

Particle selectivity, gut volume, and the response to a step change in diet for deposit-feeding polychaetes

Michael J. Bock¹ and Douglas C. Miller

University of Delaware, College of Marine Studies, Lewes, Delaware 19958

Abstract

We performed a series of experiments to examine the aspects of deposit feeding that were relevant to studies of resource variability over short time scales. We examined particle-size selectivity, gut volume, gut residence time, and the response to a change in diet in three polychaete species: *Spiochaetopterus oculatus*, *Spio setos* and *Marzelleria viridis*. All three species were particle-size selective and had similar gut volumes and gut residence times. Thus, measurements of bulk sediment characteristics are largely irrelevant to the studies of their nutrition. In response to a step change in diet, changes in the egestion rate were accomplished by smooth transitions between steady-state rates occurring over 1 to 2 h. The form of this modulation suggests that these organisms do not respond to changes in diet by temporarily retaining or flushing the material in the gut in order to increase digestive yield. The time scale of the response to a change in diet provides evidence for a foregut/midgut feedback mechanism for inducing changes in feeding rate due to sediment food concentration. If the time required to modulate the feeding rate to a new steady state is more rapid than the time scale of food-resource variability in the field, it is unlikely that a response other than a gradual transition to a new ingestion rate would provide a significant advantage.

Deposit-feeding marine polychaetes live in a temporally and spatially heterogeneous environment. Previous results have shown that food resources in surficial sediments can change on a daily time scale in response to storm-associated sediment transport (Miller et al. 1984; Bock and Miller 1995). Specifically, feeding areas can be depleted with respect to sedimentary organic matter (Miller et al. 1984; Bock and Miller 1995) and preferred particle sizes (Luckenbach et al. 1988). On large spatial scales, sediment transport can move organic matter many meters (Levinton and McCartney 1991). On small spatial scales, individual grains in a sedimentary deposit may vary in terms of grain size and organic matter per particle (Mayer 1994a,b). Deposit feeders are known to feed selectively on the basis of grain size and organic coating when presented with a choice (Taghon 1982; Self and Jumars 1988). Thus, the concentration and composition of the organic matter ingested can be highly variable in space and time and is not necessarily equivalent to the ambient, or bulk, sediment found in their feeding areas.

Organisms feeding at the sediment–water interface respond rapidly to changes in fluid flow and particle transport. Organisms capable of feeding on suspended and bedload material will do so when exposed to nutritious particles in transport (e.g., Dauer et al. 1981; Nowell et al. 1989; Miller et al. 1992; Bock and Miller 1996, 1997). Dedicated suspension feeders often alter their feeding strategy when flow and particle transport conditions change (e.g., Bricelj 1984; Bricelj et al. 1984; Rhoads et al. 1984; Bayne et al. 1987; Grizzle and Lutz 1989; Grant et al. 1990; Ward et al. 1996). Dedicated deposit feeders may adjust the size of their feed-

ing area or stop feeding altogether in response to increases in fluid flow and particle transport (e.g., Levinton 1991; Miller et al. 1992; Karrh and Miller 1996). Thus, fluid flow and particle transport clearly influence feeding behavior.

In addition to the physical factors discussed above, changes in the biochemical composition of food particles can also influence feeding behavior. Mathematical modelers have attempted to predict how the feeding rate will change in response to changes in food concentration (e.g., Penry and Jumars 1987; Dade et al. 1990). At low food concentrations, feeding rates should be low and should increase with increasing food concentration, up to intermediate values. At higher food concentrations, the feeding rate should decrease. Experimental manipulations of food concentration have revealed that this relationship in fact exists in all deposit feeders examined to date (e.g., Taghon and Greene 1990; Karrh and Miller 1994; Bock 1995). The models and experiments described above explore the steady-state response to changes in food resources, ignoring the time scale of the response. However, since changes in food resources can occur over many time scales (hours to days), an understanding of the link between the time scale of the feeding rate response and biochemical changes in food resources is critical.

The time scale of the response to changes in diet by benthic organisms feeding at the sediment–water interface has received little attention. However, Miller (1992) found that the deposit-feeding hemichordate (*Saccoglossus kowalevskii*) exhibited an increase in feeding rate after 1 h when switched from a substrate with a low organic-matter concentration to one with a high organic-matter concentration. When switched from a substrate with a high concentration of food to one with a low concentration, the feeding rate declined after 4 h. These results suggest that adjustments in the feeding rate are related to feedback from the hindgut, with the asymmetry being attributed to changes in the gut throughput time when feeding on substrates of differing nutritional quality. These changes in feeding rate, those induced by changes in food concentration, occur much more

¹Present address: University of Maine, Darling Marine Center, Walpole, Maine 04573.

