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SEDIMENT MIXING BY *LAMPSILIS RADIATA SILIQUOIDEA* (MOLLUSCA) FROM WESTERN LAKE ERIE

Peter L. McCall, Michael J. S. Tevesz,[1]
and Stephen F. Schwelgien[1]
Department of Earth Sciences
Case Western Reserve University
Cleveland, Ohio 44106

ABSTRACT. The sediment reworking activities of an abundant Lake Erie unionid bivalve, Lampsilis radiata siliquoidea, *have been studied by field observations and laboratory experiments. Unionid burrowing in laboratory microcosms increased sediment water content 10-20%, decreased water content variability, homogenized sedimentary structures, and increased tenfold the volume of oxidized sediment over that in microcosms with no unionids. Incomplete mixing of sediment took place to a depth of 10 cm during burrowing by* L. r. siliquoidea. *Burrowing by other unionids may extend the depth of maximum reworking to 20 cm. Unionid burrowing, feeding, and respiratory activities may alter the profiles of various elements and radionuclides associated with sediment particles and alter the location and intensity of microbial activity in sediments.*

INTRODUCTION

The mixing of sediments by macrobenthic organisms has been documented in both marine and freshwater habitats. This mixing has profound effects on the physical and chemical properties of sediments, including grain size, mass properties such as water content and shear strength, and diffusion coefficients for certain solutes in sediments (Rhoads 1974). Vertical profiles of sedimentary materials produced by the activities of macrobenthos are noticeably different from profiles produced in similar environments by physical processes alone (Berger and Heath 1968; Aller 1977; Robbins, Krezoski, and Mozley 1977, among others).

Except for studies on sediment reworking by the tubificid oligochaetes (cf. Davis 1974, Fisher 1979, Robbins *et al.* 1979), practically nothing is known about the biogenic alteration of sediment properties in freshwater environments. In this paper we will provide information on the sediment reworking activities of another major group of freshwater organisms, the unionid bivalves.

Numerous studies in the marine realm show that the ability of an organism to alter sedimentary properties is related to its size, abundance, and activity (see review by Rhoads 1974). Goodrich and van der Schalie (1932) reported that unionid bivalves (Mollusca) were more abundant in Lake Erie than in any of the other Great Lakes. Unionids are infaunal to semi-infaunal filter-feeding bivalves. They are very active as burrowers and crawlers on a wide variety of substrata (see for instance Coker *et al.* 1921, Tevesz and McCall 1979). The effects of these bivalves on sediment properties and the depth to which they are active are not well known, but Baker (1928) reported the occurrence of unionids as deep as 20 cm below the sediment-water interface. Wood (1953) calculated that unionids were the dominant macrobenthic secondary producers in this part of the lake, totalling 78% of the standing crop (82.5 g m^{-2}) of the non-oligochaete macroinvertebrate fauna. One unionid species, *Lampsilis radiata siliquoidea* (Barnes), totalled over 54% of the macroinvertebrate standing crop in the western basin. In addition, Wood reports that this species occurs in the western basin in population densities of up to 20 m^{-2} and its average wet weight (without shell) is 10.5 g per individual (n=147). The standing crop biomass of oligochaetes in this part of Lake Erie has not been measured directly. Using the data of Britt, Pliodzinskas, and Hair (1977) and our estimate of average individual wet weight of .04 g (n=1000), we esti-

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[1] Department of Geological Sciences, The Cleveland State University, Cleveland, Ohio 44115.

mate that the standing crop of oligochaetes is less than 12 g m^{-2}.

Because unionids are large, active, and abundant burrowers, it is reasonable to expect that they may significantly modify sediment properties. In this paper, we document by means of field and laboratory observations some of the sediment reworking activities of *L. r. siliquoidea.* On the basis of these observations, we then offer several working hypotheses about the effects of unionids on the biogeochemistry of lake bottom sediments.

MATERIALS AND METHODS

In situ observations of life habitats and collections of bivalves and associated sediments for laboratory studies were made by divers using SCUBA at two sites in the western basin of Lake Erie. (Site A 82°59.4′ long., 41°43.8′ lat.; Site B 83°11.5′ long., 41°43′ lat.). Sediment grain size distributions at these sites were determined by settling tube analysis (Royse 1970). Organic matter determinations were made by chromic acid digestion and a modified Walkley-Black titration (Gaudette *et al.* 1974).

