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THE EFFECTS OF A UNIONID BIVALVE ON THE PHYSICAL, CHEMICAL, AND MICROBIAL PROPERTIES OF COHESIVE SEDIMENTS FROM LAKE ERIE†

PETER L. McCALL*, GERALD MATISOFF*,
and MICHAEL J. S. TEVESZ**

ABSTRACT. *Lampsilis radiata* is a large, burrowing, suspension-feeding bivalve which dominates the macrofaunal standing crop biomass of the muddy sediments of western Lake Erie. Bivalve crawling mixes sediments to depths of 3 cm, while burrowing mixes sediments to maximum depths of 30 cm. Burrowing reduces sediment resistance to torque bar shear (x2) in the region near the burrow but increases resistance to shear (x1.5) at a distance of 5 cm from the burrow.

Suspension-feeding produces a layer of feces and pseudofeces at the sediment-water interface. In this layer, clay particles are tightly bound to themselves but only loosely bound to underlying sediment. Bacterial biomass is enhanced, but growth of binding filamentous bacteria is apparently inhibited. Sediment entrainment rates in a laboratory flume are increased by factors of 20 to 50 at fluid shear stresses of 1 to 2 dynes · cm^{-2} compared to sediment with no bivalves while settling velocity and aggregates are increased by a factor of 7 to 10. The entrainment effect nearly disappears at stresses $\geq$ 6 dynes · cm^{-2}.

L. radiata also alters pore water chemistry and nutrient transport in laboratory microcosms. The bivalve burrow induces radial diffusion of solutes through the burrow wall and suggests about a 30 percent increase in ammonium-nitrate flux into overlying water. However, direct measurement of ammonium + nitrate accumulation in water overlying bivalves and sediment is 1.6 times greater than expected from radial diffusion and bivalve excretion. We think this synergistic increase in flux is due to enhanced bacterial growth rates near the burrow wall.

Sediment bacteria growth rates were increased by as much as a factor of 2 in microcosms containing bivalves. This enhancement is largest at greater depths below the interface, up to at least 4 to 6 cm depths, and extends at least 5 cm from the burrow wall.

The animal-sediment-benthic boundary layer system is sufficiently complex that we cannot use these laboratory results to predict field results with confidence. Physical, chemical, and biologic effects interact, and the presence of other fauna can accentuate or counteract the effects of *L. radiata*.

† Contribution 148, Department of Geological Sciences, Case Western Reserve University, Cleveland, Ohio 44106

* Department of Geological Sciences, Case Western Reserve University, Cleveland, Ohio 44106

** Department of Geological Sciences, Cleveland State University, Cleveland, Ohio 44115

INTRODUCTION

Macrofauna can affect sediment and solute transport via a number of pathways (fig. 1), and it is important to understand the relative contribution of each pathway if we hope to understand these processes in natural systems. To give just a single example, a burrowing organism may alter the porosity of a fine-grained bottom and thereby enhance flux of a solute across the interface (fig.1, pathway 5); the burrower may also inject nutrients into sediment pore water and enhance microbial growth, which in turn may also enhance the flux of a solute by increasing its production or consumption in the sediment (fig. 1, pathway 4). Were the latter pathway a relatively important one for a particular solute, then we would know to include in future studies of that solute flux other pathways that also affect microbial growth. In a real system containing many species, enhanced microbial growth due to one organism may attract other deposit feeding macrofauna which themselves may have synergistic or antagonistic effects on the flux. The abundance of yet other species could be changed by some effect of our burrower on sediment (pathway 1A); this species may then alter solute flux by changing physical properties in such a way as to change microbial growth (pathways 3,4). Thus physical, chemical, and biologic alterations of cohesive sediment are closely interrelated. For this reason the examination of several effects together has some advantages over a more piecemeal approach. Moreover, a single macrofaunal activity (for example, burrowing) may affect a number of different sediment properties (see, for example, Grant, Boyer, and Sanford, 1982), and so a certain efficiency is achieved by examining many of them at once.

We will examine the multifarious effects of *L. radiata*, a burrowing suspension-feeding bivalve, on sediment transport, solute flux, and microbial growth, and we will give some examples of interacting pathways involving *L. radiata*.

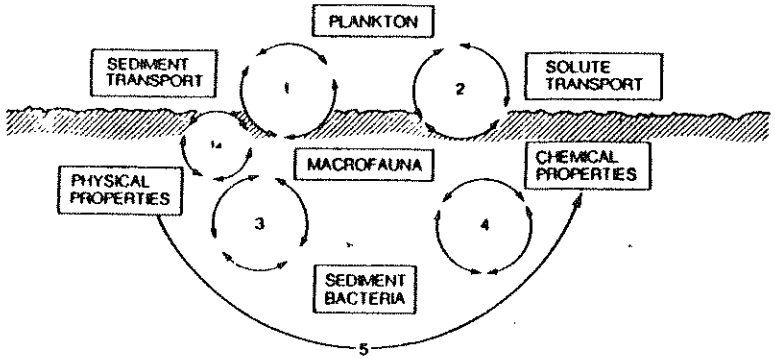


Fig. 1. Schematic depiction of animal-sediment-water interactions in muddy sediments.

L. radiata occurs throughout the Mississippi and Missouri river system, all of Canada east of the Rocky Mountains, the St. Lawrence drainage, and the Atlantic Slope south to South Carolina. It is found in lakes and streams on substrata ranging from muds to gravels and is frequently the most abundant bivalve in these environments (Burch, 1973; Clarke, 1973). Unionid bivalves have the largest standing crop (82.5 $g \cdot m^{-2}$ wet) and individual biomass (avg individual wet wt is about 10.5 g) of any invertebrate group in western Lake Erie, and *L. radiata* is the most abundant unionid (Wood, ms).

We provide here some quantitative measurements of the effect of *L. radiata* on: (1) the physical properties and the rate of entrainment of cohesive sediments; (2) vertical gradients and radial diffusion of pore water solutes; and (3) growth rates of sediment bacteria *in situ*.

STUDY AREA AND METHODS

Lake Erie is the shallowest and most productive of the Great Lakes. Its bottom sediments are thus mobile and reactive, and the benthic macrofauna are abundant. Suspension-feeding unionid bivalves are found primarily in the shallow western basin in gravels, sands, and muds. Silt-clay size sediments occupy over 80 percent of bottom area. They typically contain <5 percent sand by weight; approximate composition is 40 percent quartz, 16 percent feldspar, 6 percent dolomite, and 35 percent illite clay. Typical organic matter content is 4 percent by weight; water contents of the top 1 cm of western basin muds range from 70 to 85 percent. Both the clams and the sediments used in our experiments were collected from the western basin (41°39′58″N, 82°56′36″W, depth 8.6 m).

Burrowing behavior and physical properties.—The locomotory and burrowing of *L. radiata* were observed in three different tanks filled with western basin sediment placed within a 60-gallon aquarium filled with aerated and filtered Lake Erie water maintained at 21°C. The sizes of the tanks were as follows: tank A, 29 cm × 19 cm × 14.5 cm; tank B, 17.5 cm × 17.5 cm × 11.5 cm; tank C, 20.5 cm × 9.0 cm × 12.5 cm. Two *Lampsilis* ranging in length from 5.5 to 7.0 cm were placed on their right valves in the middle of each tank. Locomotory activities were monitored with a 16 mm movie camera equipped with an intervalometer. Two time-lapse studies 6 and 11 days long were performed.

In order to determine the depth to which *L. radiata* mixes sediments, two 17.5 cm × 4.0 cm × 11.5 cm tanks were filled with alternate layers of powdered nickel (opaque to X-rays) 2 to 3 mm thick and Lake Erie sediments (non-opaque to X-rays) approx 2 cm thick. The powdered nickel was encased in rice paper to prevent it from smearing as the natural sediment was added. The rice paper dissolved in the wet sediments in a matter of hours, leaving the powdered nickel in reasonably thin and flat layers within the sediments. Boxes with *Lampsilis* added were placed in a 60-gallon aquarium containing continuously aerated and filtered Lake

Erie water at 21°C and were radiographed weekly for a month, then the experiment was repeated. In order to determine the volume of sediment disturbed by *Lampsilis*, three large tanks (20.5 cm × 9.0 cm × 12.5 cm) were used.

To measure the extent of fabric alteration caused by *Lampsilis*, we elected to use a rotational viscometer that measured the torque necessary to turn a T-bar spindle within the sediment. We first examined the relationship of water content and torque measurements in the top 6 cm of 14 cores sliced into 1 cm thick layers collected from two tanks filled with remolded western basin sediment. To measure the effect of *Lampsilis* on sediment compactness, three 17.5 cm × 17.5 cm × 11.5 cm tanks were filled with homogenized western basin sediment and placed in a 30-gallon aquarium filled with aerated, filtered Lake Erie water maintained at 21°C. Four *L. radiata* were placed in two of the microcosms, while the third served as a control. Twenty-one days later, sediment compactness was determined.

