

The impact of population abundance on the deposit-feeding rate of a cosmopolitan polychaete worm

Abstract—The impact of population abundance on the deposit-feeding rate of *Mediomastus ambiseta* (Capitellidae: Polychaeta) was studied in still-water laboratory experiments. Mean individual pellet production rate ($\text{mg worm}^{-1} \text{d}^{-1}$) decreased monotonically with increasing worm abundance in the range of 6.5×10^3 to 1.3×10^5 worms m^{-2} . Worms fed roughly an order of magnitude slower in the high-density treatment than in the low-density treatment. The vertical distribution of pellets (i.e., sites of egestion), however, was insensitive to changes in worm abundance. Despite the high population abundances, the weight-% of pellets in the highest abundance treatments was $<20\%$. Therefore, contrary to expectations, it was unlikely that feeding rate was limited by the availability of ingestible particles. Rather, some combination of resource depletion and possibly of enhanced physical or chemical interference caused the observed decline in feeding rate at higher population abundances. These results suggest that studies that seek to transfer laboratory-based measures of deposit-feeding rate to the field must be careful to match abundances in the two domains.

Sediment displacement by organisms markedly influences the fate of particle-bound contaminants. Depending on the sign of the concentration gradient, particle bioturbation can either accelerate the penetration rate of contaminants into the seabed or facilitate the release of deeply buried constituents to the water column. A better predictive understanding of particle bioturbation would have far-ranging consequences for contaminant-transport studies in particular and benthic oceanography in general. At this time, however, mathematical models of sediment bioturbation (Boudreau 1986a,b; Boudreau and Imboden 1987) have far outpaced understanding of the controlling factors. For example, it is uncertain how changes in various abiotic (e.g., organic C, water temperature) and biotic (e.g., animal abundance, species composition) factors affect the intensity of sediment bioturbation at a particular site (Wheatcroft and Martin 1996).

Deposit feeders are key to developing a better understanding of bioturbation because, in nearly all settings, deposit feeders dominate particle displacement (Aller 1982). Nowhere is this more true than in anthropogenically affected environments such as harbors and areas near ocean outfalls, which are often dominated by small, opportunistic polychaete worms from the family Capitellidae (Grassle and Grassle 1974; Pearson and Rosenberg 1978). The abundance of these worms can vary substantially and is sometimes very high. For example, in Buzzards Bay, a large coastal embayment in southeastern Massachusetts, the capitellid *Mediomastus ambiseta* reaches abundances of $\sim 5 \times 10^5$ individuals m^{-2} , but its numbers fluctuate by an order of magnitude over the course of a year (Grant and Butman 1987). Given the dominance of such opportunistic worms in contaminated sediments, we must learn how to incorporate such fluctua-

tions into models of organism effects, such as bioturbation intensity. In particular, is it a valid assumption that ingestion rate, and hence sediment mixing rate, is independent of population abundance? To address this question, we conducted laboratory experiments to examine the impact of varying animal abundance on the deposit-feeding rate of the cosmopolitan polychaete worm *Mediomastus ambiseta*.

Sediments containing *Mediomastus ambiseta* (hereafter, *Mediomastus*) were collected using a Van Veen grab from a shallow subtidal site in western Buzzards Bay. Sediments were sieved through a 300- μm sieve and sorted for *Mediomastus*. Animals were placed in sediment-laden culture dishes and maintained in well-aerated seawater tables at 20°C for at least 10 d before the experiments started. Sediment for the experiments, collected from the same site, was put through a 300- μm sieve, sonicated for 2 min, then sieved through a 38- μm sieve. The purpose of the sonication step was to break up any fecal pellets or other aggregates in the sediment. (All particles were $<38 \mu\text{m}$ at the start of the experiment). Sediments and animals were placed into 7-cm deep by 0.6-cm diameter (“small”) or 1.4-cm diameter (“large”) tubes with surface areas of ~ 0.3 and $\sim 1.5 \text{ cm}^2$, respectively. There were five density treatments for the large tubes (nominally 1, 2, 5, 10, and 20 worms tube^{-1}), and two density treatments for the small tubes (nominally 1 and 4 worms tube^{-1}). These treatments corresponded to densities between 6.5×10^3 and 1.4×10^5 worms m^{-2} (Table 1), which encompasses much of the natural abundance range of *Mediomastus* in coastal environments (Grassle and Grassle 1974; Grassle et al. 1985; Grant and Butman 1987; Hyland et al. 1991; Hughes 1996; Wheatcroft and Martin 1996). The purpose of using two tube sizes was to test the effect of varying microcosm-edge proximity to worm density on pellet production rate.

