed juveniles). There was no difference in mean size in ponds between years ($F_{1,16} = 0.82$, $P = 0.379$) and no significant year × species interaction ($F_{1,16} = 0.01$, $P = 0.928$), but mean size of Floaters was significantly larger than Pondmussels ($F_{1,16} = 6.49$, $P = 0.022$). Mean size differed significantly among ponds for both species (Pondmussel: $F_{10,341} = 30.79$, $P < 0.0001$; Floater: $F_{8,421} = 17.05$, $P < 0.0001$; Fig. 3). Pondmussel size was more variable among ponds than for Floaters: there were more pairwise differences among ponds for Pondmussels, and Pondmussel mean size spanned a greater range among ponds (42.2–64.8 mm; Floaters = 48.3–60.5).

For Pondmussels, there was no significant effect of the infestation pressure × mussel density interaction on YOY size ($F_{1,7} = 0.17$, $P = 0.693$). A reduced model omitting the interaction term showed no significant effect of infestation pressure ($F_{1,8} = 1.37$, $P = 0.275$), but there was a significant, negative effect of mussel density ($F_{1,8} = 6.78$, $P = 0.031$). The best fitting regression model of the relationship between mussel density and YOY size explained about half of the variation in YOY size and was curvilinear, depicting a sharp decline in size at mussel densities as low as 0.2–0.5/m^2 (Fig. 4). For Floaters, there was no significant effect of the infestation pressure × mussel density interaction on YOY size ($F_{1,5} = 0.03$, $P = 0.876$), and a reduced model omitting the interaction term showed no significant effects of infestation pressure ($F_{1,6} = 2.90$, $P = 0.140$) or mussel density ($F_{1,6} = 0.02$, $P = 0.887$).

In 2011, nearly all YOY mussels of both species were sexually mature. All Pondmussels examined ($N = 238$) were mature and had well differentiated

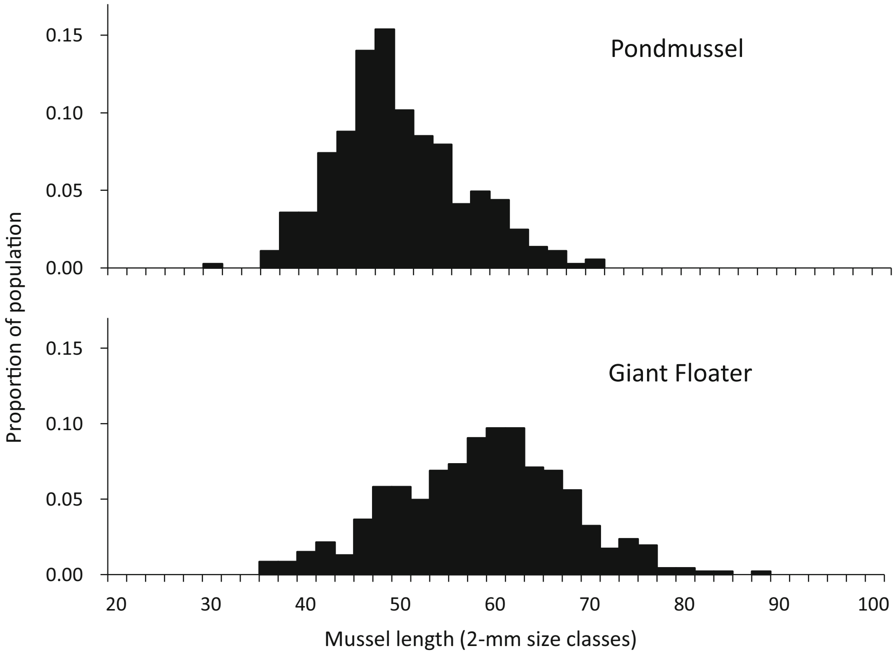


Fig. 2 Distribution of sizes of young-of-year Pondmussels and Giant Floaters across all ponds and both years ($N = 11$ ponds for Pondmussels, $N = 9$ ponds for Floaters)

