

A SIMPLE MODEL OF FLOW–SEDIMENT–ORGANISM INTERACTION

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ABSTRACT

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Previous models of organism–sediment interaction have been limited primarily to eddy diffusion-type mixing. While such models are useful in interpreting some stratigraphic records, they cannot be expected to provide mechanistic insights into the diversity of interactions among sedimentary processes, organism activities, and boundary layer flows. To provide a more general formulation capable of dealing with all three types of processes in concert, a simple, discrete-time Markov model is generated. This version of the model deals explicitly only with particulate and not liquid phases.

The initial formulation is a two-compartment, ergodic model of deposit feeding. Particle selection by deposit feeders results in incorporation of the selected particles into fecal pellets, and fecal pellet disaggregation completes the cycle. Particles which are more strongly selected or which are incorporated into more robust pellets thus spend more time and reach higher relative concentration in the fecal-pellet compartment. The next level of complexity is achieved by adding burial from the “free” sediment (non-fecal-pellet) compartment. This model predicts that particles which are more strongly selected or incorporated into more robust fecal pellets will have greater residence times in surficial sediments (both pellets and “free” sediments) before they become part of the stratigraphic record, and will therefore achieve higher concentrations in surficial sediments than will less preferred particles. The full flow–sediment–organism system is reached by adding the potential for lateral advection of particles. The probability of such advection is allowed to differ between pellets and “free” sediments. Increasing selection and robustness of fecal pellets then can either increase or decrease relative concentration and residence time of a given particle type in surficial sediments.

The model thus provides a means of explaining differences in stratigraphic patterns among materials deposited simultaneously. It also suggests that deposit-feeder selection may increase the average age (i.e., time since initial deposition) of surficial sediments by maintaining preferred particle types near the surface. Selection may likewise control the texture of surficial sediments—in a manner which is easily confused with purely physical sorting. Parameters which require careful measurement in testing these simple predictions are selectivity by deposit feeders (probability of selection), rate of fecal-pellet breakdown under realistically simulated conditions (probability of pelletal disaggregation), differential erodibilities of pellets versus “free” sediments (relative probabilities of lateral advection), and rates of burial of “free” sediments versus pelletized sediments (probabilities of burial).

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INTRODUCTION

Rhoads' (1974) landmark review consolidates organism—sediment interactions as a distinct, empirical discipline. Theoretical developments in this field have lagged seriously behind empirical studies, however, probably due to the abundant, strong feedbacks among organisms, sediments, and fluid flows. As an example of such strong feedbacks, shallow subtidal sediments are disturbed relatively frequently by episodic flow events (storms), often leading to colonization by dense stands of relatively short-lived, opportunistic tube builders such as *Ampelisca* and *Pygospio* (Rhoads et al., 1978). These dense tube mats not only alter the likelihood of invasion by other biota (Woodin, 1976), but also may cause resistance to erosion and increased rates of deposition of fine materials in the interstices among tubes—much the same way in which a shag carpet protects the floor below from shear forces and allows dirt to escape the lifting and shearing forces of the broom. Flow dynamics thus influence community composition, which in turn affects both sediment structure and the nature of flow (e.g., characteristic roughness lengths) in the bottom boundary layer, demonstrating only one of many complex interactions.

Specific models of various components of the organism—sediment—flow system have been developed previously. For example, Guinasso and Schinck (1975) review efforts aimed at modeling empirically the sediment-mixing effects of organisms, while Levinton and Lopez (1977) and Taghon et al. (1978) suggest two contrasting parameterizations of the deposit-feeding process. Such models have been crucial in determining both the ranges of possible system behaviors and the specific measurements which must be made to test the modeled concepts. None of these available modeling approaches, however, seems to generalize easily to include the effects of flow and consequent sediment transport.

An initial concern was the development of a model to relate the short-term dynamics of the deposit-feeding process with its long-term sedimentological effects. This initial focus was justified by the empirical observation that deposit feeding moves a far greater bulk of marine sediments per unit time than does any other animal activity (Aller, 1977). Deposit feeders process particles at such great rates apparently to strip them of the most easily assimilated part of the ubiquitous organic (including microbial) coating that covers marine sediments (Hargrave and Phillips, 1977). This coating is renewed quickly (Lopez et al., 1977; Lopez and Levinton, 1978).

Three salient features of deposit feeding must be included in any realistic model: (1) deposit feeders usually ingest some types of sediment particles out of proportion to their local abundances (e.g., Whitlatch, 1974; Self and Jumars, 1978); (2) egested sediments are packaged in more or less robust fecal pellets, coils, or mounds (hereafter called pellets, regardless of their specific morphologies); and (3) pellets are, with very few exceptions, deposited by the animal on the sediment surface irrespective of the animal's depth of feeding (e.g., Ronan, 1977). Selective feeding can provide the animal with

the greatest net rate of energy gain (Taghon et al., 1978). Fecal pellets are formed into recognizable morphologies, in turn, apparently to avoid unprofitable reingestion of material that has not yet been recolonized by bacteria (Levinton and Lopez, 1977). The theoretical advantages of depositing fecal material at the sediment surface have not been explored in detail, but the results of the present modeling do provide some insights into the consequences the deposit feeder may experience.

Ongoing observations further suggest that selection in deposit feeders is a stochastic process (Jumars et al., in prep.). Particles are handled in bulk by these microphages (sensu Fauchald and Jumars, 1979); individual particles are not rejected or selected, but particles of differing physical characteristics do show differing probabilities of being picked up, transported to the mouth, and ingested (e.g., Self and Jumars, 1978; Baumfalk, 1979). To reflect the stochastic nature of the deposit-feeding process, a family of Markov models will be developed, starting with a very simple, two-compartment model of deposit feeding alone. Subsequently, the effects of burial (via continued sedimentation) and of hydraulic sediment transport will be added. All of the Markov modeling terminology below comes directly from the excellent elementary text by Kemeny and Snell (1960).

