

Monitoring defecation activity of infaunal deposit feeders*

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ABSTRACT: An inexpensive, reliable thermistor device capable of monitoring infaunal foraging activity was built and used in the laboratory to examine effects of temperature on sediment reworking by the malidanid polychaete *Clymenella torquata*. The worm defecated at least once per hour 55.0 % (12.0 °C) to 88.2 % (5.5 °C) of the time. Defecation rate was linearly and positively related to temperature. Estimated volume of sediment ejected per defecation (0.015 ml) did not change with temperature. Results are compared with previous reworking studies of *C. torquata*.

INTRODUCTION

Many of the effects which deposit-feeding benthos exert on the physical, chemical, and biological properties of sediments are mediated by their feeding activity (e.g. Pryor, 1975; Goldhaber et al., 1977; Yingst and Rhoads, 1978; Baumfalk, 1979; Aller, 1980; Anderson, 1980; Eckman et al., 1981; Hammond, 1981; Nowell et al., 1981). Therefore, detailed knowledge of deposit-feeding ecology is of interest. Although techniques exist to monitor the feeding behavior of tubicolous infauna (e.g. Wells, 1953; Mangum, 1964a; Kudenov, 1978), methodological limitations commonly prevent long-term, undisturbed records of organism activity. In this paper a relatively inexpensive, reliable thermistor device for monitoring infaunal foraging activity is described. Data examining sediment reworking rates by the malidanid polychaete *Clymenella torquata* in relation to temperature are presented and compared to previously published estimates.

MATERIALS AND METHODS

Bioturbation was monitored using a flowmeter modified from LaBarbera and Vogel (1976). Matched hot bead thermistors (Fenwal Electronics GB32P38, 2000

Ohm \pm 1 %, 2.54 mm in diameter, stub ends glass encapsulated) formed arms of a bridge circuit (Fig. 1). Remaining components were fixed resistors (0.25 W rating, 5 % tolerance) and an operational amplifier (741). The bridge was connected to the op-amp using Fairchild linear integrated circuits. Power was supplied by a standard op-amp power supply. Circuit output was recorded by connecting a potentiometric strip chart recorder between the amplifier and the negative side of the bridge. To waterproof the thermistor probes, their leads were soldered to 26 gauge wire, the wire was threaded through glass tubing, and tubing and stub end of thermistor were joined and sealed with shrink tubing. The glass tubing then was placed through bored corks and held by clamps attached to a ring stand.

The apparatus was used to examine temperature effects on defecation rates of *Clymenella torquata*. This polychaete lives anterior end down in a vertically positioned sand tube and ingests sediments 10 to 15 cm below the sediment surface. To defecate, the worm moves upward to its tube opening and ejects unconsolidated feces onto the adjacent sediment surface (Mangum, 1964a, b; Rhoads, 1967). Adult worms (ca. 5 cm long) were collected from a shallow subtidal sand flat and maintained at a naturally occurring population density (ca. 700 m⁻²; Dobbs, 1981) in laboratory sediment microcosms (plastic basins 28 × 31 × 13 cm deep). Microcosms were held in running ambient seawater at least one week prior to any measurements. New microcosms were established with freshly collected worms for experiments at 18.0 °C

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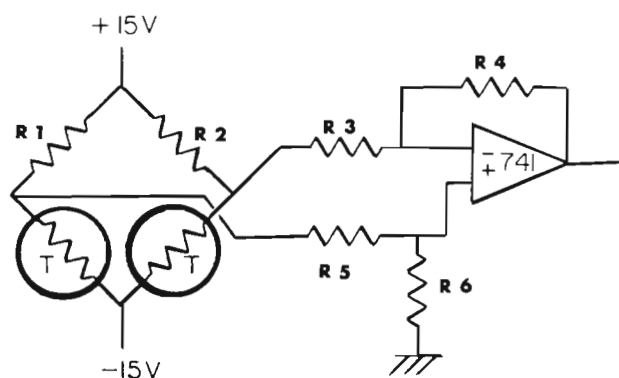


Fig. 1. *Clymenella torquata*. Schematic diagram of flowmeter used to monitor defecation episodes. T = thermistor; R1 and R2 are $2.15\text{K}\Omega$; all other resistors are $1\text{M}\Omega$; 741 = operational amplifier

(June, 1978), 12.0°C (November, 1978), and 5.5°C (January, 1979). Microcosm sediment temperatures were isothermic with the overlying water and fluctuated less than 1.0°C during each experiment. Experiments generally lasted 24 h, although activity patterns over 88 h were obtained. After each set of measurements, the microcosm was examined for tubes curved at their lower end, i.e. the head shaft, a condition which may occur if the sediment is too shallow (Mangum, 1964b; pers. obs.). In all cases, only straight tubes were found.