Because choosing whole worms and placing them in microcosms was time-consuming, only about two hundred worms could be added during a day. Therefore, two nearly identical experiments were conducted with five replicates of each abundance treatment in the large-tube experiment and four (“Day 1”) and three (“Day 2”) replicates of each abundance treatment in the small-tube experiment. The experiments were begun 2 d apart. During the experiments, all tubes were maintained in a well-aerated 3,500-liter seawater table filled with 1 μm filtered seawater maintained at 20°C. The experiments were terminated after 12 d by removing the tubes from the water tables and sectioning the sediments at 1-cm intervals. Samples were placed into 50-ml centrifuge tubes and refrigerated. To enumerate worms and pellets, each depth interval was sieved through 180- and 45- μm sieves. Worms and tube fragments remained on the 180- μm sieve, whereas pellets were retained on the 45- μm sieve. Worms were briefly placed in MgCl_2 (a narcotizing solution), then transferred to ethanol to await body-size measurements. The length of the

Table 1. Worm densities in large- and small-tube experiments.

No. of worms per tube	Density (m^{-2})	
	Large tube	Small tube
1	6.50×10^3	3.54×10^4
2	1.30×10^4	
4		1.41×10^5
5	3.25×10^4	
10	6.50×10^4	
20	1.30×10^5	

first nine setigers and the width of the ninth setiger were measured using an ocular micrometer on a dissecting microscope. Thorax volume was computed from these measurements by assuming that the worm was a cylinder. The purpose of the size measurements was to determine whether the size distribution of worms was similar in the different treatments.

Because *Mediomastus* pellets ($\sim 160 \mu\text{m}$ by $90 \mu\text{m}$) are much larger than ambient sediment grains ($< 38 \mu\text{m}$), we intended to quantify dry pellet mass (and hence egestion rate) in each sample by removing tube fragments on a $180\text{-}\mu\text{m}$ sieve and filtering the pellets retained on a $45\text{-}\mu\text{m}$ sieve onto a preweighed filter, drying the pellets, and reweighing them. However, the $45\text{-}\mu\text{m}$ sieve also retained unidentified clumps ("flocs") of material that were clearly neither pellets nor tube fragments. To address this potential problem, we separated flocs from pellets in a subset ($\sim 35\%$) of the samples by gently swirling the mixtures in petri dishes. This action resulted in a hydrodynamic fractionation, because the flocs were less dense than pellets. Floc mass was quantified from each depth interval and density combination. A split-plot analysis was performed with density and day as the main plot treatment effects and depth as the subplot treatment. This analysis indicated that floc mass did not differ between density treatments ($F = 0.15$, $\text{df} = 4$, $P = 0.96$) or among depths within treatments ($F = 0.57$, $\text{df} = 3$, $P = 0.64$). Therefore, the median floc weight (9.7 mg) for all the swirled samples ($N = 78$) was subtracted from the total mass retained on the $45\text{-}\mu\text{m}$ sieve of the nonswirled samples to yield pellet mass.

