HETEROGENEOUS GRAIN SIZE DISTRIBUTION IN TIDAL FLAT SEDIMENT CAUSED BY BIOTURBATION ACTIVITY OF ARENICOLA MARINA (POLYCHAETA)

by

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CONTENTS

I. INTRODUCTION

A great variety of infaunal organisms disturbs the primary sediment texture by burrowing, searching for prey or feeding on the sediment itself. The latter type of feeding (deposit feeding) is likely to constitute the main contribution to the total bioturbation in a given area.

VAN STRAATEN (1952, 1954) described an almost ubiquitous thin layer of coarse shell debris, with a high amount of the tests of the gastropod *Hydrobia ulvae*, at a depth of 20 to 30 cm in the subsurface of the tidal flats of the Dutch Wadden Sea. VAN STRAATEN (1952, 1954) ascribed its formation to the feeding behaviour of *Arenicola* which causes an accumulation of particles too big to be swallowed by the lugworms.

RHOADS & STANLEY (1965) in sediment cores from a tidal flat near Cape Cod, Mass., found a gradual coarsening of the tidal flat deposit from top to bottom. They supposed this gradation to be produced by selective feeding of the polychaete *Clymenella torquata* and called it biogenic graded bedding. Specimens of the worm kept in aquaria with homogenized sand, produced a positive gradation within a period of about one month. RHOADS (1967) described several forms of biogenic reworking of sediment for some intertidal and subtidal animals, including some cases of biogenic graded bedding. WARME (1967) also

reported the phenomenon of biogenic graded bedding caused by the burrowing activity of *Calianassa* spec. for a lagoon in California.

HYLLEBERG (1975) in a paper on selective feeding of the Arenicolidae *Abarenicola pacifica* and *A. vagabunda* noticed the grading effect of deposit feeding. TREWIN & WELSH (1976) studied the effect for a.o. *Arenicola marina*.

CADÉE (1976, 1979) gives more literature data on the subject and studied (CADÉE, 1976) the sediment reworking by *Arenicola marina* on the Dutch tidal flats, with special interest in the amount of sediment reworked and the seasonality thereof, and also noticed the biogenic graded bedding.

All authors cited conclude that graded bedding is caused by selective deposit feeding, which produces a relatively fine layer of faeces on top and leaving behind a relatively coarse layer at the bottom of the bioturbated zone.

This paper discusses some effects of the bioturbation caused by the polychaete *Arenicola marina* L., found mainly in laboratory experiments.

II. MATERIALS AND METHODS

Sediment samples of 40 to 60 g were dried at 60° C for about 3 days. The coarsest particles (like shells and large peat fragments) were removed and the sand was thorouhgly mixed in a mortar to separate agglutinated grains. The sediment passed a set of 9 sieves, with 1000, 500, 400, 315, 250, 200, 160, 100 and 50 μm meshes respectively, in a vibration sieving machine. The fractions were collected from the sieves and weighed (the loss in weight of the total sample during sieving and collecting was about 1%). From the weights of the fractions their weight percentage and cumulative weight percentage (from coarse to fine) were calculated.

Over a period of more than one year samples were taken from an indoor tidal mud flat ecosystem consisting of two large concrete basins filled with tidal flat sediment and inhabited by lugworms (*cf.* DE WILDE & KUIPERS, 1977). Samples were taken twice a month with a core sampler. The core was divided into 5 cm layers which were dried and stored.

For other experiments adult lugworms were caught on the tidal flat north of the NIOZ harbour and young ones on a tidal flat in the

Mok (CADÉE, 1976: fig. 1, stations A and B respectively). The lug-
worms were kept in plastic containers that were placed in a large
aquarium tank. Sediments used were tidal flat sediments (from station
A), river sand and a fine-grained pure quartz sand, or mixtures of
these.

III. RESULTS

A. FIELD OBSERVATIONS

A few cores were taken on the tidal flat near the NIOZ harbour (sta-
tion A). Some of them showed a distinct stratification which may be
caused by rather severe conditions. Layers of medium sand are inter-
bedded with silt or clay layers (Wentworth scale; WENTWORTH, 1922)
and with layers of decomposing *Ulva lactuca* and other algae. REINECK
& SINGH (1973: 323–324) report a similar stratification from Germany
caused by greater sediment transport during storms. Adult lugworms
seem to be scarce where such impenetrable layers of clay or *Ulva* are
present at a depth of less than about 10 cm. However, young lugworms
may be abundant.

