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PRECISE RADIOTRACER MEASUREMENT OF THE RATE OF SEDIMENT REWORKING BY *STYLODRILUS HERINGIANUS* AND THE EFFECTS OF VARIABLE DISSOLVED OXYGEN CONCENTRATIONS

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ABSTRACT. A radiotracer method is used to determine the rate of sediment reworking by the worm, Stylodrilus heringianus, *an organism common in profundal sediments of the Great Lakes. A submillimeter layer of sediment labeled with gamma-emitting cesium-137 is added to the surface of worm-inoculated sediments contained in cells of rectangular cross-section placed in an insulated aquarium (10°C). This layer, progressively buried by the conveyor belt feeding action of the worms, is located by scanning the cell with a well-collimated detector mounted on a hydraulically actuated elevator. Precision in locating the marked layer is greatly enhanced by Gaussian profile analysis developed in this study. Relative uncertainties in location of less than 0.01 cm allow reworking rates as low as 10^{-3} cm/hr to be determined in 1 to 2 days. The effect of variable dissolved oxygen (D.O.) concentrations on sediment reworking rates was determined by adjusting the relative proportions of N_2 and O_2 introduced into the aquarium through a continuous bubbler system. In a cell subject to gradual reductions in D.O. (about 1 mg/L every 50 hours) from saturation concentration (10.6 mg/L), sediment reworking rates remained virtually constant down to 1 mg/L. Below this value, the rate decreased, approaching zero at 0.2 mg/L. On increasing D.O. values above about 4 mg/L, reworking returned to the initial rate. Gradual decreases in D.O. induced a reversible dormant mode in these organisms. In cells subject to coarse D.O. changes (3.7 to 8.8 mg/L per step), reworking stopped at around 4 to 5 mg/L and did not resume following reinstatement of saturation values for up to 18 days. In all cases more than 70% of worms were alive at the end of the experiment. This study illustrates the potential of the gamma scan system for quantitative behavioral bioassay of the interactions of zoobenthos with altered sedimentary environments.*
ADDITIONAL INDEX WORDS: Benthos, tracers, Lake Michigan, diffusion coefficient.

INTRODUCTION

Aquatic earthworms, particularly the Tubificidae and Lumbriculidae, rework and redistribute the upper layers of sediments in lakes and ponds. Rates and modes of sediment reworking have been determined in both field and laboratory systems by Brinkhurst *et al.* (1972), Davis (1974a,b), Krezoski *et al.* (1978), Fisher *et al.* (1980), and others. Rhoads (1974) described the mode of reworking by larger marine annelids as a "conveyor belt." This mode of sediment movement also characterizes the feeding behavior of several species of the freshwater family Tubificidae. In this mode, the worms feed below the sediment surface (down to 10 cm) and deposit mucous-bound fecal pellets at the sediment-water interface. The ingestion and depo-

sition of fecal pellets alter the particle size of surficial sediments and affect subsequent sediment erosion and transport (McCall 1979). The rate at which oligochaetes feed and rework sediments depends partly on the sediment type and food content. Other factors which may influence reworking rates include physical and chemical constituents of the sediment, temperature, oxygen, species of worm, community interactions, and life history stages (Brinkhurst *et al.* 1972, Hargrave 1969, Brinkhurst and Jamieson 1971, McCall and Fisher 1980).

In the Great Lakes, there are several oligochaete families, four of which are common in the soft sediments of the open lake (Spencer 1980). At least two of these families, Tubificidae and Lumbriculidae, are known to feed in the conveyor belt mode. Most sediment reworking studies have involved zoobenthos populations from Lake Erie, where *Tubifex tubifex* and *Limnodrilus hoffmeisteri* are the dominant species. Earlier studies in our laboratory (Klahr 1981, Krezoski 1981; Krezoski *et al.* in press) have shown that the lumbriculid *Stylodrilus heringianus*, the dominant species of profundal Lakes Michigan, Huron, and Superior, reworks sediments in the same manner and at rates comparable to tubificids (Poddubnaia 1961, Wachs 1967, Appleby and Brinkhurst 1970, Davis 1974b). The biology of *Stylodrilus* in the lakes is not well known (Hiltunen 1967), and its classification as a cold water stenotherm has been questioned by Mozley and Howmiller (1977). *S. heringianus* also has been found in streams and temporary pools, both of which have very different regimes from the cold, oxygen-rich bottom waters of the Great Lakes (Cook 1969, Pickavance 1971).

As some sediments of the Great Lakes experience periodic oxygen deficiencies, this study aims to illustrate the effect of reduced dissolved oxygen (D.O.) levels on rates of sediment reworking by oligochaetes. Decreases in D.O. in water adjacent to the sediment-water interface have been shown to affect tubificid behavior. However, even at very low D.O. levels, species such as *Tubifex tubifex* and *Limnodrilus hoffmeisteri* will survive for extended periods of time (Alsterberg 1922, Brinkhurst and Jamieson 1971). Fisher and Beeton (1975) found that *Limnodrilus hoffmeisteri* burrowed more deeply in hypoxic conditions and tended to move toward sediments or water richer in oxygen. Studies of oxygen consumption in tubificids show that respiration does not change significantly until D.O. levels are very low (Berg *et al.* 1962, Palmer 1968). In other studies, the change in respiration rate is shown as an increase in respiratory undulations which continues until D.O. reaches a level at which worms collapse (Hargrave 1969, Aston 1973, Prosser 1973).

Another purpose of the present study was to improve the precision with which measurements of sediment transport and reworking rates could be made by the use of nuclear scanning methods described in detail earlier (Robbins *et al.* 1979). Precise measurements were not possible in previous studies using the methods of Alsterberg (1922), Brinkhurst *et al.* (1972), and Fisher and Beeton (1975).

