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PERIODICITY IN FECAL PELLET PRODUCTION BY THE CAPITELLID POLYCHAETE *MEDIOMASTUS AMBISETA* THROUGHOUT THE DAY

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ABSTRACT

Rates of fecal pellet production in *Mediomastus ambiseta* (Hartman), a capitellid polychaete, were determined by collecting and counting the number of pellets deposited on the sediment surface at three censusing intervals (6, 12 and 24 hours). The field-collected worms were maintained in culture in a dark incubator at near-ambient water temperature (20°C) for at least a month prior to the study. Rates of pellet production exhibited a dramatic and repeatable cycle over the course of the day. Pellet production by worms censused at 6-hour intervals was highest from 2400 to 0600 (Daylight Savings Time) and decreased by about a factor of four from 0600 to 1800; almost no pellets were produced between 1800 and 2400. From these experiments it is not possible to determine if the cycle is an innate, programmed behavior (e.g. a circadian rhythm) or a response to some cyclically occurring external stimulus. Whether genetically or externally controlled, the cycle may be for avoiding predation by a twilight- or night-active predator or it may be due to physiological constraints.

INTRODUCTION

During the course of laboratory studies to develop standard methodologies for determining rates of sediment reworking by *Mediomastus ambiseta* (Hartman) under various flow and sediment-transport conditions, a periodicity in fecal pellet production was observed. *Mediomastus ambiseta* (hereafter called *Mediomastus*), a capitellid polychaete, is a numerically dominant infaunal organism in many coastal embayments on the east coast of the United States (e.g. Grassle *et al.* 1980, Sanders *et al.* 1980, Mahoney & Livingston 1982, Dobbs & Vozarik 1983). For example, population densities of recruited postlarvae (retained on a 300-μm sieve) at a shallow, subtidal (10-m depth) site in Outer New Bedford Harbor, Buzzards Bay, Massachusetts (USA) vary between 180 000 and 720 000 individuals/m^2 throughout the year. It is the numerically dominant, macrofaunal organism at this site. *Mediomastus* is a sub-surface deposit feeder ingesting sediment at distances of millimeters to a few centimeters below the sediment-water interface and depositing discrete, cylindrical fecal pellets on the sediment surface. *Mediomastus* feeds on silt- and clay-sized particles and repackages them into pellets which may be several orders-of-magnitude larger in size (large juvenile and adult worms produce pellets that are approximately 160 μm long and 90 μm in diameter). This repackaging of free sediments into biological aggregates may have profound implications to sediment resuspension and transport, which are discussed elsewhere (Grant & Butman 1987, Butman *et al.* in prep.). In this paper, results are presented from experiments that revealed a periodicity of pellet production in *Mediomastus* throughout the day. Several hypotheses are posed which may explain the observed defecation cycle.

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MATERIALS AND METHODS

Large juvenile and adult worms (retained on a 300-μm sieve) were collected from a shallow, subtidal field site (see Introduction) and held at near-ambient water temperature (20°C) in a dark incubator for at least one month prior to the study. During this time and during the experiments, the worms were maintained in defaunated (by freezing) sediments collected from the study site. Just prior to each experiment, worms of similar size were held in seawater for several hours until their guts were devoid of pellets, then they were introduced into dishes (4.5 cm in diameter and 2.2 cm in depth) with presieved sediment and returned to the incubator. Worms were allowed two days to establish a tube and "normal" feeding activity before censusing began. Pellet production was censused by carefully removing all pellets deposited on the sediment surface by pipette with as little disturbance to the sediment as possible. The assumption was made that all pellets produced were deposited on the sediment surface.

Two experiments were conducted; the conditions are listed in Table 1. The main difference between the two experiments is that the number of pellets produced by each individual was counted at each censusing interval in the first experiment, whereas the pooled, dry weight of pellets produced by ten individuals per dish was determined in the second experiment. Both methods of censusing produced similar results.