Pellet production rate (PPR), expressed as $\text{mg worm}^{-1} \text{d}^{-1}$, monotonically decreased with increasing worm density in the large-tube experiment (Fig. 1, Table 2). Averaged over the 12 d of the experiment, worms in the highest density treatment fed roughly an order of magnitude slower than those in the lowest density treatment. PPR differed between days, but there was no density-by-day interaction (Table 2). PPR did not differ between the 1- and 2-worms tube $^{-1}$ (Tukey-Kramer HSD Test [Day and Quinn 1989], $P = 0.08$) or the 10- and 20-worms tube $^{-1}$ ($P = 0.06$) treatments. All other pairwise comparisons were statistically significant. The likely reason for the difference in PPR among days was that worms in the first experiment were significantly larger than those in the second ($0.017 \text{ mm}^3 \pm 0.0017 \text{ mm}^3$ vs. $0.011 \text{ mm}^3 \pm 0.0014 \text{ mm}^3$). There was, however, no density-by-day interaction (three-way analysis of variance on worm size: $F = 1.00$, $\text{df} = 4$, $P = 4.1$) or density effect ($F = 1.51$, $\text{df} = 4$, $P = 0.20$). Hence, within a day, worm size did not differ between densities. Therefore, the trend in PPR

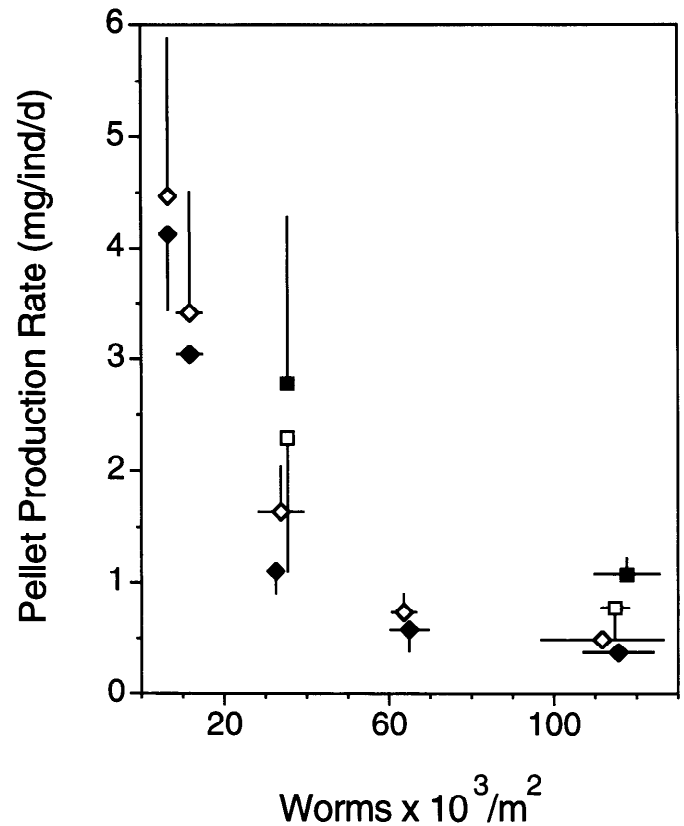


Fig. 1. Pellet production rate ($\pm \text{SD}$) versus worm density ($\pm \text{SD}$) for the large-tube (diamonds) and small-tube (squares) experiments (open and closed symbols are for Day 1 and Day 2 experiments, respectively). To prevent confusion, only one limb of each error bar for the ordinate is shown.

cannot be attributed to systematic variation in worm size as a function of treatment.

We assumed that worms in the high-density treatments would encounter the sides of the tubes more often and therefore feed more slowly than worms in the low-density treatments. This conjecture was tested by comparing PPR in the 5- and 20-worms large-tube $^{-1}$ treatments to PPR in the 1- and 4-worms small-tube $^{-1}$ treatments, respectively. These treatment pairs had similar densities (Table 1), but differed in the area of sediment that was "close" ($< 1 \text{ mm}$) to the tube sides. In fact, contrary to expectations, no decrease in PPR was observed in the small-tube experiment as compared to the large-tube experiment (Table 3). Rather, at similar densities, PPR was significantly higher in the small tubes (Fig. 1), but as expected, PPR decreased with increasing density.

Table 2. Results of two-way ANOVA on log pellet production rate from the large-tube experiments.

Source of variation	df	SS	F-ratio	P
Density	4	30.0145	129.9898	0.0000
Day	1	0.4357	7.5473	0.0095
Density \times day	4	0.1747	0.7567	0.5607
Error	34	1.9626		

Table 3. ANOVA results comparing the log pellet production rate in the large- versus small-tube experiments.