Markov models have been used widely in geology and ecology for the past twenty years, although their use was first suggested by Vistelius (1949) to compare an observed sequence of sedimentary beds with that which would occur from random superposition of beds. Markov modeling has been used by geomorphologists to analyze limestone cave development (Curl, 1959) and to distinguish between regional patterns and local random variations in river profiles (Melton, 1962). Stratigraphers have employed Markov models to identify cyclicity in stratigraphic deposits (viz. Krumbein, 1967; Krumbein and Dacey, 1969; Schwarzacher, 1975). Swift et al. (1972) developed a Markov model to describe textural gradients in deposits across a continental shelf with a source of sediment at the coast and a sink at the shelf break. They imposed the condition that at several steps across the shelf, the probability of grains being deposited was a function of grain size. Thus, even with random diffusion of material on the shelf, a textural gradient would be developed. The major use of Markov models in ecology, reviewed recently by Usher (1979), has been to examine the hypothesis that ecological succession can be considered as a non-random process. In both geological and ecological studies, the focus has been either on the formal similarity of the equilibrium transition matrix with an observed data set or on testing the assumption of stationarity of the transition probabilities. The present aim, by contrast, is to identify states and transitions that deserve further laboratory and field attention and to do so via simple, first-order Markov models.

NO BURIAL AND NO LATERAL ADVECTION

The simplest possible discrete-time, ergodic, Markov model contains two states. Those states are chosen as (1) fecal pellets and (2) "free" sediments

outside fecal pellets. In this case and in all subsequent formulations, sediment particles will be viewed as passing among states. An individual sediment grain may, by being selected (stochastically) for ingestion by a deposit feeder, move from the free state to the pelletal state. Conversely, through the interaction of fluid shear, physical abrasion, microbial degradation of the pelletal binding, and feeding activities of other organisms (including both meiofauna and macrofauna), a pellet may break down into its constituent particles, which then become available for reingestion. In the model, particles are not reingested by the species which produced the pellet until they are recolonized microbially and the pelletal structure has disintegrated (Levinton and Lopez, 1977). This two-compartment model is presented in both matrix and graph theoretic form in Fig.1.

The first-order Markovian assumption that the transition probabilities (i.e., the probabilities of selection and breakdown) depend only on the present state and not on the history of past states that the sediment particles have occupied, appears well met in this application. The additional Markovian assumption that the transition probabilities remain constant over time, may not be satisfied entirely for seasonal marine environments; nonetheless, it allows determination of the potential long-term effects of particular combinations of transition probabilities. This assumption does not imply, for example, that the probability of breakdown for an individual pellet is constant in time. It merely implies that the mean probability of breakdown for a large, random sample of pellets (of varying ages) does not change. The drawbacks of this assumption, and ways of circumventing it, will be treated in the discussion. Finally, implicit in the two-compartment representation is the assumption of horizontal homogeneity. Again, this is a simplifying assumption and can be modified as data or theories permit (e.g., Fig.12).

Figure 2 is a trend surface summarizing the model's steady-state (i.e., long-term) behavior as a function of varying transition probabilities; all

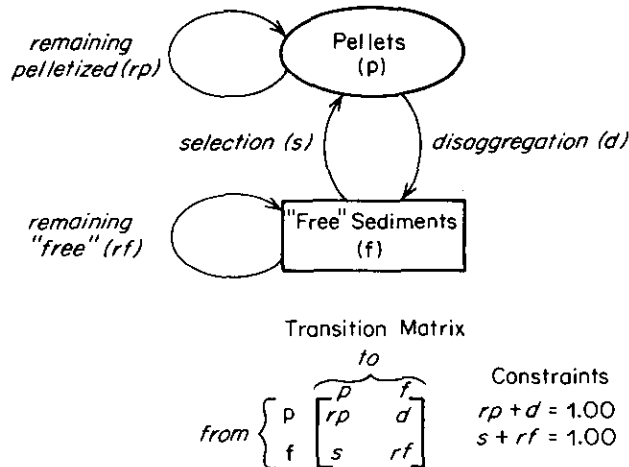


Fig.1. Graphic and matrix summary of the regular, ergodic Markov model of deposit feeding without burial and without advection.

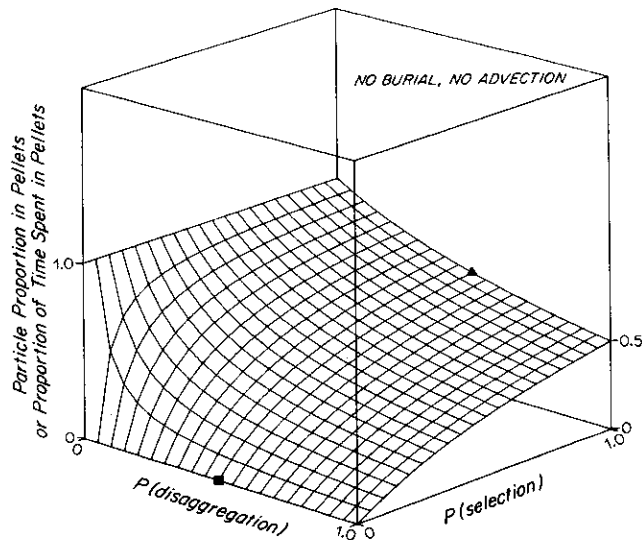


Fig.2. Trend surface summary of the behavior of the regular, ergodic Markov model of deposit feeding. Triangle: P (disaggregation) = 0.50, P (selection) = 1.00, proportion in pellets at any one time or proportion of time spent as pellets = 0.67; Square: P (disaggregation) = 0.50, P (selection) = 0, proportion in pellets at any one time or proportion of time spent as pellets = 0.00 (see text).

possibilities for the two-compartment model are covered by the diagram. It is apparent that the lower the probability of pelletal breakdown and the higher the probability of selection, the higher will be the proportion of material in pelletal form when the inevitable (Kemeny and Snell, 1960, p.70) balance between selection and breakdown rates is reached. Either of two interpretations may be applied to the trend surface; it represents both the proportion of time spent in the pelletal compartment and the proportion of material residing at any one time in the pelletal compartment. The former interpretation has the advantage that it keeps clearly in mind the fact that at steady state material still is passing between compartments.

Additional information may be gleaned by supposing more than one type of particle. Assume one kind of deposit feeder with one constant probability, say 0.50, of fecal-pellet breakdown during the chosen time interval. This time interval now bears the interpretation of the fecal-pellet half-life, and the validity of this analogy with radioactive decay is borne out by the experimental results of Levinton and Lopez (1977). Suppose two kinds of particles, one that is rejected entirely by the deposit feeder (probability of selection, $s = 0.00$, square of Fig.2) and one that is selected as soon as it becomes available ($s = 1.00$, triangle of Fig.2). All the particles of the former type will be found outside the fecal pellets, while two-thirds of the particles of the latter type will be found in the fecal pellets. This partitioning effect has stratigraphic consequences, as will be seen in the subsequent models. Note that the partitioning effect of differential selectivity becomes stronger at lower probabilities of pelletal disaggregation.