RESULTS

Rates of pellet production by *Mediomastus ambiseta* exhibited a dramatic and repeatable 24-hour cycle (Fig. 1). Pellet production by worms censused at 6-hour

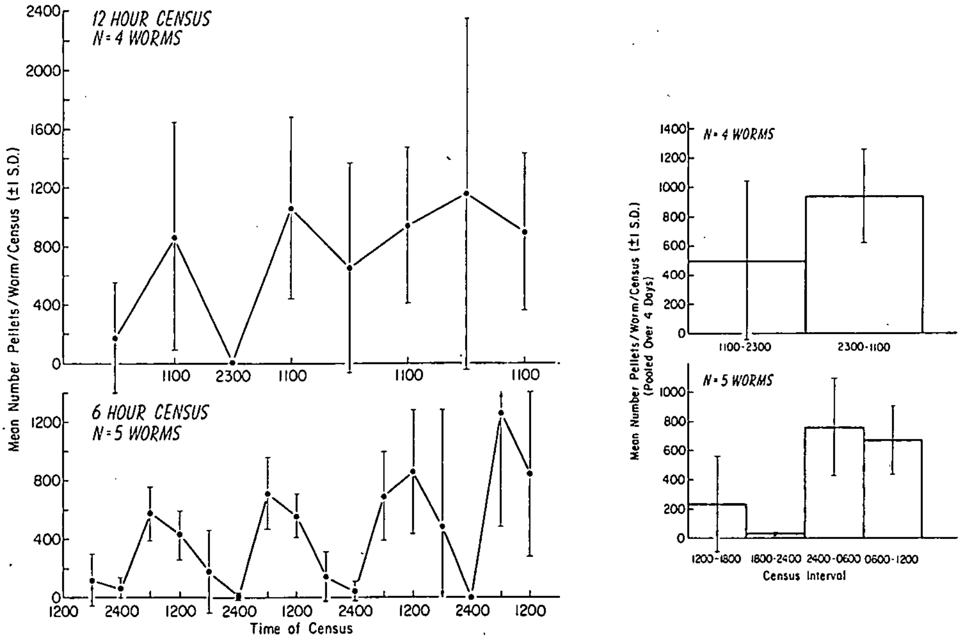

Fig. 1. Pellet production by *Mediomastus ambiseta* in Experiment 1. Mean number of pellets produced per worm (± 1 SD) at the 6-hour and 12-hour censusing intervals for the 4-day duration of the experiment (left) and these data pooled over 4 days for each censusing interval (right).

intervals was highest during the 2400 to 0600 (Daylight Savings Time) interval and decreased by about a factor of four during the 0600 to 1800 interval. Almost no pellet production occurred between 1800 and 2400 hours. Pellet production by worms censused at 12-hour intervals exhibited a similar cycle (Figs 1 and 2), with pellet production 30 to 50% higher between 2300 and 1100 hours than between 1100 and 2300 hours. (The censusing times for the 12-hour intervals were off-set by one hour compared to the 6-hour intervals, due to our technical ability to census only one group of worms at a time.)

The relatively high standard deviations associated with mean pellet production for the 6-hour censuses, especially during the last two days of the experiment (Fig. 1), reflect variability in the maximum number of pellets produced by each worm at any given census (Fig. 3) and not significant deviations from the observed 24-hour cycle. Each individual censused at 6-hour intervals exhibited a similar cycle of maximum pellet production between 2400 and 1200 hours, and minimum production between 1800 and 2400 hours (Fig. 3). In contrast, the variability in pellet production at each censusing interval for worms censused every 12 hours in the first experiment (Fig. 1) reflects real variability in the timing of peak pellet production among the four individual worms (Fig. 4). This variability is considerably reduced in the second experiment (Fig. 2), however, where an order-of-magnitude more worms were censused (see Table 1).

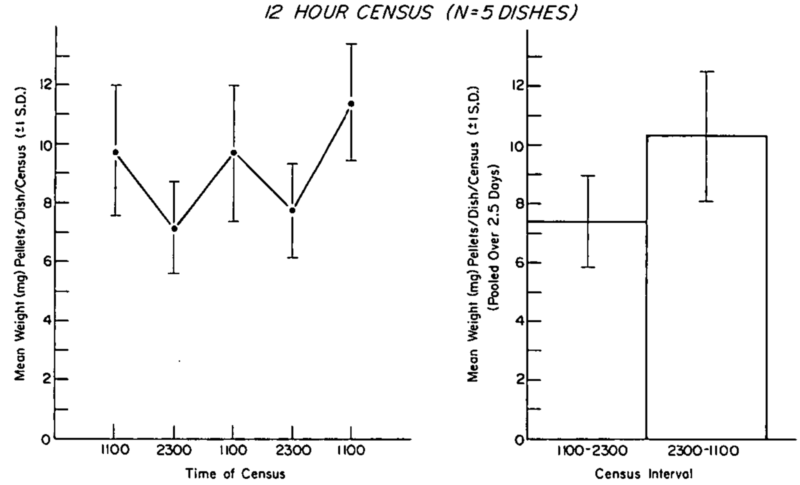

Fig. 2. Pellet production by *Mediomastus ambiseta* in Experiment 2. Mean weight of pellets produced per dish (± 1 SD) at the 12-hour censusing intervals for the 2.5 day duration of the experiment (left) and these data pooled over 2.5 days for each censusing interval (right).