Source of variation	df	SS	F-ratio	P
Experiment	1	2.4655	17.0905	0.0005
Density	1	6.5614	45.4825	0.0000
Day	1	0.0051	0.0356	0.8523
Experiment \times density	1	0.0725	0.5026	0.4865
Experiment \times day	1	0.5480	3.7989	0.6064
Density \times day	1	0.0395	0.2740	0.6064
Experiment \times density \times day	1	0.0036	0.0250	0.8760
Error	20	2.8853		

Despite the decrease in PPR in the high-density treatments, the greater number of worms in those treatments meant that the total mass of pellets at the end of the experiments was greater. For example, the percentage weight of pellets in the 0–1-cm depth interval ranged from 6.7% for the 1-worm tube⁻¹ treatment in Experiment 2 to 19% for the 20-worms tube⁻¹ treatment in Experiment 1. Thus, worms in the high-density treatments were more likely to encounter pellets during foraging.

An alternative response to crowding is for worms to feed deeper within the sediment (White et al. 1987). Consequently, pellets may be distributed at greater depths in high-density treatments, because worms are of finite length (i.e., the head cannot go deeper without taking the tail with it). Tukey's Multiple Comparison Test was used to compare pellet production among treatments within a depth interval. Overall, the results indicate few significant differences among treatments in the depth distribution of pellet mass (Fig. 2), although there were scattered exceptions. For example, in Treatment E (10 worms tube⁻¹) there was a significantly higher percentage of pellets in the 0–1-cm interval relative to Treatments B–D. In the 1–2-cm interval, treatments B (1 worm tube⁻¹) and C (2 worms tube⁻¹) had significantly higher pellet production than Treatment E. Depth distribution of pellet mass did not differ among treatments in the depth intervals of 2–3, 3–4, and 4–5 cm. The depth distribution of heads measured at the end of the experiments (not illustrated) also showed little difference among treatments; however, one must treat that finding with caution, given the many problems associated with determining animals' depth distribution.

The feeding rate of *Mediomastus* clearly decreased with increasing worm abundance. Before discussing the causes and ramifications of this result, we must clarify the potential biases associated with the experiment. One source of potential systematic error is differential pellet breakdown among treatments. If pellet breakdown was more rapid in the high-density than the low-density treatments, then the results would be invalid. Although there is no direct evidence that this did not occur, several observations suggest it was highly unlikely. First, the duration of the experiments (12 d) was short relative to the length (several months) of the pellet-enumeration phase. At no time during the enumeration phase were pellets observed to fragment, despite several episodes of sieving and swirling. Second, there was no difference among treatments in the amount of flocs, which could be a product of fragmented pellets. Third, reports from the liter-

