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Seasonal and species-specific patterns in abundance of freshwater mussel glochidia in stream drift

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Abstract. We examined seasonal patterns of abundance of mussel larvae (glochidia) in stream drift in a diverse, large-stream mussel assemblage in the Sipsey River, Alabama, across 1 y. We used recently developed techniques for glochidial identification combined with information about mussel fecundity and benthic assemblages to evaluate how well observed glochidial abundance corresponded to expected abundance based on glochidial production. Glochidia from short-term brooding species (*Amblema plicata*, *Elliptio arca*, *Fusconaia cerina*, *Pleurobema decisum*, *Obliquaria reflexa*, and *Quadrula asperata*) were abundant from May to August but did not occur in drift between November and the end of April. Long-term brooders (*Lampsilis* spp., *Medionidus acutissimus*, *Obovaria unicolor*, and *Villosa* spp.) occurred in several short peaks in spring, summer, and autumn, but generally were less abundant than short-term brooders. We estimated that the benthic assemblage at our study site produced >500,000 glochidia/m² annually and production varied widely among species. Abundance of species in the drift was positively related to benthic abundance but was only weakly related to glochidial production. The poor relationship between glochidial production and abundance in the drift suggests that release and transport of glochidia are influenced by a wide variety of abiotic and biotic factors.

Key words: drift, glochidia, reproduction, host strategy, broadcasting, fecundity, life history, Unionidae.

Adult freshwater mussels (families Unionidae and Margaritiferidae) are benthic, largely sedentary organisms for which dispersal occurs primarily during the larval stage. Larvae (glochidia) are brooded by female mussels for variable lengths of time that generally correspond to either a short-term or a long-term brooding strategy. Among short-term brooders, eggs usually are fertilized in spring or early summer, and glochidia are brooded for ~2 to 6 wk and then released (Weaver et al. 1991, Bruenderman and Neves 1993, Garner et al. 1999). Among long-term

brooders, eggs usually are fertilized in late summer or autumn, and glochidia are brooded for an extended period, usually over the winter, and released primarily in the spring or summer. However, a low level of release may occur over much of the year (Zale and Neves 1982, Watters and O'Dee 2000). Glochidia of most species are obligate ectoparasites on fishes and must encounter a suitable host fish soon after release from the female. Fish-host specificity varies widely among mussel species, which range from generalists that parasitize a wide array of fish species to specialists that can parasitize only a few closely related species (Haag and Warren 1997). Dispersal occurs primarily while glochidia are encysted on host fishes but also may occur to some extent as glochidia drift in stream currents (Schwalb et al. 2010).

Glochidia are found commonly in stream drift (Neves and Widlak 1988), but the ecological role of these individuals is poorly understood. Some mussel species are thought to be glochidial broadcasters for

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which host infection is dependent on passive, chance encounters between fishes and drifting glochidia, but this strategy is well documented for few species (Murphy 1942, Davenport and Warmuth 1965, Young and Williams 1984). In contrast, many mussel species have behavioral or anatomical adaptations that actively attract and infect specific fish species, thereby increasing chances of host–fish encounters and reducing glochidial loss through indiscriminant parasitization of unsuitable host species (Haag and Warren 2000, Barnhart et al. 2008). For these species, it is not known whether drifting glochidia represent an alternate, passive strategy for host infection or glochidia enter the drift after failed host encounters and, therefore, represent lost reproductive effort (i.e., glochidial larvae with no chance of metamorphosis into benthic juveniles). The importance of glochidial drift as a dispersal mechanism also is poorly known (Jansen et al. 2001, Schwalb et al. 2010).

Patterns of glochidial abundance in stream drift, especially in diverse assemblages of species with an array of life histories, potentially could provide information about host-infection strategies and other aspects of mussel reproductive ecology. Seasonal patterns of glochidial drift and their relationship to brooding strategies have been described previously in several streams (Zale and Neves 1982, Neves and Widlak 1988, Weaver et al. 1991, Hove and Neves 1994). However, these studies were limited to assemblages with low mussel diversity, or investigators were unable to examine species-specific patterns in abundance because of the difficulty of identifying species with similar glochidia. Nonseasonal factors that influence glochidial abundance in the drift have been examined in only one study, in which abundance of glochidia in the drift was strongly correlated with abundance of benthic adults across several sites (McLain and Ross 2005).