Fourteen live *Lampsilis radiata siliquoidea* were collected from these sites and taken to the laboratory for further observation. One set of laboratory observations was made for the purpose of describing the burrowing sequence of *L. r. siliquoidea* and the effects of burrowing and semi-infaunal crawling on the mixing of surface sediments.

Five 17.5 cm x 17.5 cm x 11.5 cm Plexiglas trays were filled with hydrated western basin sediment from the sites where unionids were collected. One unionid was placed in each tray. These trays were then put in a sixty-gallon aquarium filled with continuously aerated Lake Erie water that was maintained at 19°C. The unionids were placed in these containers the day after they were collected and their activities and sedimentary effects were visually observed and photographically recorded for a period of one month. Data on the size, orientation, and depth of burrows were collected from these trays. In addition, two sediment cores were taken in each of four randomly selected trays three days after the introduction of the unionids to determine the effect of unionids on sediment water content. One 4 cm long core was taken from the tank at a location as far away from the bivalve as possible in a part of the tray unaffected by biogenic sediment mixing. These cores were sectioned into 1 cm lengths, and sediment water content for each 1 cm interval was determined as weight loss upon drying in an oven at 90°C. Water content determinations are reported here as percent total weight of water plus sediment.

The remaining nine bivalves were held in their native sediments in the same aquarium during this time. After one month, they were placed, three to a tray, in three 30 cm x 40 cm x 11.5 cm deep trays filled with western basin sediment to determine the area covered by bivalve surface trails and the effect of surface migration on the oxidation state of the sediment in a two-week period. Sediment color is a reliable indicator of the oxidation state of most finer grain terrigenous sediments (Mortimer 1941, 1971; Berner 1971; Fenchel and Riedl 1970; Rhoads 1974), and was used here to determine the location of the boundary between the oxidized and reduced sediment layers. The presence of oxygen in sediments induces the formation of ferric hydroxides, which give the sediment a brown color. Below this zone oxygen is absent and the sediment may be grey or black. The black color in marine sediments is due to the presence of the metastable sulfides mackinawite and greigite. The grey color is found in the presence of FeS_2 (Berner 1971).

Another set of observations was made to determine the effects of bivalves on sediment laminae and to determine the depth to which *Lampsilis* disturbs sediments. Four 17.5 cm x 4 cm x 11.5 cm aquaria were filled with alternate layers of powdered nickel (1-2 mm thick) and natural lake sediment (~1 cm thick). One unionid was placed in each of the aquaria and allowed to burrow. Ten days after the introduction of the bivalves, radiographs of the aquaria were made using a continental GR-A radiography unit and Kodak X-Omat MA2 film.

RESULTS

Field Observations

The major goal of the field work was to collect living *L. r. siliquoidea* for laboratory experiments. In the course of these collections, estimates of unionid abundances were made by diver examination of fifteen randomly placed 1 m^2 quadrats. Only *L. r. siliquoidea* were found at site A; population densities ranged from 7-18 individuals m^{-2} ($\bar{x} = 10.7$, $\sigma = 1.9$). The unionid fauna at site B was comprised of *L. R. siliquoidea, Proptera alata,* and *Ligumia nasuta* (density 2-10 m^{-2}). Physical properties of the sediments at these two sites are shown in Table 1. *L. r. siliquoidea* were found both at the surface of the substratum and up to 3 cm below the sediment surface. One larger specimen of *Proptera alata* (length 12 cm) was

TABLE 1. Physical properties of bulk samples of surface sediment at two collecting localities in western Lake Erie.

	Site A	Site B
Median Grain Diam. (ϕ)	9.5	8.3
Water Content (%) ($\pm\sigma$, n=4)	80 (±2.1)	73 (±2.6)
Organic Carbon Content (%)	5.4	6.7
Water Depth (m)	9.4	7.0

found living 5 cm below the sediment surface at site B. Several unionid surface furrows up to 2 m long, 3 cm wide, and 2 cm deep were observed at site A indicating that unionids were not entirely sedentary in the field. These trails were probably made only a short time before they were observed, since time lapse photography of the bottom by us in other parts of the lake have shown that such features do not last much longer than ten days because of frequent resuspension of the lake bottom by waves and currents. However, no *in situ* measurements of the extent or frequency of unionid movements were made.

