

## EFFECTS OF TEMPERATURE AND DENSITY ON SEDIMENT REWORKING BY *STYLODRILUS HERINGIANUS* (OLIGOCHAETA: LUMBRICULIDAE)

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**ABSTRACT.** A non-destructive, radio-marker system was used to follow sediment burial, or reworking rate, by the particle-feeding oligochaete *Stylodrilus heringianus* Claparede over a range of worm densities and water temperatures in laboratory microcosms. Marker layer burial rates were monitored for seven densities (30,000 to 134,000 worms  $m^{-2}$ ) while slowly altering the temperature from 10°C down to 4°C, up to 20°C, and then back to 10°C. From 10°C to 4°C, reworking rates decreased approximately 90%. When the temperature was increased above 4°C, reworking rates approached levels shown at the initial 10°C but remained relatively constant through the remainder of the experiment. It is assumed that reproductive activities, stimulated by the 4°C period, affected feeding activity. The reworking rate per worm was shown to be independent of the initial oligochaete density. Time dependent and depth dependent models were tested to examine the decline in observed reworking rates during the latter part of the experiment. There was a weak correlation between time and decreased reworking rates and a strong correlation between density and depth of feeding. Correlations suggested that reworking rates per worm remained similar over time, but the depth to which an organism fed increased with increasing worm density.

**ADDITIONAL INDEX WORDS:** Sediment-water interface, feeding rates, Lake Michigan.

Many biotic and abiotic factors have been found to influence diagenesis or vertical mixing of lake sediments (Goreau 1977). Although wind-driven waves and bottom currents have a slight impact (Petr 1976), the most profound mixing of deeper sediments is by the larger invertebrates (McCall and Fisher 1980, Robbins 1982, Robbins *et al.* 1984). Of specific interest are oligochaete worms whose "conveyor belt" mode of sediment reworking accounts for much of the vertical transport in surficial sediments (Rhoads 1974, Robbins *et al.* 1979, Fisher *et al.* 1980, Krezoski 1981, McCall and Tevesz 1982). The action of worms feeding below the sediment-water interface and depositing fecal material on the sediment surface provides constant mixing of as much as the upper 15 cm of

sediment in the Laurentian Great Lakes (Robbins 1982).

The rate of sediment reworking by oligochaetes is a function of many variables including sediment type, available carbon, dissolved oxygen concentration, temperature, and organism density (Alsterberg 1922, Ravera 1955, Appleby and Brinkhurst 1970, Stockner and Lund 1970, Wavre and Brinkhurst 1971, Davis 1974a, Davis 1974b, Petr 1976, Pliodzinskas 1978, Husby-Coupland 1980, McCall and Fisher 1980, and others). The geochemistry of the sediment and associated bacteria influence the distribution and abundance of species (Wavre and Brinkhurst 1971, Brinkhurst and Austin 1979) as well as control the rate of passage of food through the gut (Petr 1976).

Worms feed slowly on sediments with a high nutritive content (Ravera 1955) and in laboratory microcosms are believed to decrease their feeding rate toward the end of laboratory experiments in response to depleted food resources (Appleby and Brinkhurst 1970, Davis 1974b). Stockner and Lund (1970) and Pliodzinskas (1978) found differences in invertebrate density and depth penetration among various types of lake sediments and suggested that organic matter and fluxes may be a regulatory factor. Robbins *et al.* (1987) have recently demonstrated that the rate of carbon flux to the sediment, and not the sediment organic content, is most influential in determining oligochaete density.

Temperature and dissolved oxygen concentration are usually considered together when assessing impact on aquatic organisms. An increase in temperature most often is accompanied by an increase in oxygen demand (Berg *et al.* 1962, Hargrave 1969), but it has been long known that variations in temperature have an effect on activity that cannot be accounted for solely by an increased need for oxygen (Alsterberg 1922).

Defecation rate, a measure of sediment reworking rate, has been found to be directly affected by temperature changes (Appleby and Brinkhurst 1970, Davis 1974b, McCall and Fisher 1980); increased temperature results in increased feeding activity. The bottom waters of the Great Lakes are at or near 4°C year round, yet except for fecal pellet production data (e.g., Appleby and Brinkhurst 1970, Davis 1974b), sediment reworking rates rarely have been directly established at this temperature, as most laboratory experiments have been conducted at 10°C up to 20–22°C. The first objective of this research was then to establish sediment reworking rates at several temperatures including 4°C.

The second objective was to assess the effect of organism density on the sediment reworking rate. Krezoski (1981) speculated that sediment reworking rates per worm (for *Stylogdrilus heringianus*) were density independent at 39,000 and 67,000 m<sup>-2</sup>, but little beyond this is known. Both objectives were examined in laboratory microcosms using the "gamma scan" system (Robbins *et al.* 1979, Fisher *et al.* 1980, McCall and Fisher 1980, Krezoski 1981, Robbins *et al.* 1984).