METHODS

Collection and Materials

The sediments and worms (*Stylodrilus heringianus*) used for these experiments were collected with a Ponar grab in June and July 1979 from Lake Michigan about 10 km offshore from the Cook Nuclear Power Plant, Bridgman, Michigan (41°00′63″N, 86°41′72″W). The depth was 42 m, and the temperature at the bottom is about 6°C year round. Worms were maintained in their original sediments at 10°C for about 1 month prior to initiation of experiments.

The species *S. heringianus* was chosen not only because of its numerical dominance but also because it is easily sorted from samples of mixed oligochaete species. Only large active worms were selected. Sediment for each experiment was sieved to 250 μ to remove organisms and coarse debris.

The sediment, a sandy silt, consisted of about 40% each of dolomite and quartz, and less than 5% each of calcite, the clays illite, montmorillonite, and kaolinite, and the feldspars plagioclase and microcline, as determined by x-ray diffraction. Total organic carbon content was about 3%.

Preparation of Experimental Cells

Sediment was added to plexiglass cells (12 cm × 5 cm × 3 cm) to a depth of about 10 cm and allowed to settle for 10 days or longer to re-establish approximately natural chemical conditions (Hargrave 1969) and to stabilize the sediment-water interface. Worms were transferred to the cells and allowed to acclimate to the sediments and establish a system of burrows over a 2-day period prior to the start of each experiment. The number of worms in the experimental cells was either 15 or 45

TABLE 1. Summary of experimental conditions.

	Control 1: no worms	Control 2: constant D.O.	A	B	C	D
Worms/cell	0	45	45	15	15	15
Worms/m^2	0	30,000	30,000	10,000	10,000	10,000
% Alive at Termination	–	75	73	100	87	93
Experiment Duration (hrs)	1,400	1,400	1,400	560	900	410
Average Increment in Oxygen (ppm)	0.0	0.0	1.1	4.3	3.7	8.8
Mean Dissolved Oxygen (ppm)	10.6	10.6	5.1	8.3	9.1	8.1

worms per cell corresponding to 10,000 or 30,000 worms/m^2 (Table 1). The lower value is somewhat higher than the abundance of total oligochaetes at the collection site (about 7,000/m^2).

The prepared cells were placed in a fixed position along a wall of an insulated 40-liter aquarium kept at 10°C. The cells were completely submerged to allow exchange of water and oxygen within the aquarium.

Regulation of Oxygen Concentration in the Aquarium

The desired D.O. level was maintained by adjusting relative proportions of air and nitrogen entering the aquarium. The flow of air and nitrogen from compressed gas cylinders was adjusted by low pressure gas flow regulators and measured by calibrated flowmeters. Total flow was kept constant at about 1,200 cc/min. The D.O. concentration, measured with a probe and oxygen meter, was recorded continuously on a strip chart recorder. It took an average of 4 hours for the D.O. concentration to equilibriate to a change in gas mixture, which is a short time in comparison with the times of exposure of cells to a given D.O. level.

Radiometric Measurement of the Reworking Rate

A non-destructive method was used to determine sediment reworking rates. This method was developed and described in detail by Robbins *et al.* (1979) (see also Fisher *et al.* 1980). A submillimeter layer of sediment labeled with gamma-emitting cesium-137 is added to the surface of the sediments in the experimental cells after the worm acclimation period. As the worms feed below the sediment surface while defecating on top of sediments, the labeled layer is progressively buried toward the feeding zone located at a depth of 3 to 6 cm (Krezoski *et al.* 1978). The labeled layer is located by scanning the length of the cell using a well-collimated NaI gamma detector (0.4 cm slit width) mounted on a hydraulically actuated platform. The absolute position of the slit relative to the base of the aquarium may be determined to within 0.05 cm.

The position of the labeled sediment layer was defined in two ways during this study. In two cells (B and D) the peak position refers to the distance between the labeled layer and sediment-water interface. The position of the interface was determined each time the profile was scanned. Since the sediment surface becomes uneven from reworking, its position cannot be located with a greater precision than 0.1 to 0.2 cm. Thus the location of the position of the labeled layer with respect to the sediment-water interface is poorly defined in comparison with the precision inherent in the activity profile of the labeled layer. Reworking rates measured relative to the repeatedly relocated sediment-water interface are subject to uncertainties which may result in a significant loss of information. The uncertainties are avoided by measuring the labeled layer position to the fixed base of the cell. In the other cells (A and C) and in control cells the position was defined in this way. Values are referred to the sediment-water interface on the basis of a single determination of the sediment column height made at the onset of the experiment. The layer position defined and measured in this way is sensitive in principle to changes in compaction occurring between the layer and bottom of the cell during the course of the experiments.

Treatment of Experimental Cells

Four experimental cells and two control cells were used to determine the effect of oxygen depletion on sediment reworking rates. At the end of each experiment, the worms were recollected by sieving to determine mortality. Table 1 gives the number

of worms per cell at the beginning and percent surviving at the end of each experiment and characterizes the average changes in concentration of dissolved oxygen with time in each of the cells.

In cell A the D.O. concentration was changed in a stepwise manner, averaging 1.1 ppm per step. Each D.O. concentration was maintained for an average of 55 hours during the first part of the experiment, while D.O. was decreased, and for an average of 75 hours when D.O. was later increased except for the last level, which was maintained for 240 hours until the end of the experiment (Table 2). Initially the cesium profile was scanned 4 to 5 times daily to determine if a reworking rate could be accurately measured over a short period of time, such as in 1 to 2 days if enough scans were taken within that period. Subsequent rates were measured over a period of at least 2 days, with 2 to 3 scans daily. The duration of the experiment with Cell A was 1,400 hours (58 days).

