

Glochidial release as a function of water temperature: Beyond bradyticty and tachyticty

G. Thomas Watters^{1,3} and Scott H. O'Dee²

¹ Ohio Biological Survey, The Ohio State University, 1315 Kinnear Road, Columbus, OH 43212-1157;

² School of Natural Resources, The Ohio State University, 2021 Coffey Road, Columbus, OH 43210-1087.

ABSTRACT: The timing of glochidial release in five species of freshwater mussels was compared to water temperature. The mussels were *Amblema plicata*, *Elliptio dilatata*, *Lampsilis radiata luteola*, *Leptodea fragilis*, and *Pyganodon grandis*. Mussels were maintained in outdoor enclosures at $\approx 40^\circ$ North latitude. Each species released glochidia at different temperatures, such that some were winter-releasers and others were summer-releasers. These did not necessarily correspond to the categories of "bradytictic" and "tachytictic" brooders, as widely used in the literature. Species considered "bradytictic" were actually winter-releasers, with their glochidia apparently overwintering on the host rather than being brooded in the marsupia. The applicability of the terms "bradytictic" and "tachytictic" to freshwater mussels must be reevaluated. Circumstantial evidence was found that *Lampsilis radiata luteola* and *Elliptio dilatata* spawn twice a year, resulting in a summer and a winter brood. *Amblema plicata* released at 23 °C (July); *Elliptio dilatata* at 5 and 19 °C (November and August); *Lampsilis radiata luteola* nearly year-round, but primarily from May through October, with a peak release at 19 °C; *Leptodea fragilis* at 11 °C (September through November); and *Pyganodon grandis* at 5 °C (October through February).

Keywords: Unionidae, reproduction, bradytictic, tachytictic, glochidia.

Although Call (1887) and Young (1911) did not believe that mussel reproduction was driven by temperature, other studies have demonstrated a definite connection (Schierholz 1889, Corwin 1920, Howard and Anson 1923, D'Eliscu 1972, Giusti *et al.* 1975, Hruska 1992, Kondo 1993). Although these studies largely deal with temperature as a cue for gametogenesis, temperature controls other aspects of mussel reproduction as well. We have shown that for *Lampsilis cardium*, and presumably others species, a lower threshold temperature exists below which metamorphosis either does not occur, or is significantly delayed (Watters and O'Dee 1999). An upper threshold temperature also exists, above which glochidia fail to metamorphose and are killed (Dudgeon and Morton 1984). The shedding of glochidia by a parental mussel also may be temperature dependent.

Under the existing models of tachytictic and bradytictic mussel reproduction, glochidia are either released to encounter hosts during the holarctic summer (tachytictic), or spring (bradytictic). However, glochidia are known to occur on fishes in winter. Neither tachytictic nor bradytictic reproduction can explain the presence of these glochidia. Furthermore, reports of gravid periods within a mussel genus or species often conflict to the extent that both tachytictic and bradytictic patterns may be exhibited.

We believe that mussel reproductive strategies may be more complicated than this simple two-system approach.

Methods

Mussels were maintained outdoors in 3028 L polyethylene circular pools (1.8 m base diameter, 1 m deep) fitted with standpipe drains. Twenty individuals of each of five species collected in Ohio were used for the study: ten male and ten gravid female *Lampsilis radiata luteola*; 20 unsexed individuals of *Amblema plicata*; 20 unsexed *Elliptio dilatata*; 20 unsexed *Pyganodon grandis*; and 10 male and 10 female *Leptodea fragilis*. Each species was kept in 34 cm x 28 cm x 15 cm plastic containers with ≈ 12 cm of mixed-grain sand. The pools were supplied with airstones and inoculated with an algal culture. *Lampsilis r. luteola* and *A. plicata* were kept in one pool, and the remaining species were kept in a second pool.

Lampsilis r. luteola and *A. plicata* were sampled for glochidia beginning in August 1995. The remaining species were sampled beginning October 1997. For *L. r. luteola* and *A. plicata*, each sampler consisted of three weighted plastic ice cube trays placed within a plastic storage crate that were placed adjacent to the mussel containers. The remaining species were sampled with 14 cm x 7 cm x 4 cm plastic containers

³ For correspondence contact G.T. Watters
(Email: watters.1@osu.edu)

placed within the mussel containers. The samplers were checked for the presence and abundance of glochidia every two to three days. Results are reported as estimates for each species for the entire pool. Material from the samplers was passed through a 145- μm sieve, and examined for glochidia with a stereomicroscope using the polarized light method devised for detecting zebra mussel veligers (Johnson 1995).