BURIAL BUT NO LATERAL ADVECTION

The complexity of the model is increased by adding another "compartment", the buried state. For the sake of simplicity, a particle entering this state is assumed to become part of the stratigraphic record; it can never return to the pelletal or free state. In the terminology of Markov modeling, the buried state is "absorbing," changing the model from an ergodic one to an absorbing Markov chain (Fig.3). The choice of 0.01 as the probability of burial is arbitrary, but this arbitrariness is of no consequence. The model still includes all possibilities because the time step of the model can be interpreted as that interval during which one-hundredth of the material in the free state is buried. Because pellets are deposited on the sediment surface, they have a relatively low probability of being buried intact. Some pellets are found in the stratigraphic record, but burial of pellets is not typical (Ronan, 1977). Again for the sake of simplicity, this probability is set at exactly zero. However, the qualitative behavior of the model does not change so long as the probability of burial from the pelletal state is lower than the probability of burial from the free state.

This implicit assumption of lower probability of burial from the fecal compartment than from the "free" sediment compartment certainly deserves testing in the field and laboratory. If the converse is true, the trend surfaces below will be seriously in error. Tentatively, the assumption appears justified on the basis of past observations of biologically graded bedding, wherein finer sediments are concentrated in surficial deposits (Rhoads and Stanley,

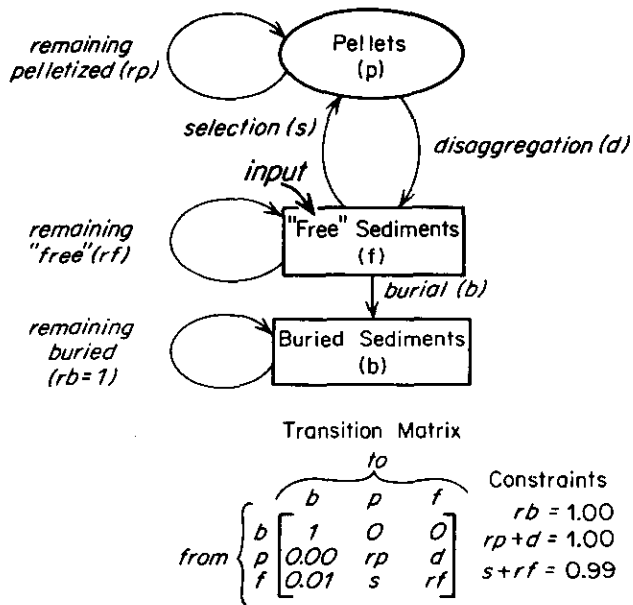


Fig.3. Graphic and canonical matrix summary of the absorbing Markov model of deposit feeding coupled with burial of sediments but excluding lateral advection.

1965; Cadée, 1976; Baumfalk, 1979; Tevesz et al., 1980). All these examples have been attributed to subsurface feeders, but similar phenomena of smaller vertical scale might be predicted for surface deposit feeders as well. The latter feed on variable thicknesses of surficial sediments and deposit their fecal material on the surface, usually outside their individual feeding areas (personal observations). Particles which are never ingested and thus never enter fecal pellets will not be returned to the interface via feeding activities and thus should show the shortest residence times at the interface. The critical test of the assumption, however, is whether the most highly preferred particle type has the greatest residence time at and near the interface.

The behavior of the model is again portrayed as a trend surface (Fig.4). Although it also bears two interpretations, they are not the same as for the ergodic model of Fig.2. One interpretation of the trend surface is as the average residence time (number of time units in either pelletal or free state) before burial of a particle initially deposited into the free sediment compartment. The other interpretation is as the steady-state standing stock of particles achieved in the sum of the non-absorbing states (pellets plus free sediments), when one unit of particles is introduced (via a constant deposition rate) into the free sediment compartment during each time step. A particularly lucid introduction to the calculation of such parameters of absorbing Markov models is given by Roberts (1976).

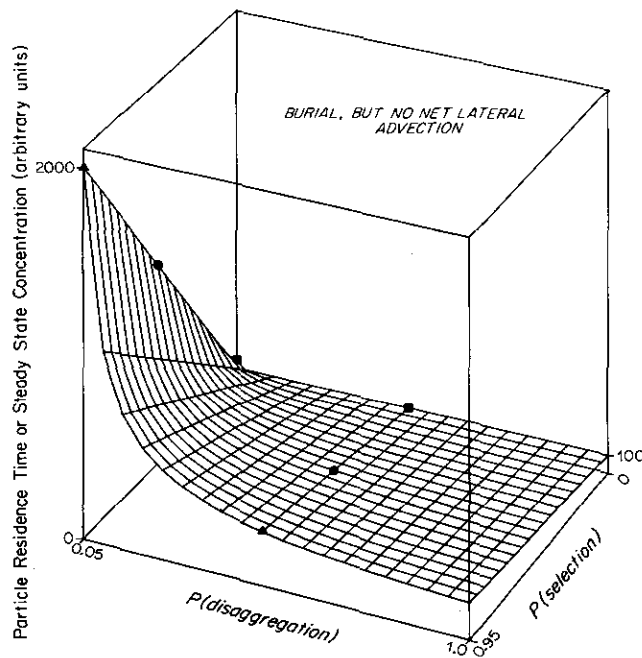


Fig.4. Trend surface of the behavior of the absorbing Markov model of deposit feeding coupled with burial or sediments but excluding lateral advection. Squares, circles, and triangles refer to Figs.5 and 6.

It is apparent that the probabilities both of particle selection and of fecal-pellet breakdown bear heavily upon the residence times of materials in surficial sediments (including both pelletal and free compartments) before burial. Particle types that are selected strongly and are incorporated into robust fecal pellets will become concentrated in surficial sediments relative to particles that either are selected to a lesser degree (or selected against) or are incorporated into less robust pellets. Deposit feeders thus can control the composition of the surficial sediments exposed to erosive forces, as discussed more fully below. Even in the absence of physical transport processes, however, dramatic stratigraphic effects are possible.

In the presence of robust fecal pellets ($d = 0.05$ during the interval in which 0.01 of the free sediments are buried), particle selection by deposit feeders can have especially large effects on stratigraphy. Fig.5 illustrates how the stratigraphic record would appear under three different probabilities of selection, given an initial input (at time = 0) of one unit of identifiable material (e.g., a volcanic ash or microtektite fall) into the free sediment compartment. The plot is generated by monitoring the proportion of this initial pulse moving into the buried state at each time interval. Fig.6 shows that, although reduced in magnitude, the effects of varying selectivity are similar at lower probabilities of pelletal disaggregation. The potential stratigraphic implications of Figs.5 and 6 can be visualized by considering a simultaneous input to the free sediments of three different types of particles which differ in the degrees to which they are selected by deposit feeders. Pulses of conservative particulate tracers arriving at the bed simultaneously thus can show markedly differing profiles.

