**DEPOSIT FEEDING**

1. Definitions

2. Significance

3. Generalizations

4. Types of deposit feeders

5. The Great Food Controversy

Definition:

**Deposit Feeder** = an animal that ingests deposited, particulate food which primarily consists of relatively inert material of low nutritional value (mineral grains, refractory organic matter, etc.)

## TABLE 1
*Weight-specific feeding rates of deposit feeders*

| Species | mg sediment ingested $\times$ mg$^{-1}$ body wt | Reference |
|---|---|---|
| **GASTROPODS** | | |
| *Ilyanassa obsoleta* | 0.4 | Connor & Edgar, 1982 |
| *Hydrobia neglecta* | 2.9 | Hylleberg, 1975[a] |
| *Hydrobia ventrosa* | 4.3 | Hylleberg, 1975[a] |
| *Potamopyrgus jenkensi* | 5.9 | Heywood & Edwards, 1962[a] |
| *Amphibola crenata* | 25 | Juniper, 1981 |
| **BIVALVES** | | |
| *Macoma nasuta* | 1–2 | Hylleberg & Gallucci, 1975[a] |
| *Macoma balthica* | 9 | Kofoed, unpub. |
| *Yoldia limatula* | 10–20 | Bender & Davis, 1984[b] |
| *Nucula annulata* | 2–5 | Cheng, 1983 |
| **ANNELIDS** | | |
| *Tubifex tubifex* | 1.6 | Ivlev, 1939[a] |
| *Capitella capitata* | 8–10 | T. Forbes, 1984 |
| *Nereis succinea* | 3.5 | Cammen, 1980a |
| *Scoloplus* sp. | 45–120 | D. Rice, unpub. |
| *Axiothella rubrocincta* | 10–30 | Kudenov, 1982 |
| *Arenicola marina* | 5.1 | Jacobsen, 1967[a] |
| *Arenicola claparedi* | 25 | Hobson, 1967[a] |
| *Pectinaria gouldii* | 21 | Gordon, 1966[a] |
| **ARTHROPODS** | | |
| *Hyalella azteca* | 1.3 | Hargrave, 1972[a] |
| *Ilyoplax pusilla* | 5.7 | Ono, 1965[a] |
| *Scopimera globosa* | 0.8 | Ono, 1965[a] |
| **VERTEBRATES** | | |
| *Liza dumerili* | 0.6 | Marais, 1980 |

[a] References cited in Cammen, 1980b. Refer to Cammen (1980b) for further details.
[b] Total sediment processing rate measured by Bender and Davis (1984) corrected for feces: pseudofeces production of 1:10 (Tantichodok, unpub.).

Lopez and Levinton, 1987
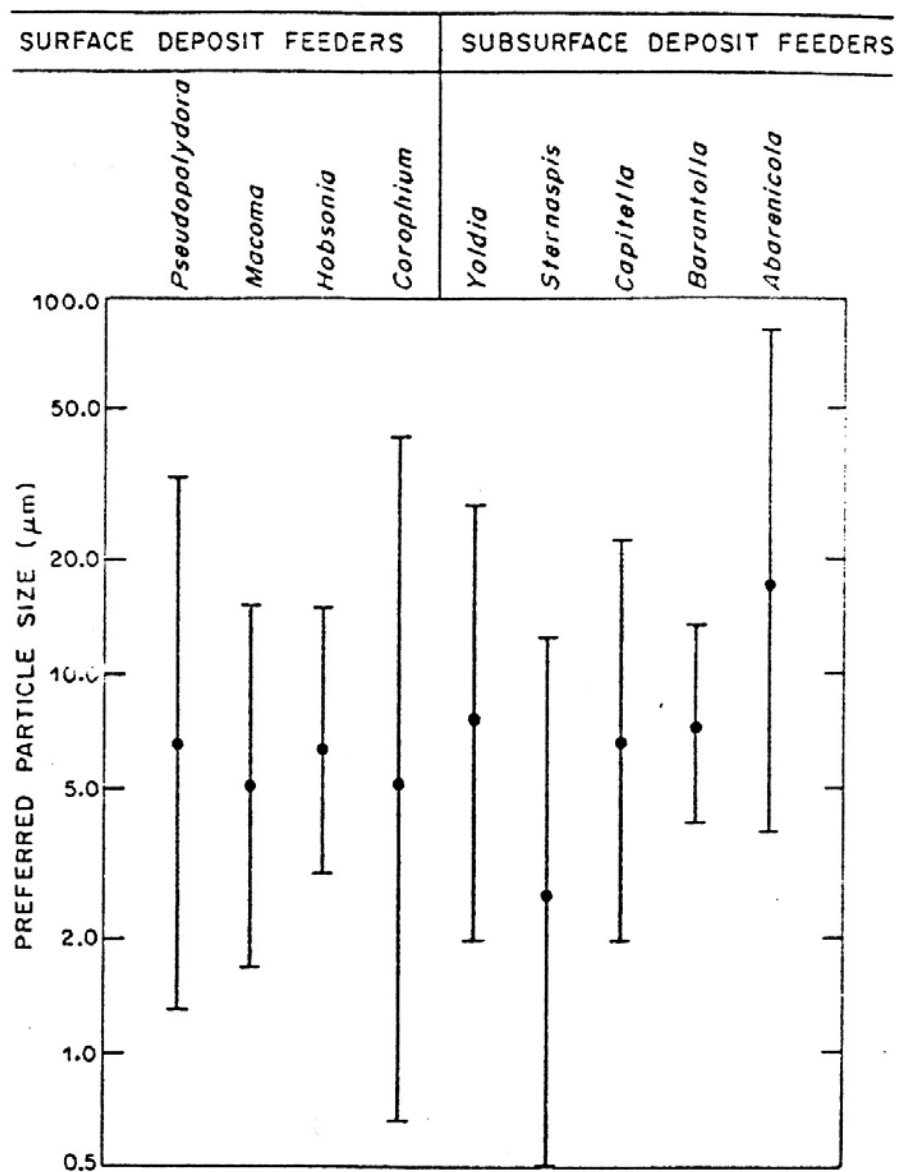
Self and Jumars, 1988

(also see Guieb et al., 2004)