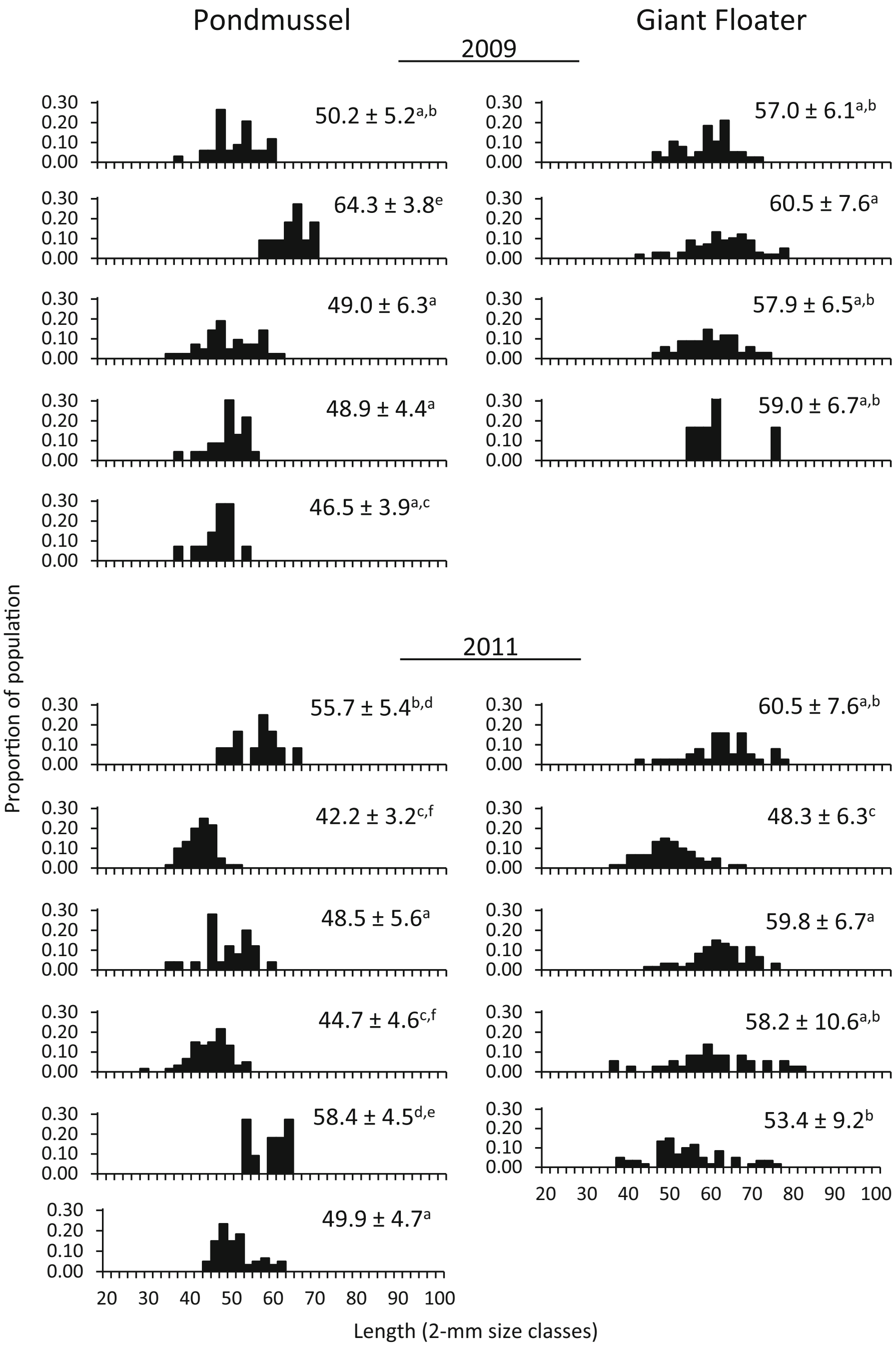
gonads. All Floaters examined ($N = 293$) were mature and had well differentiated gonads except for a single individual in which we were unable to find recognizable gonadal tissue. Sex ratios for both species were close to 1:1 on average (mean proportion of females, Pondmussel = 0.60, Floater = 0.49), but sex ratios varied widely among ponds (Fig. 5). Three Pondmussel populations were significantly female-biased, and one was significantly male-biased. For Floaters, one population was female-biased, and one was male-biased.