The Burrowing Sequence

Fourteen *L. r. siliquoidea* and associated sediments were collected from site A and returned to the laboratory for observation. After being placed on their sides in aquaria containing their native sediment, the bivalves quickly commenced water pumping but otherwise remained motionless for 30-40 minutes prior to burrowing. In burrowing, after three or four tentative probing thrusts, the foot anchored in the sediment and the shell (average length 6.3 cm; n = 14) was pulled to an erect probing orientation. The angle created by the long axis of the animal and the sediment surface measured for five individuals ranged from 33°-50°, with a mean of 39°.

Penetration in each burrowing sequence, whether vertical or with a noticeable lateral component, was always accomplished by a slow, steady dilation of the foot. This was followed by brief closing and retraction of the inhalant and exhalant apertures and rapid valve adduction, which forced a powerful jet of water from the mantle cavity through the ventral margin of the shell. Rapid contraction of pedal muscles, first anterior then posterior, resulted in the shell rocking downward into the sediment. Both the ejection of water from the ventral margin and the rocking motion of the shell loosened and resuspended particles from the underlying sediment and transported a mixture of water and sediment both anteriorly and upwards to the substratum surface and overlying water. Continual water exchange between the surrounding sediment and mantle cavity was observed during the burrowing process (cf. Trueman, 1966, 1968a, 1968b; Trueman, Brand, and Davis 1966, for marine bivalves and the freshwater bivalve *Margaritifera*).

These burrowing activities often formed in the sediments a semi-permanent vent for the water ejected from the mantle cavity by valve adduction. This vent, as determined by x-radiography, extended through the sediments from the buried anteroventral region of the clam. The vent was observable at the sediment surface as a mound 4-5 mm high with a central circular hole approximately 3-4 mm in diameter (Figure 1).

Occasionally, individuals assumed a life position with the shell posterior projecting up to 9 mm above the sediment-water interface (Figure 2). Most of the animals, however, burrowed until the posterior tip of the shell was flush with the interface. Because the sediments were cohesive, the bivalves formed small depressions while achieving life position. Thus, while the shell posterior in life was flush with a local surface, it was actually located on the bottom of a depression 2-3 cm below the general interface (Figure 1).

Effects on Sediment Properties

Laboratory animals frequently reburrowed (2-3 times per week) and also used the foot in extensive

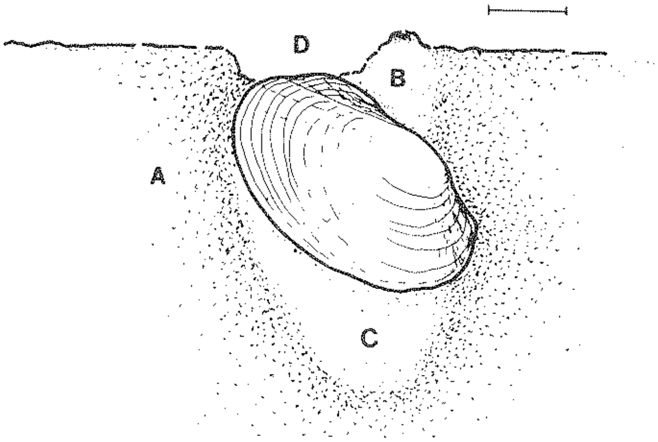

FIG. 1. L. r. **siliquoidea** *in infaunal life position. A = sediment unaffected by burrowing activities; B,C = zone of high water content produced by burrowing activity; D = depression in sediment-water interface produced by burrowing activity. Scale = 2 cm.*

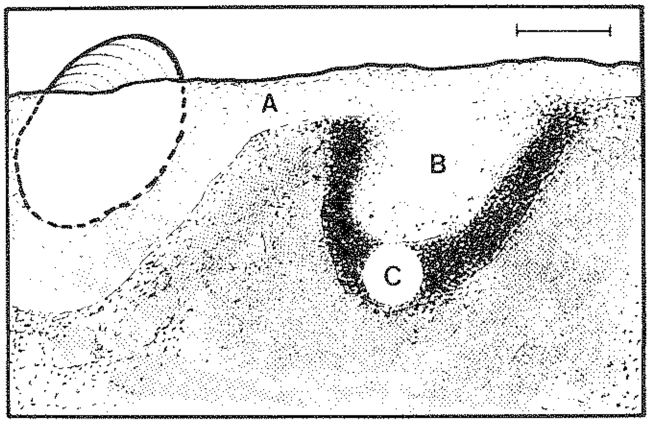

FIG. 2. Sedimentary effects of L. r. siliquoidea. *A = extensively reworked oxidized sediments; B = relict bivalve burrow containing oxidized sediments; C = rind of black sediments produced by intense bacterial reduction surrounding relict burrow. Scale = 4 cm.*