We used recently developed techniques for glochidial identification combined with information about benthic abundance and mussel fecundity to examine species-specific patterns of glochidial drift in a diverse, large-stream mussel assemblage. First, we described seasonal patterns of glochidial abundance and how these patterns differed among species. Second, we tested the hypothesis that glochidia of each species would be present in the drift in proportion to the abundances of species in the benthic assemblage. Third, because fecundity varies greatly among mussel species, we tested the hypothesis that glochidia would be present in the drift in proportion to total glochidial production by each species in the assemblage. We expected that this 2nd null hypothesis would be supported if all species released glochidia in

a similar fashion, but that interspecific differences in release behaviors and other potential factors would result in deviations from these expectations.

Study Area

The Sipsey River is a 5th-order tributary of the Tombigbee River in west-central Alabama (USA). The Sipsey River is relatively unaltered physically (Benke 1990) and supports a diverse aquatic community including >80 fish species (Boschung 1989) and one of the most intact large-stream mussel assemblages in the Mobile Basin (McCullagh et al. 2002). Our study site was an ~100-m-long reach in the lower 1/3 of the river (lat 33°05'08"N, long 87°57'37"W). The site was in a long riffle/run complex with predominantly gravel substrate and depths generally <1.5 m. Forty-two mussel species are known from the river (McCullagh et al. 2002), but only ~23 species occur commonly in the vicinity of our study site (Haag and Warren 2010).

Methods

Field sampling

We established 4 permanent sampling points in the thalweg of the study reach. On each sampling date, we placed a single drift net with detachable sample bucket (both 100- μ m mesh size, net opening = 307 \times 457 mm) at each sampling point and collected stream drift for 30 min between 1000 and 1500 h. In previous studies, glochidia were most likely to be present in drift during this time period and were least abundant at night (Neves and Widlak 1988, Bruenderman and Neves 1993). We measured water velocity and depth at the mouth of each net and later calculated the volume of water sampled (m³). We also measured water temperature in the study reach on each sampling date. We stained samples in the field with phloxine B and returned them to the laboratory. Sampling spanned 1 full y from May 2004 to April 2005. Most mussel species in the Sipsey River release glochidia in late spring and summer (Haag and Warren 2003), so we sampled approximately weekly from May to August and twice monthly for the rest of the year.

Laboratory procedures

We rinsed each sample over a 1-mm and a 100- μ m sieve to remove debris and preserved the material in 95% ethanol. We subsampled 16% of the total volume of each sample and counted and measured all glochidia in each subsample under a dissecting microscope equipped with a digital camera and video-imaging software. We measured length, height,

TABLE 1. Identifications of glochidia captured in drift samples from the Sipsey River, Alabama. A dash (–) indicates that these species were not considered in these or further analyses because of low sample sizes. The numbers 1 and 2 following *Pleurobema decisum* refer to 2 glochidial morphotypes present in the population (see Kennedy and Haag 2005). DFA = Discriminant function analysis, CI = confidence interval.

Species	Total no. glochidia identified by DFA	Mean probability of correct identification	Estimated no. of glochidia identified correctly (95% CI)
<i>Amblema plicata</i>	140	0.6251	87 (76–98)
<i>Elliptio arca</i>	130	0.7240	94 (85–103)
<i>Fusconaia cerina</i>	532	0.9278	494 (483–503)
<i>Hamiota perovalis</i>	2	–	–
<i>Lampsilis ornata</i>	28	0.6689	19 (14–23)
<i>Lampsilis straminea</i>	11	0.5945	7 (3–9)
<i>Lampsilis teres</i>	47	0.8430	40 (35–44)
<i>Medionidus acutissimus</i>	58	0.7847	46 (40–51)
<i>Obliquaria reflexa</i>	78	0.6591	51 (44–59)
<i>Obovaria unicolor</i>	34	0.8105	28 (23–31)
<i>Pleurobema decisum</i> 1	185	0.9224	171 (164–177)
<i>Pleurobema decisum</i> 2	75	0.7385	55 (48–62)
<i>Potamilus purpuratus</i>	1	–	–
<i>Quadrula asperata</i>	121	0.8876	107 (101–113)
<i>Villosa lienosa</i>	11	0.8394	9 (7–11)
<i>Villosa vibex</i>	2	–	–

and hinge length of each glochidium to the nearest 1 μm (Kennedy and Haag 2005).