To record worm activity, one probe (the sensing thermistor, T_s) was positioned in the water over an individual worm's tube opening. A plastic collar (3.5 cm in diameter, height sufficient to reach to the air-water interface) was placed on the sediment surrounding the worm's tube. The collar thus enclosed T_s and greatly reduced signal interference caused by water flow in the experiments. The other probe (the compensating thermistor, T_r) was positioned within a collar in an area of the microcosm containing no worms. Worm activity moved water past T_s , cooling it

relative to the undisturbed T_r , and the resistance change was translated as a deflection on the recorder. Each of the worm's defecations caused a spike on the trace baseline (Fig. 2). Worm feces were collected using methods modified from Rhoads (1967) and Gordon (1966) and measured volumetrically (relationship between volume in ml [X] and dry weight in g [Y] was $Y = 1.26X - 0.07$, $r = 0.99$, $n = 21$). Mean volume of material per defecation was calculated by dividing total volume of sediment defecated by each worm by number of defecations indicated on its trace.

Data were examined for differences among temperatures using a non-parametric Kruskal-Wallis test ($\alpha = 0.05$). If results were significant, then values were compared with the a posteriori Duncan's multiple range test, corrected for unequal sample sizes.

RESULTS

Analysis of nearly 500 h of records indicated that *Clymenella torquata* defecated at least once per hour 67.6 % (18.0°C), 55.0 % (12.0°C), and 88.2 % (5.5°C) of the time (Table 1). Time spent reworking, i.e. percent defecation hours, was significantly lower at 12.0°C than at 5.5°C . Due to large variability, there were no differences among temperatures in the duration of defecation activity periods (DAP), quiescence periods (QP), nor in the number of defecations per defecation activity period (refer to table legend for definitions). Defecation rate at 5.5°C was significantly lower than at 18.0°C and 12.0°C . There was a positive, linear relationship between temperature ($^\circ\text{C}$) (X) and number of defecations per hour (Y): $Y = 0.16X + 1.47$, $r = 0.74$, $n = 21$. Estimated volume of sediment ejected per defecation was 0.015 ml ($n > 1100$ defecations) and did not change with temperature, suggesting that a threshold volume of sediment must accumulate in the worm's gut to initiate a defecation episode (R. B. Whitlatch, pers. comm.).

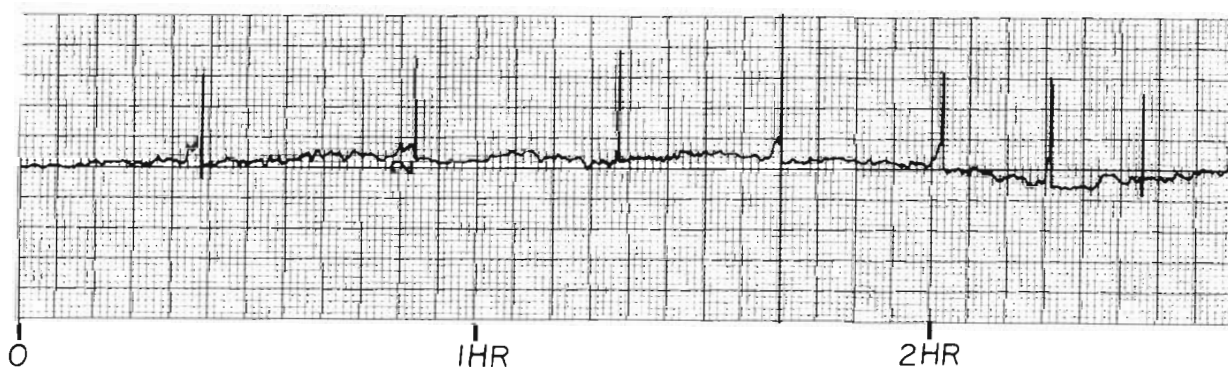


Fig. 2. *Clymenella torquata*. Representative defecation pattern. Each spike on the trace indicates a defecation episode. Total time shown is 2 h 40 min

Table 1. *Clymenella torquata*. Effects of temperature on defecation activities. Defecation hour = any hour during which one or more defecations occurred. Defecation activity period (DAP) = one or more consecutive defecation hours. Quiescence period (QP) = one or more consecutive hours during which no defecations occurred. Where there were significant differences among temperatures, results of Duncan's multiple range test (DMRT) are shown; values represented by the same letter are not significantly different