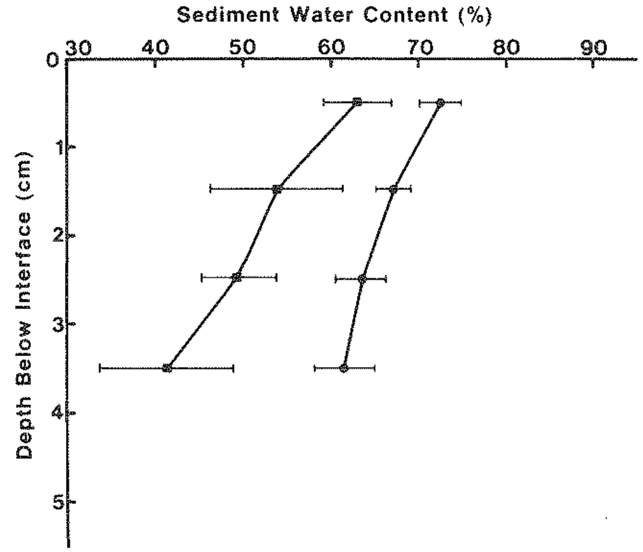

FIG. 3. Water content of laboratory aquaria containing Lake Erie sediment with (circles) and without (squares) L. r. siliquoidea. *Plotted points are means of four measurements. Bars represent 95% confidence intervals.*

semi-infaunal crawling. These activities plowed the sediment to a depth of 2-3 cm. *L. r. siliquoidea* produced two major effects on sediment physical properties. First, mucally bound pseudofeces were produced below the anteroventral margin of the shell in addition to being ejected onto the sediment surface (Figure 1). Second, burrowing increased sediment porosity and decreased compaction. Sediment water contents measured in the top 4 cm of laboratory aquaria containing western basin sediment and *L. r. siliquoidea* were 10-20% higher than in sediments without *L. r. siliquoidea* (Figure 3). Water content of sediment treated with clams falls in the range of *in situ* sediment water content (70-80%, Table 1) in this part of the lake, whereas sediment without clams does not. In addition, water content variance in sediment treated with clams was less than that with no treatment (Figure 3), indicating homogenization of the sediment by burrowing clams.

Smearing of powdered nickel laminae by unionids in thin-wall aquaria (Figure 4) is further evidence of sediment mixing and homogenization. Radiographs indicate that the unionids examined by us can mix sediments to a depth of 10 cm during burrowing. The combined widths of the shell and extended foot are about 5 cm. It is not possible to measure the width of the disturbed zone using these narrow aquaria, so we estimated that the

