

Predicting particle selection by deposit feeders: A model and its implications¹

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Abstract

A feeding model for a generalized, benthic deposit feeder is derived from a filter-feeding model and used to predict how such a deposit feeder would adjust its feeding to maximize its net energy gain. Under the assumption that deposit feeders are utilizing the bacterial fraction of the sediment or other surface organic coatings as food, the model predicts that the smallest particles should always be ingested, while the selection of larger particles depends on several parameters, including gut passage time and assimilation efficiency of the deposit feeder. The model also predicts relationships among particle size selection, assimilation efficiency, gut passage time, gut volume, and particle rejection costs.

Empirical investigations of marine deposit feeding have suggested several generalizations. Rather than using non-living organic matter directly, most deposit feeders digest the microbial epigrowth of particles (e.g. Fenchel 1970; Fenchel and Kofoed 1976; Kristensen 1972; Yingst 1976). Deposit-feeder standing stock is often inversely correlated with sediment particle size (e.g. Newell 1970). Microbial standing stock per unit surface area of sedimentary particles is surprisingly constant (Dale 1974; Hargrave 1972), and particle size appears to be important in partitioning the deposited resource (Fenchel et al. 1975).

Consideration of the filter-feeding models of Lam and Frost (1976) and Lehman (1976) suggested to us that the parameters of the deposit-feeding system might profitably be connected via a suitable feeding model. In order to accelerate the desirable iteration between theory and practice (Box 1976), we sought to develop a simple, general deposit-feeding model which might still be consistent with the above empirical observations.

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Methods

We discovered that Lehman's (1976) model could be applied with relatively little modification. The assumptions and boundary conditions used in our modification of his model are that net energy gain to the animal is optimized; that there is a maximum, finite gut volume, and the gut is always filled to its capacity; that assimilation rate is independent of particle size; that ingestion is continuous; that sediment particles are spherical mineral grains, and their supply to the immediate environment of the organism is unlimited; and that the food for the deposit feeder consists of bacteria or other organic coatings attached to the surface of the sediment particles.

These assumptions of our model thus differ from Lehman's only in geometric detail: the food for deposit feeders is made roughly proportional to surface area, rather than to volume, of the particles. When carried through the derivation, however, these seemingly minor changes have dramatic effects.

Following Lehman, let

$$Q = E_a - E_c - E_r, \quad (1)$$

where E_a is the energy gained from assimilation of bacteria, E_c is the energy expended in collecting sediment particles, and E_r is the energy required to reject an unwanted particle (all in

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cal·time⁻¹). Q (cal·time⁻¹) then represents the net energy gain to the animal, which can be partitioned among growth, reproductive, respiratory, and excretory processes. To maximize Q , the animal must strike an optimal balance among E_a , E_c , and E_r .

Now,

$$E_a = \sum \alpha_i D_i P E_i. \quad (2)$$

Here, α_i is a selectivity factor for particle type i . When α is equal to one, the particle is always ingested when it is encountered in the environment. At the other extreme, when α_i equals zero, the i th type of particle is never selected for ingestion. D_i (No. particles·ml⁻¹) is the abundance of the i th particle type, E_i (cal·particle⁻¹) is the energy gained from digestion of the bacteria associated with one of those particles, and P (ml·time⁻¹) is the "processing rate." P is used in place of F , the filtering rate, in Lehman's original model. When we substitute a "processing rate," the animal can be considered to process a certain volume of sediment in the course of selecting particles for ingestion.

Continuing to follow Lehman (1976, model 1), the energy gained from digestion, E_i , can be written as

$$E_i = E_{\max_i} (1 - e^{-T/a}). \quad (3)$$

E_{\max_i} (cal·particle⁻¹) is the amount of energy gained if all the bacteria present on the particle were digested. T (time) represents the gut passage time and $1/a$ (time⁻¹) is a measure of the time-specific assimilation efficiency. Figure 1 shows the relationships among these parameters for assumed values of $1/a$ and T . For long gut residence times, high time-specific assimilation efficiencies, or both, E_i approaches E_{\max_i} asymptotically. The data of Berrill (1929) on digestion in ascidians suggest that this simple exponential model provides a good approximation to actual rates of digestion for the group. The validity of our model to deposit feeders remains to be determined; we know of no data which contradict it. Using the