*Stylogdrilus heringianus* Claparede 1862 (Lumbriculidae) is a cold water stenotherm generally associated with northern oligotrophic lakes rich in oxygen (Poppchenko 1980), although it has been

identified from a variety of freshwater systems (Cook 1969, Pickavance 1971, Timm 1980). In the upper Laurentian Great Lakes, *Stylogdrilus* is characteristic of the profundal zone in fine-detrital mud and overall is probably the most abundant and widely distributed species (LaDronka 1984, Lauritsen *et al.* 1985). Its dominance of the open lake environment (1,600 to >8,000 worms m<sup>-2</sup>) and its easily recognizable character of intersegmental bands make it an excellent experimental organism.

## METHODS AND MATERIALS

*Stylogdrilus heringianus* and sediments were collected with a Ponar grab at Station DC-6, 10 km offshore from the Donald C. Cook nuclear power plant in Lake Michigan near Bridgman, Michigan (42°0'63"N, 086°41'72"W) (Seibel and Ayers 1974). Sediments at this depth (42 m) consist of greenish-gray to reddish-brown lacustrine muds with a range in median diameter of 2.3–10.4 phi (Cook and Johnson 1974). Worms and sediment were held in a controlled temperature chamber at 10°C for approximately 1 month prior to use.

Sediments for experimental cells were screened through a U.S. Standard Sieve #60 (mesh = 0.250 mm) to remove all coarse debris and macroinvertebrates. Some oligochaete cocoons may have remained in the sediments, but the 0.250 mm mesh has proven effective in removing immature and adult *Stylogdrilus* and tubificids. Nine rectangular, open-topped, plexiglass cells (3 cm × 5 cm × 30 cm ID, Fig. 1) were filled with sieved sediments to a depth of 12–15 cm, then positioned along the face of a 45-L aquarium (Fig. 1). Water collected in Lake Michigan was added to the aquarium to a level ~5 cm above the cells. An aerator tube (Fig. 1) circulated the water throughout the entire system at oxygen saturation (Husby-Coupland 1980, Robbins *et al.* 1984) similar to conditions at the collection site. Temperature was regulated by a Masterline™ unit to within 0.2°C. Water temperature throughout the tank was monitored by multiple thermistors. Just prior to introducing the worms, the entire aquarium was encased in black plastic, then covered with 5-cm-thick Styrofoam to close off the system from outside light and limit temperature fluctuations.

Seven densities were chosen from 30,000 to 134,000 worms m<sup>-2</sup> (Table 1). The densities begin an order of magnitude higher than normally found for *Stylogdrilus* in the open lake, but, based on past

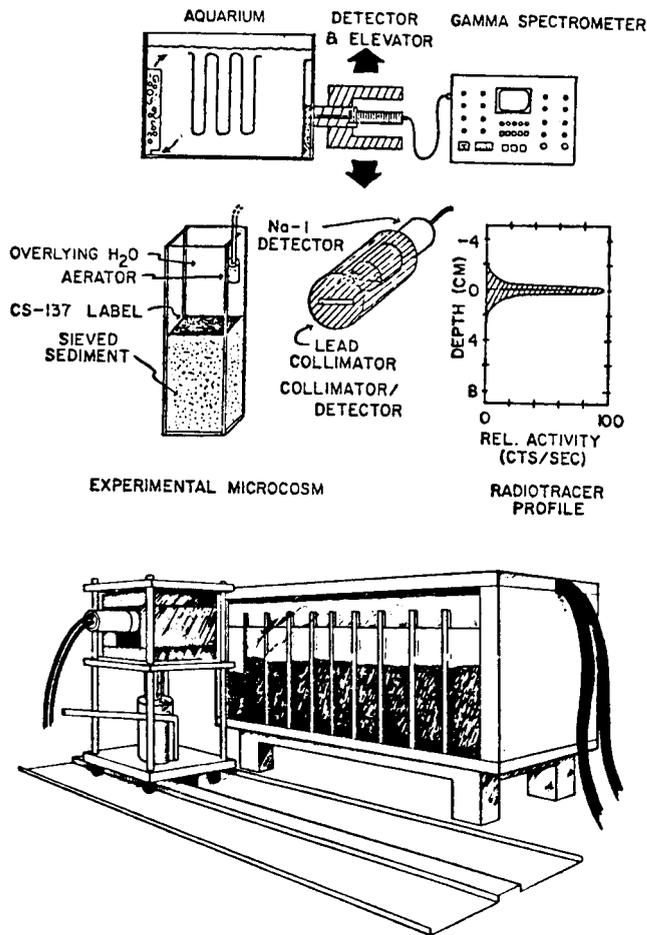


FIG. 1. Upper pannel shows aquarium with aerator, cooling coil, and cell with NaI detector connected to spectrometer. Middle pannel shows microcosm with sediment and Cs-137 layer, collimator for NaI detector, and initial sample profile (relative activity in counts per second). Lower pannel shows aquarium housing several microcosms and moveable sled for detector and elevator.

experiments, they would allow for reworking rate determinations within a reasonable period of time (Robbins *et al.* 1984). A sediment reworking rate was determined for each density at six temperatures between 4 and 20°C. The lower and upper end temperatures corresponded approximately to the normal range of temperatures in nearshore Lake Michigan. Because all of our previous reworking experiments using *Stylodrilus* had been conducted at 10°C and reworking rates per worm were well established, this temperature was chosen as the beginning and ending point.

