BIOTURBATION

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Assignment

REQUIRED READING

Boudreau, B. P. 1998. Mean mixed depth of sediments: the wherefore and the why. Limnol. Oceanogr. *43*: 524-526. *[Mixed layer depth has an mean depth of 9.8 cm [documented in* **Boudreau 1994***; BPB's model predicts 9.7 cm.]*

Cammen, L. M. 1980. Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. Oecologia (Berlin) *44*: 303-310.

Shull, D. H. 2001. Transition-matrix model of bioturbation and radionuclide digenesis. Limnol. Oceanogr. *46*: 905-916. *[Narragansett Bay Th-234 & Pb-210 profiles modeled, indicating food caching by maldanids.]*

RECOMMENDED

Boudreau, B. P. 1994. Is burial velocity a master parameter for bioturbation? Geochim. Cosmochim. Acta. *58*: 1243-1249. *[$D_b \propto$ flux of organic matter; flux of organic matter $\propto$ burial velocity. Mixing depth is 9.8±4.5cm]*

Gallagher, E. D. and K. K. Keay. 1998. Organism-sediment-contaminant interactions in Boston Harbor. Pp. 89-132 in K. D. Stolzenbach and E. E. Adams, eds., Contaminated sediments in Boston harbor. MIT Sea Grant Publication 98-1. *[Expanded version of this article available as* ***html*** *or* ***pdf*** *on Gallagher's web page*Jumars, P. A. 1993b. Concepts in biological oceanography. Oxford University Press, New York & Oxford. 348 pp. *[Please read Chapters 17 & 18, Stratigraphy & Diagenesis]*

Matisoff, G. 1982. Mathematical models of bioturbation. Pp. 289-330 *in* P. L. McCall and M. J. S. Tevesz, eds., Animal-sediment relations. Plenum Press, New York.

Miller, C. B. 2004. Biological Oceanography. Pp. 287-293.

Rhoads, D. C. 1974. Organism-sediment relations on the muddy sea floor. Oceanogr. Mar. Biol. Ann. Rev. *12*: 263-300. *[The classic review.]*

Rice, D. L. 1986. Early diagenesis in bioadvective sediments: relationships between the diagenesis of beryllium-7, sediment reworking rates, and the abundance of conveyor-belt deposit feeders. J. Mar. Res. *44*: 149-184.{**7**, **9**, **10**, **12**, **15**, **24**}

Shull, D. H. and M. Yasuda. 2001. Size-selective downward particle transport by cirratulid polychaetes. J. Mar. Res. *59*: 453-473. [**http://www.ac.wwu.edu/~shulld/JMR2001.pdf**]

Solan, M., B. J. Cardinale, A. L. Downing, K. A. M. Engelhardt, J. L. Ruesink, and D. S. Srivastava. 2004. Extinction and Ecosystem Function in the Marine Benthos. Science *306*: 1177-1180.*["Here we use data from marine invertebrate communities to parameterize models that predict how extinctions will affect sediment bioturbation, a process vital to the persistence of aquatic communities. We show that species extinction is generally expected to reduce bioturbation, but the magnitude of reduction depends on how the functional traits of individual species covary with their risk of extinction."]*.{?}

Comments on Bioturbation

In his last book, **Charles Darwin (1896)** explained a process well known to farmers, "objects of all kinds, left on the surface of pasture-land, after a time disappear, or, as they say, work themselves downward." Darwin argued that earthworm feeding caused this movement of particles. Earthworms eat at depth, deposit castings near the surface, and bury inedible large particles under their castings. Darwin estimated the number and weight of earthworms, their feeding rates, the rate of formation of new topsoil, and the rate of burial of stones and chalk layers that he had added. Darwin had proposed and tested the first model of animal-sediment reworking.

The modern term for particle reworking by animals is bioturbation. There are several key reviews of bioturbation. **Rhoads' (1974)** monograph laid the foundation for future work on animal-sediment interactions. **Aller (1982)** and **Fisher (1982)** reviewed and expanded the quantitative framework for analyzing both bioturbation and bioirrigation, the movement of porewater by animals. **Matisoff (1982)** summarized many field studies and models of bioturbation. **Thayer (1983)** reviewed the evolution of bioturbation. Boudreau (**1986a** & **1986b**), **Robbins (1986)**, and **Boudreau & Imboden (1987)** rigorously analyzed diffusive defined bioturbation models and extended these models to explain the effects of conveyor-belt feeding. **Rice & Rhoads (1989)** modeled the effects of bioturbation on organic matter profiles. **Wheatcroft *et al.* (1990)** provided a mechanistic explanation for the particle diffusion coefficient and showed why large organisms usually control particle-mixing rates. **Jumars (1993b)** discussed a variety of effects of bioturbation on stratigraphy. Virtually all of these papers stress the need for more field research, especially on the animals responsible for bioturbation. **Wheatcroft *et al.* (1994), Blair *et al.* (1996)** and Levin et al. (**1997**, **1999**), **Shull (2000)**, **Shull & Yasuda (2001)**, and **Josefson et al. (2002)** accepted this challenge and their results are startling. Food caching, believed until recently to be a minor feeding mode, is widespread from the intertidal to the deep sea and has major effects on the movement of labile organic matter and radioactive tracers in sediment.

THE ORGANISMS RESPONSIBLE AND HOW THEY FEED.

Animal activities can move particles in a number of ways. **Robbins (1986, p. 8542)** describes this well:

> *"A close encounter with the near-surface region of well-oxygenated marine and freshwater sediments reveals a scene of intense activity: organisms of many forms and sizes diving, ploughing, channeling establishing burrows, feeding, irrigating, metabolizing, respiring, defecating, reproducing, preying on their neighbors, dying and disintegrating."*

The biomass and abundance of the infauna are usually poor predictors of particle-mixing rates. Animals that feed at depth will have much greater effects than organisms that feed and defecate at the surface. **Wheatcroft *et al.* (1990)** use dimensional analysis to argue that a few large subsurface deposit feeders can affect sediment movement far in excess of their biomass or numerical contribution to the community. Feeding mode information is needed to convert animal abundance and biomass data to geochemical effects.

Polychaete worms usually constitute the largest portion of individuals, biomass, and species richness in benthic communities. **Fauchald & Jumars' (1979)** in 'The Diet of Worms' classify feeding modes by food gathering apparatus and motility. This classification was not designed to predict geochemical effects. In particular, it doesn't distinguish among a variety of subsurface deposit-feeding modes. **Boudreau (1986a)** reviewed classifications that attempted to remedy this situation. I have extended some of Boudreau's classifications in **Table 1.**

Local vs. nonlocal feeding

The major split among feeding types is whether feeding activities move particles in accord with local (biodiffusive) or non-local (bioadvective) models. **Boudreau (1986b)** defines nonlocal mixing as animal activities that displaced particles distances greater than the scale over which the concentration of tracer changes substantially. I call this tracer decay depth l_c in **Table 1**. If nonlocal mixing is occurring, the Goldberg & Koide's diffusive model of bioturbation is inappropriate. That model (**Boudreau 1986a**, Equ. 44) is:

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial z}\left[D_b(z)\frac{\partial C}{\partial z} - wC \right] - \lambda C. \tag{1}$$

where, C is the concentration of a tracer, w is the sediment accumulation rate [cm/s], λ is the decay constant [s^{-1}] (=ln(2) / half life), and D_b is the bioturbation coefficient [cm^2/s]. This equation has been applied to radioisotope profiles in dozens of different environments using a variety of radioisotopes. Wallace and Gschwend in the Boston Harbor SWEX study used ^{210}Pb and ^{234}Th., natural radioisotopes with half lives of 24.2 days and 21 years, respectively. It is usually assumed that bioturbation acts only within a bioturbation zone near the sediment-water interface.

Table 1. A classification of animal activities that affect radioisotope profiles. The major break separates biodiffusive and non-local mixing. The distinction between local and non-local is set by the distance taken for the tracer to decay substantially — a function of decay, sediment accumulation, and bioturbation rates. This distance, which can range from millimeters to many centimeters, will be called l_c. A food cache is a temporary subsurface reservoir for food or feces.