Acknowledgments

This research and manuscript were improved by advice and comments from G. Taghon, J. Grant, R. Geider, M. Palmer, and two anonymous reviewers. This work was supported by NSF grant OCE 92-17020 to D.M.

slowly than do changes induced by flow and sediment transport.

Organisms could use many strategies to deal with variability in food resources, including utilizing different digestive enzymes, altering the exposure time of the food substrate to enzymes, increasing the active uptake of digestive products, and increasing gut surface area. Penry (1993) maintains that adjustments in processing rate appear to be more easily accomplished than do reaction-adsorption adjustments, and thus, these adjustments could be an important response to diet variability. Hassett and Landry (1990) found that changes in digestive enzymes can occur on a 1–5-d time scale for zooplankton (similar data for deposit feeders are not available). It is unlikely that enzyme systems and uptake rates can be significantly altered on the same time scale as transport-induced changes in food resources, which can occur on less than a tidal or daily time scale (Bock and Miller 1995). However, these parameters could be changed in response to seasonal fluctuations in temperature and primary productivity (Levinton and McCartney 1991). Gut throughput occurs on a similar time scale to that of transport-induced phenomena, such as tidal transport and storm passage, and could provide one mechanism for organisms to use to maximize assimilation.

In these experiments, we examined particle selectivity and the response to a change in diet, since these are feeding parameters that are easily alterable in order to maximize food intake in the face of diet variability. Our goals were (1) to determine if three species of tentaculate deposit-feeding polychaetes are particle-size selective, (2) to quantify the feeding-rate response to step changes in diet, and (3) to develop hypotheses to use in exploring the observed response to a change in diet.

Methods

Species collection and housing—Two spionid polychaetes (*Spio setosa* and *Marenzelleria viridis*) and a chaetopterid polychaete (*Spiochaetopterus oculus*) were collected from an intertidal sandflat at Breakwater Harbor, Delaware (38°46'N and 75°06'W), during low tides 1–2 weeks before being used in an experiment (sites previously described by Bock and Miller 1995). Individual worms were housed in 50-ml centrifuge tubes that were filled with 1 mm sieved, macrofauna-free sediment that had been collected from the same location. Worms were then transferred to a laboratory seawater table (33‰ salinity and 20°C) with a flow speed of 2–3 cm s⁻¹. Under these conditions, all three species deposit feed exclusively (see Miller et al. 1992 and Bock and Miller 1996 for a description of feeding behavior under flow).

Particle selectivity—At least 20 individuals of each species were collected and housed as described above during the week of 5 August 1994. Particle-size selectivity experiments were performed in a laboratory seawater table on 10 August 1994. Ten randomly selected individuals of each species were allowed to feed on a mixture of two sizes of glass beads, with flake fish food added to increase the palatability (Jumars et al. 1982). The bead sizes were chosen based on

the mean grain size of Breakwater Harbor sediment (250 μm). The mixture consisted of 16 g of 88–127-μm glass beads, 126 g of 177–250-μm beads, and 0.2 g Tetramin flakes, resulting in equal numbers of both sizes in the mixture. The flakes rapidly disaggregate, leaving no visible solid particles, indicating that the beads were coated. The treated beads were spread into 6-cm-diameter plastic petri dishes to a depth of 1 mm and were frozen until use (Taghon 1982). The frozen disks were gently placed on the sediment surface, where they quickly thawed. After several hours, fecal pellets were gently removed with a pipette. We were successful in avoiding contamination of the fecal samples with beads from the feeding area (pers. observation). Ambient samples were collected by coring with a soda straw (Taghon 1982). Beads were counted on a dissecting microscope at ×120. At least three fields of view were counted for each sample, resulting in ~250 beads per ambient and fecal sample per worm. The proportion of test beads (in this case, small beads) to the total number of beads (small plus large beads) was calculated for each sample. An individual's selectivity (L) was calculated using the ambient test bead proportion (p_a) and the gut, or feces, proportion (p_g) in a base-10 logarithm of the odds ratio (Jumars et al. 1982).

$$L = \log_{10}[p_g * (1 - p_a)] / [(1 - p_g) * p_a]$$

The log odds ratio is the ratio of the probabilities of ingestion of the test and the control beads. A positive log odds ratio indicates selection for the test bead over the control bead (small versus large beads, in this case).

Gut volume and residence time—At least 22 worms of each species were collected during the week of 10 October 1994 and housed as described above. Gut volume and gut residence time were measured on all of the collected worms on 26 October 1994 using a fluorescent tracer (Miller and Ray 1988). At the start of the experiment, feces were removed and a thin layer of fresh sediment with a trace number of dyed particles (5% by mass) was added (Miller and Ray 1988). The worms were permitted to feed until dyed sediment was egested. The time elapsed for each worm was recorded, and the egested sediment was collected with a pipette. The collected sediment was rinsed with deionized water, dried, and weighed to ±1 mg to measure gut capacity. Gut capacity was converted to gut volume using an assumed sediment bulk density of 1.4 g cm⁻³ (Bock and Miller 1995). The worms were then removed from their tubes and housed in sediment-free beakers filled with seawater. After 2 d, all of the sediment in their gut was egested (as evidenced by the cessation of defecation), and the worms were measured for length, wet weight, dry weight, and ash-free dry weight. No evidence of residual ingested sediment was found in the ashed worm samples.