The sediment in experimental and control cells

TABLE 1. Initial and final numbers of *Stylodrilus heringianus* in control and experimental cells, density is equivalent number of worms  $m^{-2}$ .

| Initial Densities<br>Density | Initial Densities   |                              | Final Densities        |                      |
|------------------------------|---------------------|------------------------------|------------------------|----------------------|
|                              | Number<br>of Adults | Total Worms<br>After 2,600 h | Number of<br>Immatures | % Adult<br>Mortality |
| Control 1                    | 0                   | 0                            | 0                      | 0                    |
| Control 2                    | 0                   | 0                            | 0                      | 0                    |
| 30,000                       | 45                  | 78                           | 42                     | 20                   |
| 44,000                       | 66                  | 73                           | 19                     | 18                   |
| 72,000                       | 108                 | 146                          | 63                     | 23                   |
| 87,000                       | 130                 | 188                          | 93                     | 27                   |
| 100,000                      | 150                 | 168                          | 66                     | 32                   |
| 115,000                      | 172                 | 183                          | 59                     | 29                   |
| 134,000                      | 200                 | 245                          | 111                    | 33                   |

was allowed to settle at 10°C for 1 week prior to addition of worms. Only large (10–20 mm) and seemingly healthy organisms were selected and were allowed to acclimate under experimental conditions for 48 h. A submillimeter layer (approximately 2  $\mu$ Ci) of Cs-137 labeled sediment then was pipetted onto the sediment-water interface, and cells were scanned to determine the position of the marker-layer, sediment/water interface. Two cells containing the Cs-137 marker layer, but no worms, served as controls.

The gamma-scan system (Fig. 1), as first described by Robbins *et al.* (1979), was used to monitor the position of the Cs-137 layer. The system is composed of an insulated aquarium, a NaI gamma detector, and a single channel analyzer. The NaI detector is situated on a hydraulic jack which can be lowered or raised in 1.0 mm intervals. In this study, the detector was placed on a sled, allowing for monitoring of several cells in a single aquarium without their disturbance (Fig. 1).

The sediment reworking rate, or the distance which the Cs-137 layer is buried by oligochaete feeding over a given time, was determined following the methods of Robbins *et al.* (1984). First, a cell was vertically scanned at 1-mm intervals to create an activity profile. The activity profile was recorded from 100 sec counts per mm over a 1–1.5 cm range in the region of highest Cs-137 activity. The profile appears as a Gaussian profile due to the 4-mm-wide slit in the detector optics. The profile was then fitted with a Gaussian function to calculate the mean position of the labeled layer (Fig. 1). If the Cs-137 layer were at position  $z$  and the detector were at depth  $z'$ , the counting rate would be a fraction ( $f(z-z')$ ) of the maximum rate or

TABLE 2. Length of time at each temperature in the monitoring sequence.

| Temperature °C | Length of Monitoring Hours | Cumulative Time Hours |
|----------------|----------------------------|-----------------------|
| 10             | 200                        | 200                   |
| 7              | 325                        | 525                   |
| 4              | 380                        | 905                   |
| 7              | 300                        | 1,205                 |
| 10             | 235                        | 1,440                 |
| 13             | 220                        | 1,660                 |
| 17             | 230                        | 1,890                 |
| 20             | 160                        | 2,050                 |
| 17             | 165                        | 2,215                 |
| 13             | 175                        | 2,390                 |
| 10             | 210                        | 2,600                 |

$$f(z-z') = e^{-(z-z')^2/2\sigma^2} \quad (1)$$

where  $\sigma$  is the standard deviation related to the full width of the Gaussian profile at half the maximum peak width (FWHM) by

$$\text{FWHM} = 2.35\sigma \quad (2)$$

The observed activity versus depth ( $A_{\text{obs}}(z-z')$ ) is then

$$A_{\text{obs}}(z-z') = A_{\text{oc}} e^{-(z-z')^2/2\sigma^2} \quad (3)$$

using least-squares methods.

Each cell was scanned daily to create an activity profile and the peak position calculated using the Gaussian function. The position of the calculated peak was then used to compute an instantaneous reworking rate. The mean reworking rate (or running average reworking rate) was obtained from the slope of a least-squares regression of the first 10 successive instantaneous rates. The next mean value was obtained by dropping the first of the 10 points and adding the next in the series, etc. The mean reworking rate over time calculated in this manner, while incorporating both constant temperature periods and periods of temperature change, allowed for better examination of trends by reducing effects of fluctuations in instantaneous reworking rates (Robbins *et al.* 1984). An  $n = 10$  was chosen arbitrarily; however, Robbins *et al.* (1984) had good results with  $n = 4$ .