Temperature was recorded approximately every hour using a submersible temperature monitor. Maximum and minimum daily temperatures were compared to glochidial release. Missing temperatures due to occasional monitor failure were calculated from an air/water temperature correlation.

Results

Lampsilis r. luteola released nearly year-round, but primarily from May through October, with a peak release at 19 °C (Fig. 1). *Amblema plicata* released glochidia in July only between $\approx 20^\circ\text{C}$ and the peak water temperature of 23 °C (Fig. 2). *Pyganodon grandis* began to release in October as the water temperature decreased to $\approx 12^\circ\text{C}$ and continued through February, with a peak release occurring at 5 °C (Fig. 3). *Leptodea fragilis* glochidia were found only from September through November, with the peak of release occurring when water temperatures decreased to 11 °C (Fig. 4). *Elliptio dilatata* released glochidia in August and September, and again in November, suggesting multiple broods or asynchronous release (Fig. 5). The peak releases occurred at 5 and 19 °C.

Discussion

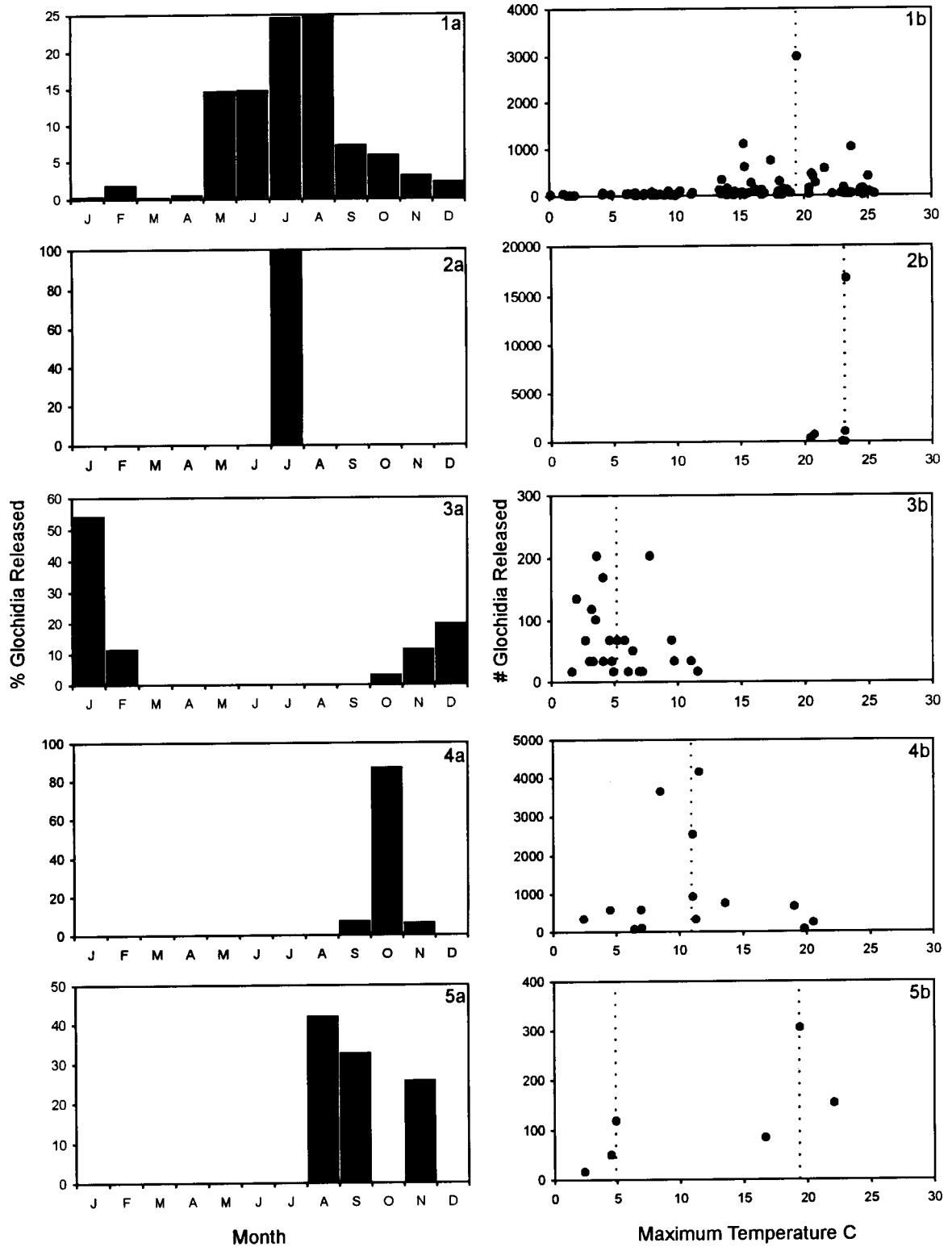
Early workers recognized a pattern in the seasonality of gravidity. Sterki (1895) first suggested the concept of summer and winter “breeders,” and believed the differences to be phylogenetically important (Sterki 1898). The terms “breed” and “brood” were used inconsistently by most early workers; Sterki (1895, 1898) was referring here to the presence of glochidia in the marsupia. Ortmann (1909) gave an extensive list of summer and winter brooders. Other lists followed (Lefevre and Curtis 1910a,b, Utterback 1916). These patterns eventually became known as bradytictic and tachytictic. Bradytictic brooders spawned in the summer, and females retained glochidia over the winter until they were released the following spring. Tachytictic brooders spawned in the spring, and released glochidia the same summer.