In several cores more than one layer with shell debris as described by
VAN STRAATEN (1952) were visible. Also, other shell debris layers, up to
5 cm in thickness could be discerned. Virtually unstratified sediment
on the other hand showed a destinct gradation (Fig. 1). Especially
from the distribution of the 80–250 μm and 250–860 μm fractions a
graded bedding is obvious. Also CADÉE (1976) reports the presence of
a graded bedding and of more than one shell debris layer (or *Hydrobia*
layer) for about the same spot.

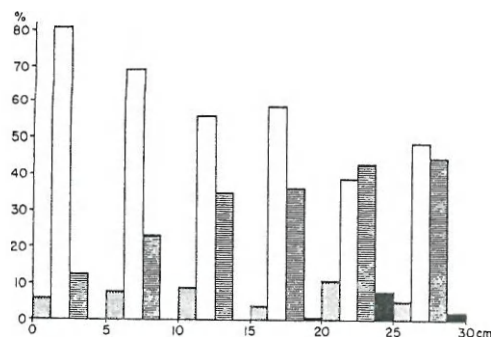Cores taken on the Balgzand, a large tidal flat area bordering the

Fig. 1. Grain size distribution in relation to depth in a core from station A; shown
are the fractions < 80 μm (dotted), 80–250 μm (blank), 250–860 μm (hatched) and
> 860 μm (black).

mainland south of Texel, showed no heterogeneous distribution of any
fraction. It must be noticed, however, that the median grain size is
much smaller (approximately 120 μm) than on the tidal flats at the
southeast coast of Texel (stations A and B); there, as in the indoor tidal
flat ecosystem (see section IIIb), median grain size is 210 μm. In the
Balgzand area about 60 per cent of the sediment samples is within the
100–160 μm fraction. The sorting coefficient $\sqrt{Q_3/Q_1}$ (after TRASK,
1932) is virtually the same (stations A and B at Texel 1.11 and Balg-
zand 1.10); the kurtosis of the sediment at Balgzand (0.95) is even less
than at stations A and B (0.99). The introduction of a 125 μm sieve to
split up the broad 100–160 μm fraction did not change this homo-
geneous picture.

B. GRAIN SIZE DISTRIBUTION IN THE COURSE OF TIME

Homogeneous sediment was brought in the indoor tidal flat ecosystem
summer 1974. Juvenile lugworms with a mean length of 11.1 mm were
introduced 1 July 1975 (day 0). In the first month of the experiment
the lugworms reached a length of about 2 cm and their burrows reached
a depth of no more than 10 cm. After 3 months they will have been
4 cm, burrowing to a depth of about 20 cm. It was estimated that
the final level of 25 to 30 cm was reached in November-December 1975
according to the lugworm's adult size at that moment.

Of the 6 levels of the 20 core samples taken during the period from
June 1975 to August 1976 the median particle size was calculated semi-
graphically (Table I). For calculation grain sizes were expressed in
φ values ($-^2$log of grain size in mm) because of the log-normal
distribution of most sediments. From this representation no clear
trend toward graded bedding can be deduced, although during the
last 5 samplings at least the lowermost level had become rather
coarser.

Heterogeneity of a sediment property can be described as the ratio
between the variation of a numerical value of that property in space
and its expected value. Here the heterogeneity has been defined as
$H = \sigma_p/p \cdot 100\%$, where σ_p is the standard deviation of a proper-
ty and p its mean value. Fig. 2 shows that the heterogeneity of the
median particle size, H_M, gradually increases with time. For an ex-
ponential relation calculated $r = 0.899$, significant ($P < 0.01$) for 16
observations.

In the same way the heterogeneity for each fraction percentage,
(H_f) as a measure for differences in percentage of fraction (f), ob-
served at the individual levels of a core. Linear regression was applied
on two sets of data points (Fig. 3): on all data (dashed lines) and on

TABLE I

Median particle size M as φ values ($-^2$log diameter in mm) at different levels of a time series of sediment samples taken from the indoor tidal flat ecosystem inhabited by *Arenicola marina*.