The Cs-137 layer position at each selected temperature (Table 2) was monitored daily (controls

weekly) until a constant reworking rate was assumed to be established by inspection of instantaneous rates. The average length of time spent monitoring each selected temperature was approximately 200 hours with the longest at 4°C (380 h) and the shortest at 20°C (160 h). All temperature changes were gradual, about 0.1°C h<sup>-1</sup>, to allow worms to acclimate.

At the end of the experiments, contents of each cell were sieved through a 0.250 mm screen to determine the final number of worms present.

## RESULTS

All cells showed varying increases in the number of worms present at the end of the experiment (Table 1), resulting from immature worms (<10 mm long) which made up between 26–54% of the final densities. Reproduction was believed to have occurred in each experimental cell, although it was possible that some cocoons hatched that were not removed by sieving. As Robbins *et al.* (1984) have shown, worms <10 mm long are too small to have much of an effect on peak burial, and, because it was not possible to determine at precisely what point adult mortality occurred, all calculations were based on the initial number of adults. In all cells, mortality of mature worms was between 18–33%.

Positions of Cs-137 layers fell slowly in both control cells over the first portion of the experiment, after which the layers slowly rose (Fig. 2). The gradual fall and rise of the Cs-137 layers corresponded directly to changes in temperature and were attributed to contraction and then expansion of the sediment column. The actual mechanisms of sediment contraction-expansion were not determined. A fourth-degree polynomial regression was calculated for the combined control cell data points and applied as a correction factor for the treatment cells. From the regression, a value was calculated for each point in the treatment cells, then added to or subtracted from the maximum peak depth for that point (Fig. 2). Corrections were made before calculations of mean reworking rates. With the exception of the 44,000 worms m<sup>-2</sup> cell, control corrected data for all experimental cells showed continual burial of the radiotracer layer over the duration of the experiment.

Responses of sediment reworking to temperature decreases were similar in each cell over the first 900 h as shown by the downward trend in the plots (Fig. 2). A significant leveling-off then

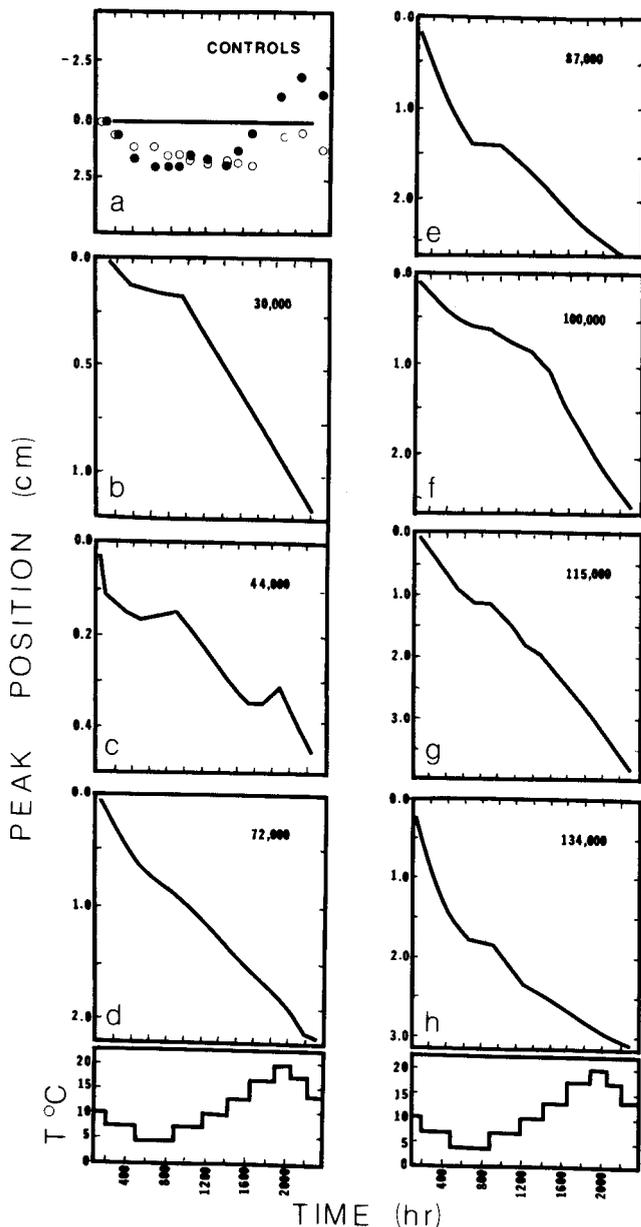


FIG. 2. Position of the Cs-137 layer relative to the sediment surface over time for control and experimental cells computed from the running averages (see text).

occurred at 4°C. Following the 4°C temperature period, there were no consistent relationships between temperature and the downward movement of the Cs-137 peaks throughout the remainder of the experiment.