Entrainment measurements.—An annular flume of outside wall radius 66 cm and channel diameter of 15 cm was used to measure the entrainment of variously treated western basin sediment. An annular ring in contact with the water surface was rotated with a 1/8 hp electric motor to produce a shear flow which, in turn, exerted a shear stress on the stationary sediment-water interface (surface area 0.65 m^2). A hot film anemometer had been used to measure vertical velocity profiles across the channel; wall shear stress was determined by fitting velocity profiles to the law of the wall, and the relation between ring rotation rate and average bottom shear stress was calculated (Fukuda and Lick, 1980). The annular design gives rise to a small secondary flow in the flume, which was not measured by Fukuda and Lick (1980); thus the stresses reported here probably underestimated the absolute value of the bottom stress by at least 10 to 15 percent (P. Sheng, personal commun.), but with- and without-bivalve comparisons should not be greatly affected.

Western basin sediment was sieved to remove macrofauna and added to the flume to a depth of several centimeters, and filtered lake water was added to a height of 7.6 cm. In one set of experiments seven bivalves were added to the sediment after 1 week; in another, no clams were added. Every 3 days thereafter, the water in each experiment was stirred with a paddle to resuspend the top few millimeters of the sediment so that it would be processed by the suspension feeders. Laboratory windows open to daylight were covered with black plastic to simulate more closely typical *in situ* light conditions. On the ninth day the entrainment experiments began. All experiments were run with the same 3-day settling interval. To begin an experiment, the ring was accelerated to increase bottom shear stress at the rate of 0.1 dynes · cm^{-2} · min^{-1} until the desired test stress was achieved (2, 3, 4, and 6 dynes · cm^{-2}). This was taken to be time zero. From this point, the concentration of suspended solids was measured at 5 or 10 min intervals until some equilibrium or quasi-equilibrium between erosion and deposition was reached. Entrainment rate was calculated as

$$E = \lim_{C \to 0} h\, dC/dt,$$

where h is the depth of overlying water and dC/dt is the slope of the concentration versus time curve (Fukuda and Lick, 1980). An exponential was fit to the data by a non-linear least squares method (James, ms) for extrapolation on the slope to zero concentration.

To measure settling velocity of eroded particles, overlying water and suspended matter were withdrawn from the flume, and concentration of sediment was corrected to ~500 mg/l by dilution or pre-settling and elutriation. This material was put in a one liter graduated cylinder and mixed, after which 20 ml samples were drawn with a pipette at a depth of 20 cm over a period of 48 hrs. Samples were filtered through 0.45 μm Gelman filters, dried, and weighed to calculate mass flux and median settling velocities.

SEM observation of the sediment surface was performed by taking a small sediment core (plastic soda straw corer) and preserving it in 2 percent gluteraldehyde. The sediment was then washed free of gluteraldehyde and dehydrated in a graded series of ethanol washes (25, 50, 75, 95 percent, and 2 washes in 100 percent ethanol). Cores were then critical point dried, sectioned, mounted on stubs, and coated with gold-palladium.

Pore water chemistry.—Two tanks containing sediment and overlying water, one with 12 bivalves and the other containing none (control), were monitored for the accumulation of dissolved solutes (NO_3^-, Fe^{2+}, HCO_3^-, Cl^-, ΣH_4SiO_4, and ΣH_3PO_4) in the overlying water, and the bivalve-containing tank was cored for pore water analyses. About 8 gallons of surficial mud was obtained from the western basin of Lake Erie by grab sampling. The mud was passed through a 250 μm sieve to remove large particles and macrobenthos and was thoroughly mixed with NaCl that served as a conservative solute tracer. The interstitial water chloride concentration rose from ~20 to ~150 ppm. Twenty liters of the sediment-water mixture were poured into each of the 29.2 cm × 44.5 cm aquaria and allowed to settle for 1 month at 24°C to a thickness of 12 cm (71-78 percent water content, 4 percent organic carbon) at which time the overlying water was carefully decanted and replaced with 11.7 l of deionized water. Twelve bivalves were then carefully placed on the sediment surface in a 4 × 3 pattern. Overlying waters were sampled over a period of 19 days, and after 28 days the sediment in the tank containing bivalves was cored with 16 mm tubes at distances of 5, 8, and 10.5 cm from the center of a clam burrow. In a helium-filled glove bag each core was sectioned into 2 cm intervals and centrifuged at 2000 rpm for 30 min to separate the interstitial water. After centrifuging the sample was drawn into a plastic syringe and filtered through a nitrogen-purged 0.2 μm Gelman Acrodisc. Only the results for the conservative pore water tracer Cl^- and the reactive nutrients NO_2^- + NO_3^- and NH_4^+ are reported here. Cl^- was determined by titration;

$NO_3^- + NO_2^-$ was determined using a Technicon AutoAnalyzer II under an inert atmosphere; NH_4^+ was determined colorimetrically with a Beckman DU Spectrophotometer.

The added bivalves were 5 to 7 cm long and averaged 2.8 g dry wt without shell. The introduction of twelve bivalves into a tank can result in clam metabolic by-products accumulating in the water. In order to distinguish this source of solutes from that that has fluxed from the sediment, we monitored the concentration of the same solutes as in the bivalve experiment in an "excretion" experiment. This consisted of placing three bivalves in 750 ml of deionized water or deionized water plus sediment and monitoring the concentration of solutes in the water for a period of 200 hrs.

Bacterial measurements.—Bacterial growth rate experiments were performed in laboratory aquaria (29.2 × 44.5 × 35.0 cm). Sediment collected from the western basin of Lake Erie was passed through a 250 μm sieve to remove macrofauna. Sieving was carried out under a helium atmosphere to avoid oxidizing reduced sediments. No water was added to the sediment during sieving. Sieved sediment was added to the microcosms and allowed to settle. Filtered Lake Erie water (17.5 l) was added on top of the sediment. A 4-week period was allowed to achieve a final sediment thickness of 12 cm and to allow pore water chemical gradients to re-establish. Then six *Lampsilis* were added to one aquarium, while no additions were made to the other. Bivalves were allowed to burrow for 4 weeks. Overlying water was changed twice a week. Temperature was held constant at 24°C.

Hesslein (ms) used a series of chambers, called "peepers," separated from surrounding sediment by dialysis membrane to study vertical profiles of pore water geochemistry. Following his idea, we constructed a set of chambers that enclosed pore water and sediment of known bacteria content but that allowed the diffusion of pore water from the surrounding sediment. A piece of 2 cm long teflon pipe (1.2 cm ID × 2.0 cm long) formed the body of the peeper; the ends were wrapped with 0.2 μm Nuclepore membranes and held in place with dental rubber bands. Sterile water was added to peepers, and they were placed in racks holding five peepers (midpoint of peepers at 1, 2, 3, 4, and 6 cm below the sediment-water interface) which were put into the aquaria for 2 weeks to equilibrate with surrounding pore water. The fraction of equilibrium reached at time t can be estimated by assuming a planar diffusion source (Hesslein, ms). The peepers are 90 percent equilibrated after 10 days, 92 percent equilibrated after 2 weeks, and 93 percent equilibrated after 3 weeks. After 2 weeks, a core of sediment was removed from each aquarium, sectioned into 1 cm intervals, and a portion of each section autoclaved. Peeper racks were removed from the aquaria. Under a helium atmosphere, about 2 g of autoclaved sediment mixed with a small innoculum of untreated sediment from the 1, 2, 3, 4, and 6 cm levels were added to peepers from the corresponding depth. A portion of this sediment was retained for counting the initial bacterial abundance. The racks were replaced into

the aquarium sediment, and then a rack was removed for counting at 1 day and then at 4 days after inoculation.

Bacteria were counted using the acridine orange direct count method of Hobbie, Daley, and Jasper (1977) as modified by Watson and others (1977). A Leitz Orthoplan outfitted with Pleomopak 2.1 and 150w xenon lamp was used for epifluorescent illumination and counting. Twenty microscope fields (100 × 100 μm) were counted in transects running from the margin of the sample toward the sample center. Mean sample bacterial abundances of sediment from the western basin of Lake Erie can usually be estimated to within 10 percent of the true sample mean by this method.

RESULTS

Burrowing.—Each bivalve burrowed into the sediments within 2 to 48 hrs after being placed in the microcosms. *Lampsilis* burrows by extending its foot away from its shell and into the sediments, dilating (thus anchoring) the foot within the sediments, and then rapidly contracting its pedal muscles (anterior, then posterior). These activities resulted in the shell rocking downward into the sediment. There is frequent water exchange between the overlying water and the bivalve's mantle cavity, and between the mantle cavity and surrounding sediments during the burrowing processes. A common life position of *Lampsilis* in western basin sediments is shown in figure 2.

After burrowing, all the clams remained largely within the sediment, and all subsequent locomotion was confined to lateral crawling. *Lampsilis* crawled semi-infaunally by orienting the anteroposterior axis of its shell at a low angle to the sediment-water interface and then moved by extending and retracting its foot.

The rate of crawing by *Lampsilis* in these two time-lapse studies is shown in table 1. This table shows that *Lampsilis* can be an active crawler.

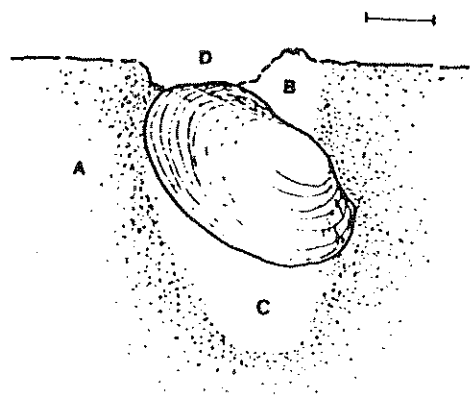


Fig. 2. Typical life position of *L. radiata*. A = sediment unmixed by burrowing; B, C = zone of complete sediment mixing; D = burrow opening. Scale bar = 2 cm.