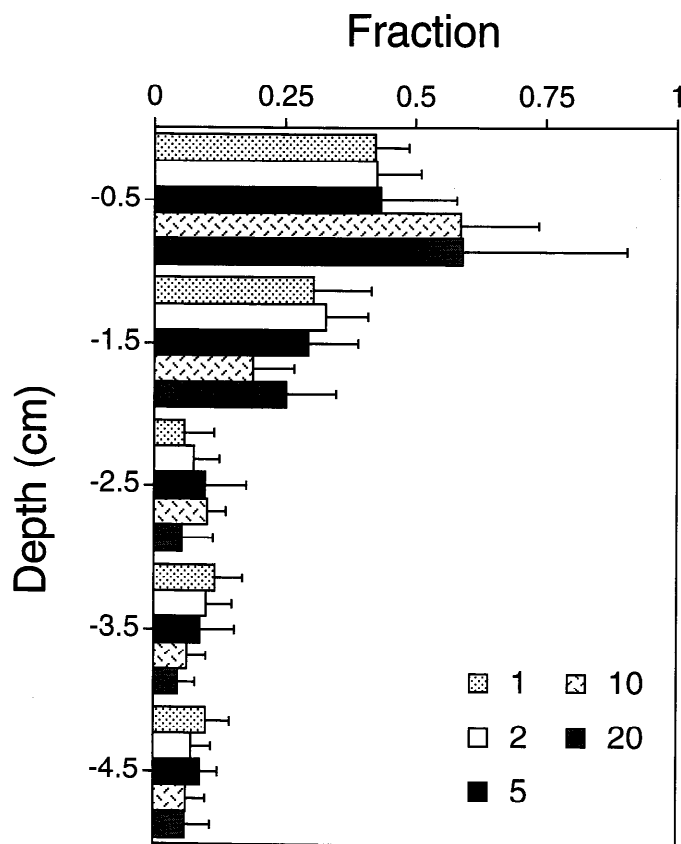


Fig. 2. Depth distribution (\pm SD) of pellets at the end of the large-tube experiments in treatments having nominally 1, 2, 5, 10, and 20 worms microcosm⁻¹.

ature (Forbes and Lopez 1987; Fuller et al. 1988; Starczak et al. 1992) suggest that capitellid pellets are notoriously robust. In summary, we are confident that a pellet, once produced, remained intact for the duration of this study.

More subtle biases might be associated with the fact that the experiments were conducted in a still-water laboratory setting. There were no other animals (macrofauna or meiofauna) in the microcosms, and there was no physical sediment transport into or out of the microcosms. The absence of other fauna from the experimental microcosms could potentially be important because such animals may accelerate breakdown rates of *Mediomastus* fecal pellets. Aside from the fact that it would be extremely difficult to include other species in the microcosms and still isolate the effect of *Mediomastus* abundance on feeding rate, the absence of other animals is unlikely to have biased our results. That is because, in many settings, *Mediomastus* is the numerically dominant animal (Grassle and Grassle 1974; Grassle et al. 1985; Grant and Butman 1987; Hyland et al. 1991; Hughes 1996; Wheatcroft and Martin 1996). Moreover, the abundance of *Mediomastus* is subject to large temporal variability, while the abundances of other species that occur with *Mediomastus* are typically more stable. Hence, the contribution of other species to pellet breakdown rates would probably be similar in different environments.

Miller and Jumars (1986) suggested that the accrual of

pellets within the foraging area of a spionid polychaete limited its egestion rate and that the physical transport of pellets, as likely occurs in the field, would ameliorate this effect. In the ocean, *Mediomastus* pellets are likely to be moved frequently as bedload because the critical shear velocity of *Mediomastus* pellets is $\sim 0.6 \text{ cm s}^{-1}$ (author's unpubl. data). This friction velocity translates to horizontal flow speeds of $\sim 10 \text{ cm s}^{-1}$ at a height of 1 m above the bed, a typical flow in coastal waters. It is not clear that the small-scale movement of pellets away from an individual has any net effect, however, since transported pellets will be replaced by pellets from adjacent individuals. Thus, it is unlikely that pellet accrual within the feeding volume of *Mediomastus* is a laboratory artifact.

Physical sediment transport is also important for the resupply of "new" or free particles (Levinton and Lopez 1977; Jumars et al. 1981) to the foraging ambit of deposit feeders (Miller et al. 1984). Because in the present experiment no particle resupply occurred, one could argue that the impact of elevated densities was artificially accentuated. It is unlikely, however, that free-particle limitation was a factor in these experiments. Recalling that the weight-% of pellets was typically quite low (6–19% in the uppermost centimeter of the bed and <5% at depths where *Mediomastus* forages), then even when pellet quantity is converted to a volume percent (<25% in all cases) it is clear that a large amount of free sediment was available for ingestion. Because all of these particles were $<38 \mu\text{m}$ —a size that is ostensibly ingestible by *Mediomastus* (cf. Self and Jumars 1988)—free-particle limitation in any of the treatments seems highly unlikely. The lack of particle limitation is a surprising result. Past models (Levinton and Lopez 1977; Jumars et al. 1981) and observations (Levinton and Lopez 1977; Levinton 1979) of deposit feeders have suggested that pelletization of free particles could limit the deposit-feeding rate and, ultimately, population abundance. The fact that we observed a drop in feeding rate in the present experiments before the effects of pelletization should have been felt by the animals suggests that an alternative (or additional) explanation is required.