The proportion of females that were gravid was highly variable among years and species (Fig. 5). In 2009, all female Pondmussels examined were gravid in all ponds, but in 2011 the mean proportion of gravid females was only 0.27 and the proportion varied among ponds from 0.00 to 0.53. The mean proportion of gravid female Floaters in 2011 was 0.91 and varied among ponds from 0.67 to 1.00. In 2009, 17–50% of all Floaters we examined (females and males combined) were gravid, but we did not determine the sex of all individuals.

Size of YOY Pondmussels did not differ between gravid and non-gravid females when variation in size among ponds was taken into account [nested ANOVA: gravidity, $F_{1,140} = 0.72$, $P = 0.398$; pond(gravidity), $F_{12,140} = 14.30$, $P < 0.001$; mean size, gravid = 44.6 mm, not gravid = 46.8]. For Floaters, mean size of gravid females was significantly larger than non-gravid females, but sums of squares indicated a larger effect of among-pond variation [gravidity, $F_{1,124} = 5.96$, $P = 0.016$; pond(gravidity), $F_{10,124} = 8.67$, $P < 0.001$; mean size, gravid = 61.0 mm, not gravid = 51.6], and the range of sizes for gravid and non-gravid females among all individuals overlapped widely (Fig. 6). In 2011, there was no relationship between the proportion of gravid females and male YOY density for either species (Pondmussels: $F_{1,5} = 0.1.68$, $P = 0.252$; Floaters: $F_{1,5} = 2.53$, $P = 0.187$; arcsine-transformed proportions; Fig. 7). Similarly, there was no relationship between the proportion of gravid females and the male/female ratio (Pondmussel: $F_{1,5} = 0.23$, $P = 0.653$; Floater: $F_{1,5} = 4.30$, $P = 0.107$).

Mean fecundity across all examined individuals was similar between species (Pondmussel = 34,311; Floater = 38,873), but fecundity was more variable for Floaters (Pondmussels, range = 12,500–56,700; Floaters = 3,750–147,000). Fecundity was positively related to length for both species, but it explained relatively little of the variation in fecundity due to the narrow range of lengths represented [Pondmussels: log fecundity = 2.595(log length) + 0.169, $R^2 = 0.329$, $P < 0.001$; Floaters: log fecundity = 3.697(log

Fig. 3 Variation in size of young-of-year Pondmussels and Giant Floaters among ponds. Each panel represents a single pond. Mean mussel size (mm ± SD) is shown for each pond; within each species, values with the same superscripted letter are not significantly different ($P < 0.05$, Tukey's HSD)



length) + 2.170, $R^2 = 0.506$, $P < 0.0001$]. Male density was not significantly related to fecundity for either species (Fig. 7). The interaction between male density and YOY size was not a significant factor for either species (Pondmussels: $F_{1,2} = 0.25$, $P = 0.669$; Floaters: $F_{1,2} = 0.01$, $P = 0.9476$), and this term was dropped from the models. For Pondmussels, there was no relationship between fecundity and male density ($F_{1,5} = 0.13$, $P = 0.774$). For Floaters, there appeared to be a decline in fecundity with increasing male density (Fig. 7), but this was due to differences in mean YOY size among ponds, and male density was not a significant factor ($F_{1,5} = 1.77$, $P = 0.276$). Similarly, there was no relationship between fecundity and the male/female ratio (Pondmussel: $F_{1,5} = 0.73$, $P = 0.431$; Floater: $F_{1,5} = 0.39$, $P = 0.566$).

Discussion

We were surprised by the large size attained by YOY mussels in our study by the end of their first growing season. We do not know the precise age of our mussels at the end of the growing season, other than the fact that mussels recruited during the year of the experiment. Mussels were stocked in ponds in January, but at the study latitude, Pondmussels and Floaters typically release glochidia and infect fishes in February or March (WRH and JAS, unpublished observations). Assuming that juvenile mussels metamorphosed and dropped off of fishes by May 1, they would be about