The greatest lateral distance traveled by a single *Lampsilis* in 1 day during this experiment was 96 cm. The table also shows that there is no apparent effect of microcosm size on rate of movement. All burrowing and crawling activity had ceased by day 5 in the first study and day 7 in the second. It was observed that both exhumation and burial stimulated vertical movement of *Lampsilis*, and Barnes (1823) and Stansbery (1961) noted seasonal differences in the behavior of mussels (buried in winter, more exposed in summer), so that *in situ* rates may well be substantially different from our laboratory values.

It was apparent that all the sediment mixing occurred during the first week of the experiment. The burrowing activity of these bivalves produced a powdered nickel "halo" that extended 1 cm away from the shell dorsally and ventrally and about 2 cm anteriorly. This halo represents an area of complete sediment mixing, because laminae were completely obliterated wherever they intersected the halo.

The depth of mixing varied with the depth of burrowing and orientation of the bivalve. The maximum depth of mixing was achieved with the antero-posterior axis of the bivalve vertical or nearly so, and the bivalve was buried completely within the sediment. The halo of complete mixing represents an area where the large and flexible foot is active. Incomplete mixing results from infrequent deep probing of the foot, and from the forceful expulsion of water during the burrowing and mantle-cavity cleansing. The maximum depth of incomplete mixing for *Lampsilis* was about twice the shell length. Since *Lampsilis* grows to lengths of over 15 cm, it likely mixes sediments to depths of 30 cm or more. This confirms the observations of *Lampsilis* burrowing behavior made by McCall, Tevesz, and Schwelgien (1979).

Even a 5 cm long bivalve will typically produce a 4 to 5 cm diameter subcircular tube of disturbed sediment extending 10 cm into the sediment. Bivalve crawling, however, completely mixes sediments only to depths of 3 cm below the sediment-water interface. Because the anteroposterior axis of the bivalve is at a low angle to the sediment-water interface, the shell and foot do not penetrate the substratum as deeply as during burrowing.

Physical properties.—The fabric of sediment in the mixed zone is altered during burrowing. Most benthic ecologists usually report fabric changes as changes in sediment water content: burrowing mixes water with sediment and decreases interparticle contacts. With increasing sediment-water content, both erodibility of particulates under flow and pore water solute flux usually increase (see reviews in McCall and Tevesz,

TABLE 1

Migration rates of *Lampsilis* in laboratory aquaria

	Experiment I (6 days)			Experiment II (11 days)		
Tank size (see text for explanation)	A	B	C	A	B	C
Rates (cm/bivalve/day)	6.3	8.1	14.0	10.1	1.3	0

1982). A few authors have measured either the torque on small shear vanes (for example, Rowe, 1974; Rhoads and Boyer, 1982) and torque bars (Myers, 1977) or sediment bearing strength with penetrometers (Bokuniewcz, Gordon, and Rhoads, 1975) to examine biogenic change in fabric. Water content is usually measured as weight loss on drying of sliced sediment cores. Sampling error increases as core diameter falls below 2 cm. Laboratory shear vane or torque bar measurements are more easily made than water content measurements and can be made on a smaller spatial scale and with less sediment disturbance. However, Rhoads and Boyer (1982) found no significant relationship between their shear vane measures and sediment water content. We found a significant correlation of torque and water content ($r = -.62$, $n = 68$, $p < 0.001$) but a linear regression of water content on torque explains only 45 percent of the variance of the data (fig. 3). These data were collected with a 3.65 cm long torque spindle. In order to investigate sediment properties near clam burrows, a smaller spindle was required so that the bivalves would not interfere with spindle rotation.

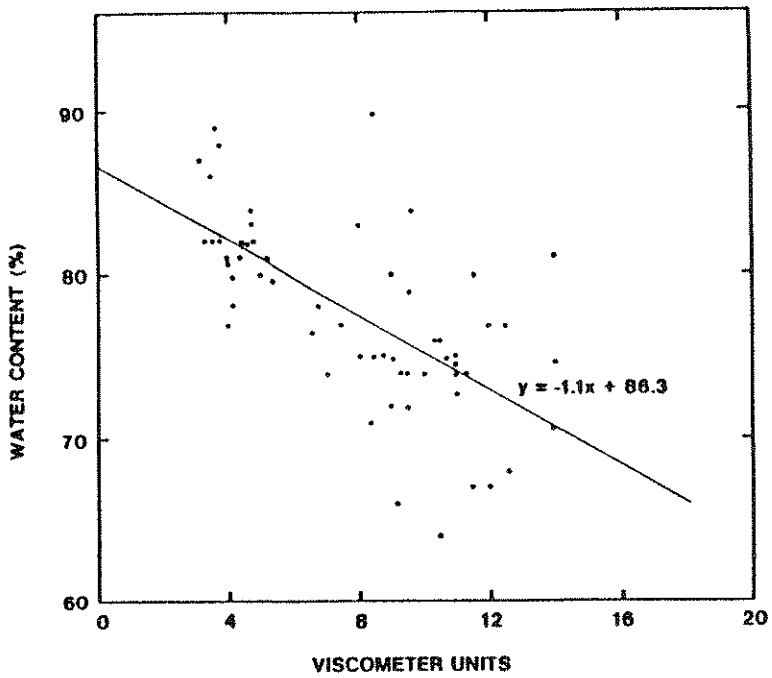


Fig. 3. Regression of water content of laboratory sediment on viscometer torque. T bar length = 3.65 cm, diameter = 0.07 cm. Rotation rate = 10 RPM One viscometer unit = 575 ergs.

Figure 4 shows that *L. radiata* reduces sediment resistance to shear by a factor of two or more in sediments immediately adjacent to it. These lower readings were taken in areas where the foot of the bivalve is highly active and where pressurized water is often ejected from the mantle cavity during burrowing and cleansing activities. The bivalves have the additional but more widespread effect of *increasing* sediment resistance by as much as a factor of 1.5 in other parts of the tank.

Sediment transport.—The usual effect of burrowers that increase sediment water content in cohesive sediments is to make sediment easier to erode. However, this is not an invariable result (McCall and Fisher, 1980; Nowell, Jumars, and Eckman, 1981). Moreover, most of the studies involve small and numerous deposit feeders and not large and less abundant suspension feeders like *Lampsilis*. We sought to discover what effects, if any, *Lampsilis* behavior had on erosion of sediment by fluid shear.

No erosion of flume sediment took place in bivalve-treated or control sediment at an estimated bottom stress of 1 dyne · cm^{-2}. Very little erosion took place in control sediment at 2 dynes · cm^{-2} (fig. 5; table 2), while very unusual behavior was observed in clam-treated sediment. A large amount of material was rapidly entrained between 1 and 2 dynes · cm^{-2},

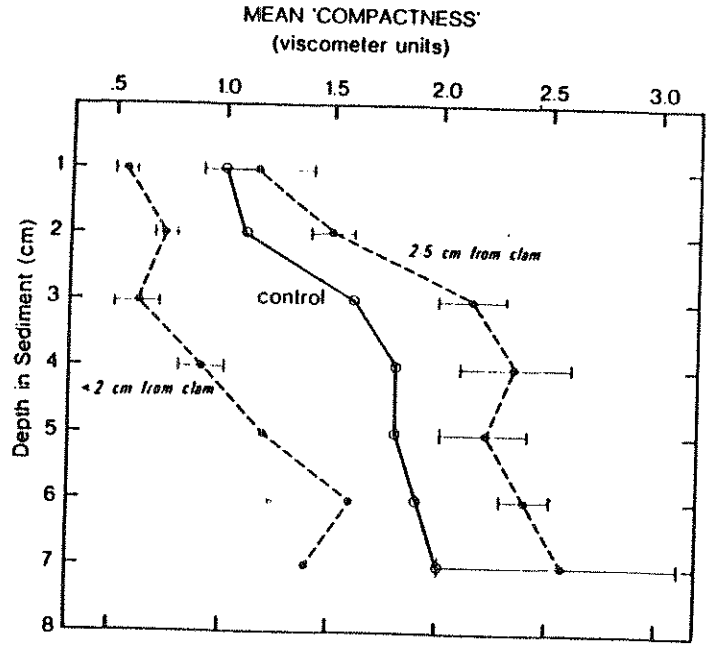


Fig. 4. Effect of *Lampsilis* on viscometer torque near and far from clam burrow. T bar length = 1.09 cm, diameter = 0.07 cm. Rotation rate = 0.5 RPM. One viscometer unit ≅ 575 ergs.