There are at least three other limiting resources that may be important in controlling the feeding rate of *Mediomastus*: (1) space, (2) pore-water oxygen, and (3) "food." Space limitation due to physical contact has been observed to decrease the time spent foraging by various surface deposit-feeding polychaetes (Levin 1982; Miller and Jumars 1986) and gastropods (Levinton 1979). Polychaetes were observed to withdraw into their tubes when their tentacles overlapped with other individuals of the same or other species (Levin 1982). Similarly, individuals of the gastropod *Hydrobia ventrosa* have been observed to frequently crawl over one another at high densities, resulting in withdrawal into the shell and thus a slower crawling rate, which in turn led to slower ingestion rates (Levinton 1979). Surface-deposit feeders, such as spionids or hydrobids, may be an extreme example of groups limited by space, however. They forage in a plane (i.e., the sediment surface) when deposit-feeding, and they either have long tentacles (e.g., the inferred foraging diameter of *Pseudopolydora kempii japonica* is roughly thirty times its tube diameter [Miller and Jumars 1986]) or are highly mobile, as hydrobids are. Space should not be as lim-

iting for subsurface deposit feeders such as *Mediomastus* because they feed in a volume, within the sediment, and they are less mobile. It should be noted, however, that the foraging ambit of *Mediomastus* in particular, and subsurface deposit feeders in general, is unknown. The lack of a clear change in the depth distribution of *Mediomastus* between treatments suggests that space was not a limiting factor. Nevertheless, the possibility exists that our experiment did not run long enough to elicit the development of spatially distinct feeding zones (cf. Rice et al. 1986). Lastly, the results of the small-tube experiment, which tested the effect of side walls on feeding rate, also suggests that physical contact is relatively insignificant for *Mediomastus*.

An intriguing but unexplored possibility involving space is that *Mediomastus* interferes with conspecifics by producing allelochemicals. These chemically diverse compounds have been shown to affect a variety of processes in marine soft-bottom systems (King 1986; Woodin et al. 1987, 1993), including recruitment and predator avoidance. Species from several families of polychaetes (Arenicolidae, Capitellidae, Cirratulidae, and Spionidae [Fielman et al. 1997]), as well as hemichordates (King 1986) and crustaceans, have been shown to secrete these compounds. If *Mediomastus* produces allelochemicals and they have an intraspecific inhibitory effect on feeding rate, then it is logical to assume that crowding would compound the effect.

Pore-water oxygen concentrations or the presence of toxic compounds such as hydrogen sulfide have a variety of effects on benthic invertebrates (Diaz and Rosenberg 1995), including cessation of feeding under low-oxygen (hypoxic) conditions (Llansó 1991). The concentration and microdistribution of pore-water oxygen depends on at least three factors: (1) the oxygen concentration in the bottom water, (2) respiration, and (3) transport processes within the seabed. In the experiments, the bottom-water oxygen concentration should have been the same for all the treatments and was most probably steady. The tank was large, well-mixed, and continuously aerated. Respiration probably was greater in the high-density treatments, simply because there were more animals. It is unlikely, however, that this greater total respiration significantly depleted pore-water oxygen, because the available 3,500-liter tank was so large, and metazoan respiration is typically small. Lastly, both molecular diffusivities and pore-water irrigation rates were likely to be higher in the high-density treatments. The former is caused by higher sediment permeability due to a greater volume-fraction of pellets (i.e., coarser sediments typically have higher permeabilities), whereas the latter is due to the larger number of tubes and animals (Aller 1982). Circumstantial evidence that pore waters were oxygenated to greater depths in the high-density treatments was provided by the greater vertical extent of light tan, as opposed to black, sediment in those treatments. Moreover, no animals in any of the treatments showed signs of acute oxygen stress such as leaving their tubes. In summary, it is unlikely that oxygen limitation caused the drop in feeding rate in the high-density treatments.