boundary conditions that the gut is always filled and that feeding is continuous, we find that

$$P = \frac{V_g}{\sum \alpha_i D_i [a(V_{o_i} - V_{f_i})(1 - e^{-T/a}) + V_{f_i} T]}, \quad (4)$$

where V_g is the maximum gut volume (ml), V_o is the volume of a sediment particle with its bacterial coating, and V_f is the particle volume when no bacteria are associated with it. The quantity $(V_{o_i} - V_{f_i})$ is thus a measure of food abundance on a particle of the i th type (in ml·particle⁻¹). Since bacteria form a relatively thin coating on sediment particles, the food abundance could also be expressed as a function of particle surface area. We chose to retain Lehman's (1976) use of volume, however, both to maintain consistency of units in Eq. 4 and to keep the model more general; food sources other than bacteria-coated mineral grains could be used in which food abundance might be more strictly related to volume (i.e. algal cells). This possibility is discussed further below.

For the energy expended to collect particles, we let

$$E_c = bP^x, \quad (5)$$

where b (cal·time^{x-1}·ml^{-x}) is a suitable processing rate constant. Several possibilities exist for the value of x . The simple linear relationship ($x = 1$) may be appropriate, but only at lower processing rates; a crossover point where E_c increases abruptly with increasing processing rate would probably exist, due to physical constraints. For a filter feeder, Lehman (1976) let $x = 3$ if the flow of water around the filtering appendages was turbulent or $x = 2$ if the flow was viscous. These values may be applicable to some varieties of deposit feeder as well. Lehman concluded that flow was well within the laminar regime and let $x = 2$. We have also used this value to facilitate comparisons between the two models. The qualitative results are not particularly sensitive to this assumption.

The last term needed to determine Q is E_r , where

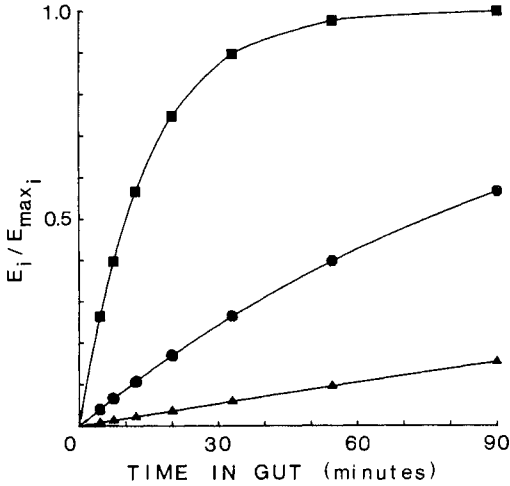


Fig. 1. Energy gain from digestion of bacteria (E_i) relative to maximum possible energy gain (E_{\max_i}) with gut passage time (T) and time-specific assimilation efficiency ($1/a$). ■— $1/a = 0.068 \cdot \text{min}^{-1}$; ●— $1/a = 0.009 \cdot \text{min}^{-1}$; ▲— $1/a = 0.002 \cdot \text{min}^{-1}$.

$$E_r = \sum (1 - \alpha_i) D_i P R_i \quad (6)$$

R_i ($\text{cal} \cdot \text{particle}^{-1}$) is the cost of rejecting a particle of type i .

These six equations were used in developing a computer program that maximizes Q , the net energy gain to the animal. Parameters which must be supplied to the program are the particle diameters, E_{\max_i} , D_i , T , $1/a$, V_g , b , and R_i . The model was run with a variety of particle sizes, but two will be used to demonstrate its basic behavior. Type 1 was $10 \mu\text{m}$ in diameter and type 2 was $20 \mu\text{m}$ in diameter. The two particle types were allowed to occupy equal volumes of space. A simple cubic packing scheme gave $D_1 = 5 \times 10^8$ particles $\cdot \text{ml}^{-1}$ and $D_2 = 6.25 \times 10^7$ particles $\cdot \text{ml}^{-1}$. The bacterial cover of these particles was assumed to be 3% of the available surface area (Fenchel 1970; Baatsoingh and Anthony 1971). Letting the dry weight of a bacterium be 2×10^{-13} g (Baker and Bradnam 1976) and the caloric value of bacteria be $5,400 \text{ cal} \cdot \text{g}^{-1}$ (Prochazka et al. 1973) gives $E_{\max_1} = 1.02 \times 10^{-8} \text{ cal} \cdot \text{particle}^{-1}$ and $E_{\max_2} = 4.07 \times 10^{-8}$. For lack of data directly applicable to deposit feeders, we let $b = 0.02$