Day number	φ values at the depths (cm):					
	0–5	5–10	10–15	15–20	20–25	25–30
1	2.27	2.26	2.27	2.27	2.25	2.27
14	2.28	2.28	2.28	2.28	2.27	2.27
28	2.26	2.28	2.29	2.27	2.27	2.26
71	2.27	2.27	2.27	2.26	2.26	2.24
85	2.27	2.24	2.26	2.27	2.25	2.24
99	2.32	2.25	2.19	2.21	2.25	
144	2.28	2.27	2.29	2.28	2.29	2.29
183	2.28	2.26	2.23	2.22	2.24	2.26
198	2.33	2.33	2.22	2.23	2.22	2.23
212	2.32	2.32	2.29	2.22	2.12	2.18
226	2.31	2.27	2.19	2.22	2.24	2.25
267	2.29	2.29	2.33	2.33	2.28	2.06
296	2.32	2.32	2.29	2.15	2.03	
324	2.31	2.33	2.29	2.35	2.30	2.07
366	2.19	2.30	2.34	2.26	1.97	
415	2.39	2.32	2.31	2.29	1.98	

those since day 140 (solid lines). The last regressions give the best fit, thus excluding the values obtained in the first 3 months when the lugworms were still small and could not yet have affected the lower levels of the sediment.

From Fig. 3 it can be seen that a relation exists between grain size and the value of H_t at a certain moment. To find out whether this is merely caused by the fact that the variation of fractions that constitute only a small portion of the total sample, will be greater than that of more important fractions, because of a greater chance of sampling
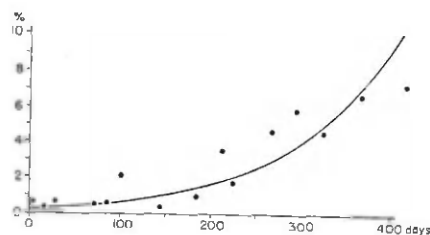

Fig. 2. Development of the heterogeneity (%) of the median particle size (data of Table I) in the indoor tidal flat ecosystem. Exponential curve calculated: $y = e^{0.0817x} - 1.05559$.

errors, or that some independent mechanism is involved, the earlier (original) and later mean heterogeneities of the separate fraction are compared (as original values are considered those that result from the cores of days 14, 28, 71 and 85 as the lugworms were still very small then). The resulting figure (Fig. 4) makes clear that indeed the expected pattern with greatest variation in the least important fractions becomes apparent. However, the heterogeneities calculated for the whole sampling period (solid line) are higher than the corresponding original values (dashed line). This must result from biogradation later on.

A regular grading of the bedding, however, cannot account for the mutual differences in the shape and symmetry of the curves. If the
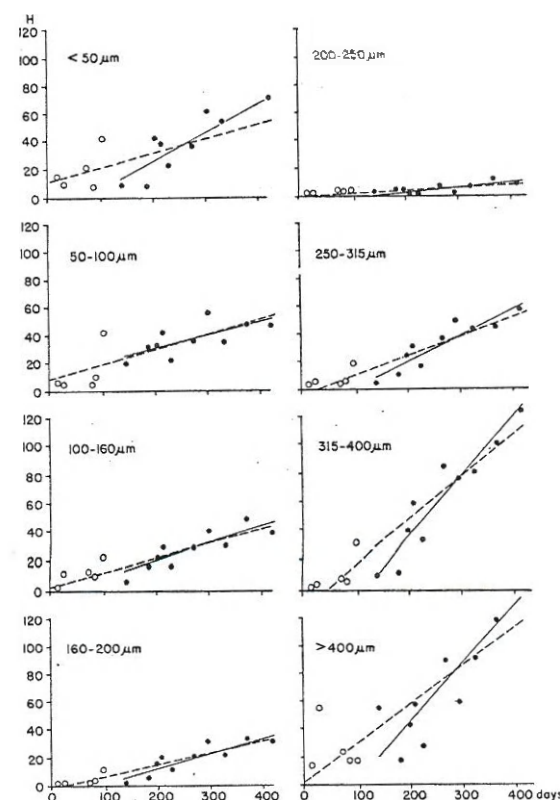

Fig. 3. For each of the separate fractions, the development of the heterogeneity H (%) of the median particle size (data of Table I) over the total period of observation (dashed lines) and over the period since day 140 (solid lines).