For the other cells (B, C, D) the reworking rate at oxygen saturation was determined over a period of 100 to 145 hours, then the rates at one to four lower D.O. concentration were measured to obtain a rough estimate of the D.O. level at which reworking was first affected. If reworking stopped, the D.O. concentration was raised to near saturation in an attempt to restart reworking activity. The length of time each D.O. concentration was maintained averaged about 100 hours, with the exception of the final concentration for Cell C, which was maintained for 440 hours. The average decrease in D.O. was 3.7 to 8.8 mg/L. Usually the Cs-137 profile in the sediment was scanned twice daily to duplicate measurements of the cesium peak position. These experiments ran for 410 to 900 hours.

Both control cells ran for the same length of time as Cell A and were subjected to oxygen saturation for the entire length of the experiment. Control 1 was used to determine possible displacement of the cesium layer in the absence of worms, and Control 2 was used to measure reworking rates with the dissolved oxygen level kept fixed at saturation. Scans were made once a week for Control 1 and once every 2 to 3 days for Control 2. All cells were kept in the dark except during scans.

RESULTS AND DISCUSSION

Precision of the Method

In a typical scan of an experimental cell the activity of the cesium-137 is determined for 100 sec. at millimeter intervals over a 1.0 to 1.5 cm span. A typical activity profile is shown in Figure 1a. The breadth of the profile (~5 mm) is due mainly to the optics of the detector system, as the thickness of the labeled layer itself is initially less than one millimeter. Previously the position of maximum counts was taken as the mean position of the radiolabeled layer (Robbins *et al.* 1979, Fisher *et al.* 1980). This method does not take optimal account of the total profile, and results in a position estimate of inferior precision. A very significant improvement in the precision of estimating the position results from approximating the profile by a Gaussian function. There is, of course, no *a priori* reason why this function should adequately describe the profile and, for sufficiently wide collimator slits, it will not. However, provided the detector optics and profile itself are symmetric about a mean position, the choice of a symmetric function enhances the accuracy in the estimate of the mean position even in the presence of small systematic departures between the observed profile and its mathematical representation. The Gaussian function is given by

$$N(x) = N_m e^{-(X-X_m)^2/2\sigma^2} \quad (1)$$

where N_m = the peak counts, x_m = the peak position, and σ is the standard deviation which is related to the full-width-at-half-maximum (FWHM) by

$$FWHM = 2.35\sigma \quad (2)$$

The total counts then are given by

$$\int_{-\infty}^{+\infty} N(x)dx = N_m\sigma\sqrt{2\pi}. \quad (3)$$

As shown in Figure 1a, this representation is in fact quite satisfactory. The three parameter least-squares fit to the first equation is based on a non-linear optimization routine described by Dams and Robbins (1970).

For Cell A the position of the peak was determined several times ($N > 3$) within a few hours. These multiple determinations, made repeatedly ($N = 25$) throughout the 1,400-hour duration of the experiment, provide a continuing measure of the reproducibility in determining peak position. Shown in Figure 2 is the standard deviation in locating the peak position (x). While considerable scatter in the data exists there is nevertheless a systematic increase over time with increasing labeled

