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Seasonal Reproductive Development of *Lampsilis cardium*, *Amblema plicata plicata*, and *Potamilus alatus* (Pelecypoda: Unionidae) in the Upper Mississippi River

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ABSTRACT

Adult specimens of three species of freshwater mussels common to the upper Mississippi River were examined histologically to determine seasonal patterns of development in gametogenesis and release of glochidia. Full maturation of gonadal materials in Lampsilis cardium (formerly L. ovata ventricosa), a long-term breeder, occurred when ambient river temperatures reached 24° to 26°C, between late July and early August. By mid-August, glochidia were present in the marsupia. Glochidia were released from late May through mid-June of the following year once water temperatures reached 20°C. The long-term breeder Potamilus alatus demonstrated full gonadal maturation earlier than seen in L. cardium with reproduction completed by late July (26°C). Glochidia of P. alatus were released over a period similar to that observed for L. cardium, late May through early July of the following year. Fully mature Amblema plicata plicata, a short-term breeder, were collected from late May through early July (18° to 21°C). Glochidia were were released from early June to early August of the same year.

INTRODUCTION

Freshwater mussels are ecologically and economically important, but effective management of this resource is hampered by limited quantitative life history information for many species. There is much general knowledge about reproductive patterns in freshwater mussels. Species are often classified by reproductive strategy and are known as either short-term (tachytictic) or long-term (bradytictic) breeders based on the length of time the female of the species retains glochidia (larvae) after fertilization. Reproductive strategy, as well as general periods of gravidity in the female and patterns of glochidial release, are known for many species (e.g. Ortmann 1909, Lefevre and Curtis 1912, Surber 1912, Howard 1914, Coker et al. 1921, Baker 1928). However, patterns of gametogenesis and release of glochidia in relation to ambient temperatures have been presented by few and generally not for species common to the upper Mississippi River (van der Schalie and van der Schalie 1963, Heard 1969, 1975, Stein 1973, Zale and Neves 1982).

We studied the annual gametogenic cycles of three species of freshwater mussels in the upper Mississippi River. The pocketbook Lampsilis cardium (formerly L. ovata ventricosa) and the pink heelsplitter Potamilus alatus are members of the subfamily Lampsilinae and are common in main channel border areas of the river. Like others in this subfamily, L. cardium is a long-term breeder with glochidia retained from late summer until they are released in mid to late summer of the following year (Ortman 1909, Lefevre and Curtis 1912, Baker 1928). Few data are available for P. alatus, but it also is a long-term breeder (Lefevre and Curtis 1912, Baker 1928) and is gravid from August to June with glochidia retained over winter and released the following June to July (Baker 1928). Both species have specialized modifications of the outer branchiae called marsupia in which developing embryos and glochidia are held (Sterki 1895). Amblema p. plicata is the

most abundant species in the river (Theil 1981, Havlik 1983) and is commercially exploited. This species is a short-term breeder (Sterki 1895) with females gravid in late spring to mid-summer (Utterback 1916, Ortmann 1919, Cocker et al. 1921, Baker 1928, Stein 1969) and glochidia released soon after they are developed. We used histological methods to provide additional details on the seasonal and temperature-related patterns of gonadal development in adults and patterns of glochidial release of these common species of the upper Mississippi River.

METHODS AND MATERIALS

Adult specimens were collected by hand on eighteen dates from late May 1982 to late April 1983, from a main channel border area of Navigation Pool 7 near River Mile 709 of the upper Mississippi River. Other species common to the site included Fusconaia flava, Quadrula pustulosa pustulosa, Obliquaria reflexa and Truncilla donaciformis. Nomenclature is as per Turgeon et al. (1988). Water temperatures were collected at the study site from just above the substrate with a Hydrolab Series 4000 water quality unit. Specimens were preserved in 70% ethyl alcohol. The gonadal-visceral mass was dissected, gonadal material excised and tissue embedded in paraffin. Eight micron serial sections were cut and Harris' hematoxylin and eosin stains applied (Humason 1979). Demibranchs were dissected and examined for the presence of glochidia under a dissecting microscope.