Response to a change in diet—At least 22 worms of each species were collected during the week of 3 January 1995. On 12 January 1995, for each species, 18 randomly selected worms were sequentially exposed to high, low, and then high organic-matter concentration treatments. Food substrates were produced by dry sieving Breakwater Harbor sediment on a shaker table. Particles that passed through a 250-μm

sieve and were retained on a 177- μm sieve were ashed overnight at 450°C and then washed with deionized water. The sediment was then dried, resieved, and re-ashed. For both treatments, bovine serum albumin and Gerber's Mixed Cereal® were added (1:5 by weight) to organic free sediment. Two organic-matter concentrations were used, 0.05-mg g⁻¹ sediment and 0.4-mg g⁻¹ sediment. The night before, a 3–4-mm thick layer of high-concentration sediment (0.4 mg organic matter per gram) was added as seawater slurry using a turkey baster. The morning of the experiment, another 3–4-mm layer was added, and feces were collected every hour for 3 h. A layer of low-concentration sediment (0.05 mg organic matter per gram) was then added, and feces were collected every hour for 4 h. Finally, a layer of high-concentration sediment was added, and feces were collected every hour for 4 h. Fecal samples were first washed with deionized water and were then dried overnight at 80°C and weighed to ± 1 mg for each worm during each time period. The results for each species were examined using repeated-measures analysis of variance (ANOVA), with time as the treatment factor and individual worms representing the repeated factor. C-Matrix multiple comparisons were performed in order that we could examine the responses to a change in diet. For each species, the last measurement from the initial high-organic-matter concentration period ($t = 3$ h) was compared to the four subsequent low-concentration measurements ($t = 4, 5, 6$ and 7 h, respectively); the P values were Bonferroni adjusted. The last low-organic-matter concentration measurement ($t = 7$ h) was compared with the four (subsequent) high-concentration measurements ($t = 8, 9, 10$ and 11 h, respectively); again, the P values were Bonferroni adjusted for the four comparisons performed for each species.

Results

Particle selectivity—For all three species, all worms exhibited a positive log odds ratio, indicating the selectivity of small beads over large beads (Fig. 1). The mean log odds ratios for each species were all significantly different from zero ($P < 0.001$, using a one-sample t -test).

Gut volume and residence time—All three species exhibited similar gut capacities and gut residence times (Fig. 2). Mean gut capacities were between about 14 and 18 mg, and the confidence intervals overlapped, resulting in gut volumes of 0.010 to 0.012 cm³ (Table 1). The mean residence times were 2–2.5 h, and the 95% confidence intervals overlapped (lower panel of Fig. 2). Pearson's correlation coefficients were calculated to test for a relationship between gut capacity, gut residence time, and the body size parameters. No significant correlations were found for any of the three species (in all cases, $P > 0.25$).

Response to a change in diet—The results were examined using repeated-measures ANOVA, and Greenhouse–Geisser-adjusted P values are reported to correct for possible violations of the sphericity assumption (Kirby 1993). There was a significant time effect for all three species, indicating a change in their egestion rates over the course of the exper-