Mixing Type	**Descriptive Name**	**Depth of:**			**Particle displacement** $l_{di} = \lvert z_i - z_d \rvert.$ $l_{ci} = \lvert z_c - z_i \rvert.$ $l_{dc} = \lvert z_c - z_d \rvert.$ $l_b = \max(l_{di}, l_{ci}, l_{dc}).$
		Ingestion z_i	**Defecation z_d**	**Food cache z_c**	
Local	Suspension feeders	Surface	Surface	—	$l_b < l_c$
	Surface deposit feeders	Surface	Surface	—	
	Small subsurface deposit feeders	Subsurface	Surface	—	
		Subsurface	Subsurface	—	
Non-local	Conveyor-belt feeders	Subsurface	Surface	—	$l_b > l_c$
	Hoers	Surface and subsurface	Surface	—	
	Miners	Relict Subsurface organic matter	Surface	—	
			Subsurface	—	
	Funnel feeders	Subsurface on rapidly subducted surface material	Surface	—	
	Subsurface deposit feeders	Subsurface	Subsurface	—	
	Suspension feeders	Surface	Subsurface	—	

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		Ingestion z_i	**Defecation** z_d	**Food cache** z_c	
		Surface to cache	Cache to Surface	Yes	
	Food caching deposit feeders	Surface to Cache	Cache to Surface	Yes	
		Surface to Cache	Cache to Subsurface	Yes	
	Reverse conveyor belt	Surface	Subsurface	No	

Equation 1 is written to permit D_b to vary within the bioturbation zone. **Boudreau (1986a)** analyzed the effects of depth variation in D_b on radioisotope profiles. So long as mixing is local, and D_b doesn't vary too rapidly in the mixed layer (L_b), then constant and depth-varying D_b models produce nearly identical profiles. With a constant D_b within a bioturbation zone (L_b) and assuming steady state, Equ 1 converts to:

$$\begin{aligned} \frac{\partial C}{\partial t} &= 0 = D_b \frac{d^2 C}{dz^2} - w \frac{dC}{dz} - \lambda\, C \ (for\ 0 < z < L_b). \\ \frac{dC}{dt} &= 0 = - w \frac{dC}{dz} - \lambda C \quad (for\ z > L_b). \end{aligned} \tag{2}$$

Jumars (1993b) notes that the bioturbation depth or mixing zone (L_b) is roughly 10 centimeters in both shallow water and the deep sea. **Boudreau (1998)** created a quantitative model that predicts that the bioturbation depth should be roughly 10 cm from shallow water to the deep sea. His model is based on the concept that subsurface deposit feeders will move sediment so long as there is labile food associated with the sediment particles. In shallow water, there is a higher food flux and higher sedimentation but the food is quickly degraded. At about 10 cm, there is little food left. In deep water, the food flux and sedimentation rates are drastically lower, but the food is more difficult to metabolize. **Santschi *et al.*'s (1990)** review found that particle mixing coefficients (D_b) range from 10^{-9} $cm^2 s^{-1}$ (0.3 $cm^2 y^{-1}$) in the oligotrophic deep sea to 10^{-5} cm^2 s^{-1} (3 x 10^3 cm^2 y^{-1}) in heavily reworked nearshore environments. **Aller *et al.* (1980)** found that typical values for nearshore sediments are about 10^{-6} cm^2 s^{-1} (3 x 10^2 cm^2 y^{-1}) and 10^{-8} cm^2 s^{-1} in the deep sea. **Martin & Sayles (1987)** estimated D_b in Buzzards Bay; it increased from 5 $cm^2 y^{-1}$ [1.6 x 10^{-7} $cm^2 s^{-1}$] in the winter to 25 cm^2 y^{-1} [≈8 x 10^{-7} $cm^2 s^{-1-1}$] in June.

In Boston Harbor, Wallace estimated D_b from ^{234}Th profiles that spanned this range. He found D_b values in the Inner Harbor and Spectacle Island of about 2 x 10^{-7} $cm^2 s^{-1}$ and 2.5 x 10^{-5} $cm^2 s^{-1}$, respectively. I sampled the infauna in the same locations sampled by Wallace. The Inner Harbor D_b values are in perfect accord with the very low infaunal abundances there. It is not surprising that the D_b values in the Inner Harbor resemble deep-sea values, since the infaunal abundance and biomass are close to deep-sea values. The D_b value of 2.5 x 10^{-5} $cm^2 s^{-1}$ for Spectacle Island seems inconceivable given the low infaunal abundances and trophic composition observed there. Unfortunately, the infaunal abundances were not recorded from the same box cores as the radioisotope profiles. Here are some possible explanations for the lack of concordance between infaunal community structure and Wallace's radioisotope profiles:

- The D_b profiles were based on real feeding activities, but I sampled a different benthic community than those that were mixing sediments in the geochemistry box cores.
- The community that mixed the sediments died or left shortly before the radioisotope profiles were determined. Their tubes and burrows might have been filled in with fine particles from the surface.
- Some unusual event, like a sediment slump, occurred weeks before the box cores were taken.
- The infauna present in the geochemistry box core were the same as those in Gallagher's box cores, but they were feeding in a manner inconsistent with either biodiffusive or conveyor-belt feeding models.

I cannot reject any of these hypotheses. Only further studies that study the seasonal change in radioisotope profiles and infaunal communities could identify whether high apparent bioturbation rates are a characteristic feature of sections of Boston Harbor that lack conveyor-belt feeders.

Rice (1986) describes the effects of bioturbation by *Leitoscoloplos* on sediment stratigraphy. In a subsequent paper, Rice analyzed the effects of sediment food quality on the growth of *Leitoscoloplos*. **Rice (1986)** is one of the only papers to couple with a quantitative model, the ingestion rate of a deposit feeder with its sedimentological consequences. **Rice (1986)** uses ^7Be as his short-lived (53 d) radioactive tracer.

Alternatives to the Goldberg-Koide biodiffusion model

For bioturbation to be regarded as biodiffusive, the characteristic bioturbation step length, l_b, for all local feeders cannot exceed the depth at which the tracer decays substantially. **Wheatcroft *et al.* (1990)** argued that the bioturbation step length is set by the difference in the depth at which food is ingested and feces are deposited (z_i and z_d in Table 1).

Suspension feeders and surface deposit feeders feed and defecate at the surface, differing only in the height above the bed at which particles are captured. They can be regarded as local mixers, but their effects on vertical particle movement are small. Many subsurface deposit feeders can be considered local feeders. A shallow subsurface deposit feeder feeding a few millimeters deep and defecating on the surface is a local mixer. All large subsurface deposit feeders are likely to begin life as local mixers.

Boudreau (1986a) warned that the diffusion analogy was inappropriate if animals move particles a greater distance than the distance it takes for tracers to decay substantially. If a single non-local feeder is added to azoic sediment, this characteristic length scale is set by sediment accumulation rate and decay rate $\left(\frac{w}{\lambda}\right)$. In the Savin Hill Cove subtidal zone, **Wallace *et al.* (1991)** estimated sediment accumulation rates of 3-4 cm per year, producing nearly vertical ^{210}Pb profiles in the upper 30 cm of sediments. A conveyor-belt feeder that fed at 10 cm and defecated at the surface under these conditions could be considered a local mixer. In an area like the Inner Harbor, where there are few animals and a lower sediment accumulation rate, a deposit feeder that displaces particles 0.5 cm might be considered a non-local mixer. If a conveyor-belt feeder is added to sediment where mixing has already taking place, then the characteristic length scale should be set by $\sqrt{\frac{D_b}{\lambda}}$. However, we do not know what D_b is before fitting the diffusion equation to a profile. The real question of whether the diffusion analogy is appropriate must be based on the application of the model. **Boudreau & Imboden (1987, p. 713)** warn:

> *"Researchers should not be misled by the apparent similarities between profiles generated by the nonlocal exchange and the diffusion models into believing that these models are functionally equivalent. When the primary object of a study is bioturbation, then conceptual and logical arguments based on an understanding of the biological and physical phenomena must be used to select the correct model. Biological data on feeding and burrowing are therefore a necessity."*

Boudreau & Imboden (1987) recommend modeling the movement of sediment particles using both biodiffusive models and non-local conveyor-belt feeding models.

The classic non-local mixers are conveyor-belt feeders. These organisms feed at depth and defecate at the surface. **Cadée (1979)** described the feeding of *Heteromastus filiformis*, which builds a tube, feeds at depths of 10-15 cm and defecates on the surface. **Rhoads (1974)** described the feeding biology of bamboo worms or maldanid polychaetes like *Clymenella torquata*, which build tubes, create a feeding cavity at depth and defecate on the surface. Not all maldanids are conveyor-belt feeders. Kudenov (**1978**, **1982**) demonstrated that *Axiothella rubrocincta*, a common maldanid on the West Coast, feeds as a funnel feeder. It lives in a J-shaped tube, feeding at the bottom end of the J. This feeding at depth creates a feeding void which causes surface sediments to subduct quickly to depth. Kudenov classifies *Axiothella* as a surface-deposit feeding funnel feeder. As did Kudenov, Word (**1978**, **1980a**, **1980b**, **1982**) classified subtidal maldanids on the California shelf and in Puget Sound as surface deposit feeders. While documenting the evidence for his infaunal trophic index, **Word (1982)** included laboratory observations of maldanids feeding on surface material to support his classification of maldanids in his "Infaunal Trophic Index" as surface deposit feeders. Shull (**2000**, **2001**) used high subsurface activities of Pb-210 to infer that maldanid polychaetes in Narragansett Bay (*Sabaco elongatus* & *Macroclymene zonalis*) might be hoeing surface sediments to the base of their tubes at 15-20 cm, a behavior noted by **Dobbs & Whitlatch (1982)** in the maldanid polychaete *Clymenella torquata*.