Stages of reproductive development were assessed in 124 L. cardium, 82 P. alatus and 229 A. plicata. The gonadal development of males and females was categorized into four stages, proceeding from the least to the most mature stage of gametogenesis as described by Yokley (1972). The stages for males and females were (1) no gamete development, (2) lumina with some spermatogonia or small ova and nutritive material, (3) males: less space between acini, more spermatogonia, and some spermatids present, females: acini spaced more closely and more large ova present (some in lumina), and (4) males: acini closely packed, lumina filled with tightly spaced spermatogonia, spermatids, and spermatozoa, females: acini closely situated with lumina filled with many mature ova, acinar walls thin. The occurrence of glochidia in the marsupia or demibranchs was classified as (1) evidence of recent release of glochidia based on ruptures of the demibranch (only observable in Lampsilinae), (2) no embryos or glochidia present, (3) few embryos and glochidia present and (4) full of embryos or mature glochidia.

Fish present along the shoreline of the study site were sampled by seine from early June to August. Young-of-the-year of all species and adult minnows (Cyprinidae) were returned to the laboratory and examined under a compound dissecting microscope for the frequency and density of glochidial attachments.

RESULTS AND DISCUSSION

Lampsilis cardium demonstrated some gonadal activity in both sexes throughout the year (stage 1 was not observed). This agrees with Zale and Neves (1982) who found that active gametogenesis occurred year-round in the four Lampsilinae species they studied. Males were in early stages of development (stage 2) until early June and females until July (Fig. 1). The first major increase in the production of spermatogonia and spermatids (male stage 3) occurred when river temperatures stabilized at 18° to 20°C for several weeks. Gonadal maturation and sperm production in males (stage 4) occurred during mid-July to late August when river temperatures peaked at about 25°C. Eggs began maturing as water temperatures increased from 20° to 25°C. Females first reached stage 4 development in late July (25°C). Fertilization appeared to occur between late July and mid-August after river