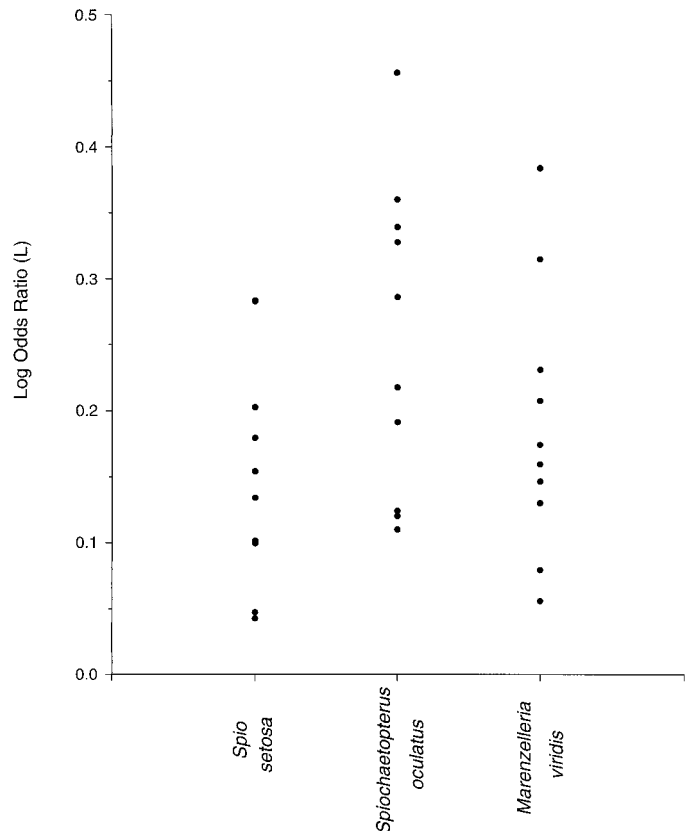


Fig. 1. Particle-size selectivity results. The log odds ratios are plotted for the three species examined. A positive log odds ratio indicates selection for the smaller bead size.

iments (*S. setosa*, $P < 0.001$; *S. oculatus*, $P < 0.001$; *M. viridis*, $P = 0.027$). The mean egestion rates and the results of the C-matrix multiple comparisons are shown graphically in Fig. 3. C-Matrix comparisons yield an F ratio using the local error terms (i.e., the error terms are composed of data from just the means being compared). This ensures that the F -tests are independent and truly distributed as F , but it limits the degrees of freedom (Kirby 1993). There was a rapid reduction in feeding rate with the addition of low-organic-matter sediment, which leveled off in about 2 h. There was a rapid increase after the addition of high-quality sediment, with egestion rates again leveling off in about 2 h. This pattern was consistent for the three species examined. *S. oculatus* and *S. setosa* exhibited a significant reduction in egestion rate after 1–2 h when switched to low-quality material and a significant increase after 1–2 h when switched to high-quality material. *M. viridis* showed significant differences in the feeding rate 3 h after the changes in food concentration. As evidenced by the variability exhibited in the initial high-organic-matter period ($t = 1$ – 3 h), other trends in the results could be attributable to within-treatment variability rather than to some experimental effect.

Discussion

All three of the species examined selected small glass beads in preference to the larger size beads. The log odds

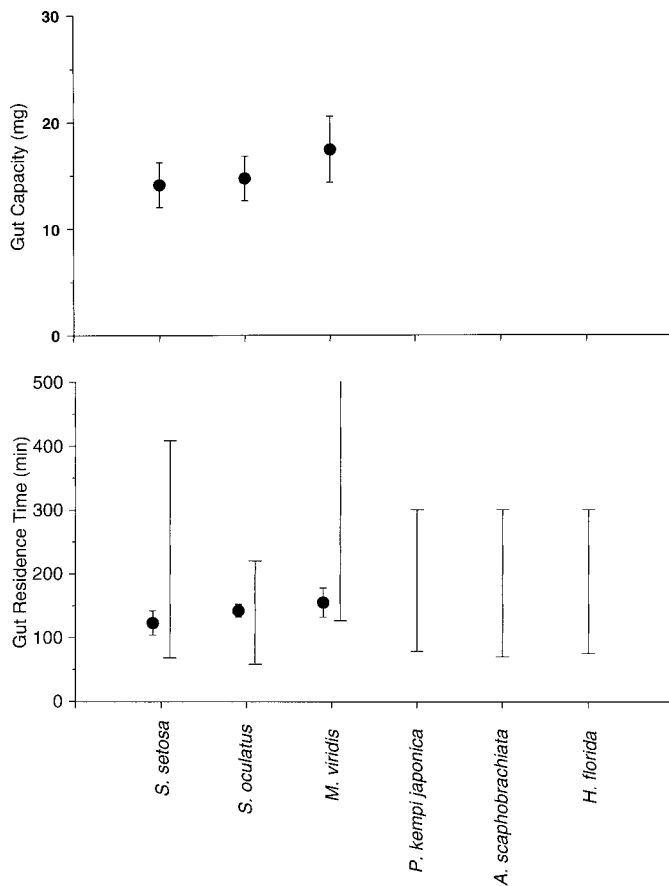


Fig. 2. Gut capacity and gut residence time results. The gut capacities were determined by weighing the feces egested before dyed sediment appeared. Gut residence times denoted by filled circles were determined using the appearance of dyed sediment; error bars = 95% confidence intervals for the means. *S. oculatus*, $n = 24$; *S. setosa*, $n = 25$; *M. viridis*, $n = 22$. Residence times denoted by the error bars with no symbols were calculated using the measured gut capacities and representative feeding rates for low- and high-concentration treatments from the change in diet experiments. The range of residence times for the species examined in Taghon and Jumars (1984) are also shown with error bars. for *M. viridis*, *P. kempji japonica*, *A. scaphobranchiata*, and *H. florida*, the upper bound residence times represent minimum values; the true upper values may be much higher.