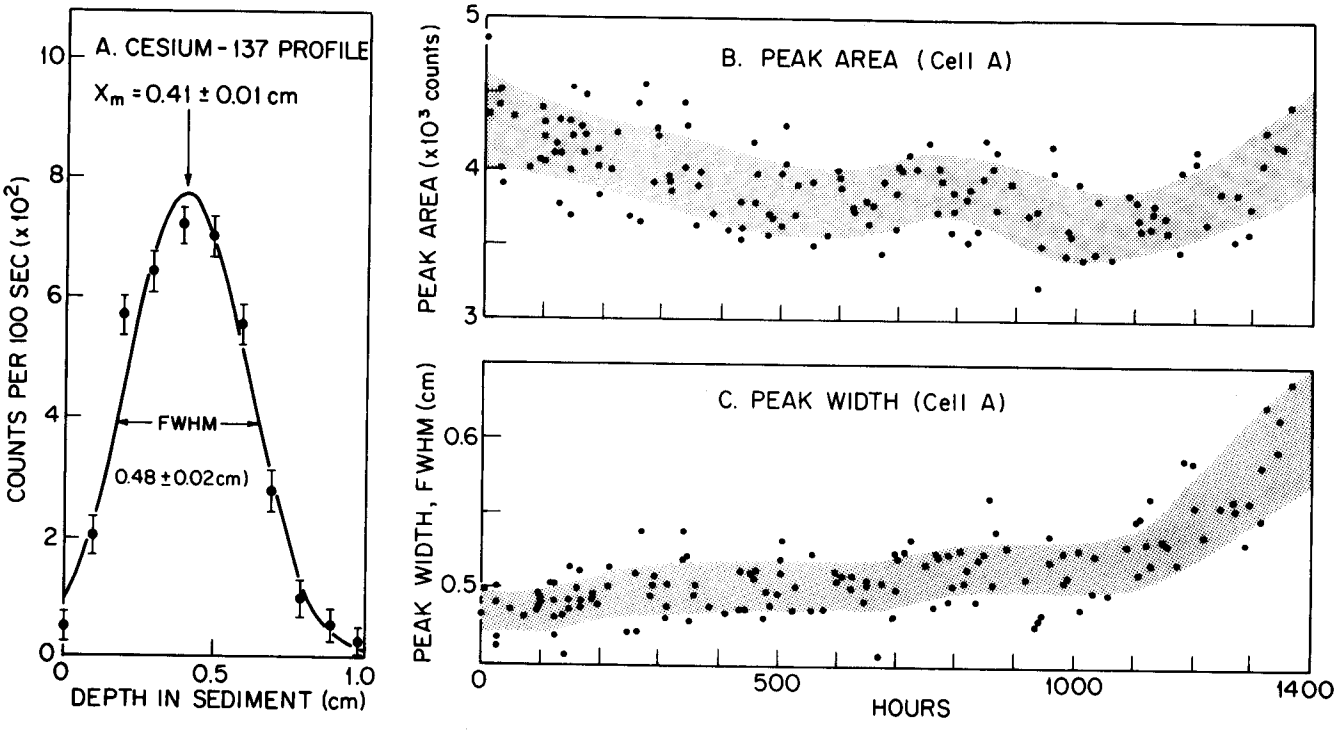

FIG. 1. a) Representative profile of cesium-137 activity in Cell A (at T = 0). The solid line is the least-squares Gaussian approximation. The mean position of the labeled layer is precisely determined (± 0.01 cm) form this theoretical fit. b) Peak area (total activity). c) Full width at half maximum (2.35 σ) versus time for Cell A. The width of the profile results primarily from detector optics as the labeled layer thickness is initially under one millimeter. The initial slight reduction in activity under the peak results from displacement of small amounts of labeled material to other parts of the cell. This loss is accompanied by a slight increase in the width of the profile. More rapid changes toward the end of the experiment follow reestablishment of oxygen saturation.

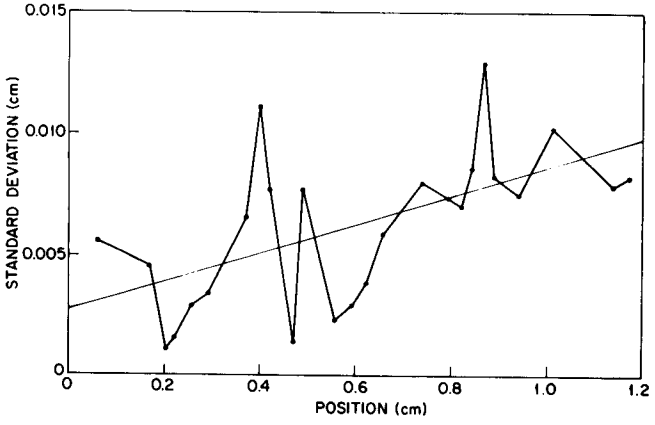

FIG. 2. Uncertainty in estimating the location of the labeled layer vs. position. The standard deviation is determined from replicate (n > 3) measurement of the cesium-137 profile and Gaussian analysis. The excellent precision in the measurement allows reworking rates the order of 10^{-3} cm hr^{-1} to be determined in 1 to 2 days.

layer depth. The regression line shown in the figure is given by:

$$SD = 0.003 + 0.006X \text{ (cm)} \quad (4)$$

with N = 25 and r = 0.6. Reasons for the increase are not clear but are probably due to a small progressive loss of symmetry in the observed profile over time. Over the course of 1,400 hours the standard deviation ranges from about 0.003 to 0.01 cm. Using this latter value as a very conservative estimate of precision, it can be seen that reworking rates characteristic ($\sim 10^{-3}$ cm/hr) of modest organism densities (10,000 m^{-2}) can be determined in a short time. Assuming a displacement of 5 SD = 0.05 cm to be sufficiently above the level precision, it can be seen that $0.05/10^{-3}$ = 50 hours are required to obtain a good measure of the reworking rate. Hence, use of the gamma scan system in combination with a least-squares Gaussian profile

analysis provides a non-destructive, rapid, and precise way of determining reworking rates and of examining the short-term characteristics of benthos-sediment interactions not previously accessible by methods employing fecal pellet collection (Appleby and Brinkhurst 1970) or pollen grain analysis (Davis 19074b).

Figures 1b and 1c indicate the peak area (the area under the Gaussian fit, proportional to the total activity) and peak width (FWHM) versus time respectively, for the experiment with Cell A. A small (~5%) but significant decrease in the activity associated with the peak occurs over the first 1,000 hours of the experiment. As the labeled layer is progressively buried, some activity is displaced from under the primary peak to other parts of the cell. Because the loss from the peak region is so small, this activity cannot be measured well in other parts of the cell. During the first 1,000 hours there is also a very small (~3%) increase in the width of the peak which results from the slightly non-uniform burial of labeled material. Beyond a thousand hours there is a significantly greater rate of increase in the peak width (25% in 40 hours) which may be associated with shallow feeding activity following reinstatement of oxygen saturation (see below). Feeding in the vicinity of the labeled layer may result in accelerated peak broadening. The broadening of the peak beyond 1,000 hours is associated with a slight increase in the activity under the peak (~10%). As the peak broadens, activity previously displaced from the peak region may be included once again in the Gaussian fit.

Worm-free Control Cell

In the cell (Control 1) with no worms, the submillimeter layer of cesium-137 moves downward by 0.1 ± 0.07 cm in 1,400 hours. This very small downward displacement corresponding to 0.08×10^{-3} cm/hr (Table 2) is almost surely due to slight compaction of the sediment during the course of the experiment. In the absence of worms, there is essentially no burial of the labeled layer. Worms must be present for the layer to move to any significant degree.

An upper limit to the effective diffusion coefficient of cesium-137 in sediments may be estimated from analysis of the profile in organism-free sediments. If there were appreciable molecular diffusion, the cesium-137 in the labeled layer would spread out in time. However, this spreading should occur to a very limited extent because of the strong affinity of the isotope for sediments (Robbins *et al.* 1977). Atoms of radiocesium diffusing away from the labeled layer are efficiently taken up by non-labeled material. Thus the extent of diffusion of the isotope in these sediments should be strongly hindered by sorption processes. And, indeed, essentially no spreading of the peak was detected over the 1,400-hour period.