Data analysis

We used Discriminant Function Analysis (DFA) to identify each glochidium to species based on shell measurements. In previous work, we developed a library of quadratic discriminant functions for glochidia of all common species in the Sipsey River based on shell dimensions of glochidia taken directly from gravid female mussels (Kennedy and Haag 2005). We identified specimens collected in drift samples by assigning each glochidium to a species based on maximum probabilities of correct classification (SAS, version 8; SAS Institute, Cary, North Carolina; Khattree and Naik 2000). Probabilities of correct classification varied among specimens and species, so we dealt with uncertainty in identifications as follows. For each specimen, we generated a random integer (0 = incorrect classification, or 1 = correct classification) from a binomial distribution based on that specimen's maximum probability of correct classification. The sum of integers of all individuals within each species gave an estimate of the number of correctly classified specimens for that particular species. We repeated this procedure 10^4 times and computed bootstrapped 95% confidence intervals around the estimated number of correctly identified glochidia. For all species, narrow confidence intervals showed that estimates of the number of correctly classified glochidia were robust (Table 1). We con-

ducted all randomizations with the Resampling Stats add-in for MS Excel (version 3.0; Resampling Stats Inc., Arlington, Virginia). We then censored our data set by retaining only the estimated mean number of correctly identified glochidia for each species and excluding glochidia with low probabilities of correct classification. For example, DFA identified 130 specimens as *Elliptio arca*, but our randomization procedure indicated only 94 of these specimens were likely to have been identified correctly (see Table 1). Therefore, we excluded the 36 specimens that had the lowest probabilities of being classified correctly as *E. arca*.

We used this censored data set for all later analyses of patterns of glochidial abundance because it provided the most conservative estimate of the true number of glochidia of each species present in our samples. We also excluded from all further analysis species that were represented by <3 glochidia (see Table 1) and species that have glochidia too small to be captured by our nets (*Leptodea fragilis*, *Quadrula rumphiana*, *Quadrula verrucosa*, and *Truncilla donaciformis*). This latter group of species composed 12% of the mussel community at our study site. Two glochidial morphotypes of *Pleurobema decisum* are present in the Sipsey River (Kennedy and Haag 2005), and both were identified in our drift samples. We combined abundances of both morphotypes for the purposes of this paper. After censoring the data set in these ways, we had estimates of glochidial abundance for 12 species that represented >85% of total mussel abundance in benthic assemblages (see below). To

examine seasonal patterns of glochidial drift, we calculated mean abundance of each of these 12 species (no./10 m³) across our 4 sampling points on each sampling date.

We tested the hypothesis that glochidia of each species would be present in the drift in proportion to the abundance of species in the benthic mussel assemblage. We obtained estimates of benthic abundance from 3 sites at and upstream of the study site from sampling done in 1999 and 2000 (Haag and Warren 2010; Table 2). One site was in the same shoal complex where drift samples were taken, and the other 2 sites were in similar habitats ~3.0 and 8.5 km upstream, respectively. Briefly, benthic abundance estimates were made by sampling quadrats within randomly located transects perpendicular to the stream (Haag and Warren 2010). Site areas ranged from 823 to 1835 m², and total area sampled at each site ranged from 18.1 to 22.6 m² (145–181, 0.125–m² quadrats). Quadrats were sampled with a portable diver-operated suction dredge, and substrate samples were taken to shore and processed across a series of 3 sieves (smallest mesh = 2.5 mm). No abundance estimates at the study site were available for 2004–2005, but mussel abundance at other sites in this section of the Sipse River was stable between 1999 and 2005 (Haag 2002, WRH and M. L. Warren, US Forest Service, unpublished data).

Fecundity varies greatly among mussel species, so we also tested the hypothesis that glochidia would be present in the drift in proportion to total glochidial production by each species. We estimated annual glochidial production by multiplying the abundance of female benthic mussels by mean individual fecundity to yield numbers of glochidia produced by each species per 1 m² of stream bottom (Table 2). We obtained fecundity estimates from Haag and Staton (2003) and unpublished data (WRH). All estimates were based on specimens from the Sipse River in the vicinity of our study site. Based on these sources, we assumed equal sex ratios for all species except *Lampsilis ornata* (0.15♀:0.85♂) and *Quadrula asperata* (0.40♀:0.60♂). We had fecundity estimates for all 12 species in our censored data set (Table 2).

Glochidia in the drift can originate from areas upstream of the sample site as well as within the site itself (Schwalb et al. 2010). We accounted for potential multiple origins of glochidia as follows. We generated estimates of glochidial production at: 1) the study site only, 2) a composite assemblage consisting of the study site and the closest upstream site, based on mean species abundance across these 2 sites, and 3) a composite assemblage including all 3 sites. This spatial hierarchy allowed us to examine the potential

influence of long-distance transport of glochidia into the study area as opposed to glochidia that originated solely from the local assemblage.