BURIAL AND LATERAL ADVECTION

The next degree of complexity and realism is added by admitting lateral transport out of the local control volume of interest (Fig.7). To allow ready comparison with earlier results, the probability of burial is left unchanged ($b = 0.01$). Lateral advection is added as the probability of transport to another absorbing state (the advected state). Fecal pellets are allowed to be more or less erodible than free sediments by fixing the probability of erosion of the free sediments at 0.1 (ten times the probability of burial) and allowing the probability of erosion of fecal pellets to vary from 0.00 to 0.25. Again for simplicity of illustration (Fig.8), the probability of pellet disaggregation is fixed at 0.50. During the half-life of a fecal pellet, then, 1% of the free sediment is buried and 10% are advected away via hydraulic sediment transport. A much wider range of variation in these parameters has been allowed in additional model runs, but the qualitative behavior of the system remains unchanged (so long as $af > b$, cf. Fig.7).

The trend surface of Fig.8 bears the same interpretation as does that of Fig.4. Residence time again refers to time spent in pelletal or free form before absorption into either the buried or the advected state. Selection can now act, however, either to increase or decrease that residence time. If sedi-

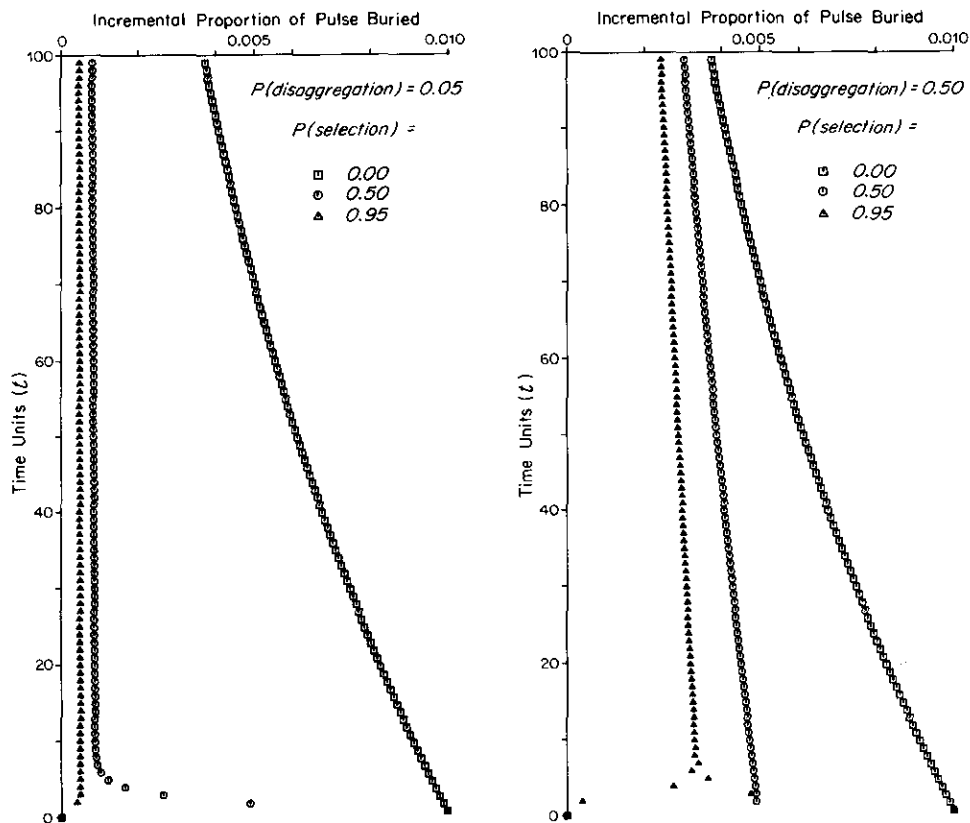


Fig. 5. Simulated stratigraphic records from the absorbing Markov model of deposit feeding without lateral advection, given a pulse of input at $t = 0$ into the "free" sediments and showing the effects of varying selection in the presence of robust fecal pellets. Squares, circles, and triangles correspond with Fig. 4.

Fig. 6. Simulated stratigraphic records, given a pulse of input at $t = 0$ into the "free" sediments, from the absorbing Markov model of deposit feeding without lateral advection, showing the effects of varying selection in the presence of less robust fecal pellets than modeled in Fig. 5. Squares, circles, and triangles correspond with Fig. 4.

ments are more readily lost (laterally advected away) from the pelletal state than they are (via the sum of advection and burial probabilities) from the free state, then increasing selection will act to decrease residence time. If pelletized sediments, on the other hand, are less likely to be absorbed or lost from the system than are the free sediments, then increasing selection will act to increase residence time. Given a constant input rate of particles, longer residence time again (cf. Fig. 4) equates with higher steady-state standing stock in pellets plus free sediments.

If pellets are eroded more easily than are free sediments, increasing selection will act to reduce the proportion of material buried at the site of interest (Fig. 9). Such an effect easily could be mistaken for purely physical winnowing of surficial sediments. If pellets are not at all erodible (probability of lateral