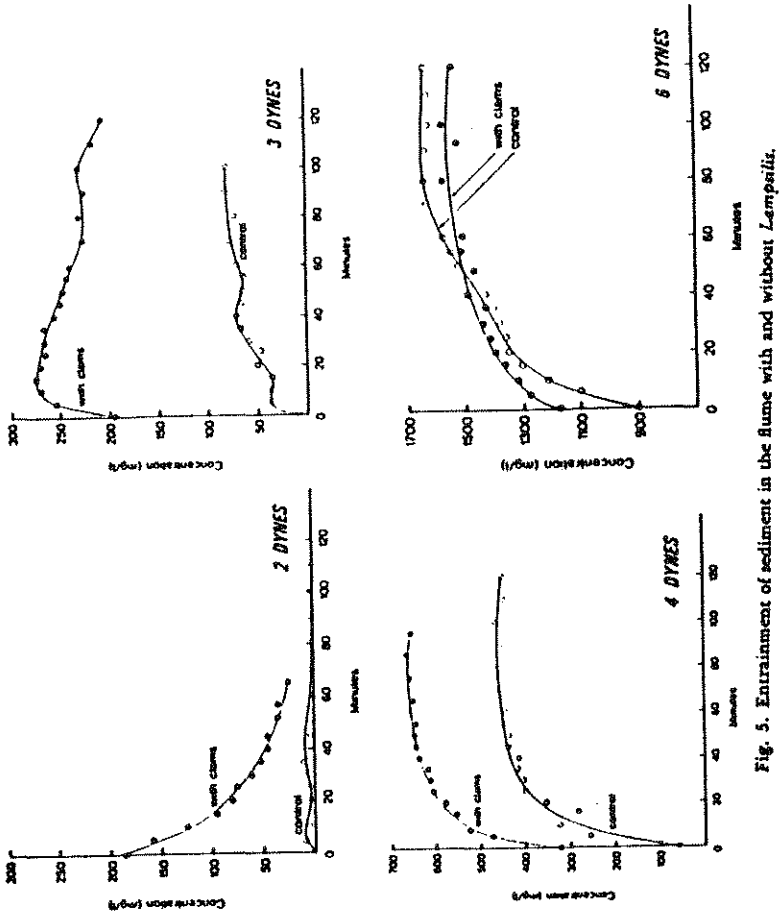


Fig. 5. Entrainment of sediment in the flume with and without *Lampsilis*.

TABLE 2

Entrainment rate of surface sediment with and without *Lampsilis*

Bottom shear stress	Control E (mg sed/cm²/sec×10⁻⁵)	With clams E (mg sed/cm²/sec×10⁻⁵)	Ratio $E_{clams}/E_{control}$
2	0.1 (est)	5.1 (est)	50
3	0.3	9.2	30
4	4.3	6.7	1.5
6	7.2	7.9	1.1

but by the time the test stress of 2 dynes · cm⁻² was achieved, this material was already settling out of suspension without being re-eroded. The entrainment rate, E, can be estimated since the stress at which entrainment began (1.5 dynes · cm⁻²) and the rate of increase of applied stress are known. An equilibrium concentration, C_{eq}, where entrainment balances deposition, does not really exist for this test, but the maximum achieved concentration was above 185 mg/l. At 3 dynes · cm⁻² this behavior is less pronounced. At 4 and 6 dynes · cm⁻², more typical kinds of entrainment curves were observed. The treatments can be compared on the basis of C_{eq} or E. We have chosen to emphasize E, since its measurement is less sensitive to unknown particle-flow interactions that increase as particle concentration increases. Entrainment rate measurements indicate that the effect of the bivalves is to make the sediment easier to erode. The effect is greatest at low shear stress, 2 to 3 dynes · cm⁻², and nearly disappears at 6 dynes · cm⁻².

The bivalve effect in these experiments was likely due to suspension-feeding activity. A large amount of feces and pseudofeces was produced by the bivalves sufficient to make a millimeter or so thick layer at the sediment-water interface. It is primarily the top few millimeters of sediment that are entrained. If just the entire top 1 mm of sediment were entrained, the overlying water concentration would be 2000 to 3000 mg/l, which is greater than that observed in our experiments (although it is unlikely that the interface is uniformly eroded). We examined the settling velocity distribution of eroded particles and found that settling velocity (size) increased with applied fluid shear stress in control beds; the opposite trend was noted in bivalve-treated beds (fig. 6). Settling velocities of particles eroded at 1-2 dynes · cm⁻² are 7 to 10 times larger in bivalve-treated sediment than in control sediment, and yet they are more easily entrained than control particles. Figure 7 shows that the median settling velocity of fresh pseudofeces is about three times greater than the parent material making up the control bed. As ejecta are colonized by bacteria (table 3), the aggregates decay and median settling velocity decreases, but after 2 weeks it is still 50 percent greater than median settling velocity of parent material. Figure 7 also shows the settling velocity distribution of material entrained from parent material at 3 dynes · cm⁻², where significant erosion begins. Were the offset of fecal material from parent material maintained during entrainment, the observed differences in median settling velocity between control and bivalve-treated sediment in figure 6 could be accounted for.

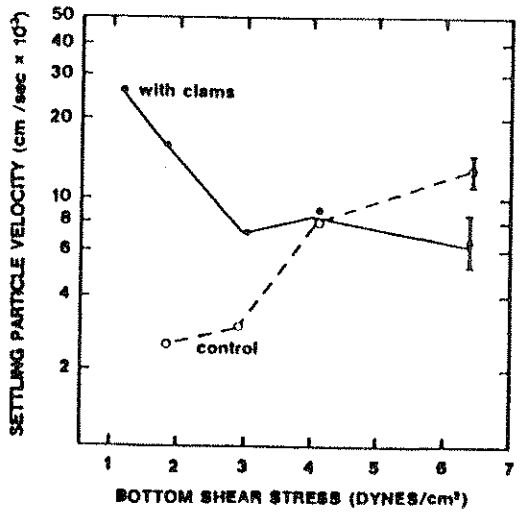


Fig. 6. Median settling velocities of sediment eroded in the flume and suspended in overlying water.

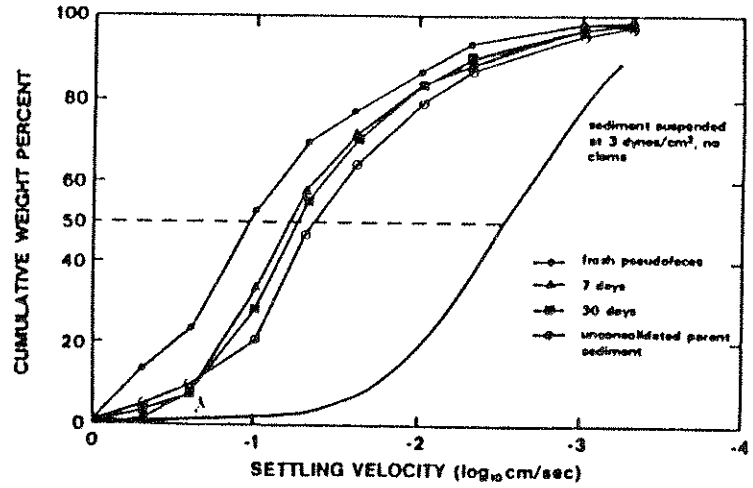


Fig. 7. Settling velocity (size) distribution of parent sediment and clam pseudofeces incubated for various amounts of time.

TABLE 5

Colonization of *Lampsilis* pseudofeces by bacteria

Material	Bacteria Abundance (Number/gm dry wt sediment × 10^9)
Parent surface sediment	2.47
Fresh pseudofeces	5.00
7 days	4.87
14 days	4.86
30 days	4.11

SEM photos of the sediment-water interface also show the effect of bivalve suspension feeding and pseudofeces production. On day 0, the first day after thorough mixing of the approx 8 cm thick sediment column, clay particles from the sediment-water interface of a tank with no bivalves have clean mineral surfaces and occur in an open fabric. No filamentous bacteria are evident (pl. 1-A). By day 4, the clay particles are covered by bacterial exopolymer and are arranged in more compact structures (pl. 1-B). A few filamentous bacteria are present. By day 8, filamentous bacteria are abundant and form a matlike covering on the sediment surface (pl. 1-C). In the tank with bivalves, already on day 0 clay particles are arranged in compact structures, and a thin drape of mucus is apparent on some grains (pl. 1-D). By day 4, grain surfaces are still not coated with bacterial exopolymers, and no bacterial filaments were observed (pl. 1-E). It is only by day 10 that exopolymer coated grains are obvious, but filamentous bacteria are still rare. One effect of the bivalves is apparently to inhibit the fouling community. Although it is clear from the bacterial counts of pseudofeces that feces are enriched in bacteria (fig. 7), they evidently do not grow as filaments on grains or excrete a large amount of exopolymer. Thus the SEM photos are compatible with the notion of a layer of clay particles tightly bound to themselves but only loosely bound to underlying sediment particles.

Pore water chemistry and solute flux.—Just as infaunal burrowing and feeding activities alter a number of different physical properties of cohesive sediments, which directly and indirectly control erodibility of interfacial particulates, so they also alter a number of chemical properties of the sediment pore water directly and indirectly control the flux of dissolved solutes across the interface (Schink, Guinasso, and Fanning, 1975; Granelli, 1979; Aller, 1978, 1980, 1982; Hammond and Fuller, 1979; McCaffrey and others, 1981; Fisher, 1982; Matisoff, Fisher, and Matis, 1985). Most previous work has examined organisms which are small by comparison to *L. radiata*.