The larger sample size of worms in the second experiment (Table 1) was expected to reduce between-replicate variability, as long as a constant number of worms per dish actually produced pellets. It was not possible to determine directly the number of worms producing pellets in each dish during the second experiment because some worms move around and produce more than one pellet pile during any given interval. However, 12 of the 15 individuals censused in the first experiment produced pellets, so it is reasonable to assume that a similar percentage also

Table 1. Experimental design

	Experiment 1	Experiment 2
Temperature	20°C	20°C
Sediment	< 90 μm 1 cm deep	< 90 μm 1 cm deep
Censusing intervals ("treatments")	24 hrs 12 hrs 6 hrs	24 hrs 12 hrs
Replicates per treatment	5	3 (24 hrs) 5 (12 hrs)
Worms per replicate	1	10
Parameter measured	number of pellets produced	weight of pellets produced
Duration of experiment	4 days	2.5 days

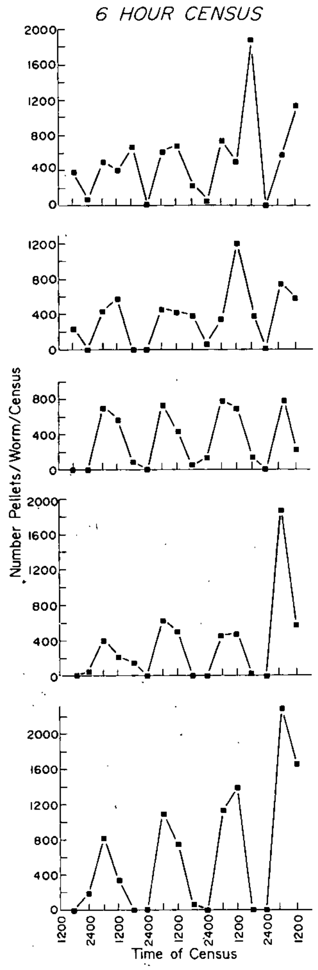

Fig. 3. Pellet production for the 5 individual worms censused at 6-hour intervals in Experiment 1.

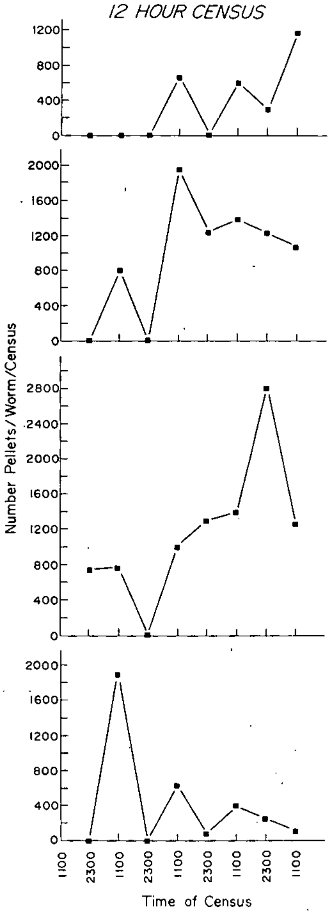

Fig. 4. Pellet production for the 4 individual worms censused at 12-hour intervals in Experiment 1.

would produce pellets during the second experiment. This assumption is supported by the fact that both methods of censusing (counting versus weighing pellets) produced similar results and that standard deviations were lower, on the average, and much more constant over time in the second experiment (compare 12-hour censuses in Figs 1 and 2).

The differential in pellets produced during the high- and low-production periods is much larger in the 6-hour than in the 12-hour censuses. For the 6-hour censuses, an average of about 1500 pellets were produced between 2400 and 1200 and 300 pellets between 1200 and 2400, whereas for the 12-hour censuses, an average of about 950 pellets were produced between 2300 and 1100 and 500 pellets between 1100 and 2300 (see Fig. 1, results pooled over four days). This may be due to the high individual variability between worms in the 12-hour census (Fig. 4), as previously discussed; however, it is interesting that all five worms censused at 6-hour intervals showed such consistency in their periodicity (Fig. 3). Alternatively, the one hour before noon and midnight may be key high and low production intervals, respectively, so that the timing of the 12-hour censusing periods obscures the magnitude of the difference in production between the high and low periods observed in the 6-hour censuses. Finally, the physical process of censusing at 6-hour intervals may induce or augment a diel periodicity in the pellet production. Whatever the cause, it appears that censusing at a minimum of 6-hour intervals is required to detect this periodicity in pellet production by *Mediomastus*.