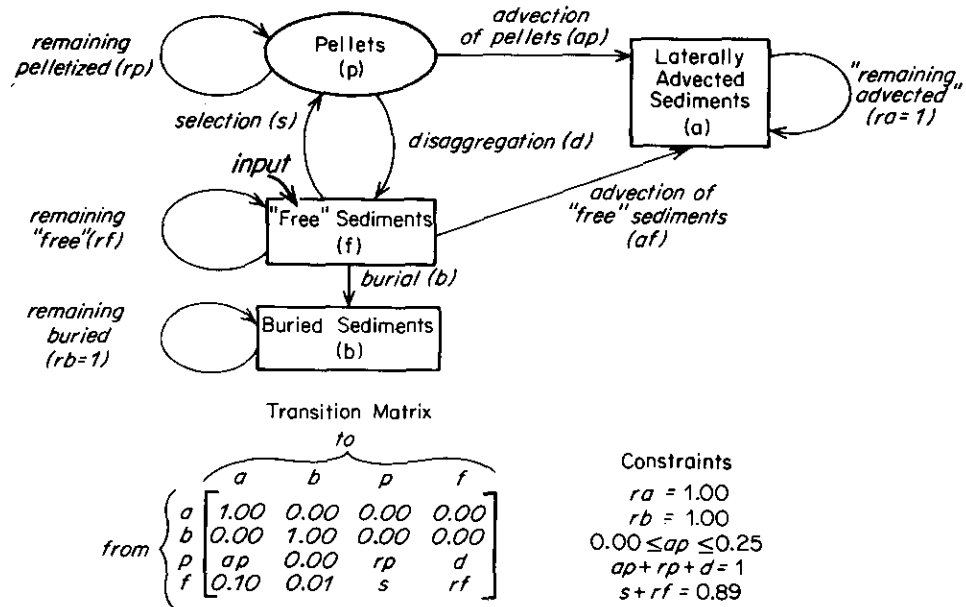


Fig.7. Graphic and canonical matrix summary of the absorbing Markov model of deposit feeding coupled with both burial of sediments and lateral advection.

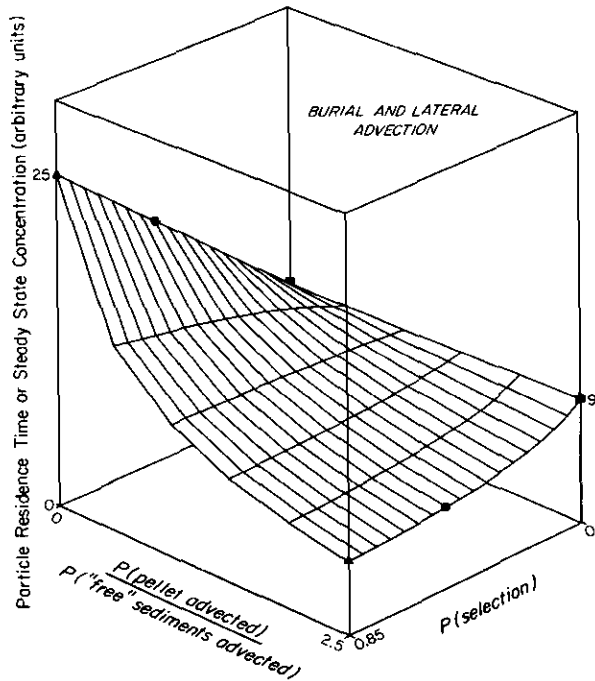


Fig.8. Trend surface of the behavior of the absorbing Markov model of deposit feeding coupled with burial of sediments and lateral advection. Probability of pelletal disaggregation set at 0.50. Squares, circles, and triangles refer to Figs.9 and 10.

transport = 0.00), then increasing selection will not alter the total amount of material buried locally (areas to the left of all histograms or “curves” of Fig.10 being equal) but will act to increase the upward skew of the depth distribution of the buried conservative tracer. Along the isoline where the probability of lateral transport of the pellets exactly equals the sum of the probabilities of burial and advection from the free compartment (= 0.11), selection has no effect whatsoever on residence time but still influences the relative proportions of the tracer lost via burial versus advection. Admitting the possibility of differential lateral transport of pellets versus free sediments thus adds substantially to the diversity of effects that selectivity and pelletal breakdown can have on the stratigraphic record.

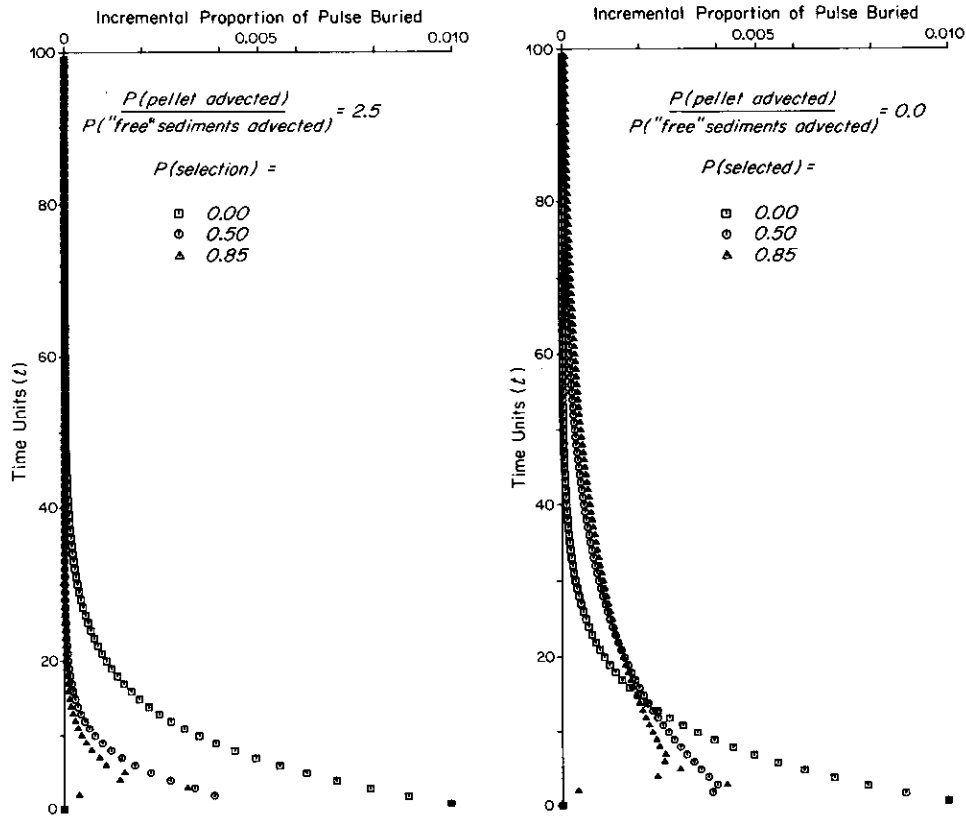


Fig.9. Simulated stratigraphic records from the absorbing Markov model of deposit feeding with lateral advection, given a pulse of input at $t = 0$ into the “free” sediments and showing the effects of varying selectivity given relatively easily erodible fecal pellets. Squares, circles, and triangles correspond with Fig.8.

Fig.10. Simulated stratigraphic records from the absorbing Markov model of deposit feeding with lateral advection, given a pulse of input at $t = 0$ into the “free” sediments and showing the effects of varying selectivity given fecal pellets of relatively low erodibility. Squares, circles, and triangles correspond with Fig.8.