Rhoads & Young (1971) described the effects of *Molpadia oolitica*, a burrowing holothuroid in Cape Cod Bay which feeds at depth and produces large fecal mounds at the surface. As shown in Fig. 1, these mounds are colonized by the suspension-feeding sabellid ('feather duster') worm *Euchone incolor*.

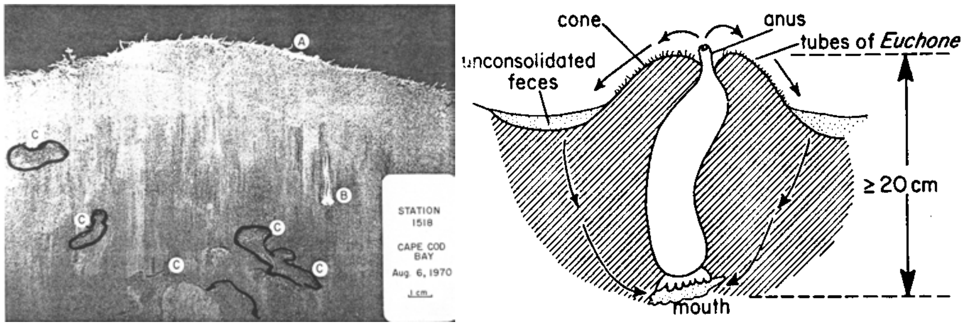


Figure 1. Sediment-profile images of the holothuroid *Molpadia oolitica* mounds in Cape Cod Bay with feeding voids **(C)**, a burrowing polychaete **(B)** and *Euchone incolor* tubes shown **(A)**. At right is a drawing of the animals' life position and direction of sediment movement. Figs 3 & 4 from **Rhoads & Young (1971)**.

Rice (1986) studied a community containing *H. filiformis*, but his dominant sediment mixer was the orbiniid polychaete *Leitoscoloplos*. *Leitoscoloplos* is a burrower — it doesn't build a tube — that feeds at 3-5 cm depth and defecates at the surface. As **Rice (1986)** experimentally demonstrated, all of these conveyor-belt species can cause surface sediments to be subducted to depth. Rice modeled the bioadvection of chalk particles and the short-lived radioisotope ^{7}Be (55-d half life) on the Lowes Cove intertidal mudflat in Maine. Chalk layers and ^{7}Be are subducted to depth at seven to eight times the local sediment accumulation rate. **Dobbs & Whitlatch (1982)** described a behavior that they called sediment hoeing, in which the head-down tube-dwelling conveyor-belt feeder *Clymenella torquata* scraped surface deposits into its tube.

Some subsurface feeders, such as lug worms (Family Arenicolidae), ice-cream cone worms (Family Pectinariidae), holothuroids (*Leptosynapta*), and some maldanids (*Axiothella rubrocincta*, see Kudenov **1978, 1982**) create feeding funnels that rapidly subduct organic rich surface material to several centimeters depth. These are called "funnel feeders." These organisms typically have a J-shaped feeding space. The organism feeds head down at the curved tip of the J and defecates through a vertical tail shaft. Some organisms live in tubes, but the lug worms and holothuroids use mucous-lined burrows. The feeding rates of these species are so high that feeding pits appear on the surface. The material being ingested was often on the surface only hours before. For this reason, **Fauchald & Jumars (1979, p. 200, 262)** followed most earlier workers in classifying funnel-feeding lug worms as surface deposit feeders because "The animal feeds by taking in sand ... much of the sand represents material that has slumped or deposited into the funnel formed by the removal of sand at the base." However, they classified ice-cream cone worms as subsurface deposit feeders, even though their feeding depends on 'small-scale slumping' and 'caved-in sediments.'

We use the term 'sediment miners' for subsurface feeders that are utilizing organic matter at depth that was produced months, years, or even decades before. These are large subsurface deposit feeders that mine organic-rich veins of sediment. **Thayer (1983)** and **Wheatcroft *et al.* (1990)** provide examples of subsurface deposit feeders that feed on old, deep organic-rich veins of subsurface deposits. These species may feed at depths a meter or more below the sediment surface. These species may defecate on the surface, but they might also defecate at depth. The distinction between funnel feeders, conveyor-belt feeders, and miners is based on how recently the organic material was on the surface. Funnel feeders feed on material subducted hours or days before, conveyor-belt feeders feed on material that is weeks or a few months old, miners feed on material that has been buried for many months to decades.

Boudreau (1986b), **Robbins (1986)**, **Boudreau & Imboden (1987)**, and **Rice (1986)** introduced non-local mixing models. The key feature of their models is that they replace or supplement the biodiffusion term, D_b, with a bioadvective term. Animals feed at one depth and defecate at another, usually the surface. Below the depth of defecation, the advection term consists of both the natural sediment accumulation rate and the bioadvection term due to deposited feces. Below the zone of ingestion, both the biodiffusion and bioadvective terms are zero.

Bioadvective, or non-local feeding, can have very different effects on stratigraphy and sediment biogeochemistry than diffusive mixing. **Boudreau (1986b)** modeled the profiles of a variety of transient tracers with non-local, conveyor-belt feeding. Bioadvective bioturbation is considerably less dispersive than biodiffusion, especially if the tracer is not ingested. A pulse of a tracer that animals don't ingest is buried in discrete layers, much like Darwin's and Rice's chalk layers or the pellets in Figures 9 and 10. Ingestion of a tracer that is continuously refreshed at the sediment-water interface will produce profiles that look like profiles generated by biodiffusive models.

Our understanding of deposit feeding may be inadequate to explain some effects of animals on geochemistry. In three studies —the Boston Harbor Sediment-water exchange (SWEX) study, **Wheatcroft *et al.* (1994)**, and **Blair *et al.* (1996)** — rapid several centimeter deep subduction of tracers was observed in areas lacking the funnel feeders or conveyor-belt feeders capable of moving that much sediment that quickly. **Wheatcroft *et al.* (1994)** labeled natural silt-clay and sand-sized particles with silver and gold to estimate bioturbation rates in MA Bay, near the proposed MWRA outfall site. They observed silt-sized particles being moved to depths of 15 cm in only 80 days. Sand-sized particles, which are less likely to be ingested, were not transported from the surface to depth as readily. Incidentally, **DeMaster & Cochran (1982)** had found that in the deep-sea that Pb-210, associated with the silt-clay component of sediment, was mixed more rapidly than the Si-32 labeled coarser deep-sea sediment. **Blair *et al.* (1996)** tracked ^{13}C-labeled phytodetritus deposited on the North Carolina continental shelf. Within 1.5 d, much of this phytodetritus had been transported to several centimeters depth. Neither **Wheatcroft *et al.* (1994)** nor **Blair *et al.* (1996)** could find conveyor-belt feeders capable of subducting that amount of material that quickly. Both studies conclude that reverse conveyor belt feeding or "food caching" was responsible.

Food caching: Why might deposit feeders do it?

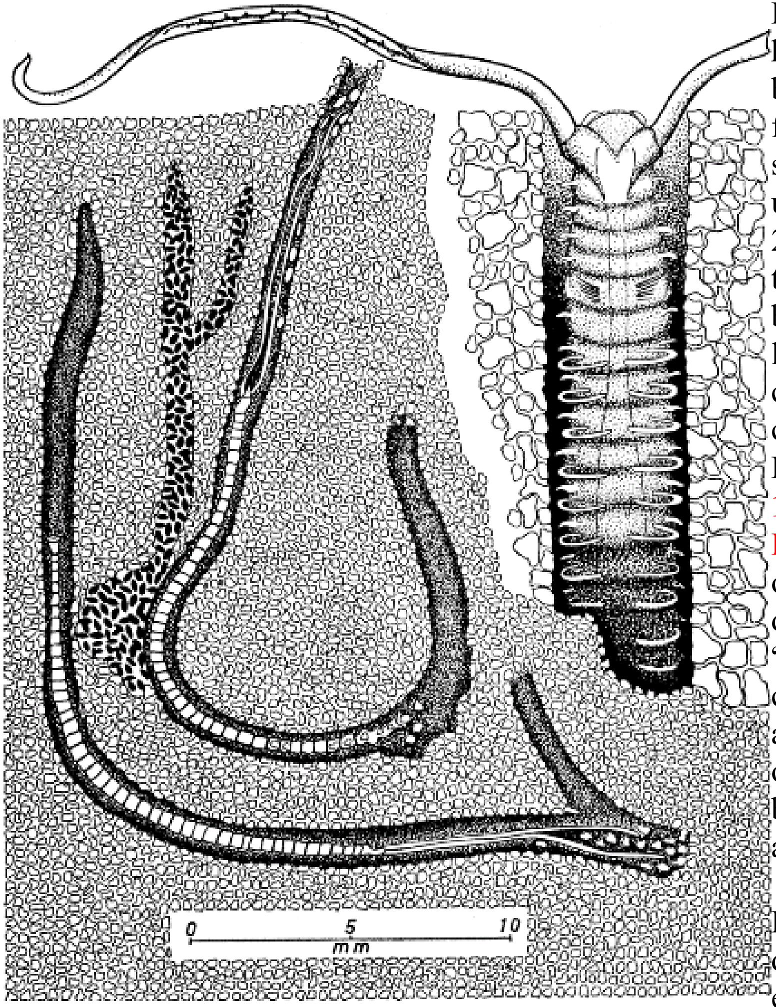


Figure 2. Food caching shown for *Polydora ciliata* in a laboratory aquarium. The spionid polychaete deposits its feces in abandoned subsurface burrows. Drawing from Schäfer (1972).