Figure 6. Estimate of most highly preferred particle diameter ± 1 standard error (68% confidence limits) for surface (particle specific gravity of 2.65 assumed) and subsurface deposit feeders.
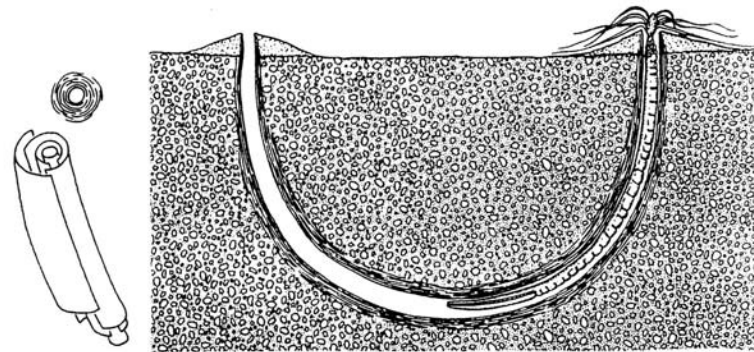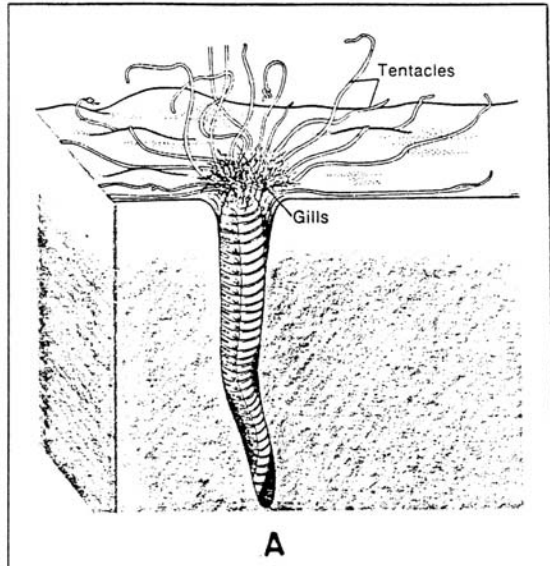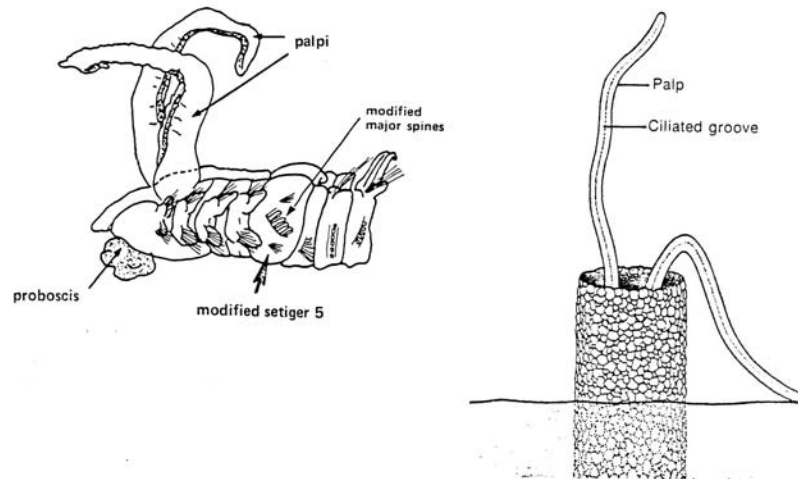
**Figure 4.20** The U-burrow of *Amphitrite ornata*, showing (left) the laminated mud wall in cross section and as an exploded constructional diagram. Data adapted from Rhoads (1967) and Aller & Yingst (1978).

*Amphitrite* (terribellid polychaete)

**Tentaculate Surface**

**Deposit Feeders**



Spionid polychaete

# Size-selective downward particle transport by cirratulid polychaetes

by David H. Shull[1,2] and Michie Yasuda[3]

## ABSTRACT

The deposition of surficial sediments many centimeters below the sediment-water interface due to the reworking activities of organisms is a potentially important but easily overlooked process in marine sediments. This kind of downward particle transport is difficult to observe in the laboratory or in the field but it has important consequences for bioturbation rates and sediment geochemistry. It is also much more likely to be size dependent than other sediment-mixing mechanisms, such as conveyor-belt feeding, and may also explain some subsurface maxima observed in sediment chemical profiles.

We examined the mechanisms behind downward particle transport in Boston Harbor. Laboratory observations indicated that a large cirratulid polychaete, *Cirriformia grandis*, collected particles (glass beads) near the sediment surface and deposited them at depth. Furthermore, particle collection by this species was size dependent. *C. grandis* preferred smaller particles in the 16- to 32-µm size range relative to larger particles.

A mathematical model was developed to simulate the feeding and burrowing mechanisms of *C. grandis* and to predict the vertical profiles of tracer particles of assorted sizes in the field. The model was tested by comparing predicted profiles with profiles of glass beads measured at the field site. These glass beads were deployed in replicated patches on the bottom of Boston Harbor. Vertical distributions of the beads after 99 d were compared to profiles predicted by the model. Good agreement between predicted and measured profiles indicated that the feeding and burrowing mechanisms of *C. grandis* were sufficient to determine observed patterns of size-dependent bioturbation rates at this site.
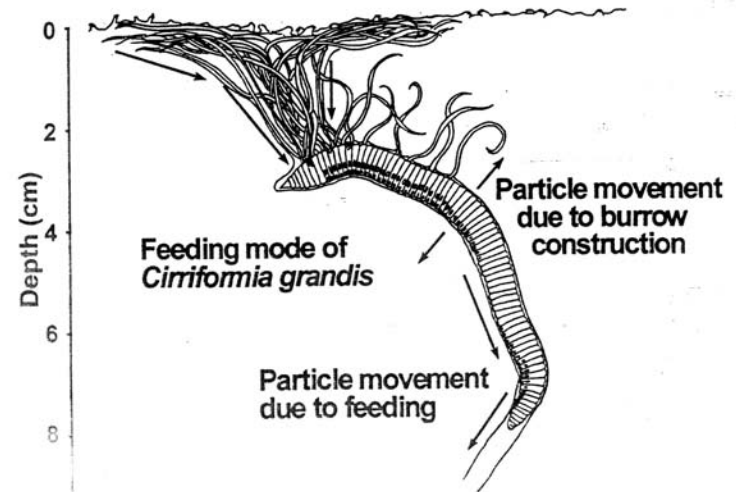


Figure 2. Feeding and burrowing mechanisms of *C. grandis*. Particles are collected near the sediment-water interface and are deposited along the entire length of the burrow. Burrows are created by displacing sediment approximately one half body width.



**Tentaculate Surface Deposit Feeders**

*Psychropotes longicauda*
Surface-deposit feeding holothurian
(5000 m central Pacific)
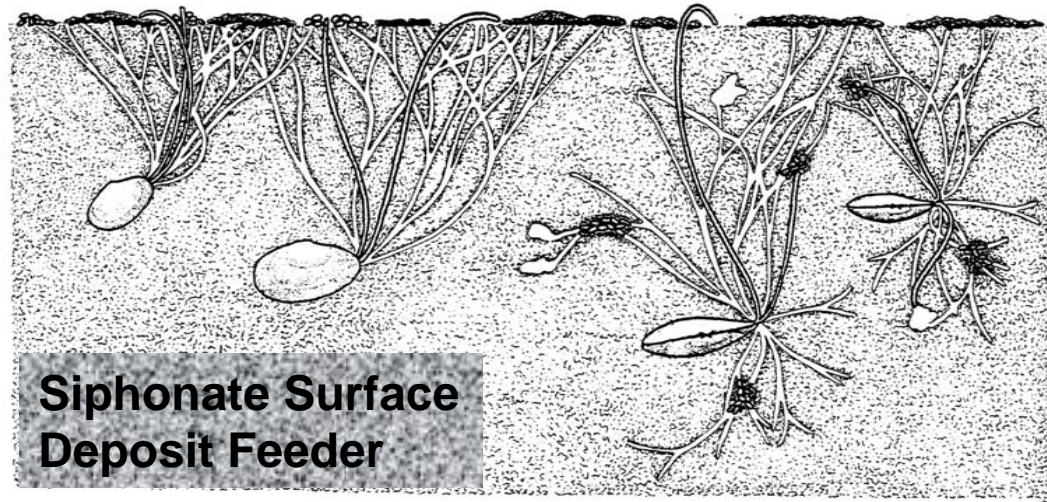
**Siphonate Surface Deposit Feeder**