We used linear regression to examine the relationships between benthic abundance, glochidial production, and mean monthly glochidial abundance of species in the drift. We tested these relationships separately at the study site only and for the 2 composite assemblages incorporating upstream sites. We log₁₀(*x*)-transformed all variables to satisfy requirements of homogeneity of variance because raw data were strongly right-skewed and variances were not normally distributed. We used mean monthly glochidial abundance of each species instead of the total number of glochidia collected to ensure that species that were present primarily during spring when sampling was more frequent were not overrepresented. Mean monthly abundance of each species was closely related to total abundance of glochidia collected during the study (monthly abundance = 0.0072[total abundance] – 0.0058; *R*² = 0.991, *F* = 1086.6, *p* < 0.0001).

We examined the relationship between glochidial abundance in the drift and glochidial production by testing how well the observed abundance of each species conformed to abundance expected under the null hypothesis that glochidia are present in proportion to glochidial production. We calculated the proportion of total glochidial production represented by each species (Table 2), then multiplied each proportion by the total number of glochidia collected (all species combined) to yield the number of glochidia of each species expected in our samples under the null hypothesis. We used a *G*-test for goodness of fit to test how well observed frequencies conformed to the expected frequencies under our null hypothesis.

Results

We collected a total of 1455 glochidia in drift nets during the study. Mean monthly glochidial abundance in the drift (all species combined) was 8.59 glochidia/10 m³. Highest overall glochidial abundances were observed on 28 May 2004 (27.62/10 m³) and 8 August 2004 (25.32/10 m³). We identified glochidia of 15 mussel species in the drift (Table 1). Our censoring procedure yielded a total of 1208 glochidia (12 species) that had a high likelihood of correct identification (83% of total; Table 1). Mean probability of correct identification of glochidia varied among species from 0.5945 to 0.9278. Nevertheless, the total number of glochidia identified by DFA was strongly correlated with the number of correctly

TABLE 2. Benthic abundance, glochidial production, and glochidial abundance in the drift for 12 species of freshwater mussels in the Sipsey River, Alabama. For benthic abundance, composite assemblage 1 is the mean abundance at the glochidia study site and the next upstream site; composite assemblage 2 is the mean for the study site and both upstream sites (see text). Estimates of glochidial production and expected glochidial abundance presented here are for the composite assemblage including all 3 sites. O = observed, E = expected.

Species	Benthic abundance (females, no./m ²)		Glochidial production (no./m ²)	Mean monthly glochidial abundance (no./10 m ³)		Log-likelihood ratio (O × ln(O/E))
	Study site	Composite 1		Composite 2	Expected	
<i>Amblyma plicata</i>	0.26	0.13	19528	0.29 (41)	0.59 (87)	65.45
<i>Eliptio arca</i>	0.90	1.10	176641	2.66 (374)	0.56 (94)	-129.81
<i>Fusconaia cerina</i>	1.00	1.36	59327	0.89 (125)	3.61 (494)	678.87
<i>Lampsilis ornata</i>	0.14	0.11	28741	0.43 (61)	0.28 (19)	-22.16
<i>Lampsilis straminea</i>	0.21	0.16	26505	0.40 (56)	0.08 (7)	-14.56
<i>Lampsilis teres</i>	0.05	0.04	12343	0.19 (26)	0.44 (40)	17.23
<i>Medionidus acutissimus</i>	0.93	0.83	19042	0.29 (40)	0.35 (46)	6.43
<i>Obliquaria reflexa</i>	0.73	0.41	9834	0.15 (21)	0.27 (51)	45.25
<i>Obovaria unicolor</i>	0.52	0.35	62326	0.94 (132)	0.19 (28)	-43.42
<i>Pleurobema decisum</i>	2.65	2.95	136222	2.05 (288)	1.56 (226)	-54.79
<i>Quadrula asperata</i>	1.89	1.38	16696	0.25 (35)	0.61 (107)	119.57
<i>Villosa lienosa</i>	0.07	0.06	4002	0.06 (9)	0.05 (9)	0.00
Totals	9.32	8.87	571207		8.59 (1208)	

identified glochidia ($r = 0.995, p < 0.001$) indicating that variation among species in the accuracy of identifications introduced little systematic bias into our data set.