Food caching is a recent addition to the known repertoire of infaunal feeding behaviors shown in Table 1. A food cache is food that is transported from the sediment surface to a burrow or tube. It may consist of uningested food or feces as shown in Figure 2. **Jumars *et al.* (1990)** proposed that the transport of surface particles into tubes and burrows may be a means to cache food for later use or to keep food away from potential competitors. Food caching is sometimes called "reverse conveyor belt feeding." Boudreau (**1986b**, **Boudreau & Imboden 1987**), Wheatcroft *et al.* (**1990**, **1994**), and **Blair *et al.* (1996)** use that term to describe organisms that feed at the surface and defecate at depth. Our distinction between "reverse conveyor belt feeding" and "food caching" is important. Food caches are used as temporary subsurface reservoirs for organic material. Much of the material might be returned to the sediment-water interface at a later time.

Food caching has never been clearly documented for any infaunal species. The evidence for food caching comes largely from geochemical studies showing subsurface peaks in tracer distributions. **Wheatcroft *et al.* (1994)** and **Blair *et al.* (1996)** describe the organisms found in their cores. **Blair *et al.* (1996)** analyzed the δ^{13} C ratios of a subset of these organisms. They found two species, a scalibregmid and paraonid polychaete (*Aricidea quadrilobata*), that showed high selection for their labeled phytodetritus. The paraonid polychaete *Aricidea catherinae* is abundant in Boston Harbor (Figures 4-6), but we do not know whether this species can or does cache food. The most abundant organisms at the Spectacle Island site were spionid polychaetes, *A. abdita*, and oligochaetes. Spionid polychaetes and ampeliscid amphipods have the ability to move particles from the sediment surface into their tubes, but the quantitative importance of this transport has not been documented.

The theory of "food caching" is in its infancy. There are three areas of ecological theory that might apply to food caching: evolutionary game theory, optimal foraging theory, and dynamic modeling. In each type of modeling, the organism faces choices of whether to cache, how to cache, and when to feed on the cache. These choices can be viewed as strategies in a game between one organism vs. Nature (="the house") or one organism *vs.* another. The modeler must choose the appropriate currency to judge winning strategies. Long-term population growth is the usual payoff, but, short-term energy assimilation can be used as a surrogate. A winning energetic strategy may be a losing long-term strategy if it exposes the organism to higher predation rates.

Individual *vs.* individual games might produce winning strategies differing from individuals *vs.* the house. A conveyor-belt feeding strategy may be turned from a winning to a losing strategy by adding another subsurface feeder feeding at a slightly shallower depth horizon. Stocking a food cache may be a losing strategy until a competitor is added. The long-term population dynamic effects of removing the food needed by a potential competitor may turn a losing strategy into a winning one. Adding a cache parasite that consumes other organisms' caches could greatly reduce the selective value of caching. Food caches will be continually consumed by heterotrophic bacteria, which can be regarded as either a second player in the game or a ubiquitous feature of "the house."

Jumars (**1993a**, **1993b**, pp. 37-45) reviews his work and that of Cammen, Dade, Levinton, Lopez, Penry, Taghon, and others on optimal foraging theory for deposit feeders and describes the advantages of fast gut passage times. The ingestion rates for most deposit feeders are high, with a modal ingestion rate of three body weights per day. **Rice (1986)** measured daily *Leitoscoloplos* ingestion rates of 120 mg dry sediments per mg dry worm (or 176 ± 55 mg dry sediment per worm), which is at the high end of weight-specific ingestion rates. These high ingestion rates severely constrain food caching strategies. A cache would soon fill with feces, and a cache filled with food would be quickly depleted.

Dynamic modeling is an extension of optimal foraging that focuses on the dynamic state variables in the system, such as the volume of the food cache and gut. If a spionid polychaete has a food particle in its feeding tentacle, it might drop it in its tube or eat it. If the spionid eats the food particle, it can defecate on the surface or in its tube. A worm's decision to cache may depend on the fullness of its gut and food cache and the amount of food remaining to be eaten. The food-storage capacity of an animal's burrow and tube may turn out to be a key variable in the food caching models of the future. **Mangel & Clark (1988)** regard specifying these dynamic state variables as the key to constructing successful models. Dynamic models also focus on the time to the end of the game. Stocking a food cache makes no evolutionary sense for an infaunal organism that is about to reproduce.

Jumars *et al.* (1990) argued that food caching is an adaptation to episodic food input. Food caching was first proposed for the deep-sea, where **Graf (1989)** observed Chl *a* from the sedimenting spring phytoplankton bloom being transported beneath the sediment surface. Many deposit feeders can scrape surface particles into their burrows or tubes, while others may defecate into their burrows or tubes. Scraping surface deposits into a cache seems to be the better strategy, but some deposit feeders may be structurally constrained to only cache feces. Moving feces into a tube or burrow for short-term storage may produce another advantage. The forager can then forage on the surface floc of phytodetritus, undiluted with recently egested feces. **Miller & Jumars (1986)** showed that the buildup of feces inhibits surface deposit feeder ingestion rates. After the surface phytodetritus concentrations are depleted or the cache reservoir is full, then feces could be moved out of the tube or burrow and back on the surface.

Food caching may be a winning strategy for deposit feeders that feed on benthic diatoms in the intertidal and shallow subtidal. Benthic diatoms vertically migrate within the sediments often forming dense mats on the surface after the tide leaves or light intensities increase. **Admiraal (1984)** and **Gould & Gallagher (1990)** describe mats of several million diatoms per cm^2. Benthic diatoms can be found in subtidal areas down to the 1% light depth and below. **Cahoon *et al.* (1993)** document high benthic diatom standing stocks on Stellwagen Bank at 0.5% light intensity. A surface deposit feeder feeding on these diatoms and defecating on the surface would soon find the diatom mat buried in feces. A winning strategy might be for a surface deposit feeder to fill its gut and defecate into its tube, or scrape the diatom mats into its tube. After the diatoms have migrated back into the sediment, the deposit feeder can then feed on its cache, or transfer its cached feces to the surface.

The geochemical implications of food caching are startling. Standard modeling approaches for assessing the effects of bioturbation on pollutant flux fail to catch the essence of food caching. A group of food caching organisms could quickly remove ^{234}Th to depth with only minor changes in the vertical transport of bulk sediments. This might account for the high bioturbation rates measured by Wallace at the Spectacle Island site. We have performed a number of Markov model simulations of the ingestion rate required to produce a D_b of 10^{-5} cm^2 s^{-1} if the infauna feed on bulk subsurface sediment. A conveyor-belt feeder would have to ingest an approximately 1-cm thick stratum at a depth of about 10 cm and deposit it on the surface each day to produce a bioturbation rate of 10^{-5} cm^2 s^{-1}. Wheatcroft and Tom Forbes have presented another rough scaling equation to predict the effects of deposit feeder ingestion on D_b:

$$\begin{aligned} D_b &\approx \frac{l_b^2}{8 \ast (Rest\ period)} \\ where,\ l_b &\approx distance\ between\ ingestion\ and\ defecation\ depths. \\ Rest\ period &\approx \left[\frac{volume\ available\ sediment}{ingestion\ rate}\right] \end{aligned} \qquad \textbf{(3)}$$

Equation 3 predicts that the infauna would have to ingest one tenth of the upper ten centimeters of sediment each day to produce a D_b of 1.4×10^{-5} cm^2 s^{-1}. It would require nearly 70,000 large *Leitoscoloplos* per m^2 to ingest sediment sufficient to produce a D_b of 1.4×10^{-5} $cm^2 s^{-1}$. *Leitoscoloplos*, with its ingestion of 120 body weights daily, has one of the highest weight-specific ingestion rates of any deposit feeder. A more typical ingestion rate on organic-rich sediments is three body weights daily (**Jumars 1993a**). Food caching, on the other hand, is a more likely explanation for the Spectacle Island ^{234}Th profiles. Fifty thousand surface deposit feeders per m^2 could scrape or move the daily input of fine particles containing ^{234}Th into their tubes. Since burrows and tubes have finite capacity, such short-term caching cannot be maintained for long. Much of the material cached at depth will eventually be brought back to the surface. Neither the diffusive mixing nor conveyor-belt feeding are appropriate analogies for food caching. An appropriate physical analogy might be "elevator feeding." Organic-rich particles are transported rapidly to depth in burrows or tubes and are rapidly returned to the surface. Finding short-lived radioisotopes or surface organic material at considerable depths does not necessarily mean that the bulk sedimentary material is being moved.