ratios compare well to those of other researchers, especially for control and test particles of diameters within a factor of two (Miller 1984; Self and Jumars 1988). This study provides additional evidence that tentaculate polychaetes are particle-size selective. This selectivity has important implications for bioturbation (e.g., Jumars et al 1981; Wheatcroft and Jumars 1987) and feeding behavior (Taghon and Greene 1990; Karrh and Miller 1994; Bock 1995). An important consequence of selectivity is that the biochemical composition of the ingested material is not represented by measurements of the bulk sediment. Given the heterogeneity of particle sizes in real sediments, the concentration of organic matter ingested by a selective deposit feeder could be many times higher than the bulk concentration. In addition, the differences between the bulk sediment and the ingested particles could be unpredictable, making it difficult to use functional-response results obtained in the laboratory to predict feeding rates in the field (but see Karrh and Miller 1994 for a possible exception). Selectivity could also complicate studies of digestive physiology and optimal digestion theory because of the attendant difficulty in determining the biochemical composition of the ingested material. Using particles with a narrow size range and similar organic coatings can solve this problem by presenting a homogeneous food source (e.g., Bock 1995); however, these results cannot be easily extrapolated to the field. A quantitative understanding of the mechanics of particle selection is required in order to effectively estimate the ingestion rate of organic matter in the field.

All three species exhibited similar gut volumes and gut residence times; however, they varied greatly in body size (Table 1). Gut residence times over a range of organic-matter concentrations, found by Taghon and Jumars (1984) for three additional species (*Amphicteis scaphobranchiata*, *Hobsonia florida*, and *Pseudopolydora kempji japonica*), compare well with the results of our experiments (Fig. 2). It is unclear if the constancy in gut residence times is indicative of a general trend relating food concentration and residence time across species. It is important to note that polychaetes have been found to adjust gut fullness (Jumars and Self 1986; Bock and Miller 1995), and, thus, our measurements of gut volume are an estimate of the amount of material in the gut and not the volume of the gut.

Table 1. Worm size parameters. The gut volume was calculated from the gut capacity using a sediment bulk density of 1.4 g cm^{-3} .

Parameter	<i>Spiochaetopterus oculatus</i> $n = 24$		<i>Spio setosa</i> $n = 25$		<i>Marenzelleria viridis</i> $n = 22$	
	Mean	SE	Mean	SE	Mean	SE
Worm size						
Length (mm)	31.1	0.7	31.5	1.8	37.3	3.1
Wet weight (mg)	18.2	0.8	83.0	8.0	54.7	7.5
Dry weight (mg)	5.6	0.2	19.0	1.7	15.0	1.9
Ash free dry weight	4.2	0.1	12.5	1.4	12.6	1.7
Gut kinematics						
Gut capacity (mg)	14.7	1.1	14.1	1.1	17.4	1.6
Gut volume (cm^3)	0.010	0.001	0.010	0.001	0.012	0.001
Throughput time (min)	142.0	5.2	122.8	9.7	154.7	11.7