Seasonal patterns

Glochidia of short-term brooders occurred abundantly in the drift from May through August, and glochidia of some species persisted in low numbers into October (Fig. 1A, B). Glochidia from short-term brooders were present only when temperatures were $\geq 20.6^\circ\text{C}$ but occurred most commonly between 22.0 and 27.8°C . Abundance of short-term brooders showed little synchrony among species within this period.

Glochidia of long-term brooders were less abundant overall than those of short-term brooders but appeared in several distinct, synchronous episodes over a longer time period and wider range of water temperatures (Fig. 1C, D). These glochidia were present during an extended period from May until early August (water temperature = 22.0 – 27.8°C), which was followed by a 1.5-mo interval during which no glochidia were present in the drift. A 2nd, shorter peak in abundance occurred throughout October and into early November (water temperature = 15.3 – 20.6°C). A 3rd peak occurred in April 2005 (water temperature = 17.1 – 18.1°C), but this peak may have represented the onset of an extended period of spring and summer drift, as observed in 2004.

Relationships between benthic abundance, glochidial production, and drift

Glochidial abundance in the drift was positively related to benthic abundance of species in assemblages at all 3 levels of our spatial hierarchy (Table 3). These relationships explained a moderate amount of the variation in glochidial abundance, but explanatory power increased with increasing spatial inclusiveness and was highest for the composite assemblage that included all 3 benthic sampling sites. The slope for this composite assemblage was significantly <1 suggesting a curvilinear relationship in which the rate of increase of glochidia in the drift decreased with increasing benthic abundance. However, the confidence interval around the slope was very wide and provided little support for specification of a relationship of this type. Confidence intervals around the slope for the other 2 assemblages included 1 and provided no support for a curvilinear relationship between benthic abundance and glochidial drift.

Estimates of glochidial production by the benthic mussel assemblage indicated prodigious output of