differences in H_t were directly related to the percentage of f, the values of *e.g.* 100 and 315 μm, and of 160 and 200 μm (lower limits of fractions) should be approximately equal. This is true for the curve of original values, but not for the curve of the total period. Especially the difference between the last two fractions remains to be explained.
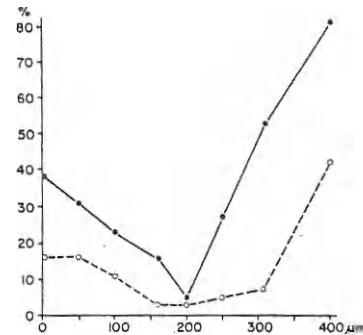

Fig. 4. Heterogeneity (%) of the median particle sizes (data of Table I) calculated for the separate fractions over the data of the first 2 months (dashed line), and over the total period of observation (solid line).

The percentages of the fractions of 100 to 160 μm and of 200 to 250 μm of some cores are shown in a series of histograms (Fig. 5). The first diagram shows approximately the original situation. By day number 99 the upper 15 cm had become graded, the lugworms still being rather small. At day number 212 a graded bedding, although not too obvious, had developed. The core of day number 366 is coarse at the top, finer at the 5–10 cm and 10–15 cm levels, while the 15–20 and 20–25 cm levels show a coarsening downward again. The core of day number 415 shows an almost perfect gradation.

C. GRAIN SIZES IN FAECES AND ORIGINAL SEDIMENT

In laboratory experiments grain size distributions in faeces of *Arenicola* were compared with the distributions in the original sediment. As a rule artificial sediments were composed as mixtures of river sand and some sediment from the tidal flats at station A or B. Faeces was collected over a period of about one month.

Two experiments were carried out with adult lugworms of about 4.5 g wet weight, each kept in a plastic container, which had been filled with a sediment mixture that was either approximately unimodal in distribution (Fig. 6a) or bimodal (Fig. 6b). Only 4 lugworms (2 in

each kind of sediment) out of 8 adapted so well, that they finally fed and defecated. Poor feeding cannot have been caused by a deficiency of food as about 20 per cent of the sand consisted of sediment, very rich in organic matter, especially living diatoms, and lugworms feed and defecate more when more food is available, as appeared from the other experiments and the study by DE WILDE & BERGHUIS (1979). Probably the animals were in a bad situation because of the small depth (about 12 cm) of the sediment in the containers. This forces the lugworm to live in a burrow of a rather unnatural form, with a much too large, horizontal part.
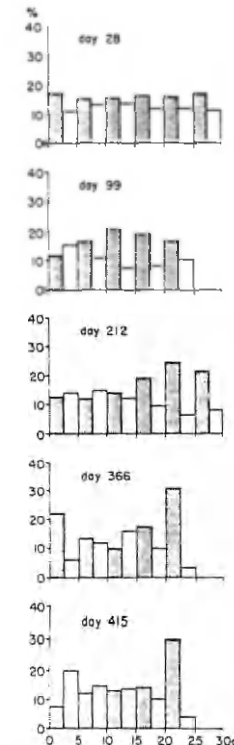

Fig. 5. Histograms showing the distribution in relation to depth of the 200–250 μm fraction (shaded) and of the 100–160 μm fraction (blank) on part of the sampling days (indoor tidal flat ecosystem).

A third experiment was carried out with 60 lugworms with a mean wet weight of 3.5 g, kept in a large aquarium tank, filled for 90% with tidal flat sediment (station A). From the histograms (Fig. 6a to c) it is

that the original sediment is coarser than the faeces produced out ... Moreover, if we look at the shape of the curves, the faeces seem ... be better sorted (more concentrated in only a few fractions) and ... distribution less skew than the distribution of the original sediment. ... TRASK's (1932) sorting $\sqrt{Q_3/Q_1}$, for the sediment and faeces of Fig. 6a are 1.22 and 1.12; for Fig. 6b 1.41 and 1.14; for Fig. 6c 1.20 ... 1.15, respectively. The TRASK's skewness, $Q_1 \cdot Q_3/Q_2{}^2$, for sediment ... faeces for Fig. 6a are 0.96 and 0.99; for Fig. 6b 0.88 and 0.98; and ... Fig. 6c 0.97 and 0.98, respectively (Q_1, Q_2 and Q_3 are the quartile ... of the cumulative percentage curve). Note that the distribution ... the faeces in Fig. 6b has become unimodal.