Peak glochidial release is associated with threshold water temperatures. Depending on the species, this may be a thermal minimum or maximum. Thermal minima as thresholds are associated with winter releasers that use host overwintering. Thermal maxima as thresholds are associated with summer releasers, which may be either tachytictic or use parent overwintering. For species having more than one reproductive strategy, both thermal minima and maxima may be important depending on the time of year.

Temperature dependent glochidial release was first suggested by Chamberlain (1934), Jungbluth and Lehmann (1976), and Young and Williams (1984). These scenarios ascribe the trigger for glochidial release to the occurrence of some spring water temperature (*i.e.*, reaching a warm-water threshold). The idea that some mussels may respond in the opposite fashion, where the trigger is the decline to a cold-water threshold, was advanced by Kondo (1993). He believed that winter “breeding” Japanese species released glochidia when temperatures were sustained below 10 °C. The dichotomy of these two triggers, one based on temperatures dropping below a threshold, the other on temperatures exceeding a threshold, has been generally unrecognized. We refer to these as *winter releasers* and *summer releasers*, respectively. The terms do not necessarily coincide with the terms *bradytictic* and *tachytictic*.

Fish sampled in winter may bear encysted glochidia (Mishra and Chubb 1969, Tedla and Fernando 1969, Dartnall 1973, Wooten 1973, Campbell 1974, Cloutman 1975, Dartnall and Walkey 1979, Jansen 1991). Furthermore, glochidia may be found in the water column year-round (Neves and Widlak 1988). The origin of these free, winter glochidia cannot be explained by either the bradytictic or tachytictic models. In the bradytictic case, glochidia should be in the marsupia; in the tachytictic case, they should not be present at all. Our results suggest that these glochidia have been released in the autumn and winter to parasitize hosts. The glochidia thus overwinter on the hosts, rather than in the marsupium. We have termed this reproductive strategy *host overwintering*, and contrast it with the traditional bradytictic pattern, which we term *parental overwintering*. Host overwintering species are winter releasers, whereas parental overwintering species are summer releasers (and hence winter brooders). Strictly tachytictic species also may be summer releasers.

The five species studied here demonstrate the problems of assigning a mussel to the tachytictic or bradytictic models:



Figures 1-5. (a) Percentage of glochidia released each month. (b) Number of glochidia released as a function of daily maximum water temperature. Dotted lines indicate peak release temperatures. 1. *Lampsilis radiata luteola* 2. *Amblema plicata* 3. *Pyganodon grandis* 4. *Leptodea fragilis* 5. *Elliptio dilatata*.