How much do deposit feeders eat?

Jumars (1993b) reviews **Cammen (1980)** who analyzed published feeding studies. Cammen analyzed published studies on the rate of ingestion of sediments and organic matter by deposit feeders. Cammen found the following regression:

$$\begin{aligned} C &= 0.381 \ast W^{0.742}. \\ where,\ C &= organic\ matter\ ingestion \left[\frac{mg\ organic\ C}{day}\right] \\ W &= individual\ weight\ [mg\ dry\ weight]. \end{aligned}$$

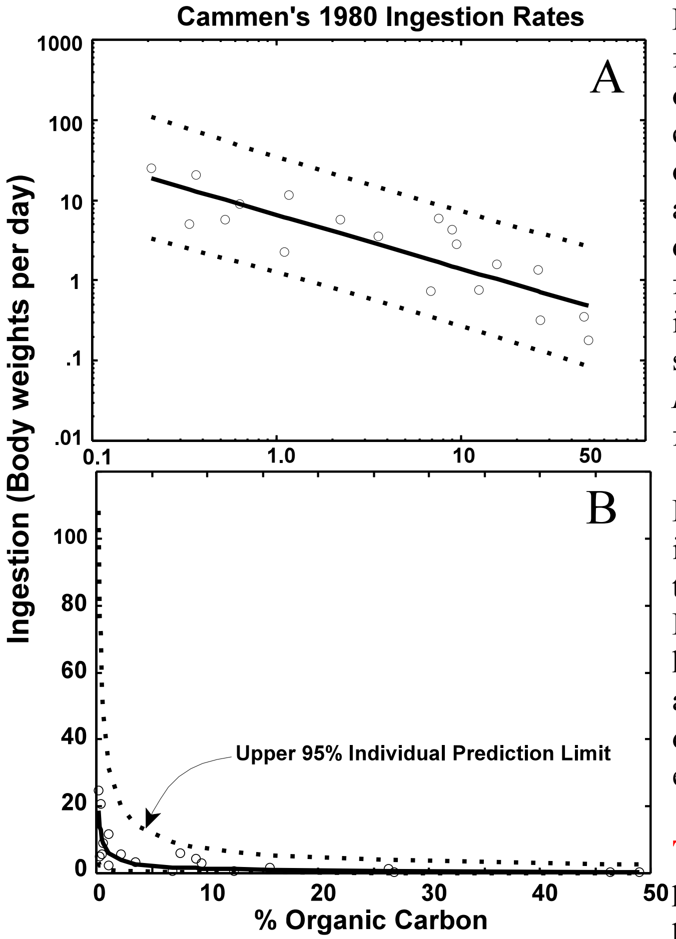


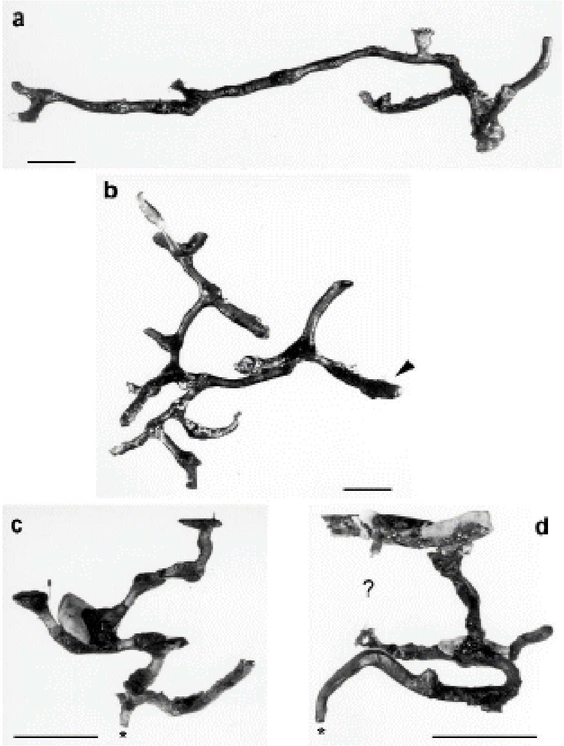
Figure 3. Log-log and linear-linear plots of **Cammen's (1980)** data and regression equation. The 95% confidence limit is for individual data points (not the means).

Figure 3 shows the relationship between deposit feeder ingestion, as body weights per day, and the organic matter content in sediments (I have converted from Cammen's % organic matter to % organic carbon). The modal deposit feeder ingests about three body weights per day in food. Smaller deposit feeders ingest more daily than large deposit feeders, and ingestion rate scales allometrically. The ingestion rates recorded by **Rice (1986)** of 120 mg sediment ingested per mg dry weight of *Leitoscoloplos* are among the highest ever recorded for a deposit feeder.

Deposit feeders in low organic carbon environments ingest much more on a weight-specific basis than those in high organic carbon environments. However, this relationship is confounded because high organic carbon environments, like those around sewer outfalls, are inhabited by much small deposit feeders than low organic carbon environments.

Thayer (1983) tabulated dozens if not hundreds of particle reworking rates from the literature. Thayer's particle reworking rates are different from Cammen's ingestion rates. Deposit feeding bivalves may bring in ten to one hundred times more material through their inhalant siphons than the amount ingested. Lamellibranch bivalves sort the edible and inedible particles on their gills (the lamellibranch). The uningested material is expelled as pseudofeces. Deposit feeding crustacea may bring ten to one hundred times more sediment into their tubes than they actually ingest. Deposit-feeding amphipods sort the particles on their maxillae, ingesting only a small fraction of the particles "reworked." Spionid polychaetes, like the one shown in Fig. 1 of Handout 25, sort particles along the feeding tentacles (heavier particles tend to fall off) and at the mouth.

The thalassinidean shrimp are among the most impressive groups of organisms responsible for deep bioturbation and bioirrigation in sediments. **Pemberton *et al.* (1976)** documented deep shrimp burrows extending to nearly 1 m depth in organic-rich estuarine sediment. They argued that the burrows from these supershrimp might have analogues in the geologic record, indicating organic-rich deposits. **Nickell & Atkinson (1995)** reviewed the trophic modes and burrow architectures of three species of these shrimp. Two of these shrimp species, even though they have deep burrows, get most of their food either from scavenging at the surface or suspension feeding. **Dworschak (2002)** published pictures of th thalassinidean shrimp, *Callianassa candida* (Fig. 4).



ig. 2. Burrows of *Callianassa candida*, Lagoon of Grado, Italy; a: resin cast #770912; b: esin cast #770914, arrow shows position where animal was entombed. Burrows of *C. hitei*, Bay of Kuvi, Croatia; c: resin cast #8307/1; d: resin cast #8307/2. All in side view, cale is 10 cm. * indicates position where cast was broken off.

Figure 4. Burrows of *Callianassa candida* & C. Whiteisobtained by filling the burrows with resin and excavating. The scale is 10 cm. Arrow shows where animal was entombed (**Dworschak 2002**, Fig. 2)

PELLETIZATION

Boston's most heavily contaminated sediments are usually heavily pelletized. This section will review the ecological and geochemical significance of fecal pellets.

What marine organisms produce fecal pellets?

Marine organisms often bind their fecal material into fecal pellets. Most benthic macrofauna produce mucous-coated feces, but the durability of the feces or fecal pellets varies greatly. Spionid feces break down rapidly, but capitellid fecal pellets degrade very slowly. Figure 5 shows the characteristic fecal pellets of *Capitella* sp. Ia from Boston's Inner Harbor. **Taghon *et al.* (1984)** studied the breakdown rate of fecal pellets being jostled in turbulent flow in a laboratory flume. The capitellids are the premier producers of robust fecal pellets. **Fleming (1989)** found that the large *Capitella* sp. Ia pellets from Boston Harbor, like those shown in Fig. 5, do not degrade during 30-minutes of pounding and shaking on a Ro-Tap shaker. After the West Falmouth oilspill in 1969, **Grassle & Grassle (1974)** described the extensive pelletization of nearshore sediments by members of the genus *Capitella*. **Fuller *et al.* (1988)** describe the diel cycle of fecal pellet production by the capitellid polychaete *M. ambiseta*. **Forbes & Lopez (1987)** document the allometry of fecal pellet production by *Capitella* sp. I. The huge pellets produced by large *Capitella* sp. Ia dwarf those produced by *Capitella* sp. I and *M. ambiseta*. **Wang et al. (2001)** document that PAHs in some of the more polluted areas in Boston Harbor are associated with the coarse sand-sized fraction of the sediments, not the fine