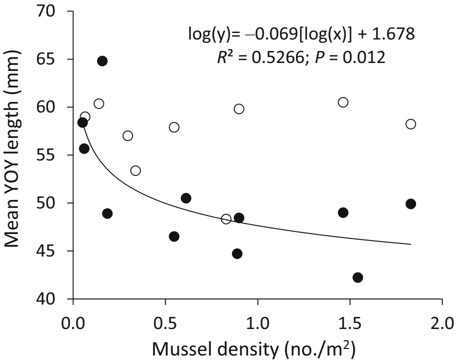


Fig. 4 Relationship between young-of-year (YOY) mussel mean size and total YOY mussel density (both species combined) in ponds. Solid circles are Pondmussels and open circles are Floaters. The regression line is for Pondmussels; there was no significant relationship for Floaters. The regression equation is based on the number of mussels in a pond, but the x-axis is depicted here as number of mussels/m^2 (based on the experimental pond area of 216 m^2) for illustrative purposes

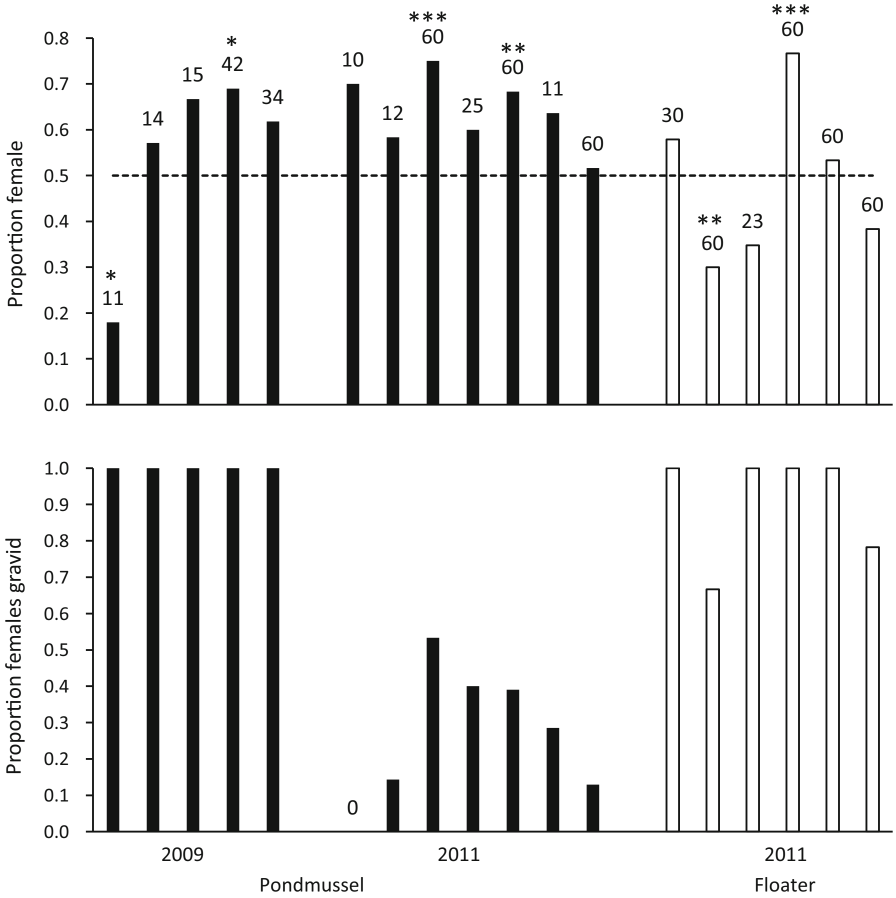


Fig. 5 Sex ratios and proportion of gravid females for young-of-year mussels in ponds. Each bar represents a single pond. Number of mussels examined in each pond is indicated on the upper panel. The dashed line on the upper panel represents a 1:1 sex ratio. Ponds in which the sex ratio deviated significantly from 1:1 are indicated by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; all P values are significant based on the Benjamini–Hochberg procedure for multiple testing with a false discovery rate of 10%)