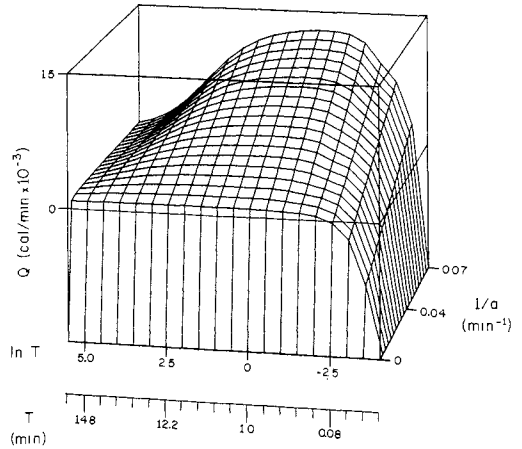


Fig. 2. Maximum rate of energy gain (Q) at various gut passage times (T) and time-specific assimilation efficiencies ($1/a$). Gut volume (V_g) = 0.01 ml , rejection costs (R_i) = $0 \text{ cal} \cdot \text{particle}^{-1}$.

$\text{cal} \cdot \text{min} \cdot \text{ml}^{-2}$ (Lehman 1976). While this constant is unlikely to be the same for any deposit feeder, the qualitative results of the model are not affected by the value of b . The remaining four input parameters were varied so that we could investigate their effects on Q , α_1 , and α_2 .

Results and discussion

By varying the input parameters T , $1/a$, V_g , and R_i we can determine which ones have the greatest effect on the results and would therefore be most profitable to measure in order to test the model.

Gut passage time and time-specific assimilation efficiency—Figure 2 is the response surface of Q , the net energy gain, at various time-specific assimilation efficiencies and gut passage times. At very low time-specific assimilation efficiencies or short gut residence times, Q is negative. When T is small, particles are rapidly passing through the gut. Due to the boundary condition that the gut always be full, P increases and the energy expended on collecting particles becomes greater than the energy gained from assimilating the associated bacteria. As $1/a$ approaches 0, enough bacterial biomass can never be assimilated to make E_a greater than E_c .

Although each point on the response surface represents the maximum value of Q at that particular gut passage time and time-specific assimilation efficiency (due to appropriate selection coefficients for the two particle types), it is clear there exists an overall maximum energy gain for any given value of T or $1/a$. This highest Q occurs at the highest elevation of the surface as one travels in the X or Y direction, corresponding to increasing time-specific assimilation efficiency or increasing time in the gut. If T is held constant, the greatest possible energy gain occurs at the highest time-specific assimilation efficiency the animal is capable of, as expected. However, when $1/a$ is fixed and gut passage time is allowed to vary, there is a definite value of T which results in the maximum energy gain to the animal. When T is too small, the particle does not remain in the gut long enough for digestion of the bacteria. As the particle is held in the gut longer, more of its bacterial coating can ultimately be removed, but Q decreases after reaching its maximum at some intermediate time in the gut. This is because Q is a time rate of energy gain. The animal gains more energy per unit time by digesting only part of the available bacteria before egesting the particle than it would by taking the additional time to digest the particle more thoroughly. The gut retention time at which this point of diminishing returns is reached becomes shorter as the time-specific assimilation efficiency increases. Also evident from Fig. 2 is that the range of T values over which Q does not change greatly decreases as the time-specific assimilation efficiency increases; the surface becomes more leptokurtic (peaked) at high time-specific assimilation efficiencies. This implies that, for an animal with a low time-specific assimilation efficiency, the gut passage time is not critical in determining the maximum possible rate of energy gain. If the time-specific assimilation efficiency is high, then the length of time food is kept in the gut becomes more crucial in regard to the maximum possible energy gain. Similarly, Q does not change greatly at long gut

residence times over most of the time-specific assimilation efficiencies used in Fig. 2. For an animal with a long gut passage time the value of the time-specific assimilation efficiency is not as important as for an animal that passes food through its gut more rapidly.