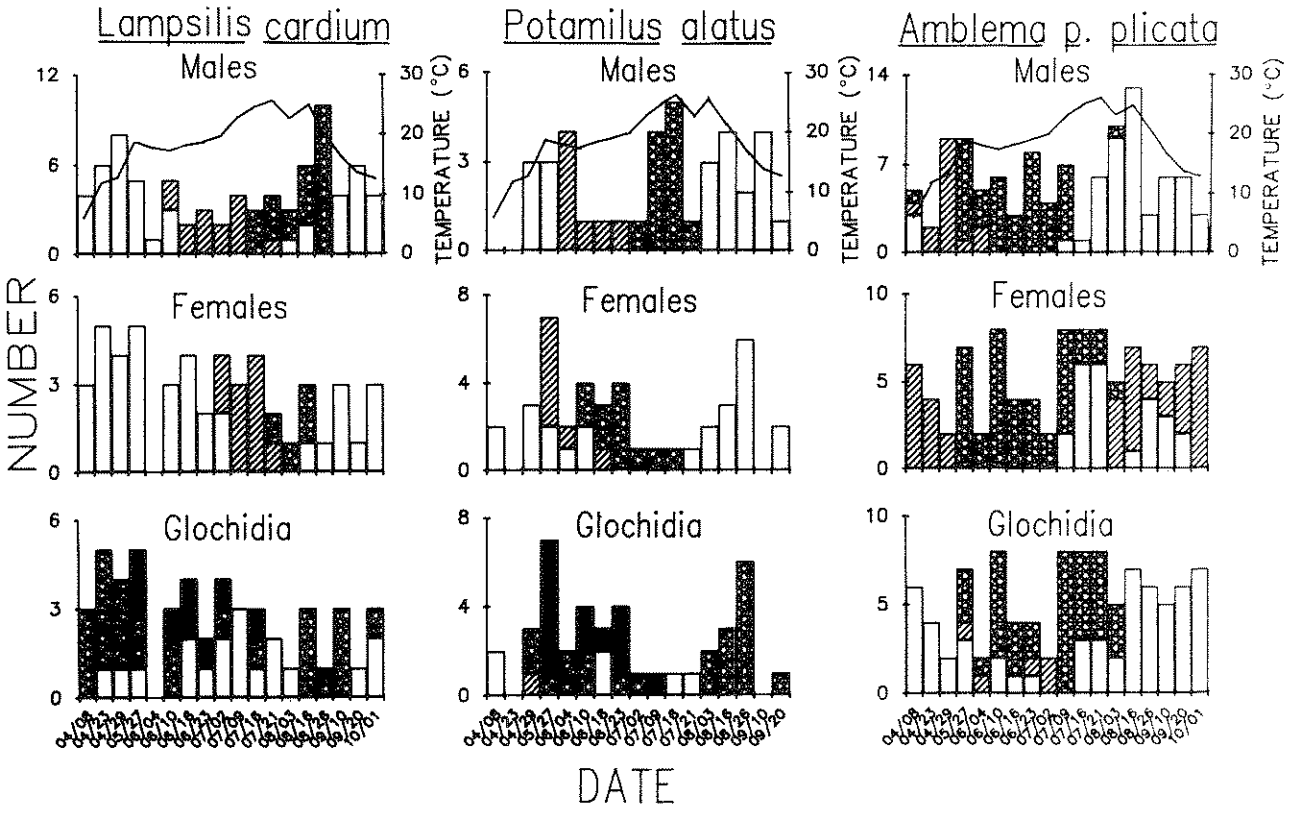

Figure 1. Seasonal pattern of gonadal development in males and females and presence of glochidia in three species of mussels, and river water temperature (line), in Pool 7 of the Upper Mississippi River from April to October. Stage 1 (black), Stage 2 (open), Stage 3 (hatched), and Stage 4 (shaded). The classification systems for adults and for glochidial presence in demibranchs are described in the text.

temperatures had peaked and were declining. Embryos were first observed in marsupia in mid-August and soon developed into glochidia (Fig. 1). They were held in the marsupia until the following year and were first released in late May, after a period of increasing water temperatures. In their study of upper Mississippi River mussels, Lefevre and Curtis (1912) found that species in the subfamily Lampsilinae had an extended period of gravidity, that release of glochidia peaked in June, and that a new reproductive cycle started in August.

As in L. cardium, gonadal activity in P. alatus persisted (no stage 1) in both sexes throughout the study period (Fig. 1). Reproductive and nutritive materials were loosely packed in the lumina (stage 2) until late May or early June, when water temperatures reached about 20°C. Males then developed to stage 3 and were fully mature by early July. Stage 2, 3, and 4 development was observed in females collected from late May to mid-June. Fully mature females were collected on June 10, nearly 3 weeks before mature males were observed. However, since our sample size was small during this period (only 9 males and 16 females were examined), mature males could have been present in the population but not collected. Potamilus alatus were fully mature earlier than L. cardium with reproduction completed by late July (26°C). A shift from stage 4 to stage 2 development was observed between specimens collected on July 21 and August 3. Some glochidia (glochidia stage 3) were observed in specimens collected in early August (Fig. 1). Marsupia were full of glochidia from fall through winter with glochidia released in late May to early July--about the same time as in L. cardium.

Specimens of Amblema p. plicata were in fairly advanced stages of reproductive development (stage 3) earlier in the year than was seen for the other species studied (April, 6°C). Lefevre and Curtis (1912) found that the entire reproductive cycle of short-term breeders like A. p. plicata extended from April to mid-August and that glochidia were discharged soon after development. In our study, progression towards full reproductive maturation occurred as water temperatures rose from 13° to 19°C; 100% of the females and 80% of the males were in stage 4 development by late May (Fig. 1). Mature adults were collected until early July when river temperatures reached 26°C. Glochidia were found in all four demibranchs and were present in specimens from late May to mid-August. Males were relatively undeveloped after late July and appeared to overwinter in stage 2, whereas females overwintered primarily in stage 3. Stein (1973), who observed a similar seasonal reproductive pattern in specimens from Lake Erie, found mature glochidia from early June (23°C) to early August (22°C).

Although the timing of full gonadal development differed among the three species, all three overlapped in their periods of glochidial release. This suggests that some competition for suitable fish hosts for the glochidia could occur. However, overlaps in hosts and in periods of glochidial release probably do not limit these species in the study area since there was an abundance of hosts and attachment sites. Of the 33 species of fish (mostly young-of-the-year) collected at the site, glochidia were found on 12 species (7 Cyprinidae and 1 species in Esocidae, Catostomidae, Percichthyidae, Centrarchidae and Percidae). Only 4% of the nearly 2,000 fish collected had attached glochidia; infected fish carried an average of three glochidia. In the perciform fishes known to comprise most of the host species for L. cardium, P. alatus and A. p. plicata (Fuller 1978, Waller and Holland-Bartels 1988), 24% of the individuals were infected and these carried an average infection of only six glochidia. This density of glochidia is below levels found to be tolerable to fish exposed under laboratory conditions (Holland-Bartels and Waller 1987).

Our analyses of gametogenesis and glochidial release support the general reproductive patterns observed in earlier works. However, our

information on the specific patterns of gametogenesis and glochidial release in relation to ambient water temperatures in the upper Mississippi River more clearly demonstrates species differences and provides an additional tool for better management of the resource. Many of the exploited and endangered mussels of this system have been targeted for renewed culture efforts and refined knowledge of all life history requirements will be required for success.

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