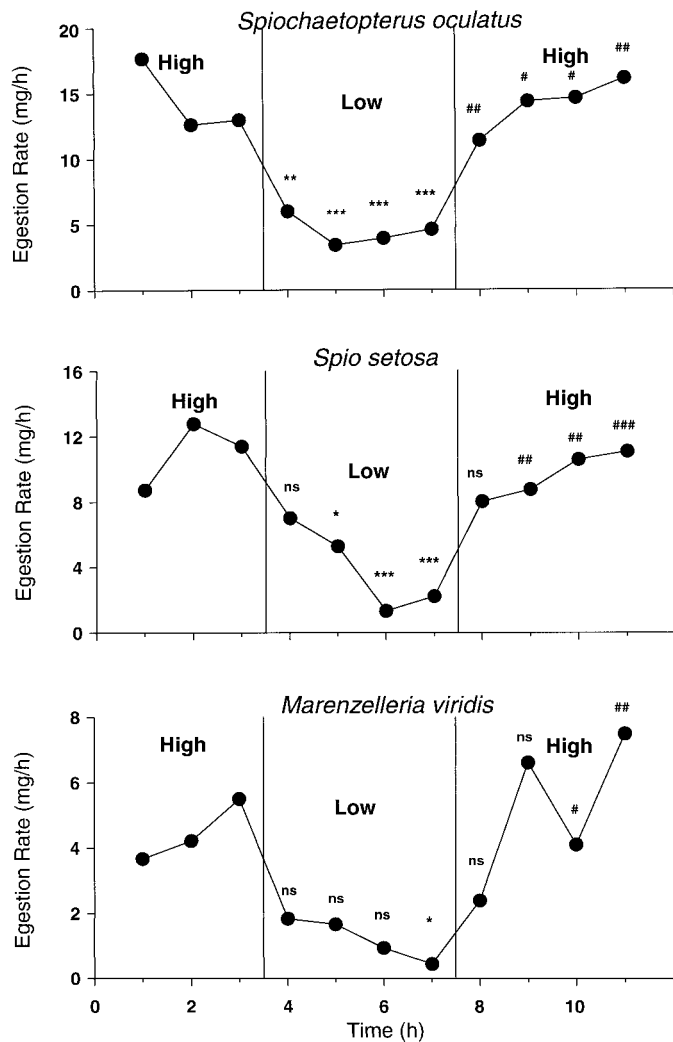


Fig. 3. Response to a change in diet. The egestion rates are plotted versus time for the three species. All three species show a response to a change in diet. The * symbols indicate the significance level of the multiple comparisons with respect to $t = 3$ h (***, $P \leq 0.001$; **, $P \leq 0.01$; *, $P \leq 0.05$.) The # symbols indicate the significance level of the multiple comparisons with respect to $t = 7$ h (###, $P \leq 0.001$; ##, $P \leq 0.01$; #, $P \leq 0.05$). $n = 18$ for each species.

For all three species, the feeding rate decreased when worms were switched from high- to low-concentration treatments and increased when they were switched from low- to high-concentration treatments. For *S. oculatus* and *S. setosa*, the change in feeding rate was significant after 1–2 h; for *M. viridis*, the trends were the same, but significant differences were only detected after 3 h. Bock (1995) examined the steady-state feeding rate response to organic-matter concentration for the same species and over the same organic matter and particle treatments used in these experiments. The steady-state feeding rates from Bock (1995) compare well with those found in our experiment a few hours after a change in diet (Fig. 3, Table 2). For *M. viridis*, the differences in the steady-state feeding rates at 0.05 and 0.4 mg organic matter (OM) g^{-1} were much less pronounced than

Table 2. The steady state feeding rates for Low and High concentration sediments, data from Bock (1995). The sediment substrate was treated in the same manner as was used in the present study.

Treatment	Feeding rate		
	<i>S. oculatus</i>	<i>S. setosa</i>	<i>M. viridis</i>
Low	8.0	0.4	0.5
High	20.6	6.6	2.8

for *S. oculatus* and *S. setosa* (Table 2), which could account for the lack of statistically significant differences at 1–2 h in the present study. Based on these results, it is unwise to speculate that the time scale of response of *M. viridis* differs from that of *S. oculatus* and *S. setosa*. For all three species, the feeding rates reached what appears to be a new steady state within about 2 h (Fig. 3). The rapid changes observed here contrast with the slower adjustment in feeding rate observed by Miller (1992) for *S. kowalevskii*, and they suggest a foregut/midgut feedback mechanism. We hypothesize that changes in the feeding rate occur in response to the early release of digestive products in the foregut/midgut. Mayer et al. (1995) incubated sediments with both commercially available enzymes and gut fluids from a deposit-feeding holothurid. Significant quantities of peptides were released in as little as 15 min, indicating that the organisms could obtain useful information by monitoring absorption in the gut. If changes in the feeding rate occur in response to conditions in the hindgut, adjustments in feeding rate would occur more slowly than the gut throughput time (about 2 h, Table 1). It is important to note that Miller (1992) rejected the foregut/midgut feedback hypothesis based on the delay in the response of *S. kowalevskii*.

Limitations in our method of measuring the feeding rate by monitoring the egestion rate may have introduced some bias. Bock and Miller (1995) reported changes in gut fullness in *M. viridis* and attributed these changes to changes in the feeding rate. *M. viridis* has about 250 setigers, and the average gut fullness changed from 25 to 75 empty setigers, translating into a gut that is 90% full and 70% full (Bock and Miller 1995). Based on the gut capacities and feeding rates we measured, this translated into a change of about 3.9 mg of sediment in the gut. *Marenzelleria* ingests this amount of material in 1–2 h, suggesting that our egestion rate experiments should have a temporal resolution of 1–2 h. Based on these calculations, it is surprising that we saw an almost immediate change in the feeding rate in response to changes in the food concentration. Jumars and Self (1986) related changes in the feeding rate to changes in gut fullness. They found that a decrease in the ingestion rate corresponded to a decrease in gut fullness. This relationship between the feeding rate and gut fullness necessitates a lag between changes in the ingestion rate and changes in the egestion rate. The implication of this lag is that we may overestimate the time it takes to detect a change in the ingestion rate by monitoring the egestion rate. Since we did detect a rapid change in the egestion rate, we conclude that changes in gut fullness occur gradually and probably did not have a significant impact on our estimates of the egestion rate. Based on

these arguments, we are confident in concluding that the three species used in our experiments changed their ingestion rates in less than 1 h when exposed to a change in diet.