DISCUSSION AND CONCLUSIONS

The simple ergodic model without burial and without advection is easy to evaluate. It is homologous with the infinite series model of deposit feeding developed by Levinton and Lopez (1977). Fig.2 thus provides a convenient summary of the behavior of Levinton and Lopez's (1977) model over its entire domain of parameter values. Their (and thus the present) model displays good fit to the standing stocks of fecal pellets observed at fixed densities of the deposit-feeding snails, *Hydrobia minuta* and *H. ventrosa*. The good fit provides strong support for the underlying Markovian assumptions of the present model. Selectivity (i.e., particle-type-specific probabilities of selection) of a deposit feeder would be particularly easy to measure under this (Fig.2) equilibrium in which pelletization is balanced exactly by pelletal breakdown. Given that the half-life of fecal pellets were known, probabilities of selection could then be estimated from the observed proportions of a particle type in pellets versus in free sediments.

The model with burial but without lateral advection seems especially germane to deep-sea stratigraphic interpretation. Its application can be generalized further to include situations with lateral advection but with inputs from lateral transport exactly balancing outputs — a fairly realistic assumption for one small, central section of an expansive habitat. Given the partitioning effects of differential selection (Figs.5 and 6), it should not be surprising that different stratigraphic markers show different apparent sedimentation and "bioturbation" rates. Such differential behaviors of different types of particles used as stratigraphic markers in the past (e.g., Berger and Johnson, 1978) have been attributed to differential mixing in eddy diffusive models of "bioturbation". Particle selection seems a biologically more realistic alternative explanation. It also (cf. Fig.4) becomes an alternative to core-top loss or to deep mixing for explaining anomalously great ages of surficial sediments.

As a simple example of potential vertical structure produced by deposit feeding, a two-layer (before burial) model is presented (Fig.11) in place of the one-layer model used above. Because deeper-dwelling deposit feeders generally are less abundant (e.g., Jumars, 1978) and appear to be less selective than do surface and near-surface deposit feeders (unpublished observations), their probability of selection is made lower than the probability assigned to the surface and near-surface deposit feeders. Besides showing the potential of multiple-layer models for explaining vertical structure in the concentration of particular sedimentary constituents, this model also shows the strong interaction to be expected between surface and subsurface deposit-feeder selectivity.

Passing to the model with both burial and horizontal advection, probably most relevant to the continental-shelf situation, one at first seems to note accord with the conventional wisdom that, in regions of extensive physical transport, organism effects are limited: compare the range of potential residence times in Fig.4 versus Fig.8. Again, however, a very important feed-

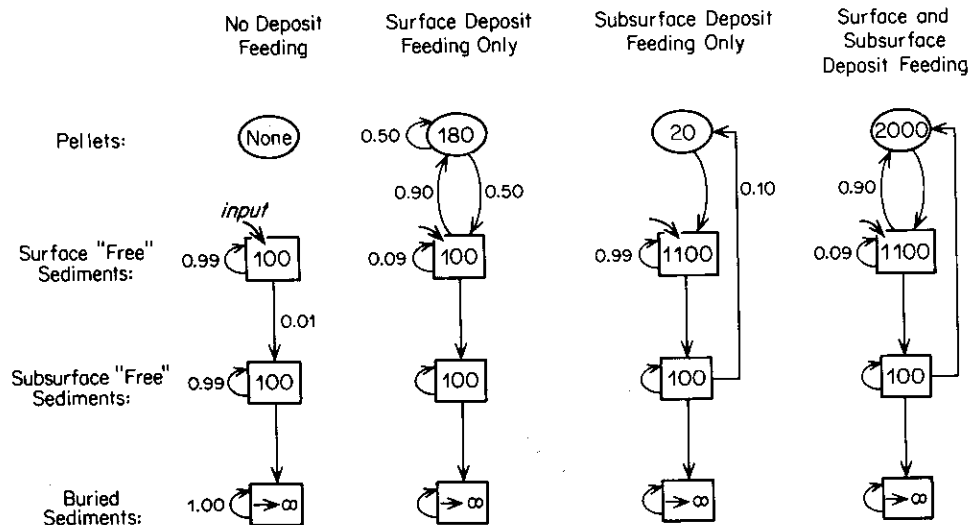
Particle Residence Times or Steady State ($t \rightarrow \infty$) Concentrations

Fig.11. Example of potential effects of deposit feeding on vertical structure of sediments in a simple two-layer (surface and subsurface "free" sediments) model. Reading from left to right, only transition probabilities that change are indicated. Note the strong interaction between surface and subsurface deposit feeding.

back is hidden. Deposit feeders tend to select smaller particles and particles of lower specific gravity (Taghon et al., 1978; Self and Jumars, 1978; Jumars et al., in prep.) — precisely those kinds of particles that are most readily transported hydraulically. As per the arguments outlined above, organism selectivity will concentrate such particles in surficial deposits where they are most easily available for transport. That this effect occurs in reality as well as in the model is borne out by the observations of Rhoads and Stanley (1965) and Cadée (1976); deposit feeders produce both biogenously graded-bedding and subsurface lag deposits of rejected material. That, in turn, fecal pellets can show transportabilities (cf. Fig.8) different from those of their constituent sediments is demonstrated by several field studies (Pryor, 1975; Risk and Moffat, 1977; McCall, 1979; Anderson, 1980) as well as by laboratory flume experiments (Nowell et al., 1981).

A slight variant (Fig.12) of the earlier model demonstrates the possible lateral effects of deposit-feeder activity more clearly. Again because deposit feeders tend to select smaller and less dense (in terms of specific gravity) particles, the biological role in the downstream hydraulic fining of deposits (such as that seen by Nittrouer, 1978, in the midshelf silts emanating from the Columbia River) may be substantial.