Three experiments were carried out with different artificial sediments Fig. 6d to f) and young lugworms with wet weights ranging

Fig. 6. Histograms showing grain size frequency distributions of sediments (solid ... in relation to the grain size distributions in faeces produced by *Arenicola* living ... these sediments (broken lines) and collected after 1 month. All sediments are ... composed except in c, that originates from station A. Left histograms adult worms; right histograms juveniles (0.2 to 0.4 g).

from 0.2 to 0.4 g. Five of them were put in one plastic container. Here again the skewness of the faeces distribution is less and the sorting is better than that of the original sediment.

The ultimate size of grains that could still be found in the faeces of adults as well as of juveniles appeared to be somewhere between 500 μm and 1000 μm. CADÉE (1976) found that *Arenicola* prefers particles smaller than some 300 to 400 μm. KRÜGER (1971) reports particles up to 2 mm in *Arenicola* faeces, but it concerns animals at least twice as big as used in my experiments.

IV. DISCUSSION AND CONCLUSIONS

From the results obtained some conclusions can be made concerning the mechanism producing the heterogeneity of the sediment. VAN STRAATEN (1952, 1954) ascribed the formation of a layer in which shell debris was concentrated, to the lugworm's inability of ingesting large particles. But this mechanism does not explain the differences between the grain size distribution of faeces and original sediment, as these large shell fragments constitute only a very small portion of the sediment. RHOADS & STANLEY (1965), RHOADS (1967), WARME (1967), HYLLEBERG (1975), and CADÉE (1976) all attribute these differences in one way or the other to selective feeding, but they do not indicate what kind of selective feeding this might be, and how this mechanism would operate.

A lugworm seems to lack the means to test the size of the particle which it is about to swallow (except perhaps by the papillae on its proboscis). Therefore, it is likely that what is called "selective" feeding, implying the animal in some way to select its food, in reality is a stochastic process. *Arenicola* feeds by protruding its proboscis into the sand, and sand grains stick to the papillae of the proboscis. Only some grains remain attached when the proboscis is withdrawn, and are swallowed. It is obvious that small particles have a greater chance to adhere firmly to the mucus-covered papillae and not to be dropped, because of their surface area being relatively larger. Sizable grains will tend to fall off more readily. Let the chance of one particle to be picked up and swallowed be P, then $P = p(x)$, where x is the grain diameter. Let the frequency of a certain particle size x be $F = f(x)$. It follows that for the chance C of any particle of diameter x to be swallowed the equation:

$$C = P \cdot F = p(x) \cdot f(x)$$

holds. If we assume the relation between "sticking chance" P and grain surface area to be linear, $p(x)$ can be plotted as a parabole. In Fig. 7 the graphs of $f(x)$ and the resulting product function C are shown.
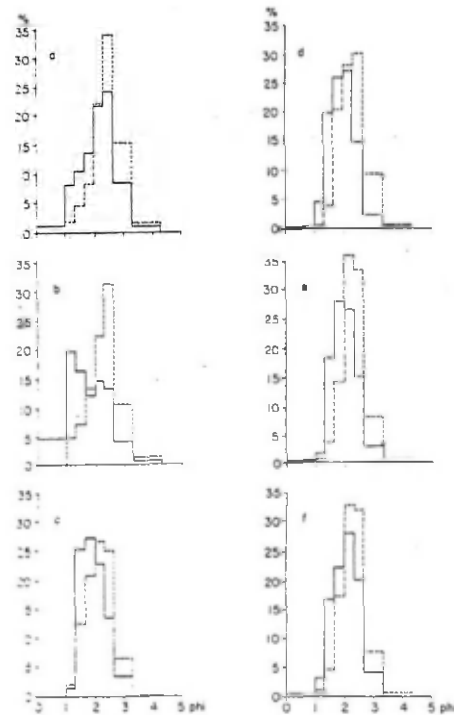
If these assumptions be correct, the result of this type of feeding will be that at first a faecal layer, which has a distribution C_1, is deposited on top of the surface layer with distribution F. It must be kept in mind that the lugworms by times shift the position of their burrows, at least of the feeding funnels (cf. RIJKEN, 1979), so that the whole area is affected.
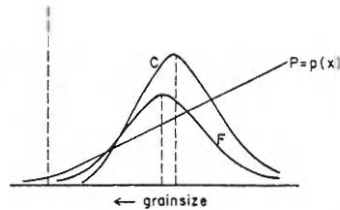

Fig. 7. Diagram showing the grain size frequency distribution of an original sediment (F), the relation of grainsize and the chance of a certain particle to be swallowed by the lugworm ($P = p(x)$), and the product curve of F and P, i.e. the hypothetical frequency distribution of the faeces (C).