The photograph in plate 2 shows a cross section through a bivalve burrow. The sediment is zoned around the burrow. The lighter material is 'oxidized' and attains its color from ferric oxyhydroxides, while the darker material attains its color from reduced compounds, especially FeS. Aller (1982) predicts that this zonation should occur due to the sequential consumption of O_2, NO_3^-, MnO_2, $Fe(OH)_3$, and SO_4^{--} during organic matter decomposition. It is clear from the photograph that the mere pres-

PLATE 1

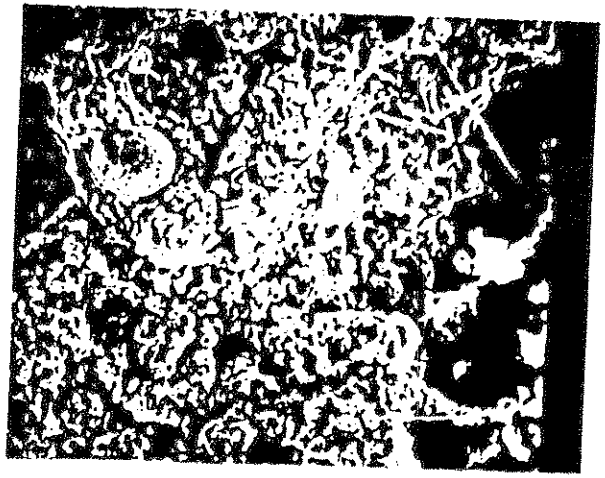
SEM photos of sediment surfaces without (A, B, C) and with (D, E, F) clams. (A) = day 0; (B) = day 4; (C) = day 10; (D) = day 0; (E) = day 5; (F) = day 10. Explanation in text.

PLATE 1 (continued)

C.

5μm

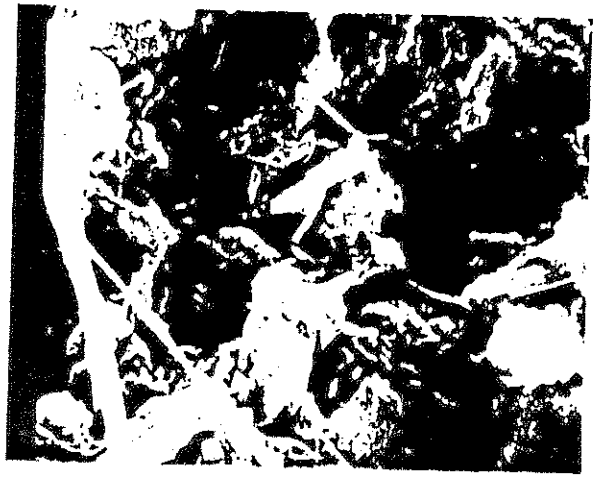
D.



50μm

PLATE 1 (continued)

E.

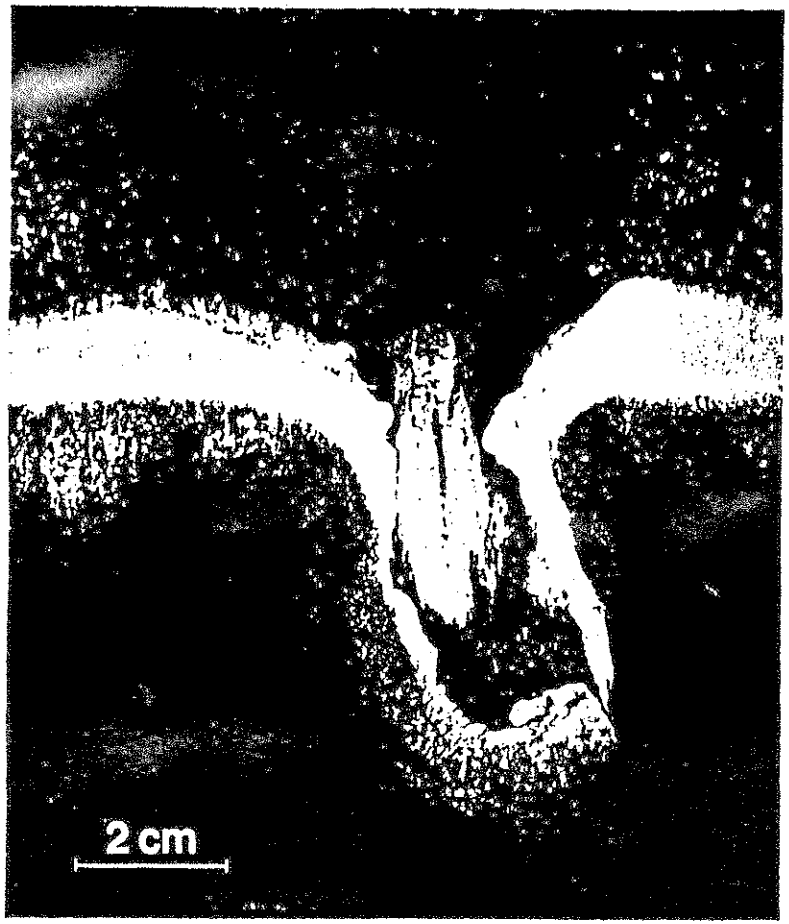


2μm

F.

1μm

PLATE 2



Cross section through a clam burrow showing color zonation around the burrow caused by zones of oxidation-reduction reactions.

ence of the burrow enables oxygenated overlying water to penetrate 6 to 8 cm into a zone that was once reduced sediment. The burrow introduces a three-dimensional geometry into the sediment and induces three-dimensional solute transport. Oxygen diffuses into the sediment from the sides of the burrow as well as from the top surface. The bivalves play a passive role: these processes will occur as long as the burrow is maintained and do not require the direct injection of oxygenated overlying water by the bivalve.

Effects of *Lampsilis* on the solute exchange between sediment and water and on rates of organic matter decomposition can be seen in the sediment pore waters at the end of the flux experiment (fig. 8). NH_4 produced from organic matter decomposition in the sediment, is fluxed toward the sediment water interface. NO_3 is produced by microbial transformation of NH_4^+ in the overlying water or in the top few millimeters below the sediment water interface. NO_3 concentrations decrease rapidly with depth in the sediment while NH_4^+ concentrations increase. Consumption of NO_3 in the sediment is rapid: it has undergone denitrification to $N_{2(g)}$ within the top 1 cm. Pore water NO_3^- concentrations are higher close to the burrow, while NH_4^+ concentrations are lower. This verifies that the burrows induce radial as well as vertical chemical mass transport. Furthermore, the effect of the burrow on ammonium concentrations is apparent over the entire depth examined (8 cm).

The pore water vertical concentration gradients are evident in figure 8 and imply vertical fluxes. Evidence for radial flux to the burrows can be seen clearly in figure 9. The relative importance of the radial and vertical fluxes can be quantitatively determined (Aller, 1980). We have estimated these fluxes by assuming average vertical gradients and average radial gradients. For ammonium, the total flux out of the sediment was

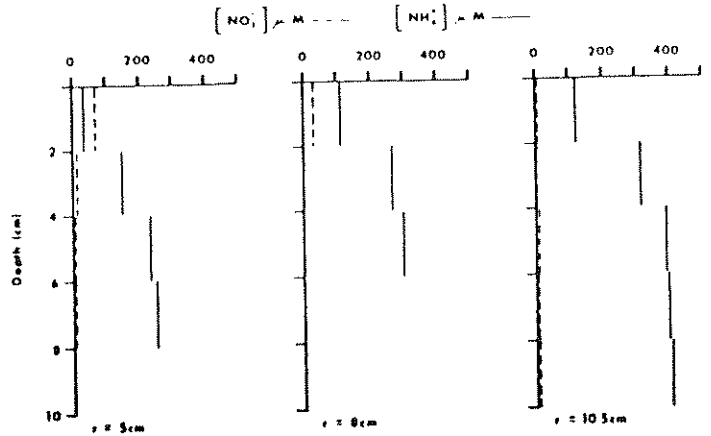


Fig. 8. Pore water nitrate concentrations (dashed lines) and ammonium concentrations (solid line) in sediments containing clams. Profiles are located 5, 8, and 10.5 cm from the center of a clam burrow (2.5, 5.5, and 8.0 cm from the burrow wall).

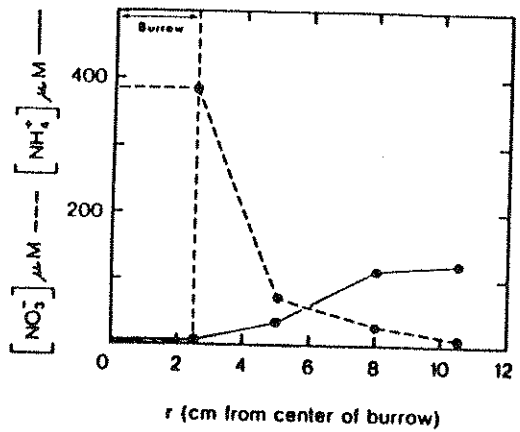


Fig. 9. Nitrate concentrations (dashed line) and ammonium concentrations (solid line) in the 0 to 2 cm interval of the cores plotted as a function of radial distance from the center of the clam burrow.

2.7×10^{-7} μ moles/cm²/sec at the end of the experiment when the cores were collected. The radial flux was 0.84×10^{-7} μ moles/cm²/sec, or 31 percent of the total.