**Figure 5.2** The deepsea tellinid bivalves *Abra nitida* (left) and *A. longicallus*, feeding. Siphonal activity zones are shown by networks of abandoned canals. *A. nitida* feeds on detritus and places both pseudofaeces and faeces on the seafloor, which is normal behaviour for tellinids. *A. longicallus*, however, deposit feeds below the surface, and while it advects pseudofaecal material up to the surface, faecal pellets are deposited at feeding level. This was interpreted by Allen (1983) as gardening activity. Modified after Wikander (1980).
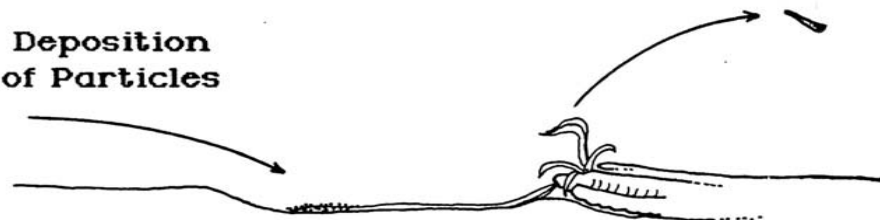
$$U(z)$$
$$\longrightarrow$$
$$C(z)$$

**Pit Feeder**

Deposition of Particles

Feeding Pit          Amphicteis

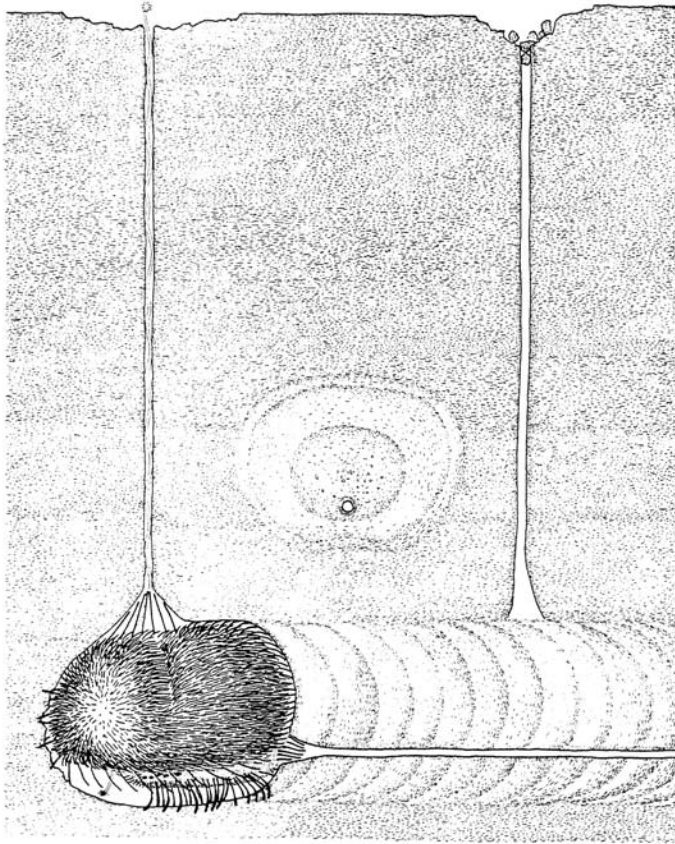**Figure 5.11** *Echinocardium cordatum* in its burrow. Behind it an abandoned shaft remains open in the muddy substrate. Above, a cross section of the backfill and subcentral drain.
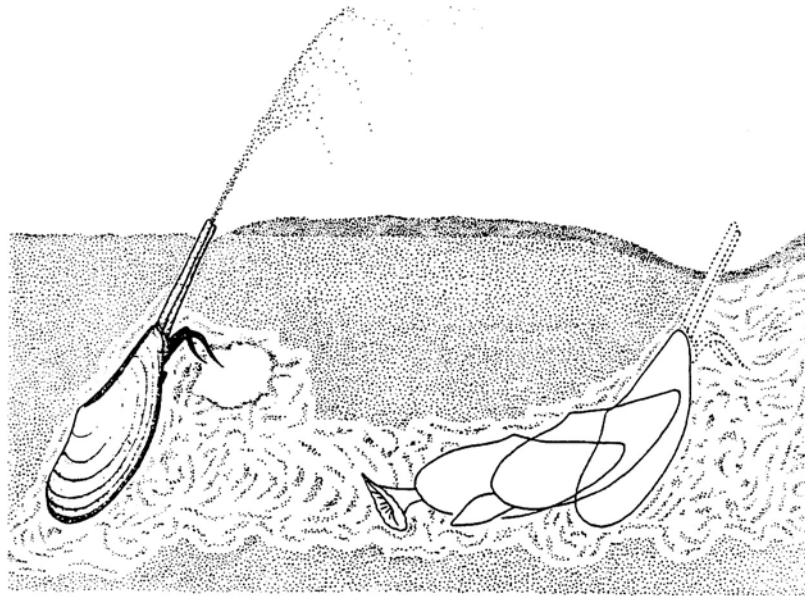
**Tentaculate Subsurface Deposit Feeders**