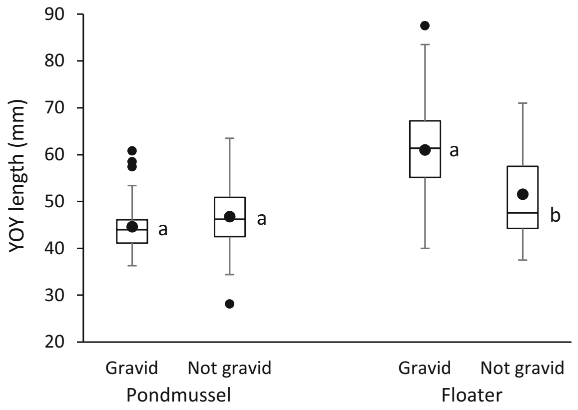


Fig. 6 Sizes of gravid and non-gravid young-of-year (YOY) mussels in ponds. Boxes represent the first and third quartiles, points within boxes are the mean, lines within boxes are the median, whiskers are 1.5 interquartile ranges, and points beyond the whiskers are observations beyond the 1.5 interquartile ranges. Within each species, means with different letters are significantly different ($P < 0.05$, see text)

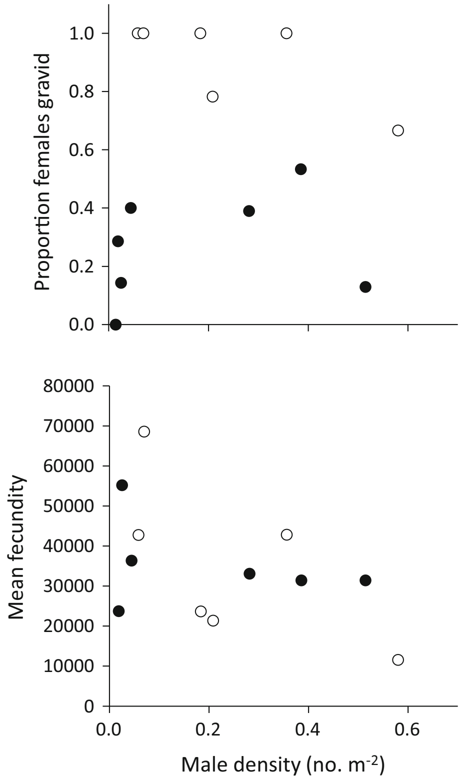


Fig. 7 Relationships of female gravidity and mean fecundity and male density for young-of-year mussels in ponds. Solid circles are Pondmussels and open circles are Floaters

6 months old by November, when we terminated the experiment.

Previous studies of juvenile mussel growth in the wild report maximum lengths of < 15 mm by the end of the first growing season, with isolated estimates as high as 31 mm (Neves & Widlak, 1987; Haag & Warren, 2010; Jones & Neves, 2011). The mean and maximum sizes we observed are 3–4 × higher than these reports. Instantaneous growth of YOY *Lampsilis cardium* Rafinesque, 1820 in 23 Kentucky streams averaged 0.008/d (as mm, range ≤ 0.001–0.015; Haag et al., 2019), which is about 3.5 × lower than our values. Some of these reports are from a similar latitude as our study (Haag & Warren, 2010), which does not support a climate explanation for the high growth we observed. Most previous reports are from riverine environments or riverine species that exhibit low to moderate growth characteristic of equilibrium or periodic life history strategies (Haag, 2012). Pondmussels and Floaters are considered opportunistic life history strategists for which rapid individual growth is a characteristic trait. Furthermore, our ponds were eutrophic and highly productive, which doubtless contributed to high mussel growth rates (see Gascho Landis et al., 2013).

Even more surprising than rapid growth was the observation that most individuals were sexually mature by the end of the first growing season. Age at maturity in freshwater mussels usually occurs at age 1–7, depending on the species, but maturity of YOY individuals is reported for several species (reviewed by Haag, 2012). However, most reports of sexual maturity of YOY or age-1 individuals either were isolated observations of larger, mature individuals within cohorts of otherwise immature individuals or they were based on incomplete demographic sampling. Our study is the first that we know of to show a high incidence of YOY maturity representative of a population-level attribute. The lack of or weak relationship between size and maturity shows that maturity was a general characteristic of the cohort and was not restricted to larger individuals. Mean fecundity of YOY Pondmussels (34,311) was about 46% of mean adult fecundity (74,000, Haag, 2013), and fecundity of YOY Floaters (38,873) was about 10% of adult fecundity (> 400,000). Nevertheless, glochidial production by YOY individuals represented substantial reproductive potential and investment.