The mean sediment reworking rates in each temperature period showed relationships to some of the temperature decreases and increases (Table 3).

For example, the 100,000 worms  $m^{-2}$  cell showed a sharp drop in mean reworking rate at 4°C, followed by a recovery period between 7 and 13°C as feeding presumably responded to increased temperature. A peak reworking rate then occurred at 13°C, followed by a lower but somewhat constant rate in the 17 to 20 to 13°C cycle and then by a sharp drop during the final 200 h at 10°C. Peak burial in other cells, again except for the 44,000  $m^{-2}$  cell, paralleled this pattern. All had significant drops in running sediment reworking rates at 4°C, approaching zero, followed by a recovery period, the length and magnitude of which varied among cells. Some distinct decline in the mean reworking rate was common in all cells during the final 200 h.

Cells containing greater numbers of worms had greater overall reworking activity than cells with fewer worms. This trend held throughout the experiment resulting in the final Cs-137 layer position to be deeper for higher densities (2.82 cm to 3.74 cm deep) than for lower worm densities (0.041–1.09 cm deep). However, on a per worm basis, the sediment reworking rate was not dependent on density (Table 3).

## DISCUSSION

### Mortality and Reproduction

Some degree of organism mortality in laboratory studies has been cited by most researchers (Appleby and Brinkhurst 1970), Davis 1974b, Fisher *et al.* 1980, Husby-Coupland 1980, Krezoski 1981, Krezoski *et al.* 1984, Robbins *et al.* 1984). The amount of organism handling and length of experiment are often cited as two major influencing factors. Estimates for worm mortality during this study, based on differences between the original density and the final number of worms > 10 mm long, fell close to reported ranges of 20–30% (Table 1) (Husby-Coupland 1980, Krezoski 1981). No macrobenthic species, other than *Stylodrilus*, were found in the cells at the end of the experiment.

Oligochaete reproduction is not unknown in laboratory microcosms, although rare (Robbins *et al.* 1984). Temperature, in itself, often serves as a biological cue to reproduce. *Stylodrilus heringianus*, which reproduces only sexually as far as is known, breeds from May through August (Pickavance 1971). Worms with sex organs are present all year but are more prevalent from late winter through early summer. Greater numbers of cocoons were

TABLE 3. Mean reworking rates (see text) ( $10^{-5}$  cm  $h^{-1}$  worm $^{-1}$  (S.E.) for *Stylocdrilus heringianus* after constant reworking rate established based on control corrected data,  $d$  = initial worm density  $m^{-2}$ .

| d       | Temperature °C |            |             |            |            |            |            |             |             |            |             |
|---------|----------------|------------|-------------|------------|------------|------------|------------|-------------|-------------|------------|-------------|
|         | 10             | 7          | 4           | 7          | 10         | 13         | 17         | 20          | 17          | 13         | 10          |
| 30,000  | 2.16 (.17)     | 0.51 (.10) | -0.06 (.42) | 0.95 (.06) | 1.58 (.09) | 1.91 (.26) | 1.62 (.18) | 1.04 (.60)  | 1.42 (.19)  | 2.22 (.33) | -0.17 (.40) |
| 44,000  | 0.82 (.11)     | 0.05 (.08) | -0.04 (.07) | 0.26 (.06) | 0.35 (.08) | 0.75 (.24) | 0.10 (.07) | -0.33 (.30) | -0.33 (.30) | 1.11 (.25) | 0.25 (.35)  |
| 72,000  | 1.30 (.05)     | 1.02 (.07) | 0.21 (.02)  | 0.77 (.06) | 0.83 (.07) | 1.11 (.25) | 0.69 (.09) | 0.65 (.28)  | 0.86 (.04)  | 1.02 (.21) | 0.24 (.13)  |
| 87,000  | 1.69 (.06)     | 1.85 (.04) | 0.06 (.03)  | 0.34 (.02) | 0.62 (.02) | 0.85 (.01) | 0.92 (.05) | 0.62 (.18)  | 0.45 (.10)  | 0.92 (.22) | 0.29 (.13)  |
| 100,000 | 0.73 (.02)     | 0.61 (.02) | 0.15 (.02)  | 0.35 (.03) | 0.53 (.04) | 1.40 (.05) | 1.07 (.06) | 1.07 (.10)  | 1.20 (.03)  | 1.13 (.12) | 0.24 (.13)  |
| 115,000 | 0.99 (.04)     | 1.34 (.04) | 0.19 (.03)  | 0.99 (.03) | 0.35 (.02) | 0.81 (.10) | 0.87 (.07) | 0.93 (.08)  | 1.14 (.08)  | 1.57 (.08) | 0.75 (.16)  |
| 134,000 | 1.48 (.03)     | 1.15 (.02) | 0.12 (.03)  | 0.55 (.01) | 0.30 (.06) | 0.28 (.05) | 0.55 (.05) | 0.09 (.14)  | 0.41 (.07)  | 0.45 (.11) | 0.05 (.04)  |

present from March through June in Britain (Cook 1969). Rising temperature in the aquarium may have possibly simulated a warming trend, causing worms to reproduce. Also, the sieved sediments may have contained some cocoons; however, no immature worms were found in the control cells. Pickavance (1971) reported that late hatching of some of the previous years cocoons was triggered by warming. The sediments for this research were collected in June from Lake Michigan which would coincide with peak cocoon abundance and highest densities of mature worms. The length of time from copulation to hatching of cocoons is unknown (LaDronka 1984).