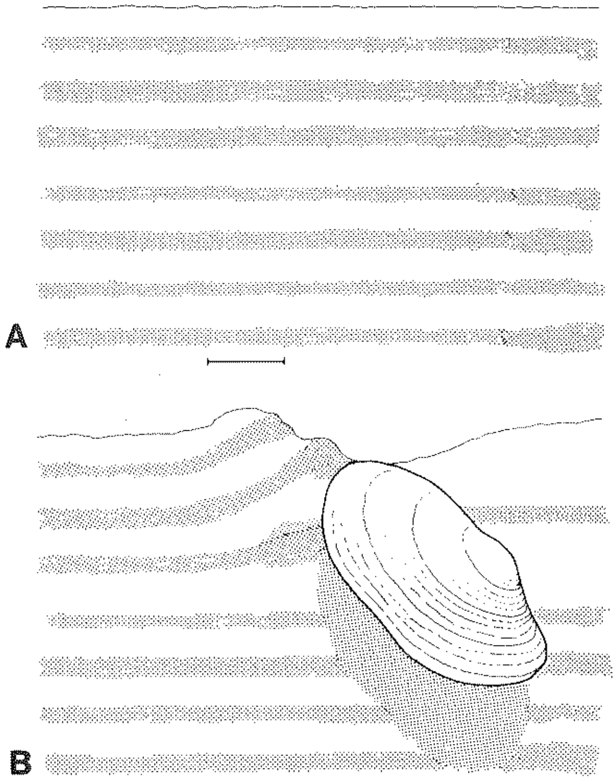

FIG. 4. Drawings made from radiographs showing bioturbation of sediments in laboratory by L. r. siliquoidea. *Opaque layers were produced by addition of a small amount of powdered nickel to sediments. A = thin-walled aquarium prior to introduction of bivalve; B = effects of one bivalve after seven days. Note destruction of sediment layers and smearing of powdered nickel. Scale = 2 cm.*

width of the disturbed zone is only a little greater than the width of the bivalve, say about 3 cm. This means that about 150 cm^3 (10 cm x 5 cm x 3 cm) of sediment are disturbed when a burrow is made by *Lampsilis*. In the large trays the volume of sediment disturbed by surface migration was measured. Surface furrows made by the clams were 2.5 cm wide and 2-3 cm deep. The clams moved 28-68 cm in the two-week observation period and averaged 42.3 cm per two weeks or about 3 cm/day/bivalve. Volume of sediment disturbed was thus about 15 cm^3/day/bivalve.

In the absence of unionid reworking, the top of the reduced zone in the laboratory sediments came to within 3-4 mm of the sediment-water interface. During unionid locomotion, both water and sediments were mixed across the redox discontinuity layer of the sediment. Coupled with water exchange during respiration, excretion, and shell cleansing, this unionid activity increased the volume of oxidized sediments. In 3-4 weeks the sediment in the small laboratory trays containing one bivalve each was oxidized to a depth of 3 cm. In addition, during burrowng the redox discontinuity layer was depressed to a depth of 10 cm around the burrowing animals whose average length was 6.3 cm. The oxic-anoxic sediment boundary at depth was sharply defined by a black zone of intense reduction and sulphide production lying immediately beneath fully oxidized sediments (Figure 2).

DISCUSSION

Sediment Mixing in Lake Erie

Sediment mixing by unionids is a function of animal density, frequency of burrowing, and life position relative to the sediment-water interface. Bivalve behavior may be altered by handling, container walls, food content of aquarium water, or any other of a variety of environmental factors that must be altered in the transition from the field to the laboratory. Allowing for these difficulties, it is still instructive to use the laboratory results to estimate the potential importance of unionids in altering sediment properties in western Lake Erie. If we allow one burrowing episode per unionid per week and the laboratory average amount of surface migration, then each unionid mixes 255 cm^3 of sediment per week [150 cm^3 + (15 cm^3/day x 7 days)]; so let us say each clam mixes 200-300 cm^3 sediment per week (at 19°C). Densities of 10-20 individuals m^{-2} are not uncommon in the western basin of Lake Erie (Wood 1953). At these population densities, unionids move 2-6% of the top 10 cm layer of western basin sediment per week at 19°C. Thus unionid burrowing activity may be of major importance in the alteration of sediment physical and chemical properties at depth in this part of Lake Erie.

Sediment mixing by unionid burrowing is not restricted to *L. r. siliquoidea*. Jernelov (1970), for instance, reported sediment reworking to a depth of 10 cm by an unidentified species of the unionid genus *Anodonta*. *L. r. siliquoidea* is not the largest bivalve in the western basin. If the same shell length/reworking depth relationship is true for the larger *Proptera alata* (found 5 cm below the sediment-water interface in one instance) as in *Lampsilis*, then biogenic reworking could occur in depths of at least 20 cm.