In another experiment, we measured the accumulation in the overlying water of chloride diffusing from chloride-rich pore waters in order to estimate the effect of burrowing and alterations of sediment fabric on flux (fig. 10). The chloride concentration in the overlying water increased more rapidly from chloride-spiked sediments with bivalves than without bivalves. The concentration of chloride in the control may be accurately described as a one-dimensional, vertical diffusional process with an apparent diffusivity of chloride in the sediment of 6.5×10^{-6} cm²/sec (solid line). The enhanced flux in the aquarium containing bivalves is more properly described by considering the geometry of the system and including radial diffusion to the burrows (Aller, 1980). A detailed cylindrical burrow model of solute transport is beyond the scope of this paper. Nevertheless, from figure 10 one can estimate that the burrows enhanced the flux by about 35 percent. This agrees well with the 31 percent value calculated from pore water data.

Figure 11 shows that the flux of nitrate plus nitrite into the overlying water in the flux experiment was substantially greater in the presence of bivalves than in the control without bivalves. Over the first 50 hrs of the experiment, the flux rates are nearly constant. Near time zero at the start of the experiment they were 2.1 μm/hr in the with-bivalves case and 0.5 μm/hr in the control without bivalves. Ammonium levels in the overlying water were at or below detection limits throughout the experiment: released ammonium is apparently completely converted to nitrate by nitrifying bacteria.

The results of the chloride experiment and the excretion experiment can be used to partition the contribution of bivalves to the increased flux of inorganic nitrogen (table 4). Near t = 0, the results from the chloride experiment indicate that the contribution of bivalve burrows to enhanced flux by radial diffusion was about 0.3 μm/hr for a total diffusion flux of 0.8 μm/hr. The excretion experiment was run for a total of 200 hrs. Figure 12 shows the concentration of nitrate in water overlying clams and clams plus sediment. As in the flux experiment, when a quantity of lake sediment is present, no ammonium accumulates in the overlying water, even though the clams are excreting large quantities of it. Even without a sediment-water interface, there are apparently sufficient nitrifying bacteria in or on the clams eventually to oxidize excreted ammonia, since it disappears from overlying water after 200 hrs. Over the first 50 hrs of the excretion experiment, the excretion rate of ammonia measured as the accumulation rate of ammonium plus nitrate in the clams plus water only

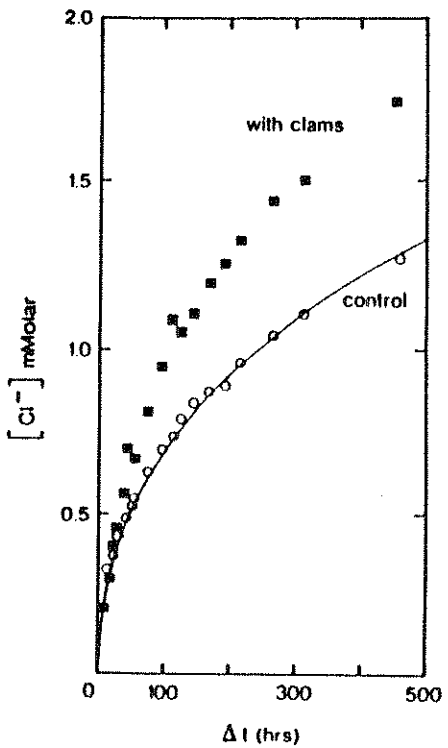


Fig. 10. Chloride concentration in water overlying chloride-spiked sediments with and without clams.

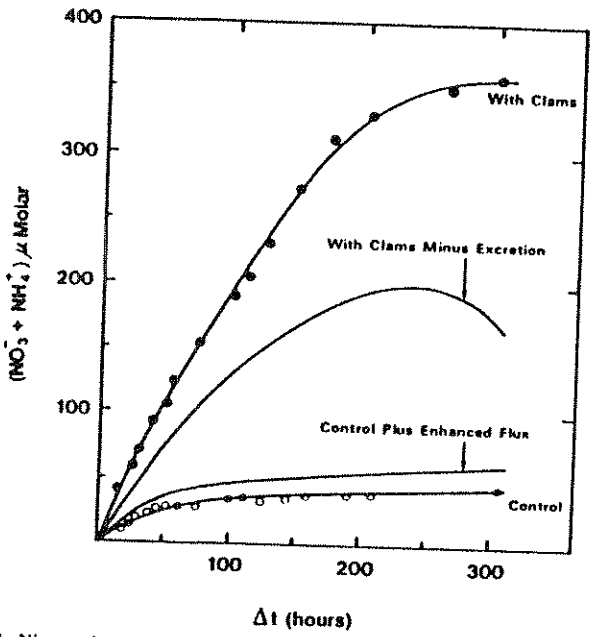


Fig. 11. Nitrate + ammonia concentrations in water overlying sediment with and without (control) *Lampsilis*. Corrections are applied for clam byproducts ("with clams minus excretion") and for enhanced flux due to the presence of burrows ("control plus enhanced flux"). Ammonia concentrations are at below detection limits in aquaria with sediments and only appear in the correction for clam metabolic excretions.

TABLE 4
Partition of flux of inorganic N (ammonium + nitrate) observed in the flux experiment

Flux due to	Flux rate at t=0 (μM/hr)	Percent of total flux	Source of data
Vertical diffusion	0.5	24	measured directly in flux experiment
Radial diffusion	0.3	14	chloride experiment
Excretion	0.7	33	excretion experiment
Bacterial growth enhancement	0.6	29	measured indirectly in flux experiment by subtraction of above ratios from total flux

treatment was 0.57 μm/g dry wt/hr. Using this value in the flux experiment, we calculate that near t = 0, the flux of nitrate due to excretion was 0.7 μm/hr or 33 percent of the total flux. We emphasize again that the clams do not excrete nitrate, but that in the presence of lake sediment, bacteria excreted ammonia appears in the overlying water as nitrate. The sum of diffusive and excretory flux, 1.5 μm/hr, is still less than the observed nitrate flux. The remainder is attributed to enhanced bacterial activity around the burrows of the clams. Bacteria in Lake Erie sediments are known to be able to generate ammonium production rates of this magnitude (Matisoff, Fisher, and McCall, 1981).

Bacterial growth rates.—There are, of course, many different kinds of bacteria that are highly stratified as a function of depth in the sediment (Sorokin, 1978; Perfilev and Gabe, 1969), and bivalve activity probably affects the growth of each differently. As a first step, however, we sought at least to measure the effect of bivalves on growth of the *total* number of bacteria as a function of depth. The method for comparing growth rates we used here — removing populations from equilibrium and measuring their rate of return in a geochemically measurable environment — could also be adapted for the enumeration of both bacterial physiologic types and bacterial activity.

In previous work with western Lake Erie sediment, periodic bacterial abundance measurements made after seeding sterilized sediment with differing amounts of untreated lake sediment showed that following a lag period of 6 to 12 hrs, there was a period of rapid linear or exponential

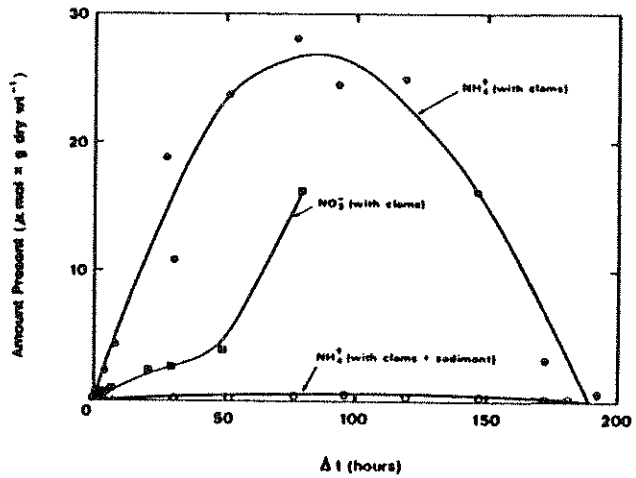


Fig. 12. Amount of nitrate and ammonium in water overlying clams and clams plus sediment. Control values of NH_4^+ and NO_3^- in deionized water above are near zero and constant for 200 hrs. Clam excretion was taken to be the sum of darkened circles and squares for the first 50 hrs.

growth that continued until day 3 to 4. There followed a stationary phase of growth where abundance changed much less (fig. 13). Accordingly, we collected data from the peepers used to compare bacterial growth rates with and without clams at days 0, 1, 4, after seeding sterilized sediment that had been incubated in the peepers for 10 days to establish *in situ* pore water gradients. Peepers were placed a radial distance of 5 cm from the center of the burrows.

Initial bacterial abundances in the peepers ranged from 0.39-.70 × 10^9 per g dry wt of sediment ($\bar{X} = 0.55 \times 10^9$ (g dry wt sed)$^{-1}$, $S = 0.08$). Standing crop bacterial abundances outside the peepers in the microcosms average 1-4 × 10^9 (g dry wt sed)$^{-1}$, depending on depth below the interface. Following Christian, Hanson, and Newell (1982), both exponential and linear growth rate constants were calculated for the periods 0 to 1 days and 1 to 4 days to measure the rate at which bacterial populations reattain equilibrium with and without the presence of clams (table 5). There is no difference in the interpretation of the effect of the clams, whether one assumes linear or exponential growth over these intervals.