It is not known why the burial of the Cs-137 marker layer and the reworking rate for the 44,000 worms  $m^{-2}$  cell were so erratic.

### Controls

The Cs-137 tracer layer in the controls without worms remained relatively stationary, 0.1–0.2 cm deep within the sediment between 400 and 1200 h of the experiment (Fig. 2). Krezoski (1981) and Robbins *et al.* (1984) demonstrated slight but significant downward movement of radiotracer layers in their control cells (about 0.1 cm in 1,400 h). They measured the depth of the radiotracer layers relative to the base of the microcosms and attributed peak movements to sediment compaction which was correlated with visual measurements of the sediment surface. Because our aquarium was sealed, we could not record the position of the sediment surface over time but assumed that control cell changes in the position of the Cs-137 layer were due to sediment compaction in combination with temperature induced contraction then expansion. Experimental cells not corrected for contraction-expansion showed some negative reworking rates, particularly at higher tempera-

tures. The control corrected data for the 44,000 worms  $m^{-2}$  and 30,000  $m^{-2}$  cells still showed some unexplainable periods of negative reworking (Table 3).

### Sediment Reworking and Temperature

Temperature is reported to have a direct effect on the defecation rate of tubificids (Appleby and Brinkhurst 1970, McCall and Fisher 1980). This relationship appeared to hold true during the early part of our experiment as measured by mean sediment reworking rates which declined in all cells when the temperature was lowered to 4°C. Between 10 and 4°C, the sediment reworking rate in the 134,000 worms  $m^{-2}$  cell dropped from  $1.48 \times 10^{-5}$  cm  $h^{-1}$  worm $^{-1}$  to  $0.12 \times 10^{-5}$  cm  $h^{-1}$  worm $^{-1}$ . Three other cells also showed over an order of magnitude decrease in the rate of sediment reworking when temperature was lowered from 10°C to 4°C (Table 3).

These data supported a direct relationship between temperature and sediment reworking rate between 10 and 4°C. McCall and Fisher (1980) found that the overall feeding rate increased linearly with temperature and concluded that the rate of defecation was most strongly dependent on water temperature and dissolved oxygen concentration. Appleby and Brinkhurst (1970) used an inverted worm technique to measure the defecation rate at various temperatures for three tubificid species. They found a temperature influence, but the magnitude varied from species to species. Their lowest temperature of 4°C produced the lowest defecation rate leading them to the conclusion that worms would be least active in winter. Data here indicate that a very slow reworking rate would occur the year around in the offshore areas of the upper Great Lakes. The average reworking rate at 4°C over the seven densities, calculated on a per

- (□) *Limnodrilus udekemianus* (Poddubnaja 1961)  
 (●) *Limnodrilus hoffmeisteri* (Poddubnaja 1961)  
 (✱) *Tubifex tubifex* (Wachs 1967)  
 (■) *Tubifex tubifex* (Appleby and Brinkhurst 1970)  
 (○) *Limnodrilus hoffmeisteri* (Appleby and Brinkhurst 1970)

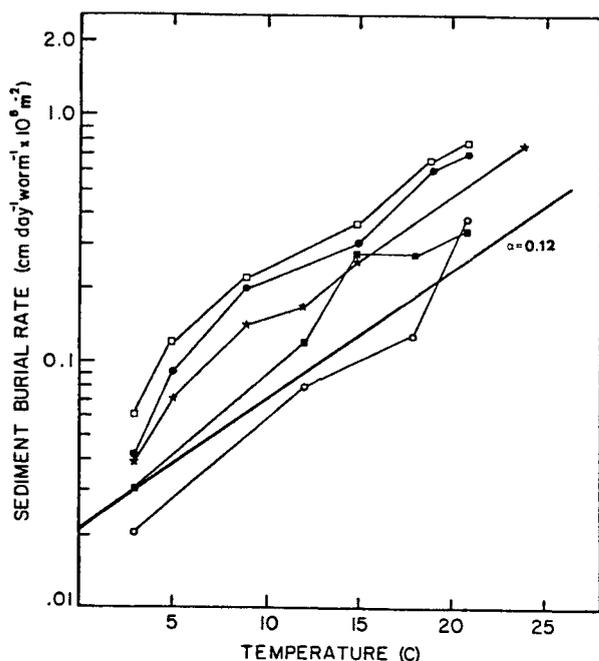


FIG. 3. Calculated reworking rates for several species of freshwater oligochaetes at various temperatures (see Fisher *et al.* 1980). Solid line is for *Stylo-drilus heringianus* from this study calculated from the depth dependent model.