Moreover, the tides and small waves will spread out the faeces mounds over the entire surface of the sediment. At the bottom of the bioturbated zone, however, a coarse residual layer, with distribution R, results from the removal of part of the finer fractions. After a certain period (in fact from the very moment the process started) the faeces will reflect the influence of $p(x)$ on distribution R. In other words, on top of the C_1 layer faeces with distribution $C_2 = R \cdot p(x)$ is deposited. If we look at the values of the median grain size in the indoor tidal flat ecosystem (Table I), the observations seems to agree with the hypothesis. Moreover, faeces collected in the experiments shown in Fig. 6d and e, after another month were slightly coarser than the faeces of the first month (median diameter differed 5 to 10 μm). The hypothesis also explains why no real graded bedding originates, but only a heterogeneous distribution of the fractions. Also in agreement is the fact that in the cores taken in the last few months in the indoor ecosystem, the lowermost level gradually became coarser. This is no contradiction, for at this end of the sediment column the concentration of oversized (not ingestible) grains goes on (this case might be considered as $p(x) = 0$). Moreover, the faeces are not only layering on at the sediment top, but there is an equal transport downward via the feeding columns of the animals causing a constant input of sediment from levels with an F distribution or even a C distribution. In the latter mixing process also other effects partake because of the presence of an open funnel at the top of the feeding column. These funnels may cave in and will act as a sediment trap (DE WILDE, 1975).

Of course, for more reasons as already indicated above, the hypothesis is an oversimplification: Other bioturbating animals will interfere; during gales, occuring mainly in autumn and winter, and with tidal movements strong enough to cause erosion, redistribution will take place.

The main process described is not unique for *Arenicola marina* and related organisms. It may be concluded that if two conditions are met, a deposit feeding animal will cause a biogenic heterogeneous bedding: (1) the animal must feed on the sediment at a lower level than where its faeces are deposited; (2) a particle's chance of being swallowed must depend on its size. Whether this chance is determined by some stochastic process as in the case of *Arenicola marina*, or by the actual preference of the animal for certain fractions, is not important.

V. SUMMARY

In a series of laboratory experiments, especially in an "indoor tidal flat ecosystem", the effects of deposit feeding by the European lugworm *Arenicola marina* L. on the sediment were studied. Feeding activity did not so much result in a biogenic graded bedding, but more in an increasing heterogeneous distribution of the several grain size fractions over the sediment. A mechanism which causes these effects is proposed: the chance of a particle to stick to the mucus covered papillae on the lugworm's proboscis and to be swallowed depends on its surface area; smaller particles have a greater chance than large ones.

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SEDIMENT REWORKING BY THE POLYCHAETE HETEROMASTUS FILIFORMIS ON A TIDAL FLAT IN THE DUTCH WADDEN SEA

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I. INTRODUCTION

Deposit feeders play an important part in many marine habitats. In various ways they have their effect on the sediment and the processes at the sediment-water interface (RHOADS, 1974). Research on sediment reworking by deposit feeders in the Dutch Wadden Sea started with work on *Arenicola marina*, the largest and most important sediment reworker in this area (VAN STRAATEN, 1950, 1952; CADÉE, 1976; BAUMFALK, 1979).

Arenicola marina is a "funnel feeder" deriving its food largely from the surface sediments, only occasionaly deeper sediment is swallowed as can be observed from black coloured faeces consisting of sediment from the anaerobic layer. *Heteromastus filiformis* is a "conveyer-belt feeder" in the terminology of RHOADS (1974) deriving all its food from sediment ingested in the anaerobic layer 10 to 30 cm below the surface. Therefore, its characteristic faecal pellets deposited at the surface, are always black in colour.

Heteromastus filiformis becomes 8 to 15 cm long and about 1 mm in