As can be seen from Figure 1c, the uncertainty (standard deviation) in estimating the peak *width* is approximately 0.02 cm. Thus any change in width due to diffusion would surely have been detected if the spread were roughly three times this value (3 SD) or 0.06 cm. For an initial line source of radioactivity located in an isotropic medium the subsequent profile resulting from diffusion is Gaussian and has a standard deviation (spread) given by Crank (1975)

$$\sigma_{diff} = \sqrt{2\, D_{eff}\, \Delta t} \tag{5}$$

where D_{eff} is the effective diffusion coefficient and Δt is the elapsed time. The overall width of the profile is given approximately by

$$\sigma_{TOT} \approx \sigma + \sigma_{diff}(t) \tag{6}$$

for small diffusional spreading. As no spreading was observed

$$\sigma_{diff} \lesssim 0.06 \text{ cm} \tag{7}$$

or

$$D_{eff} \lesssim 4 \times 10^{-10} \text{ cm}^2/\text{sec} \tag{8}$$

The effective diffusion coefficient of cesium-137 is related to that in free solution approximately by (Li and Gregory 1974)

$$D_{eff} = D_o\left(\frac{\alpha}{\Theta^2}\right)\frac{1}{1+K} \tag{9}$$

where the factor α/θ^2 is close to unity for these sediments and K is the dimensionless ratio of activity per gram of solids to activity per gram of solute (distribution coefficient). The diffusion coefficient in free solution, D_o, is about 2×10^{-5} cm²/sec. Thus the absence of detectable cesium-137 spreading in the worm-free control cell implies a distribution coefficient (K) for cesium-137 given by

$$D_o/(1 + K) \lesssim 4 \times 10^{-10} \text{ cm}^2/\text{sec} \quad (10)$$

or

$$K \gtrsim 5 \times 10^4.$$

This value is even higher than that obtained previously (4×10^3) by Robbins *et al.* (1977) from a radiotracer uptake experiment using fine-grained sediments from another location in the Great Lakes. For radiotracers whose distribution coefficients are the order of 10^3 or less, the gamma scan

TABLE 2. Reworking rates at various levels of dissolved oxygen.

Cell		D.O. (ppm)	Period (hrs)	Exposure time (hrs)	Reworking Rate[1] (10^{-8} cm hr^{-1}/no. m^{-2})
Control 1	No worms	10.6	0–1,400	1,400	0.25 ± 0.21[2]
Control 2	Constant D.O.	10.6	0–1,400	1,400	4.07 ± 0.13
A		10.6	0–60	60	4.00 ± 0.10
		7.7	60–120	60	4.40 ± 0.30
		6.3	120–165	45	3.27 ± 0.30
		5.4	165–220	55	5.13 ± 0.60
		5.2	220–265	45	3.60 ± 0.37
		4.8	265–320	55	3.40 ± 0.53
		4.2	320–380	60	2.67 ± 0.53
		3.6	380–440	60	3.47 ± 0.26
		3.2	440–495	55	4.80 ± 0.57
		2.2	495–555	60	4.00 ± 0.47
		1.5	555–600	45	3.13 ± 0.43
		0.8	600–650	50	3.70 ± 0.56
		0.2	650–715	65	1.37 ± 0.50
		1.0	715–815	100	2.77 ± 0.33
		1.9	815–855	40	1.50 ± 0.43
		2.8	855–935	80	2.06 ± 0.73
		4.2	935–1,025	90	2.93 ± 0.37
		5.9	1,025–1,105	80	3.50 ± 0.30
		7.6	1,105–1,160	55	5.73 ± 0.77
		10.1	1,160–1,400	240	4.20 ± 0.30
B		10.5	0–145	145	4.00 ± 0.30
		6.9	145–312	167	4.50 ± 0.40
		4.0	312–410	98	-1.80 ± 0.60
		10.5	410–560	150	-0.20 ± 0.50
C		10.6	0–100	100	15.10 ± 0.70
		7.5	100–180	80	8.50 ± 0.90
		9.8	180–300	120	10.80 ± 0.70
		5.6	300–360	60	7.80 ± 1.00
		3.6	360–460	100	1.30 ± 0.40
		10.6	460–530	70	1.30 ± 1.20
		10.6	530–815	285	— —
		10.6	815–900	85	1.00 ± 1.10
D		10.6	0–14	145	14.40 ± 0.80
		1.8	145–260	115	1.70 ± 1.00
		10.6	260–410	150	0.30 ± 0.30

[1]Standard deviations reflect uncertainties in position of the marked layer. Uncertainties in population density are unknown and thus not included in the estimate.

[2]Observed "burial rate" = 0.08 ± 0.06 × 10^{-3} cm/hr. For purposes of comparison, as no worms were present, this value is arbitrarily divided by 30,000 worms m^{-3} to obtain comparable numbers.

method can, in principle, be used to obtain sediment tracer diffusion coefficients by direct measurement.

Constant Dissolved Oxygen Cell

Significant variations in the rate of reworking occur for this control cell (Control 2) kept at a constant concentration of dissolved oxygen (10.6 mg/L = saturation) during the course of the experiment. The position of the labeled layer versus time is shown in Figure 3. The regression line corresponds to the following relation:

$$\text{Position (cm)} = -0.03 + 0.00122 \text{ time (hrs)} \quad (11)$$

with r = 0.997 (N = 26). During the course of the experiment (1,400 hours) the average rate of sediment burial by *Stylodrilus* was 1.22 ± 0.05 (SE) × 10^{-3} cm/hr. The linear increase in position of the labeled layer with time is consistent with the observations of both Fisher *et al.* (1980) and Krezoski (1981) that within the upper few cm of sediment the marked layer moves downward at an essentially uniform rate. At greater depths they observed that the layer moved downward at a reduced rate. Krezoski (1981) and Fisher *et al.* (1980) attributed the reduction in burial rate to entry of the labeled layer into the zone of active feeding. In the present case the uniform (or accelerated) downward movement of the labeled layer within the upper 1.8 cm of sediment indicates that no significant feeding was occurring in this zone.