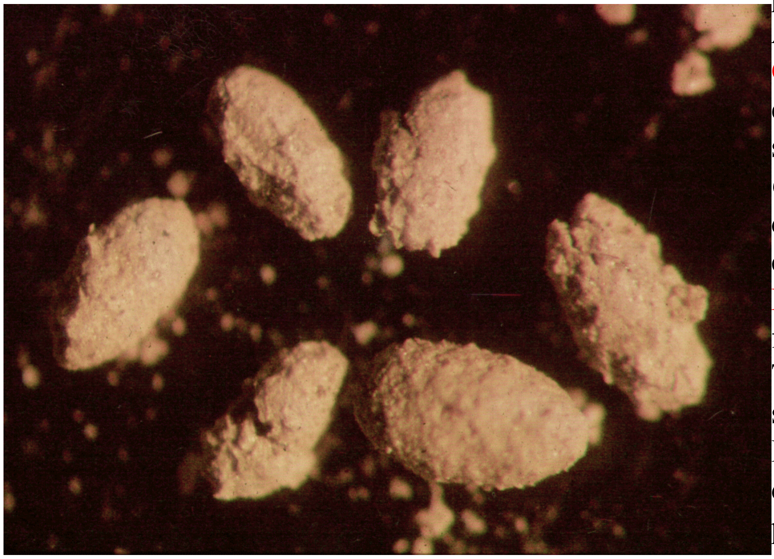


Figure 5. Freeze-dried fecal pellets from Boston's Inner Harbor. Over half the sediment weight in surface strata can be composed of these 300-µm x 500-µm pellets.

fraction as most models would predict. These coarse fractions include *Capitella* fecal pellets, plant detritus and charcoal.

Ecological significance

It isn't known why organisms produce pellets. There are two major explanations. One explanation is that deposit feeders produce pellets to reduce the probability of reingesting already ingested sediment. The second explanation is that pellets are a byproduct of deposit-feeder digestion, with no selective value once they leave the gut. One of the unusual features of *Capitella* digestion is that the pellets form in the first one eighth to one fifth of the body length. Wagenbach (pers. comm.) has studied the formation of *Capitella* pellets. *Capitella* ingests silt- and clay-sized particles with an eversible, mucous-covered proboscis. These particles are rolled and thoroughly mixed with mucous in the first few worm segments. They are probably bathed in digestive enzymes at this point in the capitellid foregut. Within about ten minutes, the complete Rugby-ball shaped fecal pellet has formed. It is mucous-coated throughout and has a continuous mucous layer shrouding the surface. The pellets are visible through the body walls of *Capitella*. Unless organic matter can diffuse through the thick mucous, the total time to extract organic matter from food particles is probably only about ten minutes. This digestive strategy may account for the presence of *Capitella* only in sediments with very high concentrations of labile organic matter (**Tsutsumi *et al.* 1990**). We can speculate that this odd digestive strategy may be advantageous in contaminated sediments where labile organic matter is associated with toxic hydrophobic pollutants. The capitellid may extract the most labile organic matter in a few minutes, and then bind the potentially toxic material in pellets to limit the assimilation of toxic contaminants as the pellet transits the gut.

Grassle & Grassle (1974) proposed that pelletization of sediments by *Capitella* might explain the crash of *Capitella* populations after oilspills. The pelletization was so extensive that small capitellids could not find sufficient food to eat. **Phillips & Tenore (1984)** documented that heavily pelletized sediments reduce the population growth rates of cultured *Capitella* sp. I.

Geochemical significance

Pellets produce an oxic/anoxic microenvironment

Greenwood (1968) and **Reise (1985)** describe the geochemical processes affected by pellet geometry. The interior of organic-rich fecal pellets is often anoxic, whereas the exterior is oxic. **Jørgensen (1977)** found high rates of sulfate reduction, a strictly anaerobic process, in oxic intertidal sediments. This process was restricted to the anoxic interiors of fecal pellets. **Henriksen *et al.* (1983)** found high rates of denitrification in the anoxic interior of fecal pellets. Denitrification rates are often limited by nitrification rates. Nitrifying bacteria, require oxygen, and ammonia or nitrite for growth. Pellets place the relevant biogeochemical gradients in close conjunction. Because deposit feeders select organic-rich sediments and their assimilation efficiency is low, pellets usually have higher organic content than the bulk sediment. **Henriksen *et al.* (1983)** found the pellets had 1.4% organic carbon, compared to the bulk sediment's 0.3%. Heterotrophic respiration of this organic carbon produces NH_4^+ which fuels high nitrification rates on the pellets outer shell. Nitrite and nitrate produced by the nitrifiers diffuses into the anoxic pellet interior where it is converted to nitrogen gas by anaerobic denitrifying bacteria.

Pellets alter sediment transport mode and rates

Deposit feeders usually ingest silt- and clay-sized particles, but their pellets are sand-sized. Pelletized sediments tend to be transported as bedload but the silt and clay particles from which pellets are made can only be transported as suspended load. **Haven & Morales-Alamo (1968)** were the first to discuss the role of fecal pellets in altering sediment transport rates. **Jumars *et al.* (1981)** produced a simple Markov model to show that pelletization can greatly enhance the residence time of particles in an area if pellets are less easily eroded than the surrounding sediment. If a contaminant were bound up in fecal pellets it would tend to be concentrated in heavily pelletized patches of sediment.

Since few deposit feeders ingest pellets, the residence time of pellets in the surface layer should be very short. Pellets would be quickly subducted to the zone beneath the zone of deposit feeding to form a lag layer. This quick subduction is due to the selective ingestion of fine particles by deposit feeders. The non-selective bumping and jostling of marine sediments by animal movement would tend to keep pellets at the surface. The mechanism for this is described by **Rosato *et al.* (1987)** in their paper, “Why the Brazil nuts are on top.”

Flux of sediment contaminants

Karichoff & Morris (1985) produced a model showing the effect of tubificid oligochaete pellets on the flux of contaminants from sediments. Their model used the same physical concepts as **Greenwood (1968)**: the diffusional path lengths within pellets are much longer than those of the silt- and clay-sized unpelletized sediment. The high organic content of pellets would also lead to a reduced diffusive flux of hydrophobic pollutants from pelletized sediments.

Wu & Gschwend (1986), **Gschwend & Wu (1986)**, **Bronawell (1986)**, and **Reynoldson (1987)** have included the effects of pelletization in their models of pollutant transfer. In general, pellets reduce the molecular diffusive transport of hydrophobic organic compounds from particles to the surrounding porewater or overlying water.

In Boston Harbor, pellets only occur where there were once populations of the large *Capitella* spp. Ia. In these areas, the pellets can often make up 20% to 70% of the sediment weight. The major effect of these pellets is to sequester contaminants within the sediments. Large pellets remain on the sediment surface only a short time before they are subducted beneath the zone of infaunal feeding. They are rarely ingested by subsurface deposit feeders. At depth, the pellet decay rate is very low, with pellet half lives that may be decades long.

Outlines

REQUIRED & SUPPLEMENTAL

Boudreau, B. P. 1994. Is burial velocity a master parameter for bioturbation? Geochim. Cosmochim. Acta. *58*: 1243-1249. *[$D_b \propto$ flux of organic matter; flux of organic matter $\propto$ burial velocity. Mixing depth is 9.8±4.5cm]*

Boudreau, B. P. 1998. Mean mixed depth of sediments: the wherefore and the why. Limnol. Oceanogr. *43*: 524-526. *[Mixed layer depth has an mean depth of 9.8 cm [documented in* ***Boudreau 1994****; BPB's model predicts 9.7 cm.]*

Jumars, P. A. 1993b. Concepts in biological oceanography. Oxford University Press, New York & Oxford. 348 pp.