**Figure 5.1** *Yoldia limatula*, deposit feeding and shifting from left to right to a new feeding site. Modified after Rhoads (1963, 1974) and Aller & Cochran (1976).
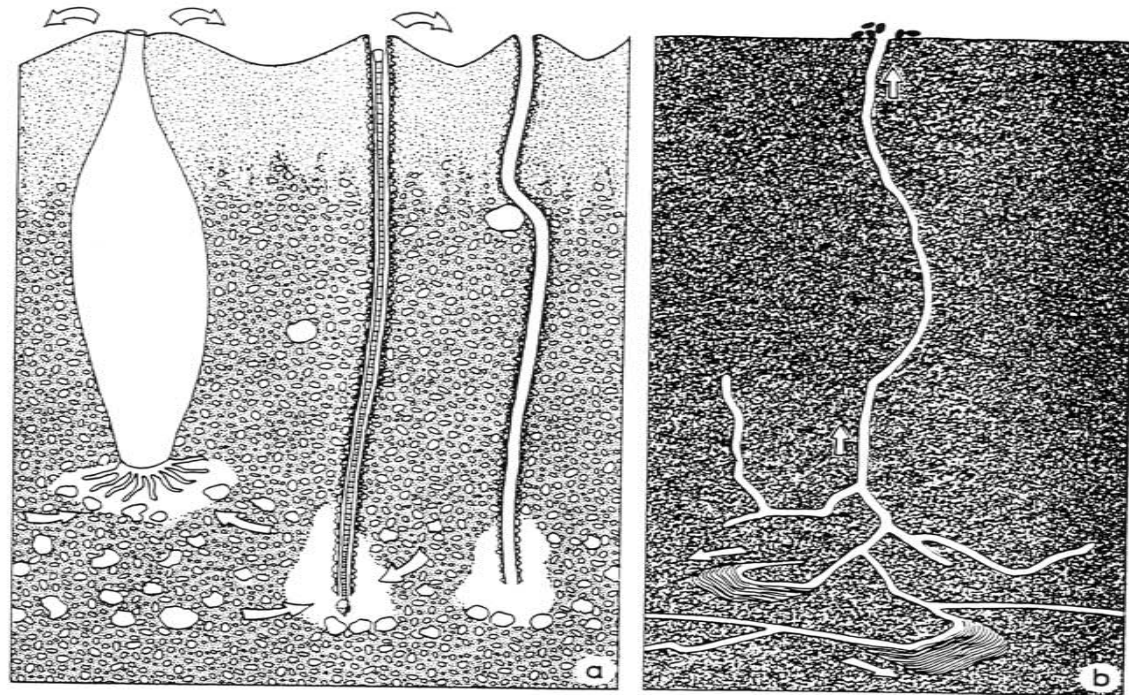
**Figure 4.15** Conveyor deposit-feeder systems. (a) *Molpadia oolitica* feeding 20 cm below seafloor together with two individuals of *Clymenella torquata* in their tubes of sand bound with mucus. Fine particles only are ingested and their advection upwards (arrows) causes the entire substrate to subside downwards, producing a graded bed and leaving a residual layer of coarse grains at head level. (b) *Heteromastus filiformis* (burrow diameter exaggerated) showing two directions of particle advection (arrows). Modified after Schäfer (1962) and Rhoads (1967, 1974).

**Conveyor-belt Feeders (Pharyngeal and tentaculate subsurface deposit feeders)**

head

Tail (pygidium)
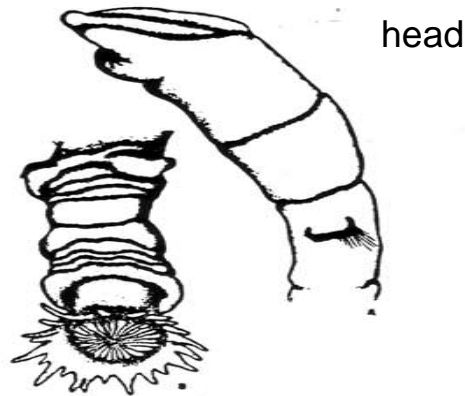
**Funnel Feeder
(Pharyngeal
subsurface deposit
feeders)**
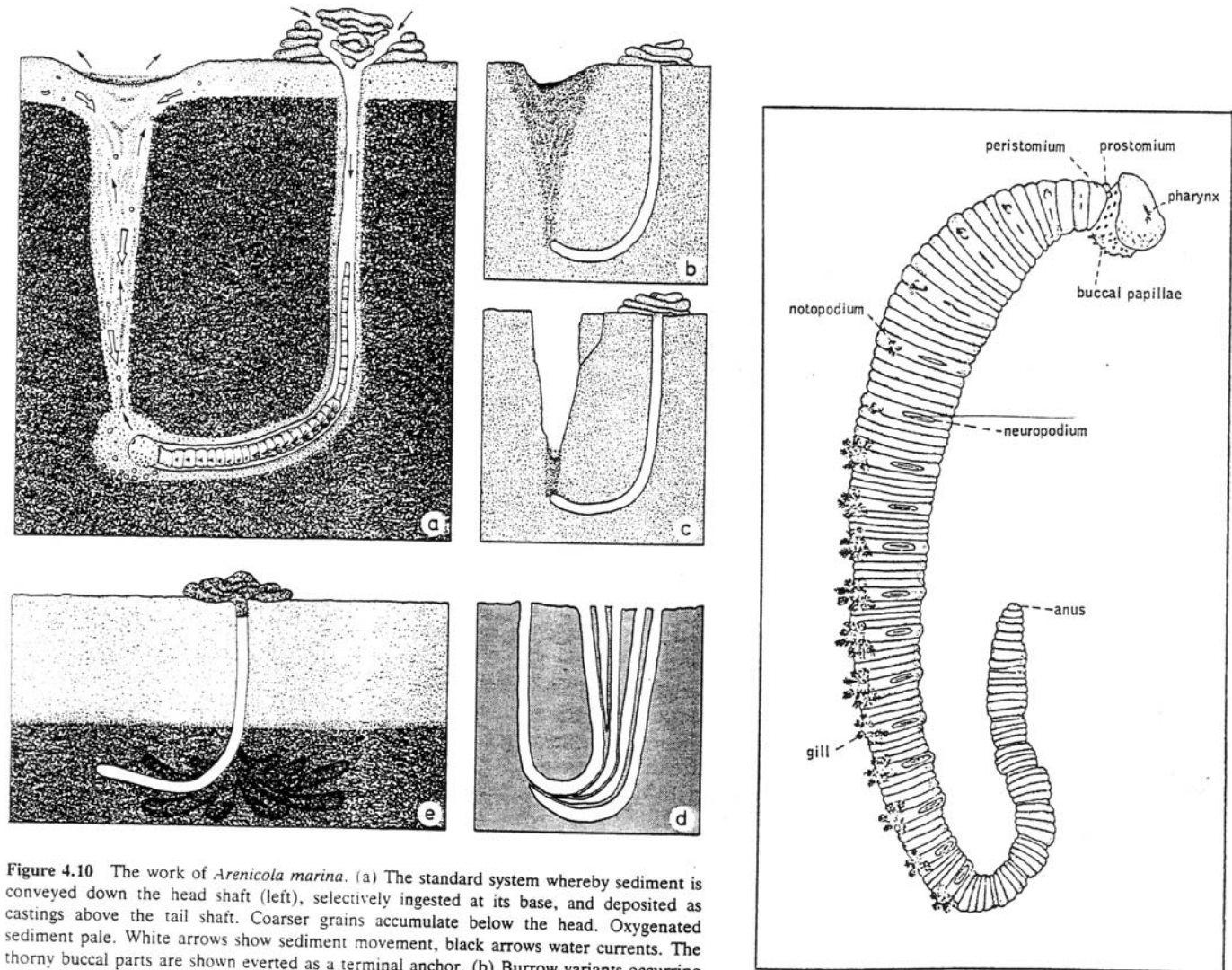