Temperature (°C)	Number of worms: number of trials	Number of hours recorded	% of total hours recorded which were defecation hours				Duration of DAP (h)		
			mean	s.d.	range	DMRT	mean	s.d.	range
18.0	5 : 5	115	67.6	26.5	37-96	AB	9.1	6.7	3-22
12.0	4 : 4	113	55.0	17.1	42-78	B	7.0	9.1	1-29
5.5	6 : 12	270	88.2	16.2	54-100	A	17.1	17.4	1-56

Temperature	Duration of QP (h)			Number of defecations DAP ⁻¹			Number of defecations h ⁻¹ (during defecation hours only)			
	mean	s.d.	range	mean	s.d.	range	mean	s.d.	range	DMRT
18.0	6.3	29.5	1-13	45.0	41.7	10-127	4.4	1.2	2.7-5.6	A
12.0	5.9	27.9	1-15	25.4	37.7	1-114	3.5	1.0	2.7-5.0	A
5.5	4.6	21.4	0-13	39.5	40.9	1-107	2.4	0.5	1.7-3.3	B

DISCUSSION

Except for a constant volume of sediment per defecation and the temperature effect on defecation rate, sediment reworking by *Clymenella torquata* may be characterized as highly variable. Considerable fluctuations in feeding activity, including temporary cessation, have been shown in other deposit feeders, e.g. a bivalve, *Scrobicularia plana* (Hughes, 1969); a polychaete, *Pectinaria gouldii* (Gordon, 1966); and a holothurian, *Leptosynapta tenuis* (Powell, 1977).

Results of this study were compared with previous investigations of *Clymenella torquata* feeding behavior (Table 2). At a mean annual water temperature of 11 °C, sediment turnover rates calculated by Rhoads (1967) and in this study differed by less than 9%. Both of these exceeded, by more than two times, the rate determined by Mangum (1964a). Rhoads and the present study determined that *C. torquata* reworked 1 ml of sediment worm⁻¹ d⁻¹ at 16 and 15.1 °C, respectively, while Mangum reported this rate

at 26 °C. Disparity in defecation rate estimates extended to lower temperatures as well. Mangum measured a rate of 0.4 ml worm⁻¹ d⁻¹ at 12.5 °C, approximately half the rate determined by Rhoads at 11 °C and the present study at 12.0 °C. Finally, the time interval between consecutive defecations observed by Mangum at 12.5 °C was nearly the same as this investigation's interval at 5.5 °C.

Neither Mangum (1964a) nor Rhoads (1967) reported the size of worms they used; therefore, it is not clear whether the above differences in reworking rates reflect size disparities. However, mean lengths of the populations Mangum studied were reported in another paper (Mangum, 1964b), 4.1 and 5.2 cm for worms from Beaufort Harbor, North Carolina and West Haven, Connecticut, respectively. The worms used in the present study were approximately 5 cm long, so it seems that differences in worm size cannot account for the rate discrepancies. An alternative explanation may lie in the length of the pre-experimental acclimation period. Although not stated specifically, Mangum

Table 2. Comparison of selected results from 3 reworking studies of *Clymenella torquata*

Reference	Estimated sediment turnover rate at mean annual water temperature of 11 °C (ml worm ⁻¹ yr ⁻¹)	Temperature at which worm defecated 1 ml of sediment d ⁻¹	Interval between consecutive defecations (min)		
			temperature	mean	range
Mangum (1964a)	136	26 °C	26-28 °C 12.5 °C	25 26	18-30 18-60
Rhoads (1967)	274	16 °C	not reported		
Present study	301	15.1 °C	18.0 °C 12.0 °C 5.5 °C	14.5 17.9 26.3	11-22 12-22 18-35

(1964a) apparently collected worms and tested them soon after. In the present study, worms were acclimated to experimental conditions for at least 1 wk. Another, functionally similar polychaete, *Pectinaria koreni*, increased its reworking rate over 8 d (Dobbs, in prep.) and this phenomenon has been qualitatively observed in *C. torquata* as well (pers. obs.).

Hot bead and hot wire anemometry have proven useful in monitoring irrigation (Scott et al., 1976; Gust and Harrison, 1981) and feeding behavior (this study) of infaunal organisms. The thermistor apparatus described here provides a detailed record of defecation episodes, as do other techniques (e.g. Wells, 1953; Mangum, 1964a; Kudenov, 1978), and offers distinct advantages. First, once microcosms are established, organisms are not subjected to pre-trial manipulation nor contact with monitoring equipment. Second, a closer approximation of environmental conditions can be achieved since the sensing thermistor can be positioned precisely to monitor a selected individual in a microcosm containing natural densities of infauna. Third, the system is maintenance-free for relatively long time periods. Fourth, the apparatus can be used to monitor activity of any organism which ejects feces, unconsolidated or pelletized, into the water immediately above the sediment surface (e.g. molpadanid holothurians and ampharetid polychaetes).

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