Unionid burrowing activity and resultant sediment redistribution may be the mechanism for the production of anomalously deep mixed profiles of sediment-associated materials in the western basin of Lake Erie. For example, Kovacik and Walters (1973) found evidence of homogenization of Hg in the top 10-20 cm of 25% of the sediment cores collected from the western basin and a portion of the adjacent central basin of Lake Erie (although they attributed this homogenization to current action). Wolery and Walters (1974) reported uniform profiles of Hg and Cr to 6 cm, while Walters, Wolery, and Myser (1974) showed profiles indicating irregular mixing to as much as 20 cm. Uniform profiles of Hg, Pb, Cr, and Zn were found by Kemp *et al.* (1976) to 8-10 cm in the western basin, suggesting intense mixing there. To reconcile sediment core profiles of *Ambrosia* pollen and Pb-210 in the western basin, Robbins, Edgington, and Kemp (1978) hypothesized deep (>15 cm) but incomplete biologic mixing that could be represented as an eddy diffusive process. We believe that this may be an accurate description of the unionid burrowing activity described here. Modelling sediment reworking by unionids is not possible without further experimentation. But unionids perform the same kind of non-directional bioturbation as the amphipod *Pontoporeia* that Robbins *et al.* (1979) modelled as an eddy diffusive process, although unionids do so on a different scale of time and space. It was not necessary to invoke any such mixing process to explain profiles in the central basin of Lake Erie and deep sections of Lake Ontario. This is consistent with the virtual absence of unionids from those areas. Mixed profiles in other parts of the Great Lakes where unionids are absent seldom extend below 5 cm (Robbins and Edgington 1975, Robbins *et al.* 1977).

It is not possible at present to completely separate the reworking effects of unionids, tubificid oligochaetes, and physical factors such as waves and currents. All are most effective in western Lake Erie where animal densities are high and the basin shallow. Annual sediment mixing rates by tubificids exceed the annual sedimentation rate by factors of 10 or more in western Lake Erie, but the depth of reworking of tubificids (~5 cm) is commonly less than that of unionids (Fisher 1979). Erosion and redeposition of sediments by waves and currents grade redeposited sediment by particle density and produce laminae visible in radiographs of sediment cores; biogenic reworking destroys these laminae (Moore and Scruton 1957, Rhoads 1970, Reineck and Singh 1973). While our examination has been limited, we have found laminated sediments in only one of six sediment cores from the western basin of the lake, from which it may be inferred that biologic reworking of sediments is an important mixing process here.

Effects on Sediment Biogeochemistry

Unionids can affect sediment biogeochemistry by their burrowing, and respiratory and excretory activities. The flushing of reduced sediments with oxidized water will alter profiles of phosphates which sorb to ferric hydroxide coatings on clay under aerobic conditions and desorb into sediment pore waters under anaerobic conditions (Mortimer 1971; Bray, Bricker, and Troup 1973). Many trace metals are likewise affected (Berner 1971, Troup and Bricker 1975). Biologic methylation of mercury and flux from the sediments are strongly dependent on the oxidation state of the sediment and reworking of macrofauna (Wolery and Walters 1974, Jernelov 1970). Biologic mixing and water exchange may stimulate microbial activity by pumping nutrients or metabolites into the sediments and purging microbial waste products from the bottom (Hylleberg 1975; Rhoads, McCall, and Yingst 1978). For instance, since reduced sediments contain already high concentrations of dissolved nutrients, oxygen supplied to reduced sediments greatly accelerates microbial activity (Hylleberg 1975). Sulphides will be oxidized to sulphates in the newly-created oxidized zone. The sulphates will diffuse into the surrounding sediment and be reduced to sulphides. The black rind of iron sulphides surrounding unionid burrows in our laboratory microcosms is evidence of this biostimulation of sulphate-reducing bacterial activity (cf. Aller 1977).

Unionids may stimulate microbial productivity in additional ways. First, the organic-rich mucus-coated pseudofeces produced by *Lampsilis* provide a labile, potentially rich microbial food resource. Second, because unionids necessarily have a large surface area of semi-permeable ctenidium exposed to the external medium and have internal tissues hypertonic to the media in which they live, they are subject to an osmotic inflow of water that must be balanced by the production of urine hypotonic to the blood but hypertonic to the external medium (Potts 1954a). Copious amounts of urine are produced. Potts (1945b), for instance, found that the unionid *Anodonta cygnea* had an excretion rate amounting to 44.7% ± 25.9% (s.d.) of individual body weight per day at 15°C. Nitrogenous wastes and salts in the urine may also stimulate microbial production.

CONCLUSION

The burrowing feeding, and respiratory activities of *Lampsilis r. siliquoidea* alter the physical and chemical properties of lake sediments. Future experiments might profitably concentrate on determining *in situ* unionid population densities and rates of sediment reworking, modelling the effects of unionid burrowing on vertical profiles of sedimentary materials, and on demonstrating the microbial 'gardening' effects of unionid activities.

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