A wide variety of Markov models can be generated to explore the potential impacts of the deposit-feeding process on sediments. All the models treated here can be (and were, with the exception of the computer-drawn summary figures) explored with no more than a desk-top calculator capable

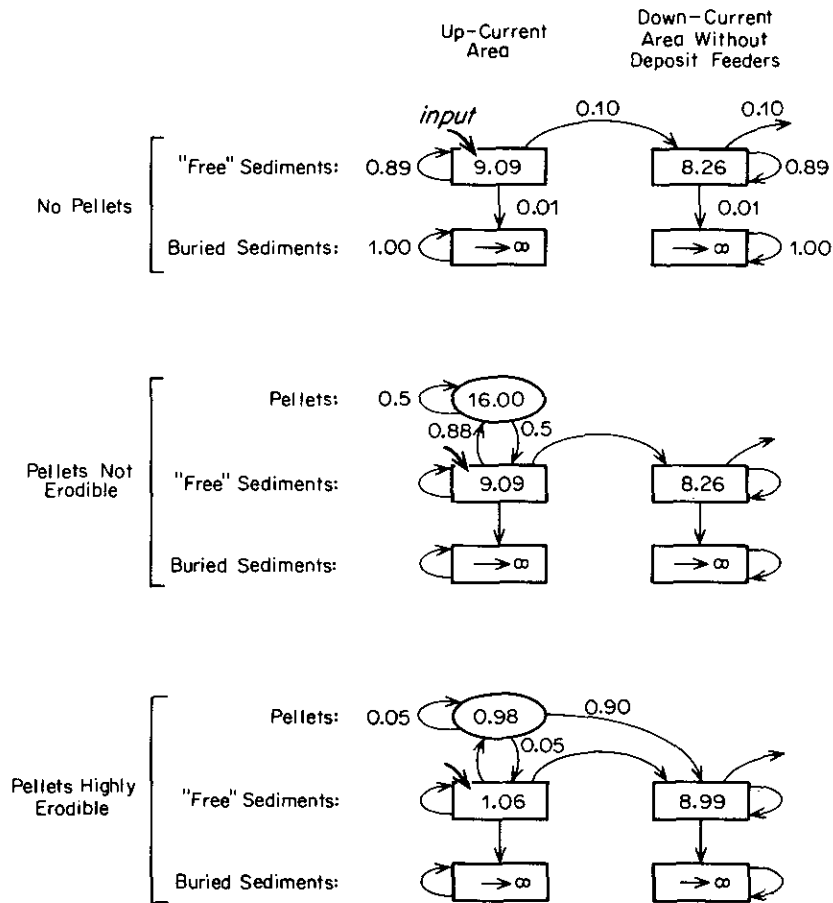
Particle Residence Times or Steady State ($t \rightarrow \infty$) Concentrations

Fig.12. Example of potential effects of deposit feeding on horizontal structure of sediments. Reading from top to bottom, only transition probabilities that change are indicated. Note the strong effect of relative erodibilities of pellets versus "free" sediments.

of inverting a three-by-three matrix. The approach generalizes easily, via widely available computer programs for matrix manipulation, to more complex systems — for example, with more compartments vertically or horizontally or with additional types of fecal pellets, each with its own characteristic probability of disaggregation.

Caution must be exercised, however, in detailed interpretations based on such simple models. The oscillatory behavior apparent in the lower (small t) parts of some of the "stratigraphic records" of Figs.5, 6, 9, and 10, especially when the probability of selection is high (triangles), is a consequence of the discrete-time nature of the model and would probably be "smoothed" in nature. At very high selection probabilities, especially when coupled with high disaggregation probabilities, the Markov models initially verge on cyclic

behavior, with the bulk of the particles alternating between pelletal and "free" sediment compartments. The oscillation in the proportion of the pulse buried with time occurs because burial takes place only from the "free" sediment compartment. Natural variability in selection and disaggregation probabilities would act to damp this initial oscillation much more quickly by spreading the particles more equitably among the compartments.

It should also be mentioned that the resemblance of Figs. 5, 6, 9, and 10 — when the probability of selection equals zero (squares in the figures) — to simulated stratigraphy from eddy diffusive models of "bioturbation" at high mixing rates (e.g., Guinasso and Schinck, 1975, fig. 1, $G = 3$) is more than circumstantial. An implicit assumption of the Markov models is homogeneity of the contents within each compartment, and one way to achieve such homogeneity is to have rapid mixing within compartments. The extent of departure from the simulated stratigraphy with zero probability of selection then becomes a measure of the degree to which (selective) deposit feeding has altered the results expected from a simple eddy diffusive mixing model. The potential extent of this departure is sobering.

Attention to the broader trends of Figs. 4 and 8 further reveals that close attention needs to be paid to obtaining realistic measures of breakdown rates of fecal pellets; the models are especially sensitive to the probability of pelletal breakdown. To date, pelletal breakdown rates have been measured only under the extremes of standing water (e.g., Levinton and Lopez, 1977) or of severe physical agitation (e.g., Risk and Moffat, 1977). Breakdown rates under realistically simulated field conditions are lacking.

The importance of pelletal breakdown rates also draws attention to even more robust biogenous structures, agglutinated tubes and tests. For those animals that carry their tubes and tests upward with ambient sedimentation (e.g., many agglutinating foraminiferans and the polychaetes *Nothria conchilega* and *Owenia fusiformis*) rather than allowing a disused lower portion to decay and become part of the deposit, one can simply substitute the label "tubes" or "tests" for pellets in all the previous models. In any case, tube building will influence the probability of burial of the sorts of materials that are selected in tube construction; over half of the sediments in the upper few centimeters of some regions are bound into animal tubes (Featherstone and Risk, 1977).

The "short memory" required of first-order Markov processes seems well substantiated in all these applications. While the additional assumption of invariant transition probabilities may hold for some (e.g., deep-sea or tropical) environments, it is unrealistic for seasonal habitats. It may be especially grossly violated if, say, physical advection is dominated by occasional winter storms. This situation is decidedly non-Markovian and is probably best handled by simulating the pattern of time-varying transition probabilities in an analog model. More gradual seasonal variation in deposit feeder activity (e.g., Nichols, 1974) can be treated similarly. While such analog models with time-varying transition probabilities can be generated relatively easily, they have the disadvantage that analytical solutions (such as those of Figs. 2, 4, 8, 11,

and 12) for the long-term behavior of the system are not, in general, possible. As R.C. Aller (personal communication) has suggested, a continuous-time, differential equation model may have decided advantages in the time-varying case.

Even without this added degree of realism, however, the simple Markov models developed above evoke stratigraphic effects which might otherwise be considered enigmatic or anomalous. The models also identify a number of parameters of the flow—sediment—organism system which require more careful measurement in the future. Some such family of simple models capable of explicitly incorporating selective feeding is necessary to address potential biological impacts on the stratigraphic record. Selective deposit feeding may either counter or amplify the apparent eddy diffusive mixing effects produced by other animal activities.