Figure 4.10 The work of *Arenicola marina*. (a) The standard system whereby sediment is conveyed down the head shaft (left), selectively ingested at its base, and deposited as castings above the tail shaft. Coarser grains accumulate below the head. Oxygenated sediment pale. White arrows show sediment movement, black arrows water currents. The thorny buccal parts are shown everted as a terminal anchor. (b) Burrow variants occurring in loose and (c) firm sediment. (d) Unusual variant where *A. marina* succeeds in exploiting clayey substrate. (e) Compound structure produced where the worm, deposit feeding in an organic rich substrate, moves the burrow radially around a stationary tail shaft. Modified after Schäfer (1962), Rijken (1979) and other sources mentioned in the text.
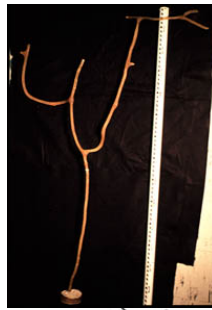
*Callianassa* (shrimp, burrow and sampling)
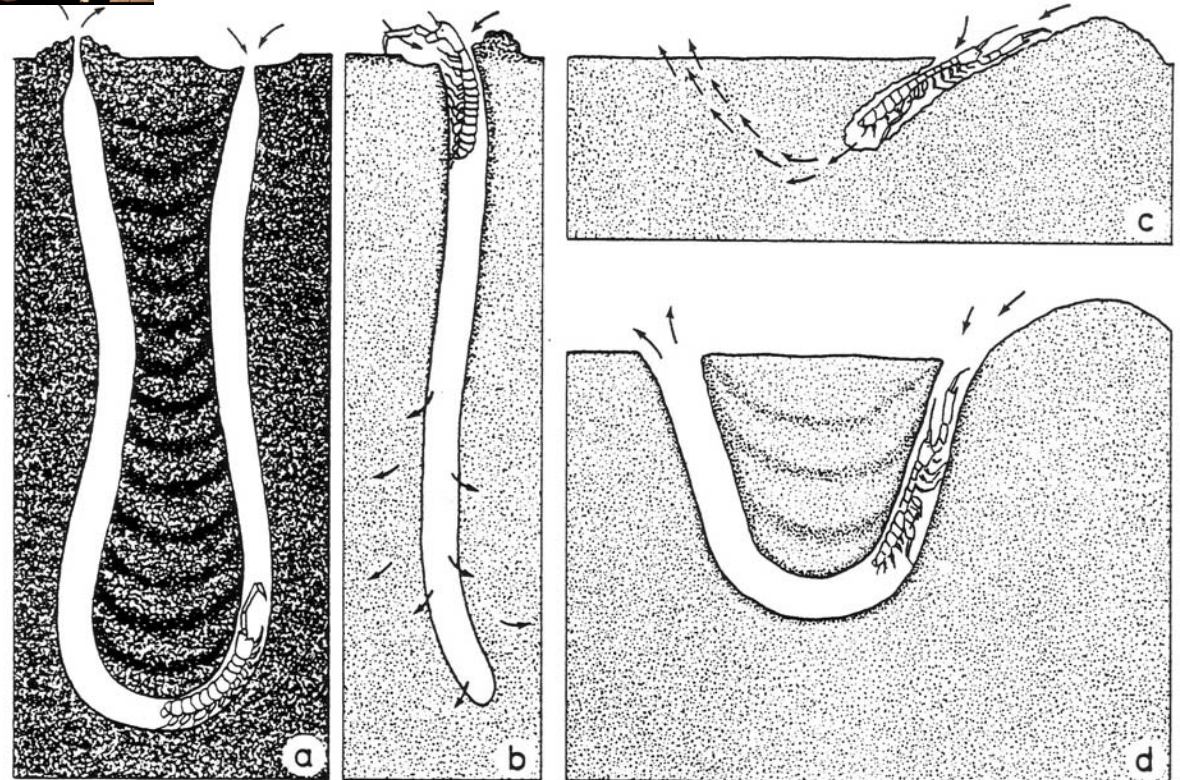
**"Shoveling"
Subsurface/Surface
Deposit Feeder**

Figure 4.9 (a) U-burrow of *Corophium volutator* in mud and (b) in sand. Arrows indicate water currents. Modified after Seilacher (1953a). (c) A stage in burrow construction by *C. arenarium*. Passage of respiration water through the sand weakens the substrate and eases construction of a second shaft. This U-burrow is then gradually deepened (d). Data from Ingle (1966).

## Nutritional needs of deposit feeders:

- Organic carbon

- Organic nitrogen

- Essential fatty acids (long chain PUFAs)

- Essential amino acids (~10)

- Sterols

- Vitamins

## Potential food sources:

- Vascular plant detritus $\longrightarrow$ $C_{org,}$ N?, sterols?

- Algae (live and dead) $\longrightarrow$ $C_{org}$, N?, sterols, PUFAs

- Sediment bacteria - SW $\longrightarrow$ $C_{org}$, N, E.A.A.s?

- Sediment bacteria – DS $\longrightarrow$ $C_{org}$, N, E.A.A.s?, PUFAs

- Protozoa and meio-

      fauna $\longrightarrow$ all nutrients

- Amorphous OM $\longrightarrow$ $C_{org}$, ?

Table 1. Partial fatty acid spectrum of some marine animals, illustrating the typical marine pattern in which the dominant polyunsaturated acids are 20:5ω3 and 22:6ω3. Values are given as the percent of total fatty acids for each specimen. NR = not reported; (−) indicates not detected

| Fatty acid | Animal | | | | | |
|---|---|---|---|---|---|---|
| | *Nephtys incisa*[a] | *Bolinopsis infundibulum*[b] | *Peneaus indicus*[c] | *Calanus helgolandicus*[d] | *Crassostrea gigas*[e] | *Fundulus heteroclitus*[f] |
| 16:0 | 16.2 | 23.2 | 15.5 | 40.0 | 7.7 | 9.0 |
| 18:0 | 13.1 | 5.2 | 8.2 | 4.1 | 2.2 | 5.1 |
| 18:1ω9 | 16.1 | 4.3 | 12.8 | 2.7 | 5.9 | 10.0 |
| 18:2ω6 | NR | 0.6 | 4.3 | — | — | 1.6 |
| 18:3ω3 | NR | 0.4 | 1.0 | — | 5.3 | 2.7 |
| 20:5ω3 | 23.2 | 22.4 | 11.2 | 13.3 | 11.4 | 7.5 |
| 22:6ω3 | 14.2 | 19.6 | 11.0 | 36.5 | 15.8 | 28.6 |

[a] Deposit feeding polychaete. Farrington et al., 1973.
[b] Ctenophore. Morris et al., 1983. Phospholipid fraction only.
[c] Crustacean (prawn). Read, 1981. Animals fed "reference diet."
[d] Crustacean (zooplankter). Lee et al., 1971. "Wild type" animals; phospholipid fraction only.
[e] Mollusc (oyster spat). Langdon and Waldock, 1981. Hatchery-reared spat; phospholipid fraction only.
[f] Salt marsh killifish. Jeffries, 1972. Muscle extract.