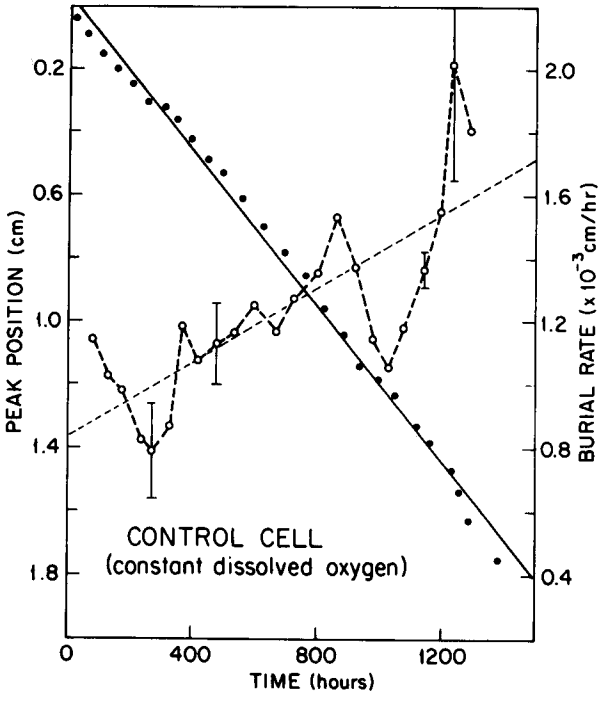

FIG. 3. (Solid circles) Position of the marked layer in the control cell (2) kept at oxygen saturation (10.6 ppm) for 1,400 hours (~2 months). The solid regression line corresponds to a mean burial rate of 1.22 × 10^{-3} cm hr^{-1}. (Open circles) The running average reworking rate. The dashed straight line through the points is the linear regression. Under conditions of D.O. saturation, the rate systematically increases during the experiment.

It is clear from comparison of the fit with data points that the small deviations from linearity are not entirely random. Their non-random character may be exhibited by computing a running average reworking rate. The running average is obtained by least-squares regression of position versus time for the first n points. The calculated slope is associated with the mean time for the n points and taken as the working rate for that time. The next set of n points is obtained by dropping the first point and adding n + 1 in the least-squares analysis. Estimates for subsequent times are obtained by advancing the set of n points through the data set. In calculating the running reworking rate, four points were somewhat arbitrarily chosen (n = 4). Error bars (90% confidence limits) associated with several of the values shown in Figure 3 indicate typical uncertainties in estimating the slope. Such uncertainties depend strongly on the goodness of fit and range in the present case from 2 to 23%. The least-squares line shown in Figure 3 corresponds to the following relation:

$$\text{Burial rate } (10^{-3} \text{ cm/hr}) = 0.85 + 0.00058 \text{ t (hrs)} \quad (12)$$

with r = 0.76 and N = 23. The excursions of the individual values about the trend line are generally of marginal significance. Note that the rate of reworking increased by roughly 50% in 1,400 hours. This increase occurred despite a 25% worm mortality during the experiment (see Table 1).

Reasons for the increase in reworking rate must remain a matter of speculation. As noted previously, the rate must eventually tend toward zero as the marked layer approaches and enters the zone of active feeding. While studies of Krezoski (1981) and Fisher *et al.* (1980) predict a uniform rate over this zone of sediment, neither previous study provides any reason or indication of an initially increasing rate of burial. It seems likely that this increase is an expression of the organisms' acclimatization to the experimental conditions.

Cell A: Gradually Incremented Dissolved Oxygen

The position of the labeled layer and D.O. concentration versus time for Cell A are shown in Figure 4. The clusters of points illustrate the reproducibility in determining the peak location. It can be seen that reworking slow down measurably around 1.5 mg/L and stops altogether at 0.2 mg/L. As the concentration is increased once again, the rate of reworking does not resume its former value until about 950 hours have elapsed (4.2 mg/L). Without further experiments it is not possible to determine if the lag in reinstatement of sediment reworking involves an altered D.O. threshold or is simply a time delay reflecting organism recovery. In any case, under the experimental conditions it has been possible to switch on and off sediment reworking by adjustments in the supply of oxygen.

A least squares line through all the points with 550 hours yields an average reworking rate of 1.19 ± 0.03 (SE) × 10^{-3} cm hr^{-1} (n = 24, r = 0.999). Similarly for all points with T > 1,000 hours, the average reworking rate is 1.20 ± 0.08 (SE) × 10^{-3} cm hr^{-1} (N = 16, r = 0.94). These values are close to the average reworking rate in the control cell: 1.22 ± 0.05 × 10^{-3} cm hr^{-1}. Thus average reworking rates before and after the period of reduced D.O. are indistinguishable from the average rate for the control cell.

The time-dependent reworking rate, based on the four point running average, and D.O. concentration versus time is shown in figure 5 for both

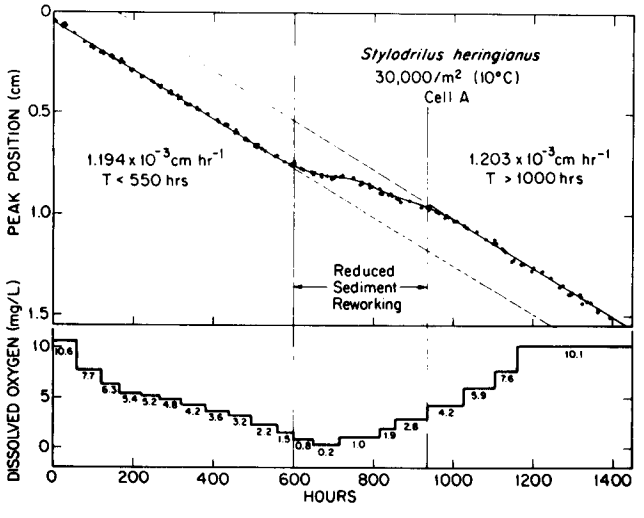

FIG. 4. Upper Panel: Position of the marked layer in Cell A subject to systematic variations in dissolved oxygen. Regression lines for T ≤ 550 hrs and T ≥ 1,000 hrs define a zone within which sediment reworking is reduced as a result of lowered D.O. concentrations. Note that the total movement of the marked layer during the course of the entire experiment is only 1.5 cm. Lower panel: Dissolved oxygen in Cell A versus time. Note that with increasing D.O. the return to normal reworking is delayed.