worm basis, was  $0.9 \times 10^{-6} \text{ cm} \cdot \text{h}^{-1} \text{ worm}^{-1}$  or  $0.78 \times 10^{-2} \text{ cm worm}^{-1} \text{ year}^{-1}$ . This corresponded to  $0.15 \text{ g dry sediment worm}^{-1} \text{ year}^{-1}$  using the conversion factors from Robbins *et al.* (1979) and is a significant drop from  $4^\circ\text{C}$  projected rates based on experiments run at temperatures between 10 and  $20^\circ\text{C}$ : Krezoski (1981),  $1.44 \pm 0.07 \text{ g dry sediment worm}^{-1} \text{ year}^{-1}$ ; Robbins *et al.* (1979),  $1.0 \text{ g dry sediment worm}^{-1} \text{ year}^{-1}$ ; and Fisher *et al.* (1980),  $1.36 \text{ g dry sediment worm}^{-1} \text{ year}^{-1}$ .  $20^\circ\text{C}$  (Fig. 3).

While the reworking rate responses to the temperature decrease from 10 to  $4^\circ\text{C}$  followed our predictions and agreed with the literature, responses during the remaining 1,700 h of the experiment did not. The most probable explanation at this time seems to be a stopping or slowing of feeding which may have accompanied reproduction.

### Feeding Models

The sediment reworking rate is essentially a measure of the worms feeding rate. The bulk of the diet consists of detrital organic particles and the associated bacteria found within the sediments (reviewed by McCall and Fisher 1980). The zone of maximum feeding for many species is 3–6 cm below the sediment water interface (McCall and Fisher 1980). Worms feed in a vertical position and deposit the undigested portion on the sediment surface (Davis 1974b, Robbins *et al.* 1979, Krezoski 1981). Feeding oligochaetes can completely utilize the nutritive content of sediments leaving only mineral particles (Petr 1976). Davis (1974b) suggested exhaustion of the food resource as an explanation for the decline of feeding and defecating rates of tubificids toward the end of experiments in small containers.

The particle reworking rate for *Tubifex tubifex*, as calculated by Fisher *et al.* (1980), showed an exponential decay over time where the rate of burial of a Cs-137 labeled sediment layer was constant until it reached a depth of 7 cm, after which the burial rate diminished and approached 0.0 at a depth near 8.5 cm. Other investigators have noticed a similar exponential shape to oligochaete feeding rate data (Appleby and Brinkhurst 1970, Davis 1974b). Krezoski (1981) fitted an exponential function to the marker layer burial rates of *Stylo-drilus heringianus* as determined by gamma-scan analysis. His data showed that the sediment burial rate was linear in the first 500 h and then decreased over time as it approached a maximum burial depth of 4.5 cm. In light of the above, we examined two models to describe our data: 1) a time dependent model, which would explain the exponential decay of the reworking rate as a time related phenomenon, and 2) a depth dependent model based on the observed decrease in sediment reworking with increasing sediment depth as cited by Fisher *et al.* (1980) and Krezoski (1981).

The time dependent model was based on one proposed by Krezoski (1981) which describes the rate of sediment burial by *Stylo-drilus heringianus* as advective sediment transport:

$$V = \frac{dz}{dt} = Z_{\max} \beta e^{-\beta t} \quad (4)$$

The above then was combined with an equation to account for the effect of temperature on feeding rate. The slope of the best fit line (alpha in Fig. 3)

TABLE 4. Results of feeding models based on time dependency (Equation 7) and on depth dependency (Equation 11).

| Density | Time Dependent |          |         |            | Depth Dependent |          |            |            |
|---------|----------------|----------|---------|------------|-----------------|----------|------------|------------|
|         | r              | $\alpha$ | $\beta$ | $Z_{\max}$ | r               | $\alpha$ | $\ln\beta$ | $Z_{\max}$ |
| 30,000  | .35            | .01      | .16     | -.2        | .60             | .11      | -0.73      | 1.37       |
| 44,000  | .32            | .09      | -.19    | .4         | .45             | .15      | -1.21      | 0.51       |
| 72,000  | .61            | .08      | -.49    | .5         | .68             | .10      | -1.58      | 2.51       |
| 87,000  | .57            | .14      | -.68    | .7         | .62             | .14      | -1.96      | 2.75       |
| 100,000 | .81            | .15      | -.30    | .3         | .87             | .15      | -3.13      | 3.85       |
| 115,000 | .45            | .06      | -.59    | .6         | .57             | .09      | -2.42      | 5.27       |
| 134,000 | .68            | .06      | -.10    | .1         | .39             | .08      | -1.36      | 2.96       |

as determined by linear least squares regression analysis was 0.12. Therefore,

$$V \approx e^{\alpha T} \quad (5)$$

Combining (5) with (1) resulted in a time dependent model with an additional term attributed to the temperature dependency

$$v(t, T) = Z_{\max} \beta e^{\alpha T} e^{\beta t} \quad (6)$$

Taking the natural logarithm resulted in a multiple linear regression equation

$$\ln V = \ln V_0 + \alpha T + \beta t \quad (7)$$

where  $V = Z_{\max}$ .