The importance of a rapid response to a change in diet is unclear. We hypothesized earlier that an organism should retain high-quality material in its gut when subjected to low-food concentration material and should flush low-concentration material from its gut when exposed to high-concentration material. The results show that this does not occur and that the response to a change in diet is simply a modulation of the feeding rate to a new steady state. Does this really represent a "mistake" by the organisms? Field data suggest that food resources in the field change on many time scales, from seasonal to daily or hourly scales (Karrh and Miller 1994; Bock and Miller 1995). If most changes occur on an hourly or greater time scale, the organisms are probably not exposed to step changes in diet, such as those explored here. In order to benefit from retaining or flushing material from the gut in response to a change in food resources, these changes must occur rapidly in relation to gut throughput times. Tidal bores in shallow areas represent one such possible mechanism for step changes in diet. Anderson and Mayer (1984) found that tidal flood fronts can transport a large amount of high-quality material to feeding areas. Jumars and Self (1986) examined the feeding response of *Pseudoploydora kempii japonica* to the pulse of particle transport associated with the incoming tide and found that the organisms dramatically increased their feeding rate. Thus, tidal fronts clearly represent a possible source of a step change in diet to which organisms could respond. The influence of tidal fronts in shallow water compared with other more gradual sources of variability is unknown. Further, the effects of tidal fronts are rapidly attenuated with depth. Thus, only some benthic organisms are exposed to such a step change in diet. Regardless, our results show that laboratory studies with a moderate acclimation period (several hours) will be affected by preacclimation effects on the feeding rate. This underscores the importance of adequate acclimation periods in experimental studies of feeding rate.

References

- ANDERSON, F. E., AND L. M. MAYER. 1984. Seasonal and spatial variability of particulate matter of a muddy intertidal flood front. *Sedimentology* **31**: 383–394.
- BAYNE, B. L., A. J. S. HAWKINS, AND E. NAVARRO. 1987. Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. *J. Exp. Mar. Biol. Ecol.* **111**: 1–22.
- BOCK, M. J. 1995. The feeding response of benthic polychaetes: Food resources and hydrodynamics. Ph.D. thesis, Univ. of Delaware.
- , AND D. C. MILLER. 1995. Storm effects on particulate food resources on an intertidal sandflat. *J. Exp. Mar. Biol. Ecol.* **187**: 81–101.
- , AND ———. 1996. Fluid flow and suspended particulates as determinants of polychaete feeding behavior. *J. Mar. Res.* **54**: 565–588.
- , AND ———. 1997. Particle-bound organic matter as a cue for suspension feeding in tentaculate polychaetes. *J. Exp. Mar. Biol. Ecol.* **215**: 65–80.
- BRICELI, V. M. 1984. Effects of suspended sediments on the feeding physiology of the hard clam *Mercenaria mercenaria* (Linne). *J. Shellfish Res.* **4**: 82.
- , R. E. MALOUF, AND C. D. QUILLFELDT. 1984. Growth of juvenile *Mercenaria mercenaria* and the effect of resuspended bottom sediments. *Mar. Biol.* **84**: 167–173.
- DADE, W. B., P. A. JUMARS, AND D. L. PENRY. 1990. Supply-side optimization: Maximizing absorptive rates, p. 531–555. *In* R. N. Hughes [ed.], *Behavioral mechanisms of food selection*. Springer.
- DAUER, D. M., C. A. MAYBURY, AND R. M. EWING. 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.* **54**: 21–38.
- GRANT, J., C. T. ENRIGHT, AND A. GRISWOLD. 1990. Resuspension and growth of *Ostrea edulis*: A field experiment. *Mar. Biol.* **104**: 51–59.
- GRIZZLE, R. E., AND R. A. LUTZ. 1989. A statistical model relating horizontal seston fluxes and bottom sediment characteristics to growth of *Mercenaria mercenaria*. *Mar. Biol.* **102**: 95–105.
- HASSETT, R. P., AND M. R. LANDRY. 1990. Effects of diet and starvation on digestive enzyme activity and feeding behavior of the marine copepod *Calanus pacificus*. *J. Plankton Res.* **12**: 991–1010.
- JUMARS, P. A., A. R. NOWELL, AND R. F. SELF. 1981. A simple model of flow–sediment–organism interaction. *Mar. Geol.* **42**: 155–172.
- , AND R. F. SELF. 1986. Gut-marker and gut-fullness methods for estimating field and laboratory effects of sediment transport on ingestion rates of deposit-feeders. *J. Exp. Mar. Biol. Ecol.* **98**: 293–310.
- , ———, AND A. R. NOWELL. 1982. Mechanics of particle selection by tentaculate deposit-feeders. *J. Exp. Mar. Biol. Ecol.* **64**: 47–70.
- KARRH, R. R., AND D. C. MILLER. 1994. Functional response of a surface-deposit feeder: *Saccoglossus kowalevskii*. *Limnol. Oceanogr.* **39**: 1455–1464.
- , AND ———. 1996. Effect of flow and sediment transport on feeding rate of the surface-deposit feeder *Saccoglossus kowalevskii*. *Mar. Ecol. Prog. Ser.* **130**: 1–3.
- KIRBY, K. N. 1993. *Advanced data analysis with SYSTAT*. Van Nostrand Reinhold.
- LEVINTON, J. S. 1991. Variable feeding behavior in three species of *Macoma* (Bivalvia: Tellinacea) as a response to water flow and sediment transport. *Mar. Biol.* **110**: 375–383.
- , AND M. MCCARTNEY. 1991. Use of photosynthetic pigments in sediment as a tracer for sources and fates of macrophyte organic matter. *Mar. Ecol. Prog. Ser.* **78**: 87–96.
- LUCKENBACH, M. W., D. V. HUGGET, AND E. C. ZOBRIST. 1988. Sediment transport, biotic modifications and selection of grain size in a surface deposit-feeder. *Estuaries* **11**: 134–139.
- MAYER, L. M. 1994a. Relationships between mineral surfaces and organic carbon concentrations in soils and sediments. *Chem. Geol.* **114**: 347–363.
- . 1994b. Surface area control of organic carbon accumulation in continental shelf sediments. *Geochim. Cosmochim. Acta* **58**: 1271–1284.
- , L. L. SCHICK, T. SAWYER, C. J. PLANTE, P. A. JUMARS, AND R. F. SELF. 1995. Bioavailable amino acids in sediments: A biomimetic, kinetics-based approach. *Limnol. Oceanogr.* **40**: 511–520.
- MILLER, D. C. 1984. Mechanical post-capture particle selection by suspension- and deposit-feeding *Corophium*. *J. Exp. Mar. Biol. Ecol.* **82**: 59–76.
- . 1992. Response of *Saccoglossus kowalevskii* (phylum Hemichordata, class Enteropneusta) to changes in diet. *Mar. Ecol. Prog. Ser.* **78**: 41–54.
- , M. J. BOCK, AND E. J. TURNER. 1992. Deposit and sus-