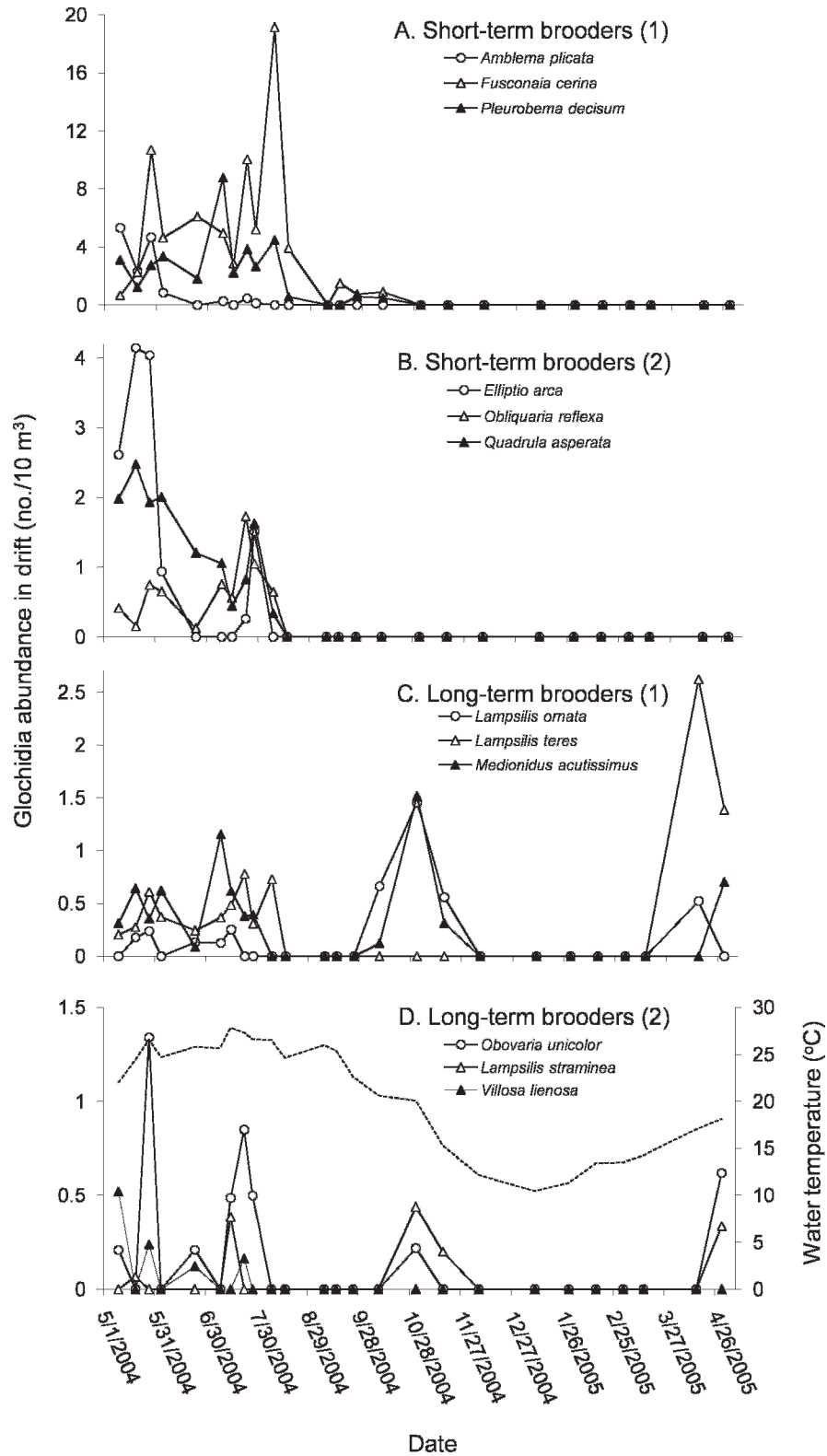


FIG. 1. Seasonal abundance of glochidia of short-term (A, B) and long-term (C, D) brooders in the drift in the Sipse River, Alabama. To reduce clutter and to accommodate the wide variation in individual species abundances, species within each brooding strategy were plotted in either a high- (A, C) or low- (B, D) abundance group (1 or 2, respectively). The dashed line on the bottom panel represents water temperature.

TABLE 3. Regression results for mean monthly glochidial abundance of species in the drift as a function of benthic mussel abundance and glochidial production (all variables were $\log_{10}[x]$ -transformed). See Table 2 heading and text for explanation of composite assemblages. CI = confidence interval.

Factor/ Assemblage	F	p<	R ²	Slope	95% CI slope
Benthic abundance					
Study site only	5.34	0.044	0.348	0.542	0.011–1.072
Composite 1	7.24	0.023	0.420	0.548	0.087–1.008
Composite 2	9.56	0.012	0.486	0.533	0.141–0.925
Glochidial production					
Study site only	1.21	0.297	–	–	–
Composite 1	2.47	0.147	–	–	–
Composite 2	4.82	0.053	0.3252	0.613	–0.019–1.245

>500,000 glochidia/m² for the 12 species studied (Table 2). In a single 1000-m² stream reach (comparable to our study site), this output represents production of nearly 10⁸ glochidia annually. Glochidial production by species in the benthic assemblage was not a strong predictor of abundance of glochidia in the drift. We found a marginally significant, positive relationship between glochidial production and glochidial abundance for the composite assemblage including all 3 benthic sampling sites, but this relationship explained a low percentage of variation in glochidial abundance. We found no significant relationship for the other 2 spatial levels (Table 3). For the composite assemblage, the confidence interval around the slope was wide and included 1 and provided no support for a curvilinear relationship. Observed abundance of glochidia of individual species in the drift departed widely from expectations based on glochidial production ($p < 0.0001$, $G = 1333.7$, 11 df). Log-likelihood ratios were especially large for 3 species, *E. arca*, *Fusconaia cerina*, and *Q. asperata*, indicating relatively greater departure from expectations (Table 2).

Discussion

We found glochidia of a wide variety of species in the drift throughout much of the year. Our DFA approach to identifying glochidia effectively allowed us to study species-specific patterns of glochidial abundance in a diverse mussel assemblage with many morphologically similar glochidia. We were able to identify confidently 83% of captured glochidia to species, and patterns of abundance in the drift generally were concordant with features of the benthic assemblage. We identified glochidia of most species present in the benthic assemblage whose glochidia were large enough to be captured by our nets, and the 3 most common species in the drift also

were the 3 most common species in the benthic assemblage (*F. cerina*, *P. decisum*, *Q. asperata*). Furthermore, the temporal occurrence of glochidia of each species coincided with previously identified periods of gravidity for those species (Haag and Warren 2003).