1) The reported gravid periods for *P. grandis* are contradictory. Jansen (1991) found gravid individuals from January to May, suggesting parental overwintering. Penn (1939) gave October and November as gravid periods, while Lewis (1985) reported July and August. But Huebner (1980) believed this species was tachytictic. Released glochidia were found only in the autumn and winter in this study, and thus we categorize it as a winter releaser following a host overwintering reproductive strategy. But the range of reported gravid periods cannot be ignored, suggesting a more complicated reproductive strategy that may vary from population to population. Future research may indicate that this species may exhibit host overwintering, parental overwintering, and/or tachytictic strategies, or that *P. grandis* represents a species complex.

2) *Lampsilis r. luteola* likewise is controversial. Huebner (1980) stated that this species did not show adult overwintering, but Trdan (1981) disagreed. Conner (1907) reported gravidity year-round. Evermann and Clark (1917) gave May and August as gravid periods. In this study, *Lampsilis r. luteola* released glochidia nearly year-round, with a peak release in May. Some glochidia were shed throughout the autumn into winter. As with *P. grandis*, this species may be capable of both host overwintering and parental overwintering.

3) The few studies of gravid periods for *Elliptio* are contradictory as well. Conner (1907) gave April to August as the gravid period for *E. complanata*, but Raulerson and Burbanck (1962) regarded *E. hopetonensis* as bradytictic. *Elliptio dilatata* was assumed to be tachytictic (Ortmann 1919). Indeed, Jirka and Neves (1992) found *E. dilatata* gravid from March into July. We found glochidia for *E. dilatata* released in August, but then again in November. This suggests that *E. dilatata* is iteroparous (multiple broods within an individual) or has asynchronous release within a population, such that both tachytictic and host overwintering reproductive strategies occur.

4) Ortmann (1919) found glochidia in *L. fragilis* from September to May. In this study, glochidia were released from September through November. No release was seen in the spring or summer. Our individuals thus were winter releasers. This species apparently is able to employ more than one reproductive strategy.

5) Of the five species studied, only *A. plicata* behaved according to our pre-conceived notion of being

tachytictic. It was gravid in July, as reported by Holland-Bartels and Kammer (1989). Unlike *E. dilatata*, the only other amblyemine examined, there was no evidence of multiple broods or multiple reproductive strategies.

It is possible that there are species interactions such that some aspect of reproductive behavior in one species affects the behavior of another species. If this is so, then results seen here may have been different than in experiments where each species was kept in separate pools. However, there is no published evidence that these interactions exist, and all of the species used here occur together in streams of Ohio.

Clearly, some mussels are either iteroparous (Heard, 1975), or belong to populations having asynchronous glochidial release (e.g., *E. dilatata*, this study). Reports of iteroparity for temperate mussel species are rare. *Cumberlandia monodonta* may breed twice a year (Howard 1915, Gordon and Smith 1990), as may *Glebula rotundata* (Parker *et al.* 1979, 1984). Harms (1909) found that *Margaritifera margaritifera* had two broods. The second annual brood occurred such that glochidia overwintered on its host (Young *et al.* 1987). We were not able to determine if any species included in our study were iteroparous, since mussels were held and sampled simultaneously.

Whether the multiple releases seen in *E. dilatata* and *L. r. luteola* are attributable to iteroparity or asynchronous release, the result is the same: a single species may be tachytictic in one brood, and exhibit parental or host overwintering in the second. Thus, different reproductive strategies may be employed among individuals of a single species, or perhaps by a single individual. At the extreme, a single individual could spawn, have a tachytictic brood, spawn again, and release some glochidia in the fall (host overwintering), while retaining other glochidia in the marsupia (parental overwintering). Host overwintering may provide the greatest dispersal potential for the species. Furthermore, because host overwintered glochidia would metamorphose earlier in the year than either parental overwintered or tachytictic glochidia, host overwintering may confer the greatest growing period before winter to juveniles. But it may be the riskiest for a glochidium. If the chances for death of the glochidium and/or the host are a function of time, then the least time spent on the host is the least risky. Thus, there are tradeoffs. But if an individual or population could use several strategies, they may "hedge their bets." In any event reproductive

strategies of mussels clearly are more complicated than just the classic tachytictic and bradytictic patterns. At least, a third option must be recognized: host overwintering.

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