Table 2. Partial fatty acid spectrum of some representative detrital substrates and microbes. Values are given as percent of total fatty acids for each sample. (−) indicates not detected

| Fatty acid | Detrital component | | | | | |
|---|---|---|---|---|---|---|
| | Marsh grass[a] | Marsh fungi[b] | Sediment bacteria[c] | Diatoms[d] | Seaweed[e] | Protozoans[f] |
| 16:0 | 24.1 | 20.4 | 22.0 | 6.3 | 23.8 | 5.3 |
| 18:0 | 3.1 | 7.0 | 6.7 | NR | 0.8 | 10.8 |
| 18:1ω9 | 7.8 | 27.4 | 0.2 | 10.1 | 16.1 | 2.5 |
| 18:2ω6 | 17.3 | 33.0 | — | 14.3 | 4.0 | 1.5 |
| 18:3ω3 | 40.3 | 2.0 | — | — | 5.6 | NR |
| 20:5ω3 | — | — | — | 18.1 | 6.0 | 19.7 |
| 22:6ω3 | — | — | — | 0.7 | 1.0 | 32.1 |

[a] *Spartina alterniflora*, stems and leaves. Schultz and Quinn, 1973. The percentage of 18:3ω3 varies from 40 in October to about 8 in April, with complementary changes in 18:1ω9 and 18:2ω6.
[b] *Sphaerulina pedicellata*. Schultz and Quinn, 1973.
[c] Aerobic bacteria isolated from Loch Eil sediment. Parkes and Taylor, 1983.
[d] *Skeletonema costatum*. Lee et al., 1971. Phospholipid fraction only.
[e] *Laminaria pallida* (kelp), frond portion. Velimirov, 1979.
[f] *Noctiluca miliaris*. Dikarev et al., 1982.

Phillips, 1984

Table 3. Essential amino acid levels as percentages of total amino acids for a variety of marine invertebrates

| Amino acid | Animal | | | | | | Composite marine invertebrate |
|---|---|---|---|---|---|---|---|
| | Dungeness crab[a] | Red abalone[b] | Euphausiid[c] | Tunicate[d] | Hard coral[e] | Sea urchin[f] | |
| THR | 6.1 | 5.6 | 4.8 | 5.3 | 5.0 | 4.1 | 5.2 |
| VAL | 6.7 | 6.0 | 5.2 | 5.4 | 4.6 | 4.2 | 5.4 |
| MET | 2.2 | 2.6 | 3.2 | 2.4 | 2.1 | 0.7[g] | 2.5 |
| ILEU | 5.2 | 4.4 | 5.2 | 4.6 | 3.7 | 4.2 | 4.6 |
| LEU | 7.5 | 8.7 | 7.8 | 7.3 | 5.9 | 6.7 | 7.3 |
| PHE | 7.4 | 3.9 | 6.5 | 4.8 | 3.8 | 4.2 | 5.1 |
| HIS | 2.5 | 2.0 | 2.2 | 2.6 | 2.6 | 0.3[g] | 2.4 |
| LYS | 4.9 | 6.0 | 7.8 | 7.6 | 9.7[g] | 5.8 | 6.4 |
| TRYP | NR | NR | 1.6 | NR | NR | NR | 1.6 |
| ARG | 5.0 | 6.6 | 6.0 | 8.5 | 7.1 | 8.8 | 7.0 |

[a] *Cancer magister*. Lasser and Allen, 1976.
[b] *Haliotus rufescens*. Allen and Kilgore, 1975.
[c] *Euphausia pacifica*. Suyama et al., 1965.
[d] *Pyrosoma* sp. Raymont et al., 1975.
[e] *Caryophyllia smithii*. Raymont et al., 1975.
[f] *Strongylocentrotus droebachiensis*. Fong and Mann, 1980. Values are approximate averages over one year of field collections of the animals.
[g] Value not included in calculations for composite marine invertebrate.

Table 4. Relative deficiencies or excesses of essential amino acids (EAA) in various foods, in comparison to the tissue EAA profile of a composite marine invertebrate (see Table 3). Percent deficiency was calculated as $[(C_r - C_a)/(C_a)] \times 100$, where $C_r$ is the percentage of the particular EAA in food (percent of total amino acids) and $C_a$ is the same for animal tissue (Fong and Mann, 1980). Negative values indicate deficiencies and positive values indicate excesses of each EAA. The four most deficient EAA are listed below each column

| Amino acid | Potential food | | | | | | Estuarine particulate material[g] |
|---|---|---|---|---|---|---|---|
| | Live eelgrass[a] | Dead eelgrass[b] | Eelgrass detritus[c] | Green seaweed[d] | Microalgae[e] | Fungi[f] | |
| THR | 17.6 | 21.6 | 13.7 | 15.7 | 5.9 | 3.1 | 3.8 |
| VAL | 33.3 | 29.6 | 46.3 | 14.8 | −25.9 | −8.3 | 14.8 |
| MET | −32.0 | −44.0 | −36.0 | 36.0 | −12.0 | −58.0 | −8.0 |
| ILEU | 23.9 | 23.9 | 4.4 | 8.7 | −10.9 | −11.3 | 8.7 |
| LEU | 31.5 | 26.0 | 1.4 | 6.8 | 26.0 | −8.4 | 23.3 |
| PHE | 23.5 | 11.8 | −5.9 | 2.0 | 15.7 | −41.2 | 21.6 |
| HIS | −33.3 | −41.7 | −8.3 | −45.8 | −45.8 | 45.8 | 29.2 |
| LYS | −37.5 | −32.8 | −6.2 | −20.3 | 7.8 | 58.8 | −9.4 |
| ARG | −50.0 | −40.0 | −24.3 | −11.4 | −21.4 | 66.3 | −14.3 |
| | ARG | MET | MET | HIS | HIS | MET | ARG |
| | LYS | HIS | ARG | LYS | VAL | PHE | LYS |
| | HIS | ARG | HIS | ARG | ARG | ILEU | MET |
| | MET | LYS | LYS | | MET | LEU | |

[a,b] *Zostera marina*. Thayer et al., 1977.
[d] *Ulva lactuca* (sea lettuce). Munda and Gubensek, 1976.
[e] 25 species of phytoplanktonic algae. Chuecas and Riley, 1969.
[f] Single-cell protein from *Candida* sp. (an alkane yeast). Mahnken et al., 1980.
[g] Particulate material (>40 μm) from Chesapeake Bay near mouth of the Patuxent River (Sigleo et al., 1983).

Phillips, 1984

## TABLE 2
### Absorption of microbes and sedimentary organic matter by deposit feeders

| Species | % absorption | | |
|---|---|---|---|
| | Bacteria | Microalgae | Organics[a] |
| **GASTROPODS** | | | |
| *Potamopyrgus jenkensi* (Heywood & Edwards, 1962) | — | — | 4 |
| *Hydrobia ventrosa* (Kofoed, 1975) | 75 | 60–71 | 34[b] |
| *Hydrobia totteni* (Lopez & Cheng, 1983) | 36–49 | 30–48 | 29 |
| *Amphibola crenata* (Juniper, 1981) | 56 | — | — |
| **BIVALVES** | | | |
| *Nucula annulata* (Cheng, 1983 & unpub.) | 66–78 | — | 0–76 |
| *Nucula proxima* (Cheng, 1983 & unpub.) | 87–92 | — | 0–16 |
| **ANNELIDS** | | | |
| *Tubifex tubifex* (Brinkhurst & Austin, 1979) | — | — | 3.0 |
| *Limnodrilus hoffmeisteri* (Brinkhurst & Austin, 1979) | — | — | 5.2 |
| *Nereis succinnea* (Cammen, 1980a) | 57–62 | — | 10.5[c] |
| *Cirriformia tentaculata* (George, 1964) | — | — | 7.9 |
| *Capitella capitata* 1 (Forbes, 1984) | 33 | — | 38 |
| **ARTHROPODS** | | | |
| *Hyallela azteca* (Hargrave, 1970) | 60–83 | 45–75 | 6–15 |
| *Corophium volutator* (Nielsen and Kofoed, 1982) | — | 80–92 | — |
| *Chironomus plumosus* (Johannsson, 1980) | — | — | 0–14 |
| **ECHINODERMATA** | | | |
| *Parastichopus parvimensis* (Yingst, 1976) | 43 | 47 | 11–43 |