The concept of "food" for deposit feeders is notoriously complex (Lopez and Levinton 1987; Mayer 1989). That, plus the fact that we did not quantify nutritional aspects of

the sediments used in the experiments, severely limits our ability to discuss this aspect of the problem. It is worth noting, however, that resource limitation has been invoked before to explain the results of a density-dependent *Mediomastus* growth-rate experiment. In a 9-d experiment, Hughes (1996) found that *Mediomastus* grew more at moderate (1.5×10^4 worms m^{-2}) than at high (4.4×10^4 worms m^{-2}) densities. Higher worm densities led to enhanced heterotrophic activity within the feeding zone of *Mediomastus*, which in turn led to lowered bulk organic C and total N values. In essence, there was resource competition between *Mediomastus* and sedimentary bacteria, and *Mediomastus* lost. Whether this competition existed in our experiments, and whether it led to the observed results, is unknown.

Although the mechanisms that inhibited feeding in the high-density treatments remain unknown, the result has several interesting ramifications. For example, assuming that pelletization (i.e., the lack of free sediment) was responsible for the observed drop in feeding rate with increasing animal abundance, we can estimate the sedimentation rate required to replenish the pelletized sediment. For the high-density treatments, there was roughly 67 mg cm^{-2} bound into pellets over the 12-d period. This translates to an annual pelletization flux of $2 \text{ g cm}^{-2} \text{ d}^{-1}$, which, assuming a bulk density of $\sim 1.2 \text{ g cm}^{-3}$, results in a sediment accumulation rate of roughly 1.7 cm yr^{-1} . Sediment accumulation rates of this magnitude are rare in fine-grained systems, but could occur either off the mouths of major rivers or proximal to sewage outfalls (Pearson and Rosenberg 1978). Rivers deliver relatively refractory organic matter, and capitellids are typically absent. Sewage outfalls provide a ready source of labile organic matter, and it is here that capitellids such as *Mediomastus* are most common (Grassle and Grassle 1974; Pearson and Rosenberg 1978; Wheatcroft and Martin 1996). Are periodically high sediment accumulation rates of labile organic matter a necessary condition for the persistence of capitellids?

From the standpoint of bioturbation, the results of this study have obvious implications. Head-down deposit feeders like *Mediomastus* create convective, conveyor-belt transport that moves particles vertically (Rhoads 1974; Boudreau 1986b). Particle transport velocity in the upward "limb" of the convection cell depends directly on ingestion rate and is essentially instantaneous. Particle transport velocity in the downward limb, or burial velocity, also depends on ingestion rate as well as on the distribution of ingestion sites, or heads. If ingestion sites are spread out vertically, then burial velocity will slow with depth. These results clearly indicate a reduction in individual ingestion rate with increasing animal abundance; thus, abundance-based models of convective mixing should take this effect into account. The vertical distribution of sites of egestion (Fig. 2) and ingestion, however, were insensitive to changes in population abundance.

Feeding inhibition caused by pellets was invoked by Wheatcroft and Martin (1996) to explain the results of a recent study of bioturbation intensity along an organic-C gradient. They measured lower bioturbation intensities in regions containing high numbers of *Mediomastus* along with similar numbers and types of other species. They conjectured that the pellets and tubes produced by *Mediomastus* could

have depressed feeding and burrowing and hence mixing rates of this and other species at the sites. Our results lend some support to their speculations.

Laboratory studies like ours have, in most cases, observed reductions in feeding rate under higher population abundances (Levinton 1979; Rice et al. 1986; Miller and Jumars 1986). Animals in these studies included both surface deposit-feeding gastropods (Levinton 1979) and polychaetes (Miller and Jumars 1986), as well as subsurface or head-down deposit-feeding polychaetes (Rice et al. 1986). A different result was obtained by White et al. (1987) in their study of particle-transport rate, a surrogate for deposit-feeding rate, by a freshwater oligochaete. They saw no relationship between sediment reworking rate and animal density. However, they noted that the depth of maximum feeding increased markedly at higher densities and ascribed this to competition. The commonality of the results in these studies, in conjunction with those reported herein, suggests that it may not be valid to transfer a deposit-feeding rate measured at one abundance to other abundances.

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