These considerations point out the desirability of determining both the gut passage time and the time-specific assimilation efficiency of an organism. The often-measured assimilation efficiency, by itself, does not provide an unambiguous assessment of an animal's energy uptake abilities. As the model suggests, an animal that extracts most of the available energy from a food item (high assimilation efficiency) but takes a long time to accomplish this will not gain as much energy per unit time as will an animal that does not digest its food as completely (lower assimilation efficiency) but processes more food items in the same amount of time. Methods used for determining assimilation efficiencies in animals (e.g. gravimetric measurement of some component of the food source and feces: George 1964; Gordon 1966; Bolton and Phillipson 1976; Davidson 1976; radiotracers: Hargrave 1970; Calow and Fletcher 1972; Duncan et al. 1974; etc.), and the additional measurement of gut passage time, permit calculation of the time-specific assimilation efficiency ($1/a$) by suitable substitutions into Eq. 3. Although the occurrence of selective ingestion makes field estimates of assimilation efficiency difficult to interpret (Hylleberg and Gallucci 1975), a properly designed laboratory experiment would not be subject to these uncertainties. Use of the gut passage time and time-specific assimilation efficiency parameters provides a more quantitative picture of feeding energetics that may be of interest from a species-interaction viewpoint (e.g. Fenchel et al. 1975).

For all values of T and $1/a$, α_1 is optimally equal to 1—that is, the model predicts that the smaller particle should always be selected. Only the selectivity coefficient for the larger particle varies, and this variation is shown in Fig. 3. At

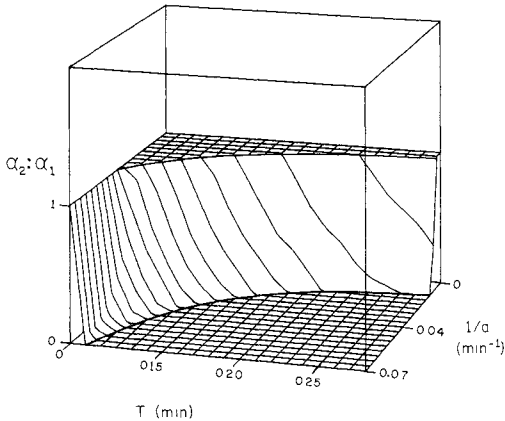


Fig. 3. Ratio of selectivity coefficients, α_2 to α_1 , that maximize net energy gain for various gut passage times (T) and time-specific assimilation efficiencies ($1/a$). Gut volume (V_g) = 0.01 ml, rejection costs (R_i) = 0 cal · particle⁻¹.

higher time-specific assimilation efficiencies and longer gut passage times, optimal results are obtained when $\alpha_2 = 0$; it is energetically more profitable to the deposit feeder to ingest only the smaller particle. This is understandable in view of the higher surface area:volume ratio for the smaller particle. Since the total amount of bacteria is directly related to the total surface area of the substrate (Odum and de la Cruz 1967; Newell 1965; Fenchel 1970; Hargrave 1972; Dale 1974), the smaller particles represent more food per unit volume and are selectively ingested. As gut passage time decreases, E_a also decreases because there is less time available for digestion, while E_c increases because the gut is being filled and emptied more rapidly at faster gut passage times. As time-specific assimilation efficiency decreases, E_a decreases because of less efficient digestion, while in this case E_c remains relatively constant. To most effectively maximize Q in these situations, the deposit feeder should act to decrease the energy expended on collecting particles. E_c can be decreased by reducing the volume of sediment processed. To accomplish this while still maintaining a full gut, the deposit feeder can also begin to ingest the larger particle. This trend is

evident in Fig. 3. At very low time-specific assimilation efficiencies or rapid gut passages, α_2 is also equal to 1; both particles are always selected to maximize Q .

Gut volume—As before, for optimal results, α_1 always equaled 1 for any gut volume used in the model. The variations of the optimal value of α_2 and the corresponding energy gain with changes in V_g are shown in Fig. 4. As V_g initially increases, Q rises due to the animal's ability to ingest a greater volume of particles. With further increases in V_g , E_c begins to increase at a faster rate than E_a . To minimize the rate of increase of E_c , the animal also begins to select the larger particle, shown by the increasing $\alpha_2:\alpha_1$ ratio. Finally, a gut volume is reached at which, due to the boundary condition that the gut always be full, E_c becomes equal to E_a , and there is no net energy gain to the animal; all energy gained from assimilating bacteria is used for collecting more particles.