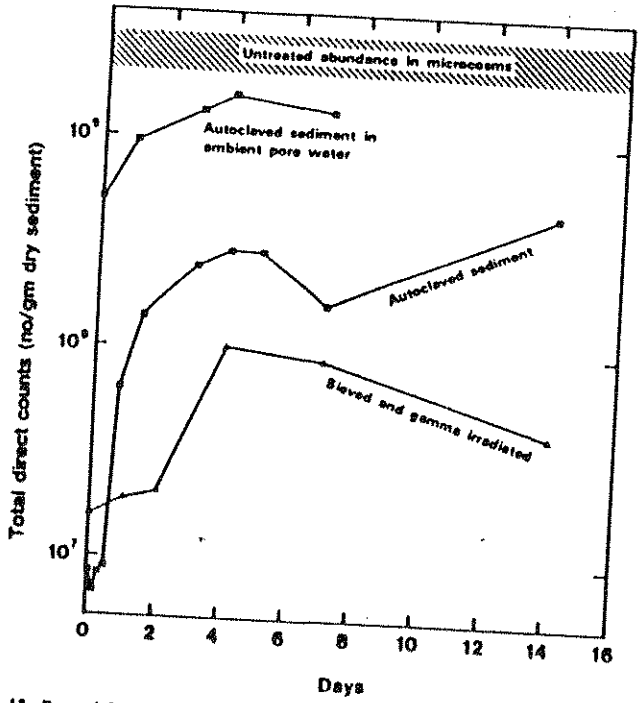


Fig. 13. Bacterial growth in sterile sediments seeded with different amounts of western Lake Erie sediment.

TABLE 5

Specific growth rates of bacteria in pore water peepers incubated *in situ* in aquaria with ("clams") and without ("control") *Lampsilis*

Depth		Time period: 0-24 hrs Clam	0-24 hrs Control	24-96 hrs Clam	24-96 hrs Control
1 cm					
	Δ*	0.036	0.045	0.010	0.006
	μ**	0.026	0.030	0.008	0.005
2 cm					
	Δ	0.022	0.013	0.010	0.003
	μ	0.017	0.011	0.011	0.003
3 cm					
	Δ	0.006	0.005	0.007	0.009
	μ	0.005	0.004	0.006	0.007
4 cm					
	Δ	0.017	0.014	0.005	0.002
	μ	0.014	0.012	0.004	0.002
6 cm					
	Δ	0.015	0.006	0.004	0.002
	μ	0.013	0.006	0.003	0.002

* $\Delta = (x_{t+1} - x_t)/(x_*(t_{t+1} - t_t))$
** $\mu = (\ln x_{t+1} - \ln x_t)/(t_{t+1} - t_t)$
x_t = abundance at tth interval, t = time in hrs

In eight out of ten comparisons (five depths × (clam + control microcosms)), growth rate constants were higher in microcosms with clams than in control microcosms. Bacteria grew faster and for longer periods of time when clams were present (in another experiment, growth rate constants in the presence of clams for days 4 to 7 were ≦0.001; in all but one case, control values were <0.001 or negative). Another effect of the clams was the alteration of the vertical gradient of bacterial growth rates. From 0 to 6 cm, 0 to 24 hr growth rates decrease by a factor of 5 to 7 without clams and by only a factor of about 2 with clams. Clams stimulate growth at depth to a greater extent than growth at the aerobic surface of the sediment.

It is not possible quantitatively to calculate the contribution of this enhanced growth to inorganic nitrogen flux, because we do not know the exact relationship between total bacterial growth rate or standing crop and ammonifier or nitrifier growth rates; nor is the relation of these growth rates to inorganic nitrogen production known. However, higher bacterial growth rates and standing crops have been reported to increase the flux of organic decomposition products (Barsdate, Prentki, and Fenchel, 1975; Fenchel and Jorgensen, 1977; Aller and Yingst, 1978; Henriksen, Hanson, and Blackburn, 1981). We note that the volume of highly reactive, apparently oxidized (light colored) sediment in the microcosm with clams was 166 percent of the equivalent volume in the control microcosms (due to the 1 cm thick layer of oxidized sediment around the clam burrows), and that both bacterial growth rates and standing crops are 2 or more times greater in the 0 to 1 cm layer of sediment than in deeper, more highly reduced and more organically depleted layers. Additional

NH_4^+ is produced by the bacteria that grow rapidly and in great abundance on the thin layer of clam feces and pseudofeces at the sediment-water interface (table 3). In the flux experiment, the total minus excreted flux is 178 percent of the control plus enhanced diffusion flux. It seems possible that this increase could be due to clam-induced increases in bacterial activity.

DISCUSSION

Physical properties and particle entrainment.—While the migration of *Lampsilis* along the sediment-water interface can alter the physical properties of the top 3 cm of cohesive sediments, our experiments show that such migration is episodic; lateral migration slows after a few days, and the clams take up a relatively sedentary position in their burrows. Most likely it is the establishment of these burrows and continued suspension-feeding that have the largest effect on sediment properties. Near the burrow wall, water content of the sediment is increased, and resistance of the sediment to a shearing device is decreased. Farther away from the burrow wall, the resistance of the sediment to the shearing device is actually increased over that of sediment with no clams. It is possible that this effect was due to the confining walls of the aquarium, but since water contents near the aquarium walls are unaltered and the clams were located at least 10 cm from the walls, we think this is unlikely. The increased resistance may result from the copious amounts of mucus observed to be produced by the bivalves as a result of mantle cleansing activities, but more likely it is the result of the redistribution of particles that occurs during burrowing. Rowe (1974) also detected this phenomenon among burrowing marine anemones. This is another example of what Rhoads and Boyer (1982) have called "far-field" effects. This one extends more than 5 cm from the bivalve.

There is no one satisfactory method of measuring the biogenic alteration of the fabric of cohesive sediments. While viscometer measurements of sediment strength and water content measurements are significantly correlated, less than half the variance of the data is accounted for by a linear regression, so it is clear that the two methods do not measure the same aspect of sediment fabric. It is not clear what aspect(s) we *should* be measuring to assess biogenic effects on sediments. A large change in tortuosity of sediment could occur with no change in water content (McCall and Fisher, 1980) and a small change in grain orientation that is not evident in water content measurement could have a large effect on sediment shear strength and bearing strength. Macroinvertebrate and microbial exopolymers can have large effects on erodibility and yet not be evident in most measurements of sediment physical properties. This study examined the erosion of sediment within a few millimeters of the sediment-water interface. We are not now able to make accurate physical property measurements on such a small scale, which is one reason that there is often poor correlation of measured physical properties of cohesive sediment and erosion (Parthenaides and Paaswell, 1970; McCall and Fisher, 1980; Rhoads and Boyer, 1982).

The effects of fauna on erosion are usually determined by measuring τ_c (critical entrainment stress) or U_c^* (critical friction velocity), the points above which particles are entrained from the bed into the flow, of sediment with and without organisms added (Rhoads, Yingst, and Ullman, 1978; Young and Southard, 1978; McCall and Fisher, 1980; Nowell, Jumars, and Eckman, 1981; Rhoads and Boyer, 1982; Grant, Boyer, and Sanford, 1982). But this tells little about the actual *flux* of particles across the interface. To study this, it is better to measure the entrainment rate and the deposition rate of sediments as affected by organisms.

Compared to the non-bivalves case, *L. radiata* in densities that mimic field abundances ($\sim 10\ m^{-2}$) increase the entrainment rate of cohesive lake sediment by a factor of 30 to 50 at estimated interfacial shear stresses of 2 to 3 dynes $\cdot$ cm^{-2}. At 6 dynes $\cdot$ cm^{-2} the bivalve effect disappears. What accounts for this large effect produced by bivalves? It is unlikely that the clam-control difference is due solely to the change in sediment water content that clams produce. The *Lampsilis* used in these experiments did not undergo extensive migrations in the flume, so there were only local changes in water content due to burrowing, and water content is increased in one part of the bottom and decreased in another. Water content changes take place over at least the entire top centimeter of sediment surrounding the burrow and should be observed over the entire range of applied shear stress, not just the low stress. Finally, we have observed in other experiments equally large alteration in E with no accompanying change in sediment-water content. The bivalves also produce microtopographic changes in the sediment surface (the effects of microtopography are reviewed most recently by Rhoads and Boyer, 1982), but it is unlikely that the bivalve effect is due primarily to this activity for the same reason that the bivalves did not move a great deal to produce much topography. In addition, entrainment tests performed on smooth beds without bivalves and on beds with artificially created topography differed by no more than 20 percent in C_{eq}.

It is the effects of suspension feeding on the microfabric of the surface layer of sediment that are most likely responsible for the observed difference. Sediment particles processed by *Lampsilis* are wrapped in mucus and ejected into the overlying water and onto the sediment surface. While the effective size of the new aggregates is quite large, it may be that they are not immediately cemented to the bed by electrostatic forces or bacterial and fungal filaments. This would explain the unusual entrainment behavior of bivalve-treated sediment at low shear stresses. The aggregates are easily eroded, but they are also large and have high settling velocities that cannot be supported by the flow. At higher stresses more and more particles unprocessed by bivalves are eroded, until there is no difference in entrainment between the treatment and the control. Measurement of the settling velocity of particles eroded at different stresses supports this notion.