Mussel size varied substantially among ponds for both species, but size did not differ among years. This suggests that small-scale variation in physical conditions among ponds was more important than larger-scale, climatic variation among years. Our ponds were of identical size and construction and received water from a common source, which further suggests that subtle differences in physical or biotic factors can have measurable effects on mussel growth. We do not have comprehensive physical or biological measurements from our ponds, but mean water temperature in 2009 was similar in the two ponds most distant from each other (28.2°C ± 4.4 SD and 28.6° ± 4.2; based on hourly measurements, May–November). Genetic traits of adult mussels stocked in ponds at the beginning of the experiment also could have affected YOY size. We were unable to measure the contribution of each adult mussel to the YOY cohort, but unequal reproductive success among adults, coupled with the small size of the adult founder group, could have resulted in YOY populations dominated by individuals having traits for lower or higher growth.

Mussel density in the ponds also may have influenced growth. The negative relationship between Pondmussel size and mussel density raises the interesting possibility of competition for food or other resources. Most direct evidence for food competition among bivalves is associated with very high bivalve densities (Eldridge et al., 1979; reviewed by Strayer, 2008). It is difficult to imagine food competition in our highly productive ponds, particularly given that our results suggest such interactions at overall densities as low as 0.2–0.5/m^2. However, YOY mussels, particularly Pondmussels, were highly aggregated in localized areas along the shore and against the netting that demarcated the experimental portion of the pond. These higher-density aggregations could have produced localized zones of food depletion, which are especially likely in shallow, imperfectly mixed lentic environments such as our ponds (Strayer, 2008). Floater size was not related to mussel density. We did not quantify aggregation of Pondmussels and Floaters, but differences in spatial distribution between species may influence the potential for food competition.

Other variation in demographic characteristics of YOY mussel populations showed little relationship to the factors we measured. There was no apparent effect of fish infestation pressure on YOY size. This is similar to the lack of evidence for effects of acquired immunity on mussel recruitment in our ponds (Haag & Stoeckel, 2015), but we were unable to directly measure the intensity of infection on host fishes. The much lower proportion of gravid female Pondmussels in 2011 compared with 2009 was not related to female size or male density, and the reasons for this difference are unknown. The lack of relationship between male density and female gravidity or fecundity is particularly noteworthy because it does not support previous ideas about the importance of high mussel density for fertilization success (Downing et al., 1993). Instead, our results support other evidence showing that efficient egg fertilization can occur even in sparse populations (Moles & Layzer, 2008; Mosley et al., 2014). Overall, high variation among ponds in YOY size, sex ratios, and fertilization illustrates the extent to which stochastic factors may influence populations at small scales.

Our results show that some species depart substantially from the traditional view of mussel life history, which generally assumes slow individual growth, late maturity, and low population growth. A more recent view proposed that faster individual growth and earlier maturity of opportunistic life history strategists can allow high population growth for those species (Haag, 2012). Our results support this view and emphasize the great extent to which life history traits can vary among mussel species, which precludes broad life history generalizations. Production of YOY populations in our ponds from small founding populations (9–10 adult females) represented exceptionally high population growth (λ as high as 34.3/year; Haag & Stoeckel, 2015). Rapid individual growth, early maturity, efficient fertilization, and high fecundity of YOY individuals indicates the potential for continued exponential population growth from a small founder group. Pondmussels and Floaters often occur in disturbed, unstable habitats, and their life history traits appear well-adapted for allowing them to rapidly colonize such environments.

Acknowledgements We thank S. Nichols and M. Hart, who assisted with all aspects of the experiments. We also thank the following people for their various contributions to the study: M. Bland, A. Commens-Carson, D. Foree, A. Gascho Landis, R. Kennedy, T. Mosley, G. Moyer, I. Palmer, N. Rankin, B. Staton, and M. Warren. This study was supported by the U.S. Forest Service, Southern Research Station, the Alabama Agricultural Experiment Station, and the Hatch program of the National

Institute of Food and Agriculture, U.S. Department of Agriculture.

References

Barnhart, C. E., W. R. Haag & W. Roston, 2008. Adaptations to larval parasitism in the Unionoida. Journal of the North American Benthological Society 27: 370–394.