It is admittedly unrealistic to maintain T , $1/a$, food gathering ability, and the amount of energy allocated to basal metabolism constant, while varying the size of the organism's gut. Figure 4 thus should not be interpreted as a prediction of the behavior of organisms of differing sizes. Instead, the purpose of this aspect of the sensitivity analysis is to demonstrate that gut size per se can have a marked effect on both particle selectivity (α) and net energy gain (Q) under the assumptions of the model.

Rejection costs—In all the results presented so far, all R_i have equaled 0; it has not cost the deposit feeder any energy to reject a particle already collected. There are many ways in which a cost for rejecting a particle can be levied. Two ways considered here are that R_i may be a function of the individual particle's characteristics, that is, some percentage of $E_{\max i}$, or that R_i may be a constant for all particle types. The effects on Q , α_1 , and α_2 of varying the cost of rejection according to these two schemes are shown in Fig. 5. Again, for maximum Q , α_1 is always 1 and α_2 is initially 0; therefore, particle 1 is never rejected, while at first par-

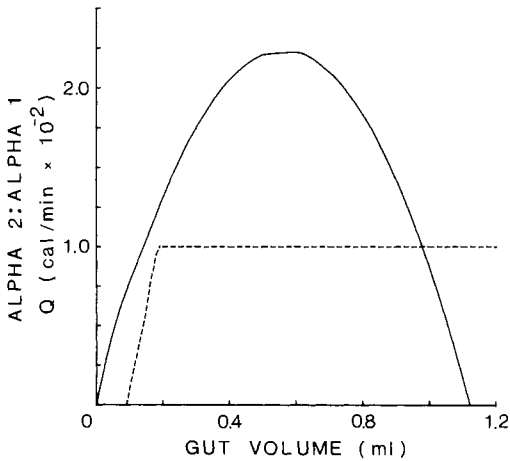


Fig. 4. Net energy gain Q (—) and ratio of α_2 to α_1 (---) at various gut volumes. Gut passage time (T) = 1.0 min, time-specific assimilation efficiency ($1/a$) = $0.0055 \cdot \text{min}^{-1}$, rejection costs (R_i) = $0 \text{ cal} \cdot \text{particle}^{-1}$.

article 2 is always rejected. As the cost of rejecting the unwanted particle type increases, the net energy gain to the animal decreases. With increasing R , it eventually becomes too expensive to reject the larger particle. At this point α_2 goes to 1 and Q levels off.

When R is expressed as the percentage of $E_{\text{max}1}$, the energy content of the smaller particle, the cost of rejection on a percentage basis is lower, as is seen by the smaller rate of decrease in Q . The value of Q in calories per minute when α_2 goes to 1 is the same whether R is expressed as a percentage of $E_{\text{max}i}$ or $E_{\text{max}1}$.

Rejection mechanisms differ among deposit-feeding groups, and the cost of rejection may be related to the mechanism used. Among the deposit-feeding crustaceans, for example hermit crabs (Roberts 1968) and crayfish (Caine 1975), sediment is sifted through setae on the mouthparts. However, whereas a filter feeder would ingest the particles retained by such a sieving process, deposit-feeding crustaceans apparently reject those larger, heavier components of the sediment retained by the setae and ingest the smaller "detritus" which passes through (Caine 1975). This type of sorting process may keep the cost of rejecting

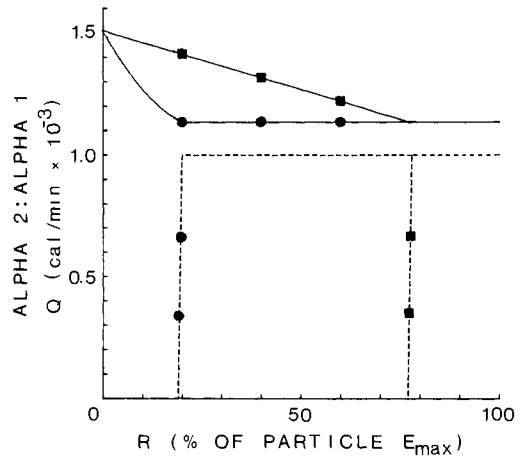


Fig. 5. Rate of energy gain Q (—) and ratio of α_2 to α_1 (---) when costs of rejection are measured as percentage of individual particle's maximum energy content (●) and as percentage of smaller particle's maximum energy content (■). Gut volume (V_g) = 0.01 ml, gut passage time (T) = 50 min, time-specific assimilation efficiency ($1/a$) = $0.01 \cdot \text{min}^{-1}$.