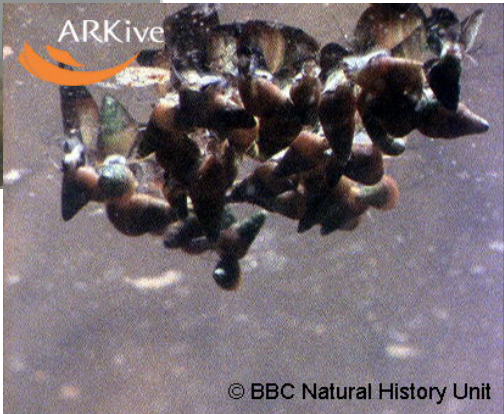[a] Bulk sedimentary organic matter, including detrital and microbial fractions.
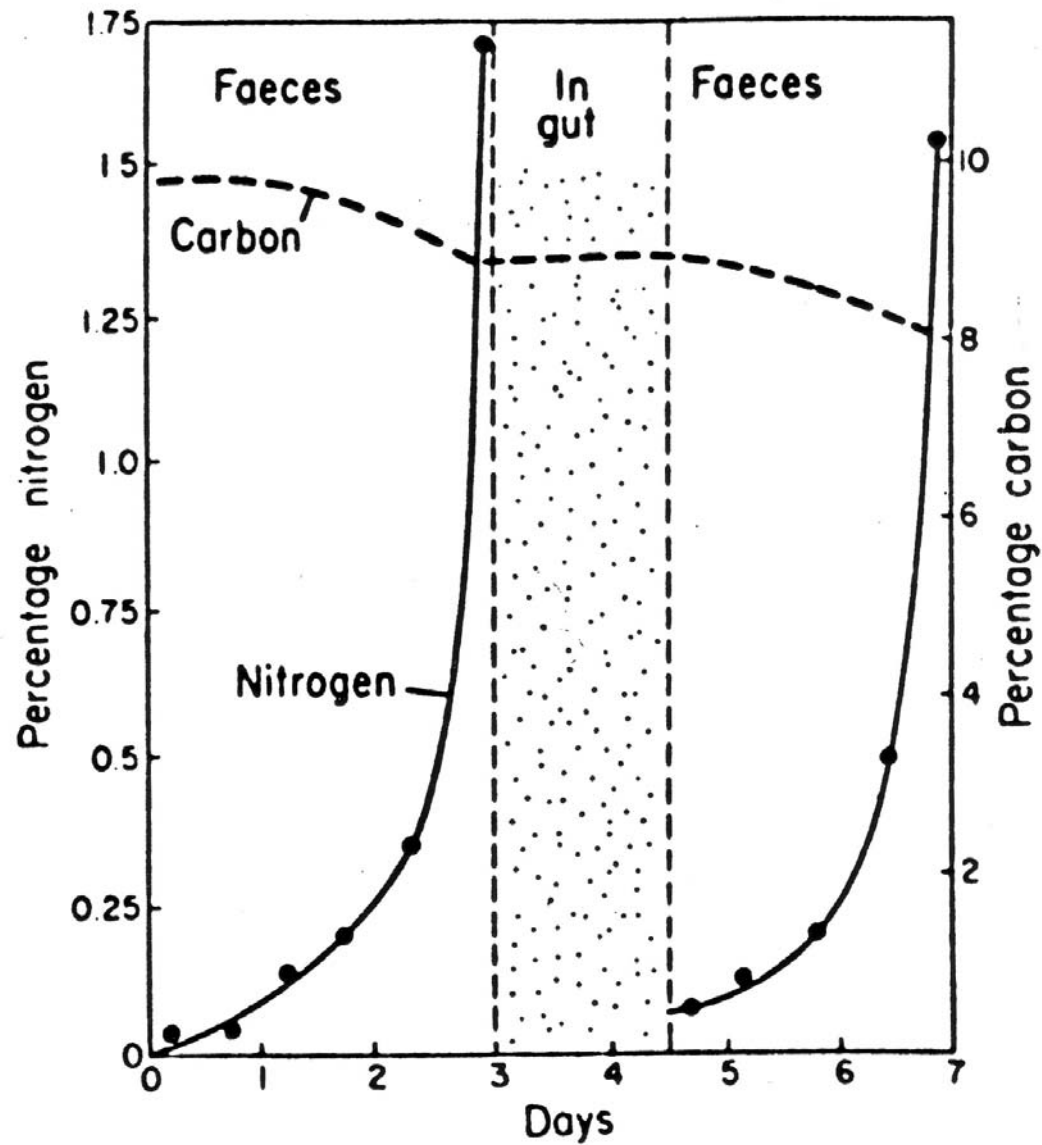[b] Barley hay
[c] *Spartina* detritus

Lopez and Levinton, 1987

Danish spartina marsh

*Hydrobia*

© BBC Natural History Unit

*Hydrobia*

Fig. 10. - Changes in carbon and nitrogen content of faeces of *Hydrobia ulvae* (I) during 3 days in sea water, (II) during passage through the gut and (III) during a second period of exposure to sea water. From Newell (1965).

# Potential impact on bacteria of grazing by a macrofaunal deposit-feeder, and the fate of bacterial production

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ABSTRACT: Bacterial biomass and production were compared to the carbon requirement and sediment processing capability of the deposit-feeding polychaete *Euzonus mucronata* (Treadwell) on a sand beach in Oregon, USA. Mean bacterial abundance ranged between sampling dates from 5.2 to 12.0 $\times$ $10^7$ cells g$^{-1}$ sediment and mean biomass ranged from 1.5 to 3.4 µg C g$^{-1}$ sediment (0.36 to 0.84 g C m$^{-2}$ to 15 cm depth). Daily bacterial production based on tritiated thymidine incorporation on 7 December 1982 is approximately 55 mg C m$^{-2}$ d$^{-1}$. The carbon requirement of *E. mucronata*, equal to the sum of annual production and respiratory loss of carbon, was 7.0 to 8.0 g C m$^{-2}$ yr$^{-1}$ (19.3 to 21.9 mg C m$^{-2}$ d$^{-1}$). Although bacterial production exceeded the carbon requirement of *E. mucronata*, the low bacterial density limits direct utilization of bacterial carbon to <10% of the average daily carbon requirement of *E. mucronata*, despite its relatively high sediment-processing capability. Conversely, *E. mucronata* ingests <10% of bacterial production per day. Because of their low density, sediment bacteria are probably not a major carbon source to other sand beach macrofauna. Bacterial turnover times (mean = 10 d) were similar to reported turnover times at much higher cell densities in other sediments, indicating that bacterial production exceeds macrofaunal production by one or more orders of magnitude in many environments. It is likely that macrofauna seldom consume more than a few percent of benthic bacterial production. Future studies of the fate of benthic bacterial production should examine the role of microbial and meiofaunal grazers.