The SEM photos indicate that the bivalves also inhibit the growth of filamentous bacteria and bacteria that secrete copious amounts of exo-

polymer, whereas direct counts indicate that they increase total bacteria abundance at the sediment-water interface. We do not know how this effect is produced: it may be due to properties of feces and pseudofeces; it may be due to altered flux of pore water solutes through the sediment-water interface; or it may be due to altered abundances of meiofaunal bacterial feeders. Filamentous bacterial mats and microbial exopolymers are thought to bind sediments and make them more difficult to erode, but we really know little about their effects. Whatever the exact mechanisms, it is becoming clear that these bivalves produce a number of effects on sediment properties that are related to particle flux — effects on mass properties, aggregate size distribution, and biochemical microenvironments — and that these changes affect microbial populations which in turn can affect both particulate and solute flux (fig. 1, pathways 3 and 4).

Pore water biogeochemistry and solute flux.—The flux of pore water solutes across the sediment-water interface is increased by the burrowing behavior of *L. radiata*. The increase is due ultimately to the maintenance of a burrow connected to overlying water and that possesses a zone of decreased sediment compaction which enhances radial diffusion of pore water solutes. The flux of conservative materials such as chloride in these experiments is increased by a factor of 1.3 to 1.4. The increase in the flux of the nutrients ammonium and nitrate is greater by a factor of four and is much greater than the "With-Bivalves" pore water profiles predict. A portion of the increase, about 44 percent of it, is due to metabolic by-products of the bivalve. A greater portion, 56 percent, is due to changes in sediment fabric and radial diffusion and enhanced bacterial activity due to the presence of the clam burrow.

There is another possibility that needs to be addressed. According to this argument, the effect of the bivalves is to alter the balance between nitrifiers and denitrifiers in the sediment and decrease denitrification of nitrate to N_2, thus allowing a greater buildup of NH_4^+ and NO_3^- in the "With-Bivalves" flux experiment. There are a number of reasons for thinking that *Lampsilis* does not "turn off" the denitrifiers. First, the vertical profile of nitrate in the sediment pore water away from the clams (10.5 cm) shows no nitrate at all even though the nitrate concentration in the overlying water is very high (~400 μM). This means there is significant denitrification in that area of the aquarium. Second, nitrate concentrations in the sediment pore waters decrease radially from the burrow wall. This indicates that denitrification is also occurring around the burrows. Furthermore, because the burrows create an enhanced area of sediment-water interface, the actual area of denitrification is expected to increase (Aller, 1982). Chatarpaul, Robinson, and Kaushik (1980) found that other burrowing macrobenthos, tubificid oligochaetes, increased both nitrification (×2.4) and denitrification (×1.8) in surficial river sediments. The fact that radial nitrate concentration gradients are less near the burrows than vertical concentration gradients away from the clams does not indicate that the clams are locally inhibiting denitrifying bacteria. We have already demonstrated that *Lampsilis* modifies the sediment texture

and fabric in a manner that should enhance nitrate diffusion into the sediment through the burrow wall. This is consistent with observed nitrate concentration gradients. Finally, it is possible to compare the observed rate of appearance of nitrate in the with-bivalve aquaria with that predicted in the complete absence of denitrification. Fendinger (1981) calculates an N_2 loss from western basin sediments of 223 $mMm^{-2}yr^{-1}$ (=0.00127 μM-Nitrogen/cm^2/hr). In the absence of denitrification, then, this aquarium would accumulate nitrate in the overlying water at a rate equal to that of the "Control Plus Enhanced Flux" (=0.8 μM/hr) plus this estimated denitrification rate (=1.6 μM/hr). This sum (2.4 μM/hr) is greater than the observed rate ("With Clams Minus Exudate" = 1.4 μM/hr). While the rate of nitrate appearance is consistent with the interpretation that *Lampsilis* could modify the balance between denitrifiers and nitrifiers, it is inconsistent with complete absence of denitrification. The observations indicating enhanced denitrification suggest to us that most of the nitrate increase is due to relative increase in the activity of other bacteria.

The increase in inorganic N flux due to the unionids in this experiment was 229 percent of the unionid excretion rate. Henriksen, Rasmussen, and Jensen (1983) found that the increase in inorganic N flux due to marine bivalves was close to the measured NH_4^+-excretion rate in both their "poor" (80 percent) and "rich" (145 percent) sediments and that excretion rate could be used as an estimate of inorganic flux due to benthic macrofauna. But their estuarine sediments were sandy and contained only 0.3 to 1.3 percent organic carbon. Our freshwater sediments are 90 percent silt-clay and contain ~4 percent organic carbon. As correctly predicted by Henriksen, Rasmussen, and Jensen (1983), the stimulation of microbial activity near the burrow wall takes on increased importance as microbial remineralization rates increase. Similar stimulatory effects in organic rich marine sediments have been detected by Aller and Yingst (1978). Our results show that the stimulatory effect of clam burrows on microbial activity also extends several centimeters away from the burrow. This is probably the result of enhanced radial diffusion around the burrow.

Where the flux across the interface of ammonium-nitrate produced during organic matter decomposition is concerned, the effect of *Lampsilis* burrowing and respiration is to alter the surface area topography and physical properties of sediment at the sediment-water interface. This alters the diffusion geometry of the sediment and pore water chemistry. This in turn increases bacterial activity which makes the greatest contribution to increased flux into the overlying water (fig. 1, pathways 4 and 5).

Further interactions.—Of course, not all macrobenthos have the same effects on sediment properties. Some benthos may accentuate the effect produced by *Lampsilis* and some may counteract them. Neither are macrobenthic interactions restricted to competition and predation. We outline one scenario to show the close relation of physical, chemical, and biological processes in lake sediments. Suspension-feeding unionid bivalves increase the growth rate of bacteria within the sediment by altering sediment

geometry, solute diffusion, and pore water microenvironments. Deposit-feeding tubificid oligochaetes are attracted to microenvironments that exhibit high bacterial growth rates (Brinkhurst, Chua, and Kaushik, 1972; McCall and Tevesz, 1982). Tubificids are the most abundant macrobenthos in Lake Erie. They feed at depth and deposit discrete, large (120 × 75 μm) fecal pellets at the sediment-water interface. These pellets are made up of tightly packed silt and clay particles that are difficult to erode and have very high settling velocities (McCall and Fisher, 1980). Thus the *in situ* effect of *Lampsilis* on particulate entrainment rate may well be opposite the result predicted by a single species laboratory study. The macrofauna of cohesive sediments live in an environment of steep vertical gradients of physical and chemical properties, and they are large relative to these gradients, so their effects can be quite large. Furthermore, since the macrofauna live in a viscous sediment-water mixture, the changes they effect in these properties are not so transient as those in aqueous or subaerial environments but last long enough to affect micro-, meio- and other macrobenthos.

At present, the laboratory results on substratum properties and the flux of solutes and particulates cannot be confidently applied to Lake Erie. To estimate *in situ* fluxes we would need to know the time between disturbances of the bottom, the spatial pattern of benthos abundance, behavioral differences of bivalves between the laboratory and the field, and the temperature dependency of macroinvertebrate behavior and particular microbial activities, as well as the antagonistic or synergistic effects of other macrobenthos. However, there is little doubt that sediment transport and solute flux are important processes in the shallow western basin of the lake.

Resuspension of bottom sediments in the shallow western basin (8 m depth) by waves and currents is frequent, and both calculated instantaneous (hours-days) fluxes (up to 5 mm/event; Sheng and Lick, 1979) and sediment trap fluxes averaged over a summer (1 mm/day; Herdendorf, 1968) greatly exceed the net accumulation rate measured over periods of 10^3-10^4 yrs (~0.3-3 mm/yr; Kemp, MacInnis, and Harper, 1977). Even in the deeper, more stable eastern basin, Bloesch (1982) found that from 83 to 99 percent of the material collected in sediment traps 1 to 3 m off the bottom at depths of 9 to 40 m had been resuspended from the bottom. Acting alone, the effect of unionids during warm months will be to increase the flux of sediment both from the interface (higher entrainment rates) and to the interface (higher settling velocities) and enlarge the area of bottom subject to erosion (by lowering the fluid stress at which interfacial sediment entrains).

Increasing attention has been focused on nitrogen limitation of photosynthesis in lakes and the ability of nitrogen to modify the biologic response to phosphorus limitation (Smith, 1982; Jones and Simon, 1981; Fee, 1979). Burns (1976) found that inorganic N in Lake Erie waters undergoes a major depletion during the summer months and exerts a significant control on phytoplankton growth. No detailed nitrogen budget

incorporating sediment processes is available for Lake Erie, but recycling of nitrogen from bottom sediments may be significant. Kemp and others (1976) estimated the annual deposition rate of nitrogen in the Western Basin of Lake Erie to be 1145 μg/cm^2/yr (= 818 mM/m^2/yr). The control aquarium gives an estimate of the rate of nitrogen release in the absence of benthos of 40 mM/m^2/yr or about 5 percent of the annual input. Extrapolating the "With-Bivalve" experimental results using natural bottom densities gives estimates that are ~7 percent of the annual input and on the order of 5 percent of the annual primary production in this part of the Lake.

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