The values for mean time and the rate of sediment reworking at each temperature were tested in this model (Table 4). Only the 100,000 worms  $m^{-2}$  cell had a significant correlation coefficient ( $P < 0.05$ ).

The second model tested depth dependency and also was derived from Krezoski (1981). The equation describing exponential decay based on depth was

$$Z = Z_{\max}(1 - e^{-\beta T}) \quad (8)$$

where  $Z$  was the depth below the sediment-water interface and  $Z_{\max}$  corresponded to the asymptotic depth of this curve. Solving for  $e^{-\beta T}$  yields

$$e^{-\beta T} = \frac{Z_{\max} - Z}{Z_{\max}} \quad (9)$$

Substituting in (4) and solving for  $V$  resulted in

$$V(Z) = \beta(Z_{\max} - Z) \quad (10)$$

Combining (10) with (5) to account for the temperature dependency and taking the log resulted in a multiple linear regression equation, this time with the three dependent variables of mean depth,  $Z_{\max}$ , and temperature (Table 4).

$$\ln V - \ln(Z_{\max} - Z) = \ln \beta + \alpha T \quad (11)$$

The correlation coefficients for the depth dependent model were higher than for the time dependent model in all cases except one, but this model also contained an additional degree of freedom. Only Cell 6 (100,000 worms  $m^{-2}$ ) had a significant value for  $r$  ( $P < 0.05$ ).

Of the two, the depth dependent model appeared to more closely describe the system. Not only were the correlation coefficients ( $r$ ) higher, but there was less spread in the values for the temperature coefficients ( $\alpha$ ). The average value for  $\alpha$  as calculated by the depth dependent model was  $0.12 \pm 0.01$ , and when plotted (Fig. 3) the temperature coefficient correlated highly with previous observations, depicting a strong logarithmic association between temperature and the rate of sediment reworking.

#### Sediment Reworking and Organism Density

Krezoski (1981) speculated that sediment reworking rates for *Stylocdrilus* were density independent. This theory was tested by a regression of the rate of sediment reworking ( $V_0$ ) on organism density ( $\rho$ ). The rate was not correlated with density ( $r = 0.2$ ). Of more importance was the observation that organism density was highly correlated ( $r = 0.78$ ) with  $Z_{\max}$  (the depth of maximum feeding). Organisms tended to feed deeper at higher densities in homog-

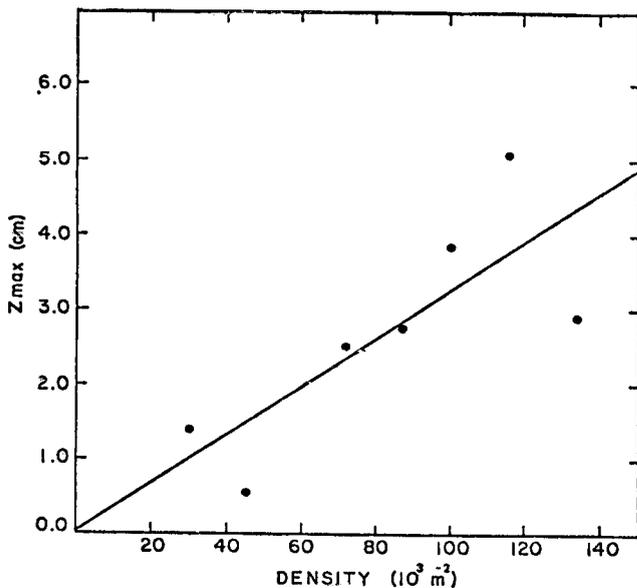


FIG. 4. Relationship between organism density and depth of feeding for *Stylodrilus heringianus* in the experimental cells,  $r = 0.78$ .

enized sediments (Fig. 4), presumably because of competition. Other researchers have described similar relationships between organism density and depth of sediment penetration (Poddubnaya 1961). Schumacher (1963) found the depth of the oxidized zoned to be extended deeper by higher densities. Thus, oligochaetes may compensate for higher densities by increasing the depth to which they feed but not the rate at which individuals feed.

#### ACKNOWLEDGMENTS

We wish to thank T. Bloom, C. Millenbach, K. Husby-Coupland, and J. Krezoski for assistance in many phases of the study. Sediment and worms were obtained in cooperation with a grant from the Indiana & Michigan Power Company. Support was provided by the National Science Foundation grant OCE-7825680. Contribution No. 418 from the Great Lakes Research Division.

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