Carey, C. S., J. W. Jones, E. M. Hallerman & R. S. Butler, 2013. Determining optimum temperature for growth and survival of laboratory-propagated juvenile freshwater mussels. North American Journal of Aquaculture 75: 532–542.

Dodd, B. J., M. C. Barnhart, C. L. Rogers-Lowery, T. B. Fobian & R. V. Dimock, 2006. Persistence of host response against glochidia larvae in *Micropterus salmoides*. Fish and Shellfish Immunology 21: 473–484.

Downing, J. A., Y. Rochon, M. Pérusse & H. Harvey, 1993. Spatial aggregation, body size, and reproductive success in the freshwater mussel *Elliptio complanata*. Journal of the North American Benthological Society 12: 148–156.

Eldridge, P. J., A. G. Eversole & J. M. Whetstone, 1979. Comparative survival and growth rates of hard clams, *Mercenaria mercenaria*, planted in trays subtidally and intertidally at varying densities in a South Carolina estuary. Proceedings of the National Shellfish Association 69: 30–39.

Gascho-Landis, A. M., W. R. Haag & J. A. Stoeckel, 2013. High suspended solids as a factor in reproductive failure of a freshwater mussel. Freshwater Science 32: 70–81.

Haag, W. R., 2012. North American Freshwater Mussels: Natural History, Ecology, and Conservation. Cambridge University Press, Cambridge.

Haag, W. R., 2013. The role of fecundity and reproductive effort in defining life history strategies of North American freshwater mussels. Biological Reviews 88: 745–766.

Haag, W. R. & J. L. Staton, 2003. Variation in fecundity and other reproductive traits in freshwater mussels. Freshwater Biology 48: 2118–2130.

Haag, W. R. & J. A. Stoeckel, 2015. The role of host abundance in regulating populations of freshwater mussels with parasitic larvae. Oecologia 178: 1159–1168.

Haag, W. R. & M. L. Warren, 2010. Diversity, abundance, and size structure of bivalve assemblages in the Sipsey River, Alabama. Aquatic Conservation: Marine and Freshwater Ecosystems 20: 655–667.

Haag, W. R., J. J. Culp, M. A. McGregor, R. Bringolf & J. A. Stoeckel, 2019. Growth and survival of juvenile freshwater mussels in streams: implications for understanding enigmatic mussel declines. Freshwater Science 38: 753–770.

Jones, J. W. & R. J. Neves, 2011. Influence of life-history variation on demographic responses of three freshwater mussel species (Bivalvia: Unionidae) in the Clinch River, USA. Aquatic Conservation: Marine and Freshwater Ecosystems 21: 57–73.

Moles, K. R. & J. B. Layzer, 2008. Reproductive ecology of *Actinonaias ligamentina* (Bivalvia: Unionidae) in a regulated river. Journal of the North American Benthological Society 27: 212–222.

Mosley, T. L., W. R. Haag & J. A. Stoeckel, 2014. Egg fertilisation in a freshwater mussel: effects of distance, flow, and male density. Freshwater Biology 59: 2137–2149.

Neves, R.J., 1993. A state-of-the-unionids address. In K.S. Cummings, A.C. Buchanan & L.M. Koch (eds), Conservation and Management of Freshwater Mussels. Proceedings of the Upper Mississippi River Conservation Commission Symposium, Rock Island, IL: 1–10.

Neves, R. J. & J. C. Widlak, 1987. Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. American Malacological Bulletin 5: 1–7.

Saha, S. & J. B. Layzer, 2008. Evaluation of a nonlethal technique for determining sex of freshwater mussels. Journal of the North American Benthological Society 27: 84–89.

Shea, C. P., J. T. Peterson, M. J. Conroy & J. M. Wisniewski, 2013. Evaluating the influence of land use, drought and reach isolation on the occurrence of freshwater mussel species in the lower Flint River Basin, Georgia (U.S.A.). Freshwater Biology 58: 382–395.

Strayer, D. L., 1999. Effects of alien species on freshwater mollusks in North America. Journal of the North American Benthological Society 18: 74–98.

Strayer, D. L., 2008. Freshwater Mussel Ecology: A Multifactor Approach to Distribution and Abundance. University of California Press, Berkeley.