17. Organism effects on strata
    - a. Both currents and animals rework sediments
    - b. Single vertical dimension usually used in models.
    - c. Simplest quantitative description (**Berger & Heath 1968**):

$$\frac{\partial C}{\partial t} = D_b \frac{\partial^2 C}{\partial z^2} - A \frac{\partial C}{\partial z} \pm R.$$
$$\begin{aligned} where,\ D_b &= eddy\ diffusion\ coefficient\ [L^2\ T^{-1}]. \\ A &= net\ accumulation\ of\ sediments\ [L\ T^{-1}]. \\ R &= reaction\ rate\ [C\ T^{-1}]. \end{aligned} \qquad \textbf{(17.1)}$$

    - d. Below the depth L_b, mixing is assumed to be absent entirely
    - e. **Guinasso & Schink (1975)**:
        - i. Nondimensionalization of mixing intensity (G) by scaling mixing rate, against sediment accumulation rate, forming and inverse Sherwood number (1/Sh, the mass-transfer equivalent of an inverse Peclet number):

$$G = \frac{D_B}{A\ L_b}.$$
$$\begin{aligned} where,\ A &= Sedimentation\ rate \left[\frac{L}{T}\right]. \\ D_B &= Bioturbation\ coefficient \left[\frac{L^2}{T}\right]. \\ G &= Non\text{-}dimensional\ mixing\ intensity. \\ L_b &= Depth\ of\ animal\ feeding\ [L]. \end{aligned} \qquad \textbf{(17.2)}$$

        - ii. Fig. 17.1. **Guinasso & Schink (1975)** mixing curves. Tracer thickness h≤0.1 L_b Depth on ordinate is given as multiples of the mixed-layer depth
    - f. Nittrouer & Sternberg (1981): Low G (<0.2_ clear mode in abundance of an impulse tracer that arrives on the seabed and buried within about 0.3 L_b of the depth at which it would be found if mixing did not occur
    - g. For G>1, the results are homologous with **Berger & Heath's (1968)**
    - h. **Wheatcroft et al. (1990)**
        - i. Nondimensionalization
        - ii. Time that bioturbation can operate is limited to L_b /A.
        - iii. Modify that transit time of a layer of finite thickness h (<L_b) to:

$$t_m = \frac{L_b - \frac{h}{2}}{A}. \qquad \textbf{(17.3)}$$

iv. Equations 17.4 and 17.5 are normal distribution equations to predict effect of bioturbation on a pulse of tracer

i. Radionuclides used to estimate parameters of Equ. 17.1, solving for A by working below a depth of L_b and then solving for D_b
  - i. Typical deep-sea D_b's range from 0.1 to 1 cm^2y^{-1}, though organically rich nearshore sites and physically disturbed sites can reach typical values for the continental shelves - of order 10 $cm^2\ y^{-1}$
  - ii. L_b is curiously constant- ranging from 4-18 cm and usually being very near 10 cm.
  - iii. Outside regions of high A, it is difficult to resolve stratigraphically events separated by less than about 3 x 10^3 yr [what about my fecal pellet profiles!]

j. **Wheatcroft *et al.* (1990)** decomposition of D_b
  - i. In accord with Boudreau (**1986a**), analogy with Fickian diffusion doubtful.
  - ii. Only deposit feeding is important in determining the magnitude of D_b
  - iii. In feeding, particles moved a body length, this excursion length called L_s.
  - iv. Unlike water-column turbulence most particles in the seabed spend most of their time sitting still. The natural choice for a time scale is the time between successive displacements (*i.e.*, the rest interval, Ω). For the one-dimensional, isotropic case:

$$D_b = \frac{L^2}{2\Omega}. \qquad \textbf{\{17.6)}$$

k. Feedbacks that narrow the range of G:
  - i. **Cammen (1980)**
    - (1) Animals feeding on food poor sediments process more food, to the $M^{0.7}$ power
    - (2) Higher organic matter flux supports higher sediment organic concentration and both larger deposit-feeding individuals and more of them (Rowe 1983)

  *"Nor does defining a biomass-specific mixing coefficient (**Matisoff 1982**) narrow the range of mixing values as much as one might suspect; whether the animal is a deposit feeder or suspension feeder is key in whether it displaces sediments in feeding. Therefore, body size-frequency data are poor predictors of step lengths or rest intervals."*
  - ii. Reasons for the constancy of L_b
  - iii. Animals capable of burrowing deeper than L_b are known from all benthic communities; they are simply to rare to have affected L_b in most estimates. And they are too rare to be routinely sampled.
  - iv. Some deep burrowing species mine rich veins of organic material (Griggs *et al*. 1969)
  - v. **Jumars & Wheatcroft (1989)** speculated that L_b is set instead by rapidly increasing gross costs of burrowing unmatched by gross gains, with resultant net gains sharply decreasing with a sedimentary overburden of 10 cm.

l. **Wheatcroft *et al.* (1990)**: horizontal displacements exceed in distance and frequency, vertical displacements.
  -Horizontal mixing makes profiles look diffusive

m. Conveyor-belt species (**Rhoads 1974**)
  - i. Add an advective or "nonlocal" term to Eq. 17.1
  - ii. Particle selectivity important

  Graded bedding (Rhoads & Stanley 1965) can result.

n. Reverse conveyor-belt feeding. Surface sediments are dragged down and deposited well below the sediment water interface (see J. N. Smith *et al*. 1986 and Chapter 18).

o. Other modifications of 17.1

    - i. **Officer & Lynch (1982)** quantified the effects of compaction
    - ii. **Carpenter *et al.* (1982)** found that even a low rate of mixing below the nominal depth L_b could greatly affect estimates of A.
    - iii. Burrowing depth and body size are positively correlated.
    - iv. Trace distributions
  - p. Episodic food input
  - q. **Graf (1989)** exciting observations suggest that large animals respond to the episodic organic input by drawing material from the surface and depositing it at depth.
  - r. Burrowing in excess of 2 m from the sedimentary surface is well known from regions where turbidites or other unsteady or unusual deposition regimes bury organic-rich deposits below the normal extent of L_b (Griggs et al 1969; **Pemberton *et al.* 1976**).
  - s. Mn nodules discussed.

Matisoff, G. 1982. Mathematical models of bioturbation. Pp. 289-330 *in* P. L. McCall and M. J. S. Tevesz, *eds*., Animal-sediment relations. Plenum Press, New York

- 1. Introduction
  - a. **Processes to be modeled**
    - i. matter in 3 states: particle solid and matter.
    - ii. bioturbation can obscure stratigraphy.
      graded bedding.
    - iii. effects on diagenesis
  - b. **Kinds of models and their objectives**
    - i. types of models
      deterministic vs. stochastic models
    - ii. Diffusion models.
    - iii. Box models
      introduced by Berger and Heath.
    - iv. Signal-theory-based model of **Goureau (1977)**
    - v. Markov models.
- 2. **Particle transport models**
  - a. **Diffusion models**
    - i. particles don't diffuse
    - ii. **Goldberg & Koide (1962)**: ionium to thorium ratio in upper portion of pelagic sediment column [an oxymoron]
    - iii. Applications.
    - iv. Equations.

$$\frac{\partial A}{\partial t} = \frac{\partial}{\partial z}\left[D_b \frac{\partial A}{\partial z}\right] - \omega \frac{\partial A}{\partial z} - \lambda A. \qquad \textbf{(8)}$$

      D_b can be assumed constant or can be assigned a variety of functional dependencies (see **Robbins 1986**)
      $\delta/\delta z[D_b\ (\delta A_1/\delta z)]-\omega(\delta A_1/\delta z)-\lambda\ A=0\ z<m$ (2)
      $-\omega(\delta A_2/\delta z)-\lambda\ A_2=0\ z<m$
      {His equation 2, both parts, are wrong. See **Aller 1982 p. 60**)
    - v. **Guinasso & Schink (1975)** dimensional analysis:
      $D_b=mv_c$, (5)
      where v_c is the apparent sedimentation rate.
    - vi. Benninger *et al.* (1979) modeled deep burrows filling in with surface material.
    - vii. Fisher modeled bioturbation as an advective process:
      $\delta A/\delta t=\delta/\delta z[D_b\ (\delta A/\delta z)]-\omega(\delta A/\delta z)-S(z)$ (6)
      S(z) is the radioactive surface loss due to feeding.
    - viii. Table 2. P. 304.

Table II. Comparison of selected values of D_b from Table 1 with values corrected for biomass density (g/dry weight/cm^2).

- b. Box models
- c. Signal processing models
- d. Markov models

3. Fluid transport models
   - a. Diffusion-reaction models
   - b. Advection models

4. Conclusions
   - a. References.

Rice, D. L. 1986. Early diagenesis in bioadvective sediments: relationships between the diagenesis of beryllium-7, sediment reworking rates, and the abundance of conveyor-belt deposit feeders. J. Mar. Res. *44*: 149-184.{**7**, **9**, **10**, **12**, **15**, **24**}

I. **Abstract**
   - A. *Scoloplos* spp. in Lowes Cove Maine
   - B. laboratory rates incorporated into steady-state and transient state models
   - C. Be-7 tracer (53.3 d half life)
   - D. bioadvective mixing of marker peak
   - E. *Scoloplos* accounted for all of the particle subduction
   - F. conveyor-belt diagenetic model
     - 1. seasonal variation of the surface biodeposition
     - 2. constant Be-7 at surface

II. **Introduction**
   - A. Aller and Fisher reviewed.
   - B. bioturbation and radioactive tracers
     - 1. slow: ^{210}Pb
     - 2. fast ^{234}Th and ^{7}Be
     - 3. **Goldberg-Koide (1962)** advection-diffusion equation
   - C. Conveyor-belt feeders
     - 1. late stage of succession
     - 2. tubificid oligochaetes
   - D. Scoloplos
   - E. **Study area**
     - 1. Lowes cove
     - 2. 9 mm/yr sedimentation rate
   - F. Macrobenthos
     - 1. *Macoma*, *Mya*, *Mytilus*
     - 2. *Hydrobia*
     - 3. *Nereis succinea*
     - 4. *Streblospio benedicti*, *Polydora ligni*
     - 5. *Tharyx acutus*
     - 6. *Heteromastus filiformis*
     - 7. **Scoloplos** (200-3000 m^{-2})
     - 8. *Saccoglossus kowaleskii* (Harrimanidae: Hemichordata
     - 9. *Corophium volutator* to 4000/m^2
   - G. Standing stock 1.6 g dry weight/m^2
   - H. 4 species: *S. robustus., S. acutus, S. fragilis* and *S. armiger*.
     S. armiger is small

III. **Methods**
   - **A.** **temporal and spatial distributions**
     - 1. 3 stations sampled 6-7 times
     - 2. 500-µm mesh sieved
   - B. **Biodeposition rates**
     -calculated per unit biomass
   - C. **bioadvection in incubated cores**
     - 1. August 1982
     - 2. **Aller & Dodge (1974)** methods, thin marker layer

D. **^{7}Be profiles**
  non-destructive γ (γ) spectrometry
    Larsen and Cutshall, 1981
    coaxial ≥ detector shielded by 20 cm of low background milled steel

IV. **Results.**

A. temporal and spatial variation in *Scoloplos* abundance

Fig. 4. Highest abundances at station 8.