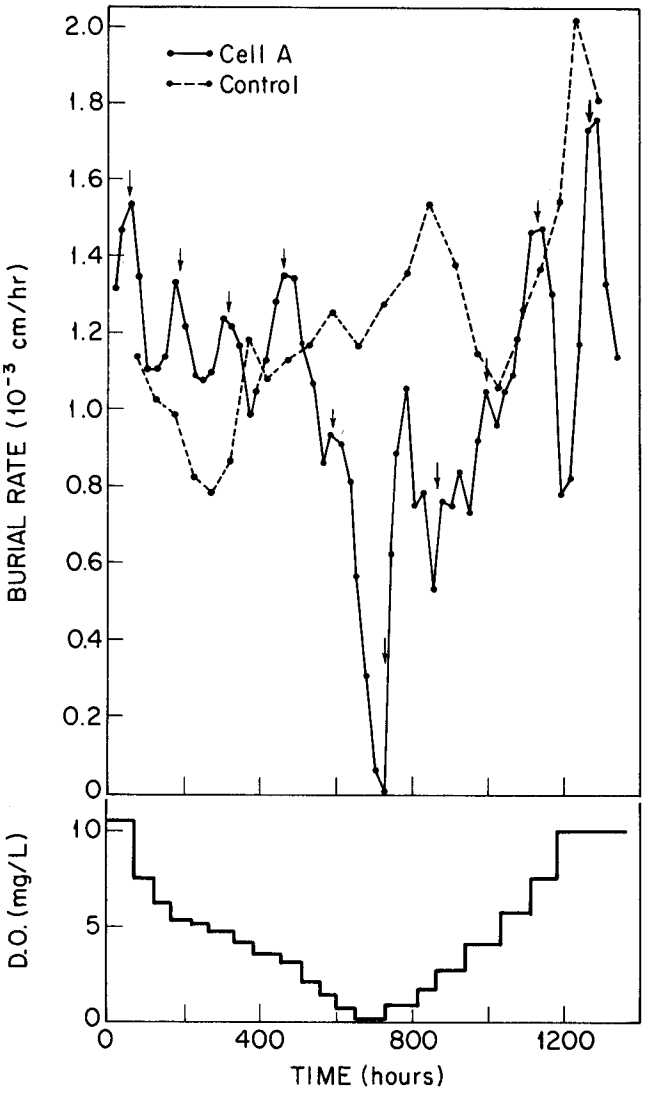

FIG. 5. Rate of sediment burial in Cell A and in the control cell. Mean rates are comparable before and after the period of oxygen depletion. Instantaneous rates, while subject to large fluctuations, appear to increase along with those in the control cell for T > 1,000 hours. Arrows indicate maxima associated with a 135-hour cycle in reworking rate observed in Cell A but not in the control.

Cell A and the control cell. It can be seen that the time-dependent rates in the Cell A and the control cell "track" before and after the period of oxygen depletion. For times greater than about 1,000 hours, rates in both cells appear to increase. This increase is not reflected in the mean for Cell A because of the large dip in rate at around 1,200 hours. The reduction in burial rate corresponding to low D.O. concentrations is clearly seen in the contrast between Cell A and the control cell. In Cell A but not in the control cell there are series of maxima (for $T < 500$ hours and $T > 1{,}000$ hours) that have a period of about 135 hours. While the periodicity is significant and not an artifact of the mathematical analysis, the cause is unclear.

While average sediment reworking rates in Cell A are virtually identical at the beginning ($T < 500$ hr) and end of the experiment ($T > 1{,}000$ hr), the worm population experienced significant changes during the period. At the end of the experiment, 73% of the original number of large active worms placed in the cell remained alive. However, about 20% of the total living worms were much smaller than the original ones. Either reproduction took place during the experiment or very small worms and cocoons were not removed by initial sieving. The close agreement between initial and final reworking rates therefore indicates that either population changes were irrelevant or were compensatory in nature. Reworking would not be affected by overall mortality if, for example, the die-off of worms occurred at the very beginning of the experiment. Alternatively, if the die-off were distributed in time, reworking rates would still not be altered if those worms which died were not effective in reworking sediments anyway. Reasons for the absence of a mortality effect, however, must remain a matter of speculation.

Cells B, C, and D: Coarse Increments in Dissolved Oxygen

In Cell A, the average change in dissolved oxygen was 1.1 mg/L, whereas in Cells B, C, D the corresponding values were 4.3, 3.7 and 8.8 mg/L, respectively (Table 1). Hence on average the increments in D.O. were three to eight times higher in the latter three cells. Cells B, C, and D differ from Cell A in another important way. Cell A had an initial worm density of 30,000 m^{-2}, whereas the other cells had an initial density of 10,000 m^{-2}, and worms for Cells C and D were drawn from separate *Stylodrilus* populations. In all other respects the cells were equivalent.