*Euzonus* = ophiliid polychaete

# The trophic significance of bacterial carbon in a marine intertidal sediment: Results of an in situ stable isotope labeling study

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*Abstract*

We report the results of an in situ tracer experiment in an intertidal sediment, where bacterial carbon was tagged with stable carbon–isotope label, after the injection of $^{13}$C-glucose. The appearance of label in bacteria (based on label incorporation in bacteria-specific, phospholipid-derived fatty acids) and subsequent transfer to meiobenthos (group level) and macrobenthos (species level) was followed for 36 days. The label dynamics of benthic taxa were either fitted with a simple-isotope model or evaluated against enrichment in bacteria, to derive the importance of bacterially derived carbon for the meiobenthos and macrobenthos. Although selective uptake of bacteria was evident, as 2.4 times more bacterial carbon was grazed as expected from indiscriminate feeding, bacterial carbon accounted on average for only 0.08 and 0.11 of the carbon requirements of meiobenthic and macrobenthic taxa, respectively. Additionally, the contribution of bacterial carbon to total carbon requirements did not depend on the living/feeding depth in the sediment or organism size (evaluated over a size range of four orders of magnitude). The observed overall low contribution of bacterial carbon implies that most intertidal benthic fauna depend primarily on other carbon resources that may assert a stronger control on the structure of intertidal-sediment communities.

# Intraspecific Variations in $\delta^{13}C$ Indicate
# Ontogenetic Diet Changes in Deposit-Feeding Polychaetes

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***Abstract.*** Many species change diets during development. Often, these ontogenetic changes are discrete and coincide with metamorphosis (e.g., amphibians), but more gradual niche changes can occur during growth. Identifying non-discrete changes in diet and understanding their implications at the population and community levels are especially difficult for ecologists who study detritivores and other species that have poorly characterized diets. Theory and several lines of evidence suggest, however, that benthic juveniles of species that deposit feed as adults may be unable to meet their nutritional demands by deposit feeding. To reject the null hypothesis that both juveniles and adults of deposit-feeding species assimilate the same diet and to infer ontogenetic changes in diet, I used stable carbon isotopes as a natural diet tracer. I quantified body-size-dependent variations in the $\delta^{13}C$ of four species of tentaculate, surface-deposit-feeding polychaetes: the ampharetid *Hobsonia florida* and the spionids *Pseudopolydora kempi japonica*, *Polydora cornuta*, and *Pygospio elegans*. In addition to worm tissues, I measured the isotopic compositions of the most likely primary producers at each field site (benthic diatoms, macroalgae, and saltmarsh grasses) to predict the worms' carbon sources.

All species showed significant size-dependent variations in $\delta^{13}C$. Furthermore, populations of *P. kempi japonica* at two different sandflats had similar ontogenetic trends despite isotopic differences in available foods at each site. Individuals fed a fixed diet in the laboratory, however, did not show significant size-dependent variation in $\delta^{13}C$, leaving ontogenetic changes in diet as the most parsimonious explanation of the field data. Regression analyses indicated that the gradual change in $\delta^{13}C$ with body size was nonlinear, with most of the change in $\delta^{13}C$ occurring before individuals reach sexual maturity. The complex life cycle of these species, therefore, includes both a radical change in niche when larvae metamorphose to juveniles and a gradual niche shift as benthic juveniles grow. The isotopic data indicate that the smallest juveniles assimilated much of their carbon from benthic diatoms ($\delta^{13}C \approx -20$ ‰), while adults assimilated most of their carbon from detritus derived from macroalgae ($\delta^{13}C \approx -9$ ‰) or saltmarsh grasses ($\delta^{13}C \approx -14$ ‰). Because abundances of benthic diatoms or other high-quality components of sediment are variable and more likely to be in limiting supply than detritus or bulk sedimentary organics, populations of species that deposit feed as adults may experience food-related recruitment bottlenecks during the juvenile stage.
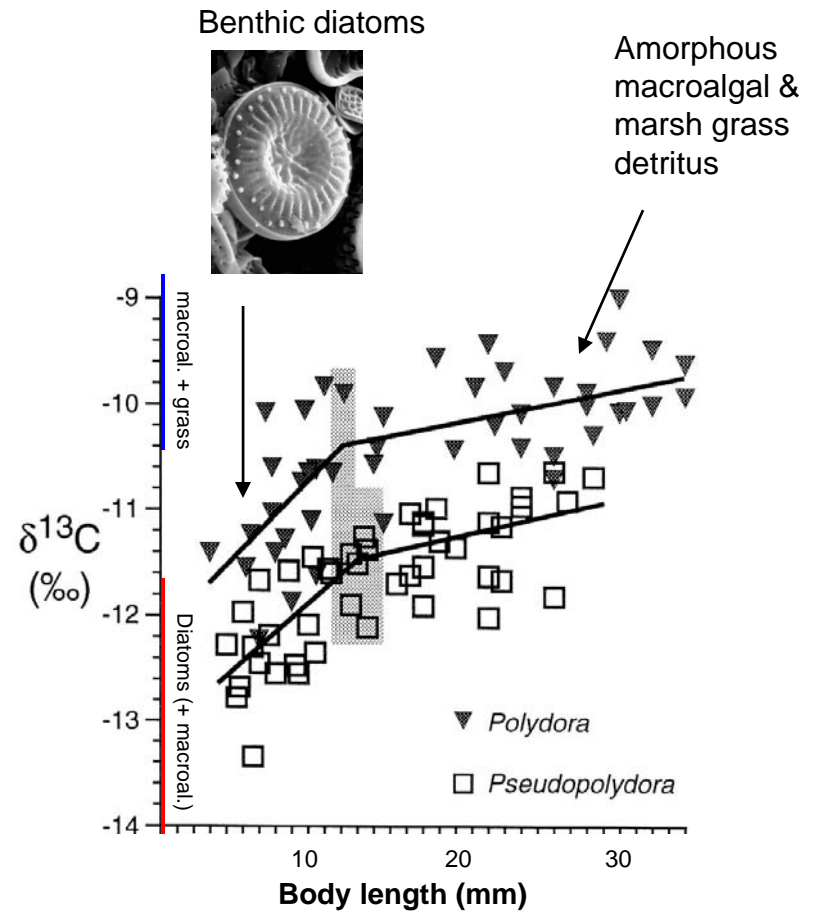
Figure 8. Comparison of the body-size-dependent variations in delta-$^{13}$C between the two polychaetes collected from False Bay. Shaded regions indicate body lengths within the 95% confidence interval around the estimated breakpoint in the piecewise linear model for each species.

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