- pension feeding in oscillatory flows and sediment fluxes. *J. Mar. Res.* **50**: 489–520.
- , P. A. JUMARS, AND A. R. NOWELL. 1984. Effects of sediment transport on deposit feeding: Scaling arguments. *Limnol. Oceanogr.* **29**: 1202–1217.
- , AND A. J. RAY. 1988. AGU abstract. Estimating sediment transport rates on spatial scales relevant for deposit feeding organisms. *EOS* **69**: 1123.
- NOWELL, A. R. M., P. A. JUMARS, R. F. L. SELF, AND J. B. SOUTHARD. 1989. The effects of sediment transport and deposition on infauna: Results obtained in a specifically designed flume, p. 247–268. *In* G. Lopez, G. Taghom, and J. Levinton [eds.], *Ecology of marine deposit feeders*. Springer-Verlag.
- PENRY, D. L. 1993. Digestive constraints on diet selection, p. 32–55. *In* R. N. Hughes [ed.], *Diet selection: An interdisciplinary approach to foraging behavior*. Blackwell.
- , AND P. A. JUMARS. 1987. Modeling animal guts as chemical reactors. *Am. Nat.* **129**: 69–96.
- RHOADS D. C., L. F. BOYER, B. L. WELSH, AND G. R. HAMPSON. 1984. Seasonal dynamics of detritus in the benthic turbidity zone (BTZ): Implications for bottom-rack molluscan mariculture. *Bull. Mar. Sci.* **35**: 536–549.
- SELF, R. F., AND P. A. JUMARS. 1988. Cross phyletic patterns of particle selection by deposit feeders. *J. Mar. Res.* **46**: 119–143.
- TAGHON, G. L. 1982. Optimal foraging by deposit-feeding invertebrates: Roles of particle size and organic coating. *Oecologia* **52**: 295–304.
- , AND R. L. GREENE. 1990. Effects of sediment–protein concentration on feeding and growth rates of *Abarenicola pacifica* Healy et Wells (Polychaete: Arenicolidae). *J. Exp. Mar. Biol. Ecol.* **136**: 197–216.
- , AND P. A. JUMARS. 1984. Variable ingestion rate and its role in optimal foraging behavior of marine deposit feeders. *Ecology* **65**: 549–558.
- WARD, E. J., J. LEVINTON, S. SHUMWAY, AND T. CUCCI. 1996. Looking into the “black box”: Feeding strategies and limitations of suspension-feeding bivalves. *J. Shellfish Res.* **15**: 507.
- WHEATCROFT, R. A., AND P. A. JUMARS. 1987. Statistical re-analysis for size dependency in deep-sea mixing. *Mar. Geol.* **77**: 157–163.

Received: 16 July 1997
Accepted: 27 November 1998
Amended: 18 February 1999