The results of the reworking experiments are summarized in Table 2. Reworking rates are expressed in terms of centimeters per hour per worm per square meter. In Cell B the initial rate of 4.00×10^{-8} cm hr^{-1}/worm m^{-2} is comparable to that in the control cell (2) (4.07×10^{-8} cm hr^{-1}/worm m^{-2}) and in Cell A (4.00×10^{-8} cm hr^{-1}/worm m^{-2}). However, the initial rates in Cells C and D are considerably higher but comparable to each other (15.1 and 14.4×10^{-8} cm hr^{-1}/worm m^{-2} respectively). Reasons for the higher initial rates in these two cells are not known. Over a wide range of densities, reworking rates are essentially proportional to organism densities (Fisher *et al.* 1980, and others) so it is likely that unknown factors other than organism density (e.g., nonequivalent *Stylodrilus* populations in Cells C and D) have produced this variability. In Cell B a reduction in D.O. from saturation to 6.9 mg/L does not result in any significant change in reworking rate. However, a subsequent reduction to 4.0 mg/L reduces the burial rate to a slightly negative value. (Negative values, rarely seen, are due to slight sediment column expansion.) On return to saturation levels, sediment reworking does not restart.

This behavior is exhibited in Cells C and D as well. In Cell C reworking is essentially unaffected by the variation of D.O. from saturation (10.1 mg/L) to 7.5 mg/L and back to near saturation (9.8 mg/L) and by the subsequent excursion to 5.6 mg/L. However, the drop to 3.6 mg/L is accompanied by a cessation in reworking. On returning the dissolved oxygen to saturation no reworking occurs. During the 18-day period following this sequence, the dissolved oxygen was kept at saturation, but the organisms did not begin reworking sediments again. Failure to recommence feeding activity cannot be explained by mortality as 87% of the organisms in Cell B were still alive at the end of the experiment. A similar response occurred in Cell D which was subjected to a single major dissolved oxygen excursion from saturation to 1.8 mg/L and back again. On reducing the D.O. to 1.8 mg/L, reworking essentially stopped and did not start again on reestablishing saturation. In this cell 93% of the worms were still alive at the end of the experiment.

Systems of sediment, organisms, and overlying water are sufficiently complicated that it is difficult to assure adequate control of all significant experimental variables. The shutdown of the sys-

tem, with the worms alive but in an inactive mode, could of course be attributed to factors not examined in the present experiments. However, there is the strong indication that the abrupt changes in levels of D.O. force the organisms into a non-reworking mode. Gradual reductions in D.O. apparently allow the organisms to continue reworking at normal rates until levels under 1.0 mg/L are reached. The sequence of gradual reductions followed by gradual increases toward saturation evidently allows the organisms to enter a "reversible" dormancy mode. While reworking stops temporarily, it begins again when favorable oxygen conditions are reestablished. In Cell C, however, 18 days of oxygen saturation were not sufficient to induce sediment reworking although most organisms were still alive. Further experiments are required to determine whether (1) coarse D.O. adjustments are really the determining variable in this "dormancy" effect and (2) whether "reversible" and "irreversible" dormancy periods really exist in laboratory microcosms subject to variable dissolved oxygen regimens.

Relation to Respiration Studies

The independence of the rate of sediment reworking by *Stylodrilus heringianus* above a certain critical level is consistent with the results of respiratory experiments by Berg *et al.* (1962) and Palmer (1968). These investigators measured the oxygen consumption of *Tubifex tubifex* at varying percentages of oxygen in gas mixtures introduced into their experimental systems. Berg *et al.* measured respiratory rates for a group of 20 worms at 11°C, while Palmer measured the respiration of individual worms at 20°C. Both groups found that oxygen uptake in *T. tubifex* is independent of the available oxygen supply above a certain level (Prosser and Brown 1962). Below this level, oxygen consumption decreases rapidly when the D.O. concentration is decreased. Berg *et al.* found that the critical level in their experiment was at about 2.5% oxygen, or 0.3 mg/L at 11°C, and Palmer found that it was about 1.5% oxygen, or 0.1 mg/L, at 20°C. In the present experiments the critical level is close to 1 ppm, significantly higher than found in the respiratory experiments. Whether this difference is due to the use of different organisms, to experimental conditions, or to the use of a different measure of the critical level is uncertain. However, it is reasonable to expect that reworking would be more sensitive than respiration to decreased D.O. since organisms might reduce their rate of reworking under conditions of declining dissolved oxygen in advance of their suffering any respiratory decline.

Since in the Great Lakes *S. heringianus* is not normally subjected to low oxygen levels, these experiments would predict more how *S. heringianus* is affected in smaller bodies of water that undergo marked changes in the D.O. concentration. If *S. heringianus* is a cold water stenotherm, it should have exhibited significantly different responses than from *T. tubifex* and *L. hoffmeisteri*.

Survival of organisms in long-term, low oxygenated conditions depends on their ability to store energy, produce energy anaerobically, or on their capacity to utilize oxygen from environments low in oxygen. The organisms that tolerate low oxygen levels best are usually the smaller, less active forms that do not use much energy. They may respond to low levels by hibernating or suspending activities (Davis 1975), or in the case of oligochaetes, by encysting. This includes certain tubificids which survive well in the laboratory at low D.O. levels by ceasing reworking activity until better conditions are reestablished. *S. heringianus* however is not known to encyst. Also, tolerance to low oxygen levels varies among individuals of the same species living in different habitats (Davis 1975). This was demonstrated to some extent in the reworking experiments. Worms subjected to relatively large decreases in D.O. over a short period of time did not tolerate the low levels as well as the worms in Cell A, which had time to acclimate to gradual changes in D.O.

Further studies are required to understand the relationship between the prior history of exposure of these organisms to reduced oxygen levels and their ability to recommence sediment reworking activities. The approach described here, which provides a sensitive measure of the response of *Stylodrilus* to changes in oxygen concentration, can be applied generally to determining the response of conveyor-belt feeding oligochaetes to natural and anthropogenic alterations of the sedimentary environment. Studies of the effect of contaminants on sediment reworking are of particular significance in the Great Lakes since it is believed that biological mixing, in combination with resuspension, plays an important role in the persistence of contaminants in the water column (Robbins 1982, Thomann and Di Toro 1983).

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