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REFERENCES

- Aller, R.C., 1977. The Influence of Macrobenthos on Chemical Diagenesis of Marine Sediments. Thesis, Yale University, New Haven, Conn., 600 pp.
- Anderson, F.E., 1980. The variation in suspended-sediment and water properties in the flood-water front traversing the tidal flat. *Estuaries*, 3: 28–37.
- Baumfalk, Y.A., 1979. Heterogeneous grain-size distribution in tidal-flat sediment caused by bioturbation activity of *Arenicola marina* (Polychaeta). *Neth. J. Sea Res.*, 13: 428–440.
- Berger, W.H. and Johnson, R.F., 1978. On the thickness and the ¹⁴C age of the mixed layer in deep-sea carbonates. *Earth Planet. Sci. Lett.*, 41: 223–227.
- Cadée, G.C., 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea Res.*, 10: 440–460.
- Curl, R.L., 1959. Stochastic models of cavern development. *Bull. Geol. Soc. Am.*, 70: 1802.
- Fauchald, K. and Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.*, 17: 193–284.
- Featherstone, R.P. and Risk, M.J., 1977. Effect of tube-building polychaetes on intertidal sediments of the Minas Basin, Bay of Fundy. *J. Sediment. Petrol.*, 47: 446–450.
- Guinasso, N.L., Jr. and Schinck, D.R., 1975. Quantitative estimates of biological mixing rates in abyssal sediments. *J. Geophys. Res.*, 80: 3032–3043.
- Hargrave, B.T. and Phillips, G.A., 1977. Oxygen uptake of microbial communities on solid surfaces. In: J. Cairns, Jr. (Editor), *Aquatic Microbial Communities*. Garland Publ., New York, N.Y., pp.545–587.
- Jumars, P.A., 1978. Spatial autocorrelation with RUM (Remote Underwater Manipulator): vertical and horizontal structure of a bathyal benthic community. *Deep-Sea Res.*, 25: 589–604.

- Jumars, P.A., Self, R.F.L. and Nowell, A.R.M., in prep. Mechanics of tentaculate deposit feeding.
- Kemeny, J.G. and Snell, J.L., 1960. Finite Markov Chains. D. Van Nostrand, Princeton, N.J., 210 pp.
- Krumbein, W.C., 1967. FORTRAN IV programs for Markov chain experiments in geology. Kans. Geol. Surv. Comput. Contrib., 13: 1-38.
- Krumbein, W.C. and Dacey, M.C., 1969. Markov chains and embedded Markov chains in geology. J. Int. Assoc. Math. Geol., 1: 79-96.
- Levinton, J.S. and Lopez, G.R., 1977. A model of renewable resources and limitation of deposit-feeding benthic populations. *Oecologia*, 31: 177-190.
- Lopez, G.R. and Levinton, J.S., 1978. The availability of microorganisms attached to sediment particles as food for *Hydrobia ventrosa* Montagu (Gastropoda: Prosobranchia). *Oecologia*, 32: 263-275.
- Lopez, G.R., Levinton, J.S. and Slobodkin, L.B., 1977. The effect of grazing by the detritivore *Orchestia grillus* on *Spartina* litter and its associated microbial community. *Oecologia*, 30: 111-127.
- McCall, P.L., 1979. The effects of deposit-feeding oligochaetes on particle size and settling velocity of Lake Erie sediments. *J. Sediment. Petrol.*, 49: 813-818.
- Melton, M.A., 1962. Methods for measuring the effects of environmental factors on channel properties. *J. Geophys. Res.*, 67: 1485-1490.
- Nichols, F.H., 1974. Sediment turnover by a deposit-feeding polychaete. *Limnol. Oceanogr.*, 19: 945-950.
- Nittrouer, C.A., 1978. The Process of Detrital Sediment Accumulation in a Continental Shelf Environment: An Examination of the Washington Shelf. Thesis, Univ. Washington, Seattle, Wash., 243 pp.
- Nowell, A.R.M., Jumars, P.A. and Eckman, J.E., 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.*, 42: 133-153 (this volume).
- Pryor, W.A., 1975. Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments. *Geol. Soc. Am. Bull.*, 86: 1244-1254.
- Rhoads, D.C., 1974. Organism-sediment relations on the muddy sea floor. *Oceanogr. Mar. Biol. Annu. Rev.*, 12: 263-300.
- Rhoads, D.C. and Stanley, D.J., 1965. Biogenic graded bedding. *J. Sediment. Petrol.*, 35: 956-963.
- Rhoads, D.C., McCall, P.L. and Yingst, J.Y., 1978. Disturbance and production on the estuarine seafloor. *Am. Sci.*, 66: 577-586.
- Risk, M.J. and Moffat, J.S., 1977. Sedimentological significance of fecal pellets of *Macoma balthica* in the Minas Basin. *J. Sediment. Petrol.*, 47: 1425-1436.
- Roberts, F.S., 1976. Discrete Mathematical Models. Prentice-Hall, Englewood Cliffs, N.J., 559 pp.
- Ronan, T.E., Jr., 1977. Formation and paleontologic recognition of structures caused by marine annelids. *Paleobiology*, 3: 389-403.
- Schwarzacher, W., 1975. Sedimentation Models and Quantitative Stratigraphy (Developments in Sedimentology, 19). Elsevier, Amsterdam, 384 pp.
- Self, R.F.L. and Jumars, P.A., 1978. New resource axes for deposit feeders? *J. Mar. Res.*, 36: 627-641.
- Swift, D.J.P., Ludwick, J.C. and Boehmer, W.R., 1972. Shelf sediment transport: a probability model. In: D.J.P. Swift, D.B. Duane, and O.H. Pilkey, (Editors), Shelf Sediment Transport-Process and Pattern. Dowden, Hutchinson and Ross, Stroudsburg, Pa., pp. 195-223.
- Taghon, G.L., Self, R.F.L. and Jumars, P.A., 1978. Predicting particle selection by deposit feeders: a model and its implications. *Limnol. Oceanogr.*, 23: 752-759.
- Tevesz, M.J.S., Soster, F.M. and McCall, P.L., 1980. The effects of size-selective feeding by oligochaetes on the physical properties of river sediments. *J. Sediment. Petrol.*, 50: 561-568.
- Usher, M.B., 1979. Markovian approaches to ecological succession. *J. Anim. Ecol.*, 48: 413-436.

- Vistelius, A.B., 1949. On the question of the mechanism of the formation of strata. Dokl. Akad. Nauk. S.S.S.R., 65: 191-194.
- Whitlatch, R.B., 1974. Food-resource partitioning in the deposit feeding polychaete *Pectinaria gouldii*. Biol. Bull., 147(1): 227-235.
- Woodin, S.A., 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. Mar. Res., 34(1): 25-41.