Seasonal patterns

Abundance of glochidia in the Sipsy River showed marked seasonality that was consistent with previous studies of glochidial drift and corresponded to the brooding pattern of each species. All species of short-term brooders in the Sipsy River are gravid and release glochidia primarily from May to early August (Haag and Warren 2003, this study). The duration and timing of glochidial release was nearly identical for short-term brooders in other studies, including *Fusconaia cuneolus* (late May–early August; Bruenderman and Neves 1993), *Pleurobema oviforme* (late April–July; Weaver et al. 1991), and *Fusconaia cor*, *Fusconaia barnesiana*, *Pleurobema oviforme*, and *Lexingtonia dollabelloides* (in aggregate, June–mid August; Neves and Widlak 1988). Glochidia of *Pleurobema collina* were present for a shorter time but within the same period (June–July; Hove and Neves 1994). *Fusconaia*, *Lexingtonia*, and *Pleurobema* all produce pelagic conglomerates that drift in the current, use minnows as hosts, and are members of the tribe Pleurobemini (Haag and Warren 2003, Campbell et al. 2005, Barnhart et al. 2008). We found a similar glochidial release period for other short-term brooders with different life histories and phylogenetic relationships: *E. arca* (no conglomerates, darter hosts, Pleurobemini), *Obliquaria reflexa* (demersal conglomerates, unknown host, Lampsilini), and *Q. asperata* (no conglomerates, catfish hosts, Quadrulini) (Haag and Staton 2003, Haag and Warren 2003). These consistent patterns across a wide phylogenetic and life-history cross-section of unionid

diversity show that a short brooding period is characteristically accompanied by a short period of glochidial release in spring and summer followed by a long period of relative reproductive inactivity.

Glochidia of long-term brooders were present in the drift throughout much of the year. This pattern is generally similar to that of other long-term brooders, but glochidial release of these species has been studied less extensively in the wild and is more variable than that of short-term brooders. In the Sipsy River, glochidia of long-term brooders were present in the drift throughout spring and summer and during a short period in autumn, but were absent in late summer and winter. With minor exceptions, these patterns were exhibited by all long-term brooding species in our study. In contrast, the release period of 4 long-term brooders in a small Virginia stream varied widely among species. *Lampsilis fasciola* and *Villosa iris* (as *V. nebulosa*) occurred in the drift in spring and summer, *Villosa vanuxemensis* occurred in autumn and winter, and *Medionidus conradicus* was present for much of the year (Zale and Neves 1982). The only common feature of glochidial release patterns among these 4 species and among long-term brooding species in our study was the absence of glochidia in the drift during the spawning period in late summer (Zale and Neves 1982, Haag and Warren 2003). In captivity, *Lampsilis siliquoidea* (as *Lampsilis radiata luteola*) released glochidia nearly year-round, and *Pyganodon grandis* released glochidia in autumn and winter (Watters and O'Dee 2000). An exception to the protracted release period of long-term brooders was documented for a population of *L. siliquoidea* (as *L. radiata luteola*) in Minnesota in which glochidial release occurred synchronously over 3 wk in June (Trdan 1981). In the Sipsy River, all long-term brooders appeared to respond to similar cues for glochidial release, but these cues evidently differ widely in other streams and among other species, a pattern suggesting that long-term brooding includes a wider array of release and host-infection strategies than does short-term brooding.

Factors affecting abundance in the drift

Mussel species vary widely in fecundity (Haag and Staton 2003), so we were surprised that abundance of species in the benthic assemblage was a more robust predictor of glochidial abundance in the drift than glochidial production. However, benthic abundance explained relatively little of the variation in glochidial abundance, and the form of this relationship was difficult to specify. A curvilinear relationship was suggested, but support for this type of relationship

was weak, and we are unable to propose a mechanism by which greater abundance of adult mussels would result in proportionally fewer glochidia in the drift. This relationship may simply reflect an expected, general increase in glochidial abundance with increasing adult abundance (McLain and Ross 2005), but also suggests that species-specific life-history traits other than fecundity are involved in determining glochidial abundance in the drift.