- characteristic numbers and biomass maintained

B. rates of biodeposition by *Scoloplos*
1. 120 mg dry sediments per mg dry biomass per day
2. **or** 176 +/- 55 mg dry sediment/worm per day
3. The data indicate that individual ingestion/egestion rates are proportional to biomass and that population biodeposition rates may be predicted with greater certainty on the basis of standing biomass rather than population or numerical density.

C. **Macrofauna and sediment turnover in incubated cores.**
1. sediment similar to ambient
2. dispersion of chalk layer, mode of transport was advective

Fig. 5. Subduction of marker horizons [chalk] during laboratory incubation at 21°C at stations C7, low abundances and C8, high abundances.

3. Final marker thickness in C7 was 2mm in C9, 9mm.
4. Subduction of the marker layer was about 4.5 times faster in C8 than C7.

D. **^{7}Be activity-depth relations**
  -monotonic roughly exponential decrease to 3-3.5 cm

Table 4. ^{7}Be activity and porosity depth variation at station 84-6 (August 1984)

V. **Discussion**

A. Biodeposition rates 120 g dry sediment/g (dry weight) worm/day

B. proportionality of deposition rates is similar to the rates observed for *Tubifix*

C. Field reworking rates:

$$R_o = B*r/[\rho[1-\Phi_s] \quad (1)$$

R_o is the rate of *Scoloplos* particle biodeposit accretion.
where, B is *Scoloplos* standing crop
r is biomass-specific particle ingestion rate
ρ is the average density of the particle
Φ_s is the porosity of the deposit

1. example 0.75 cm/month subduction velocity.
2. annually, it is 7 cm/yr or 8 times the local sedimentation rate.

D. ***Scoloplos* abundance and bioadvective subduction velocity. P 163**
1. movement of chalk layer
2. *Scoloplos* feeding accounts for the difference in movement of chalk layers.
3. One dimensional diagenetic equation. **Berner (1980)**
   a. particle advection is broken down into two components. allochthonous burial and autochthonous=s
   b. assumes constant surface activity

“...conveyor belt subduction of a horizon at any depth x is due to feeding activity occurring below that horizon, provided that the steady-state porosity profile is maintained. It is also clear that conveyor-belt subduction of all particles is due to transport of those particles which the deposit feeder selects for ingestion.”

E. Bioadvective contribution to sediment mixing in Lowes Cove.

- ingest particles less than 250 µm.

F. **Steady state: constant biodeposition rate and constant surface concentration.**
1. physical processes control surface transport

Fig. 7. **^{7}Be depth profiles at station 84-6**. and steady state bioadvection profiles

2. conclusion: model fits the data quite well
3. random mixing coefficient

Fig. 8. Curve fits of the usual random mixing model [**Goldberg-Koide** and calculated mixing coefficients. [a poor fit]

G. **transient state: Case 1: cyclic annual variation in biodeposition rate and constant ^{7}Be surface concentration.**

1. assume biodeposition rate r is a function only of temperature.
2. use the Arrhenius equation:

$r(T) = A\, e^{[-Ea/RT(t)]}$, where $A = 1.39 \times 10^{22}\ g*g^{-1}*d^{-1}m$, $E_a = 27.0$ kcal/mol and $R = 1.987 \times 10^{-3}\ kcal*°^{-1}*mol^{-1}$ (**Rice et al. 1986**)

3. temperature fluctuations improved the fit.

Fig. 9. Fit using seasonally varying temperature-dependent ingestion. Assumes constant surface concentration. *Nevertheless, it is still clear that the steady-state prediction is in remarkably good agreement with the data and with this transient-state prediction." p. 174*

4. Is ^{7}Be surface concentration maintained?

H. **transient sate: cyclic annual variation in biodeposition rate with variable ^{7}Be surface concentration due to variations in atmospheric deposition and/or conveyor-belt dilution.**

1. S_o is constant only if
   a. the concentration in new and recycled material change seasonally in such a way as to perfectly balance varying w_s. or
   b. if the boundary condition is ineffective because of external buffering.
2. Case 2
3. the hypothetical conveyor-belt boundary condition appears to be so strongly controlled externally as to be almost ineffective in influencing $S_o(t)$
4. differences in atmospheric input is also buffered.

I. **Relationships between the abundance of *Scoloplos* and other benthic biogeochemical phenomena.** p. 179

1. positive correlation with depth average POM
2. labile organic matter brought to depth

VI. **Conclusions**

A. Biological reworking by *Scoloplos* important
B. ^{7}Be can be explained by an bioadvective diagenetic model and constant surface concentration of ^{7}Be
C. seasonal variation in atmospheric deposition of ^{7}Be and dilution of ^{7}Be on the sediment surface did not improve upon a diagenetic model in which ^{7}Be concentration was constant

Rice, D. L., T. S. Bianchi, and E. H. Roper. 1986. Experimental studies of sediment reworking and growth of *Scoloplos* spp. (Orbiniidae: Polychaeta) Marine Ecology Progress Series *30*: 9-19{24}

1. Abstract:
   a. surface biodeposition
   b. particle reworking rates proportional to worm biomass
   c. 24% carbon assimilation efficiency
   d. Gross growth efficiencies of 2.4% and 8.3%, respectively.
   e. 4% of the total nitrogen in the experimental sediment from Flax Pond, New York was nutritionally available to the worms.
   f. most of the organic nitrogen required must be met by utilizing organic detritus.

Shull, D. H. 2001. Transition-matrix model of bioturbation and radionuclide digenesis. Limnol. Oceanogr. *46*: 905-916. *[Narragansett Bay Th-234 & Pb-210 profiles modeled, indicating food caching by maldanids.]*

Solan, M., B. J. Cardinale, A. L. Downing, K. A. M. Engelhardt, J. L. Ruesink, and D. S. Srivastava. 2004. Extinction and Ecosystem Function in the Marine Benthos. Science *306*: 1177-1180.*["Here we use data from marine invertebrate communities to parameterize models that predict how extinctions will affect sediment bioturbation, a process vital to the persistence of aquatic communities. We show that species extinction is generally expected to reduce bioturbation, but the magnitude of reduction depends on how the functional traits of individual species covary with their risk of extinction."]* {?}

Web Resources

Table 2. Web Resources on bioturbation

URL	Site	Description
http://www.epa.gov/aed/html/ct/index.html	EPA Atlantic Ecology Division	CT Analysis and 3D Visualization of Marine Sediment Communities
http://seis.natsci.csulb.edu/bperry/Sedimentary%20Rocks%20Tour/bioturbation.htm	Sedimentary Rocks Tour	Bioturbation traces in rock
http://massbay.mit.edu/marinecenter/Publications/publication002/shull1998a.htm	MIT Sea Grant program	Predicting Dredged-Material Cap Thickness from Data on Benthic Community Structure David H. Shull and Eugene D. Gallagher

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Gray, J. S. 1974. Animal-sediment relationships. Oceanogr. Mar. Biol. Ann. Rev. *12*: 233-261. *[Focuses mainly on the ecological aspects - little on bioturbation or geochemistry]*

Jumars, P. A. 1993a. Gourmands of mud: diet selection in marine deposit feeders. Pp. 124-157 *in* R. N. Hughes, *ed*., Mechanisms of Diet Choice. Blackwell Scientific Publishers, Oxford.

Jumars, P. A. 1993b. Concepts in biological oceanography. Oxford University Press, New York & Oxford. 348 pp. *[Chapter 17 is an insightful review of the effects of bioturbation on stratigraphy, including synopses of* ***Wheatcroft et al.'s (1990)*** *work on mechanistic interpretations of* D_b*]*

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ON FECAL PELLETS

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