The weight of sediment incorporated into fecal pellets (rather than the number of pellets produced) is a more useful measure of sediment reworking by *Mediomastus* in terms of the implications to sediment transport, since the weight- or volume-concentration of sediment eroded and transported by the flow can be calculated from sediment-transport models (e.g. Grant & Glenn 1983). Assuming that the worms in both experiments produced the same amount of fecal pellets, it is interesting to note that about 10 mg weight of sediment is equal to about 1000 pellets (compare pooled results for the 12-hour censuses in Figs 1 and 2).

DISCUSSION

Periodicity in biological processes of marine organisms, such as activity patterns (Trueman 1971), color change (Fingerman *et al.* 1961), vertical migration (Harris & Wolfe 1955) and defecation (Wells 1953) has long been recognized. More recently, feeding periodicity also has been observed (Mayzaud *et al.* 1984, Mayzaud 1985). Periodicities may be twelve-hourly (e.g. when governed by the tides), daily, monthly or even yearly rhythms.

In the present study, periodicity of pellet production in *Mediomastus ambiseta* occurred on a 24-hour cycle, even when the worms were held in a dark incubator at near-ambient seawater temperature for a month prior to and during the experiments, except for the brief intervals when the worms were censused. The cycle was most pronounced in worms censused at 6-hour intervals. Peak pellet production occurred during the 2400 to 0600 hour interval and decreased by about a factor of four during the 0600 to 1800 hour interval; almost no pellet production occurred between 1800 and 2400 hours. This periodicity of pellet production may be due to an innate, programmed behavior (i.e. a circadian rhythm) or may be a response to some cyclically occurring stimulus. Our experiments were not designed to distinguish between these possibilities.

It is tempting to suggest that this diel cycle of pellet production is among the category of innate, behavioral or physiological responses known as circadian rhythms because the worms show this daily periodicity in the (seemingly) absence of cues from their natural environment. Circadian rhythms have been ascribed to activity patterns of several marine organisms (Stephens 1962, Fuentes-Parob & Ramos-Carvajal 1983, Williams 1983, Powers & Barlow 1985). Considerably more research is required to establish whether or not pellet production is a circadian rhythm in *Mediomastus*.

Whether genetically or externally controlled, the cycle may be a response to a twilight- or night-active predator such as *Crangon septemspinosus* or small crabs that prey on the exposed posterior ends of *Mediomastus* during defecation (Grassle & Grassle 1984, Grassle *et al.* 1985). In the Wadden Sea, flatfish are thought to prey on the posterior ends of another capitellid polychaete, *Heteromastus filiformis* (DeVlas 1979). Alternatively, it may be due to physiological constraints (Mayzaud *et al.* 1984, Mayzaud 1985, Nott *et al.* 1985). Other explanations most certainly are possible, but these are the only reasonable alternatives of which the authors are aware.

The results of this study suggest that it may be necessary to control for the time of day in feeding studies of infaunal deposit feeders. Experiments that measure feeding rates based on short or one-time intervals (Cammen 1980, Lopez & Kofoed 1980, Lopez & Cheng 1983, Taghon & Jumars 1984, Miller & Jumars 1986), without first testing for a natural periodicity, may have under- or over-estimated even the mean daily feeding rates, if feeding follows a diel rhythm similar to that found in *Mediomastus*.

These results also have important implications for studies of interactions between benthic organisms and sediment transport. *Mediomastus* changes the sediment texture by repackaging small particles ingested from below the sediment-water interface into pellets several orders-of-magnitude larger in size and deposits them onto the sediment surface, where they are exposed to the flow. The synchrony of a daily cycle of pellet production with diel physical phenomena (e.g. resuspension by tidal flows) may determine the type and amount of sediment that is resuspended by the flow each day. Likewise, the coincidence of strong tidal currents and irregular storm events with periods of high or low pellet production may determine the amount of sediment in suspension and available for transport by the flow.

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