A number of factors could explain the weak relationship between glochidial production and abundance in the drift. The degree to which mussel fecundity varies among years is unknown, but substantial departures from our fecundity estimates (which were determined primarily in 1999–2000) because of annual variation in egg production or fertilization could be partly responsible for observed patterns. Variations in flow or other hydrological variables could alter patterns of glochidial abundance and transport, particularly if these events occurred during selected time periods and disproportionately affected species with different release periods. 2004 and 2005 were average flow years for the Sipsy River (US Geological Survey recording gage 02450250; <http://waterdata.usgs.gov/al/nwis/rt>), but we could not evaluate how different flow regimes affected glochidial abundance. Our censoring procedure could have introduced bias into our data set because probabilities of correct identification varied among species. However, the strong correlation between our raw and corrected identifications shows that censoring introduced little systematic bias across species. Furthermore, the magnitude of departures of observed glochidial abundance from expected values for several species (e.g., *E. arca*, *F. cerina*) cannot be explained by a reduction in observed abundance caused by censoring. Some species may release glochidia primarily at night (Haag and Warren 2000), and the restriction of our sampling to daylight hours may have resulted in underestimation of abundances of these species. However, if glochidia remain in the drift for extended periods (>1 d), then diurnal differences in release may be largely obscured. Apart from these potential confounding factors, differences among species in life-history traits other than fecundity, especially host-infection strategies, probably have a major influence on patterns of glochidial abundance in the drift.

Mussel species in the Sipsy River show a variety of glochidial-release strategies ranging from highly specialized adaptations to attract specific fish species to lack of such adaptations among potential broadcasters (Haag and Warren 1997, 2003, Haag and Staton 2003). Therefore, drifting glochidia could

represent either: 1) lost reproductive effort (individuals that have entered the drift after failed host encounters and subsequently have little chance of infecting suitable hosts), 2) a secondary, passive infection strategy for species that primarily use active host attraction, or 3) a primary strategy for host infection by species with no adaptations for host attraction. Which of these categories best describes the role of drifting glochidia probably varies among species based on host use, strategies for host attraction, and the timing of glochidial release. Consequently, the diversity of glochidial release and host-infection strategies predicts strong departures from expectations of glochidial abundance in the drift based simply on passive release and occurrence of glochidia in proportion to differences in production among species. Furthermore, glochidial release and infection strategies that may influence glochidial abundance in the drift probably have evolved in concert with co-adapted suites of life-history traits (e.g., Winemiller and Rose 1992), thereby optimizing the effectiveness of these strategies given great differences among species in energetic investment in offspring.

Most proposed host-infection strategies are based on laboratory observations, but interspecific differences in glochidial abundance and release periods can provide clues to strategies that are used in the wild. In the laboratory, *E. arca* releases glochidia in thick aggregations of mucus that can entangle host fishes (Haag and Warren 2003) but that reduce the likelihood that glochidia will enter the drift. This strategy could explain the substantial underrepresentation of this species in our samples. Conversely, *F. cerina* forcefully ejects conglutinates into the water column where they are preyed upon by drift-feeding minnows (Haag and Warren 2003). The disproportionately high abundance of these glochidia in our study probably is attributable to this release strategy. The few species that appear to infect hosts primarily by broadcasting free glochidia overcome the low probability of encountering fishes by releasing prodigious numbers of glochidia during a short time period to maximize glochidial abundance in the drift (Murphy 1942, Davenport and Warmuth 1965, Young and Williams 1984). Glochidia of *Amblema plicata* were found in the drift for the shortest duration (primarily during May) of any species in our study, and a short release period was documented for this species in captivity (Watters and O'Dee 2000). These traits together with its apparent lack of adaptations for host attraction (Haag and Staton 2003) and its wide host usage (Watters 1994, O'Brien and Williams 2002) are compatible with an infection strategy oriented toward broadcasting and passive encounters with host fishes.

In our study, glochidial abundance was predicted best by a composite benthic assemblage from the study site and 2 upstream sites (for both benthic abundance and glochidial production), a result suggesting that glochidia may be transported considerable distances by stream currents (but see Jansen et al. 2001). Glochidial survival after release varies among species but decreases rapidly with increasing temperature. Above 20°C, glochidia may survive only 1 to 5 d (Jansen et al. 2001, Zimmerman and Neves 2002). Most glochidial release in our study occurred above 25°C. Thus, even if glochidia are likely to parasitize fishes in the drift, drifting may be an important means of long-distance dispersal in the Sipsey River only for long-term brooders whose glochidia are present when water temperatures are cooler.

The availability of supporting data on mussel assemblage composition and fecundity provided us with a unique opportunity to examine dynamics of glochidial abundance in the drift to an extent not previously possible. The lack of a strong relationship between glochidial production and abundance in the drift shows that release and transport of glochidia are dynamic processes influenced by many factors.

To date, no investigators have published studies of multiyear patterns of glochidial drift at a single site. Longer-term drift studies that encompass annual variation in flow, mussel fecundity, and other variables could provide important information about host-infection strategies used by mussel species in the wild and about factors that influence mussel reproduction and recruitment.

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