unwanted particles relatively low. Deposit-feeding bivalves commonly eject unwanted particles as pseudofeces, which may entail a greater energetic cost than the sieving mechanism of crustaceans. Little is known concerning rejecting mechanisms in deposit-feeding polychaetes (Fauchald and Jumars in press), a third major group of deposit feeders.

Whichever of the many possible schemes of rejection costs applies, the cost of rejecting a particle would be difficult to measure. The importance of having at least some estimate of R is evident from its effects on Q and α (Fig. 5). More studies on the mechanisms and energetics of particle rejection are therefore needed to clarify the economics of deposit feeding.

Comparison with filter feeder—For a herbivorous copepod, the caloric values of possible food items are generally proportional to the volumes of phytoplankton cells. For a herbivorous filter feeder, the energy optimization model thus predicts that particles which are larger than those with the greatest abundance will show the highest α_i (Lehman 1976).

These results are the exact opposite of the deposit-feeding case, where the model predicts that the smallest particle should be preferentially ingested and larger particles may or may not be eaten depending on various parameters already discussed. The caloric value of an organically coated mineral particle is proportional to its surface area, and a given volume of small particles has a greater total surface area than the same volume of larger particles.

Complicating factors—In aphotic environments bacteria no doubt constitute a major food resource for benthos. In the intertidal and shallow subtidal, however, phytobenthos may serve as food for a deposit feeder. If the algae are epiphytic on particles (e.g. Fenchel and Kofoed 1976), little modification of the present model would be required; if algal cells are selected individually, Lehman's (1976) model may apply directly. However, if algae and bacteria are both digested and if different particles contain these food items in differing proportions (an extreme case being that in which diatoms are treated as individual particles), the time-specific assimilation efficiency would probably vary among particle types. A food item-specific efficiency—the use of an a_i term in place of a —would allow for this. This approach might be particularly useful for those benthic or planktonic filter feeders that ingest both phytoplankton and detrital particles (with their associated microflora).

The question of variable gut passage time should also be addressed. Evidence for a food item-specific gut passage time exists (Hill 1976). The components of a mixture of particle types pass through the gut of a deposit-feeding ampharetid polychaete at different rates (Self and Jumars unpublished). If this ability is widespread among deposit feeders, the use of a single variable to describe gut passage time would be an oversimplification. Again, however, the model could be generalized by inclusion of a particle-specific gut passage time, T_i .

Testing the model—This incomplete list of complications (e.g. no considera-

tion being given to varying sediment packing configurations) and the seeming tenuousness of the longer list of explicit and implicit assumptions would suggest that the model might readily be mortally endangered (cf. Platt 1964). We are unaware, however, of any published body of data sufficient for disproof. Although Whitlatch (1974), for example, demonstrated a preference for larger ($>75 \mu\text{m}$) particles by *Pectinaria gouldii*, he also found that the smaller particles ($<25 \mu\text{m}$) lacked an organic coating. The avoidance of the smaller particles in this environment might therefore be explained by their unsuitability as food items (low $E_{\text{max},i}$).

There have been many other studies on particle selection by deposit feeders. We have chosen not to apply data generated by these studies toward testing our deposit-feeding model. As we have already mentioned, we do not know of any study or combination of studies including all input parameters needed by even this simple model. Indeed, one of the prime purposes of this—and any—model is to identify the parameters needed to develop a predictive ability. With suitable values used for the unknown input variables, the model can successfully hindcast most observed results, but this sort of a posteriori testing is uninformative and dangerous. For these reasons we feel any attempt to review the deposit-feeding literature now through the eyes of our model would not be worthwhile.

We are, therefore, currently attempting disproof of those component assumptions which can be most easily tested. It appears unlikely that the same model would hold over the wide diversity of foraging methods among deposit feeders (e.g. Newell 1970; Jumars and Fauchald 1977), and the best approach to outlining the model's utility seems to be a testing of its basic assumptions among a small selection of widely divergent deposit-feeding strategies.

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