

Effects of Tubicolous Polychaetes
On Intertidal Substrates
In Cobequid Bay, Nova Scotia.

Effects of Tubicolous Polychaetes
on Intertidal Substrates in
Cobequid Bay, Nova Scotia.

By

Raymond Paul Featherstone

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AUTHOR: Raymond Paul Featherstone

SUPERVISOR: Dr. M. J. Risk

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Abstract

Populations of three tubicolous polychaetes, Clymenella torquata, Spiophanes wisleyi and Sabellaria vulgaris located in the intertidal zone of the south shore of Cobequid Bay, Nova Scotia were studied for their effects on the surrounding sediment. Grain size measurements were made of the tubes and the surrounding sediment. T-tests were made on the resultant differences between the Inman sorting and mean statistics of the two sand populations. The percentages of heavy and light minerals were also measured with the use of a binocular microscope. The differences in sorting and mean grain size between the tubes and substrate may affect stability and porosity of the sediment and effect sediment structures easily identifiable in the geologic record.

Clymenella torquata inhabits a low energy intertidal sandy environment and increases the porosity of the sediment by its feeding habits. Stabilization of the sediment may be effected by high population densities of Clymenella (densities around $420/m^2$). Tubes were built with preferential grain sizes. Spiophanes wisleyi exists in phenomenally high population densities in low-energy areas. The large numbers of tubes (up to $98,000/m^2$) bind the sediment; tubes are made of virtually the same grain sizes as the substrate; no bioturbation occurs during the construction of the tubes. The latter two factors make preservation potential very low in the geologic record. Sabellaria vulgaris in the study area is of little sedimentological importance. Population densities are too low to affect the surrounding substrate. This species exists in a high energy zone - a characteristic of fauna which build reefs. Reef formation by sabellariids may have been important in the geologic past and is locally

important today in the North Sea (Schafer, 1972) and Florida (Gram, 1968).

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Introduction

During the summer of 1973, the author worked in Nova Scotia, on the intertidal mud and sand flats of the south shore of Cobequid Bay.

In the course of the work, field observations made by the author and co-workers produced impressions about the faunal distributions: the fauna varied not so much with tidal height, but with the grain size of the sediment. Diversity of fauna was low throughout the intertidal zone; total number of species was less than thirty. Deposit feeders existed in the majority e.g. Corophium volutator (an amphipod), Macoma balthica in the muddy silt areas whereas scavengers e.g. Pagurus sp. (a hermit crab), became prominent in the sandy zones. Such distributions occur as a result of the type of food available; this, in turn is related to the stability of the sediment. The sandy zones are much more mobile in character; this hinders the growth of populations of deposit feeders because unicellular algae cannot establish on shifting substrates (Sanders et al., 1962). The finer sediments intertidally indicate weaker energy regimes, hence detritus is likely to accumulate on such substrates, therefore presenting other food (in addition to the algal crop) to deposit feeders.

In particular areas of the intertidal "mudflats" three species of tubicolous polychaetes were identified. The species were identified as Clymenella torquata, a maldanid polychaete (deposit feeder); Spiophanes wisleyi, a spionid polychaete (deposit feeder); and Sabellaria vulgaris, a sabellariid polychaete (filter feeder), (identifications courtesy of D. L. Peer, 1973).

Clymenella torquata in feeding upside down, produces a very "spongy" substrate as a result of effecting a higher porosity and saturation level

4.

(Sanders et al., 1962). The substrate is planar in areas of extensive populations of Clymenella torquata; adjacent areas with few Clymenella tubes showed rippling. This species seemed, therefore, to have a stabilizing effect on the substrate. Such an effect has also been reported by Fager (1964) for populations of Owenia fusiformis at subtidal depths of eight to twelve metres.

The tubes of Spiophanes wisleyi were very numerous at Cambridge. The high population densities gave exposed areas a matted appearance. This species also appears to lend stability to the substrate as a result of binding the sediment by the high densities of tubes. The tubes are much smaller than those of Clymenella and a significant drop in the population density allowed the formation of ripples. Tidal creeks often exposed the intense matting (even at depth) on the banks.

Sabellaria vulgaris is the acharacteristic member of the group of three tubicolous polychaetes in that it is a filter feeder. This species was noted to bind sand grains into a tube cemented onto a gravelly substrate. Grains of granule size (Udden-Wentworth scale) were often found bound together by two or three tubes of this species. Pebbles and cobbles were much more numerous than granules, however and served as solitary bases for numerous tubes. A related species, Sabellaria alveolata, builds outstanding sand reefs in the North Sea (Schafer, 1972). Schafer states that S. alvolata can change a substrate from one of mobile sand character to a stable ragged reef character; such a marked change in substrate was not observable in the area of study although sabellariid reefs have been reported off Kingsport in the Avon estuary (Bleakney, 1973) near the study area. The change in substrate described here would most certainly be

accompanied by a change in the surrounding fauna (Schafer, 1972).

The author investigated the effects of the tube-building activities of these three tubicolous polychaetes on the surrounding sediment. Mineralogy and grain size of the tubes of each species and the surrounding sediment have been compared in order to define these effects.

Region of Study

The study area was located on the south shore of Cobequid Bay, Nova Scotia. The author and co-workers stayed in a farmhouse in Noel Shore, Nova Scotia centrally located in the study area. Twelve transects were surveyed at various points along a stretch of fifty miles ranging from Bramber to Selmah (see Figure 1). These transects were set up for the master's thesis work of H. D. Craig and research project of Dr. M. J. Risk carried out by Miss V. J. Tunnicliffe.

Two of the tubicolous polychaete species were almost exclusively located along two transects: Clymenella torquata was found on the Pembroke transect (Plate 1) and Spiophanes wisleyi was located at Cambridge (Plate 3). The polychaete, Sabellaria vulgaris was located sporadically along the shore; localized populations were found at East Noel (Plate 5) and Noel Shore in five "pockets".

The supratidal zone is extremely variable due to the topographic relief along the coastline. This zone is either composed of saltmarsh separated from the upper intertidal zone by a one metre displacement (approximately) or coniferous forest separated from the upper intertidal zone by more than eight metres height difference. Coastal relief is due to the presence of rock outcrops. Excellent exposures of Triassic cross-

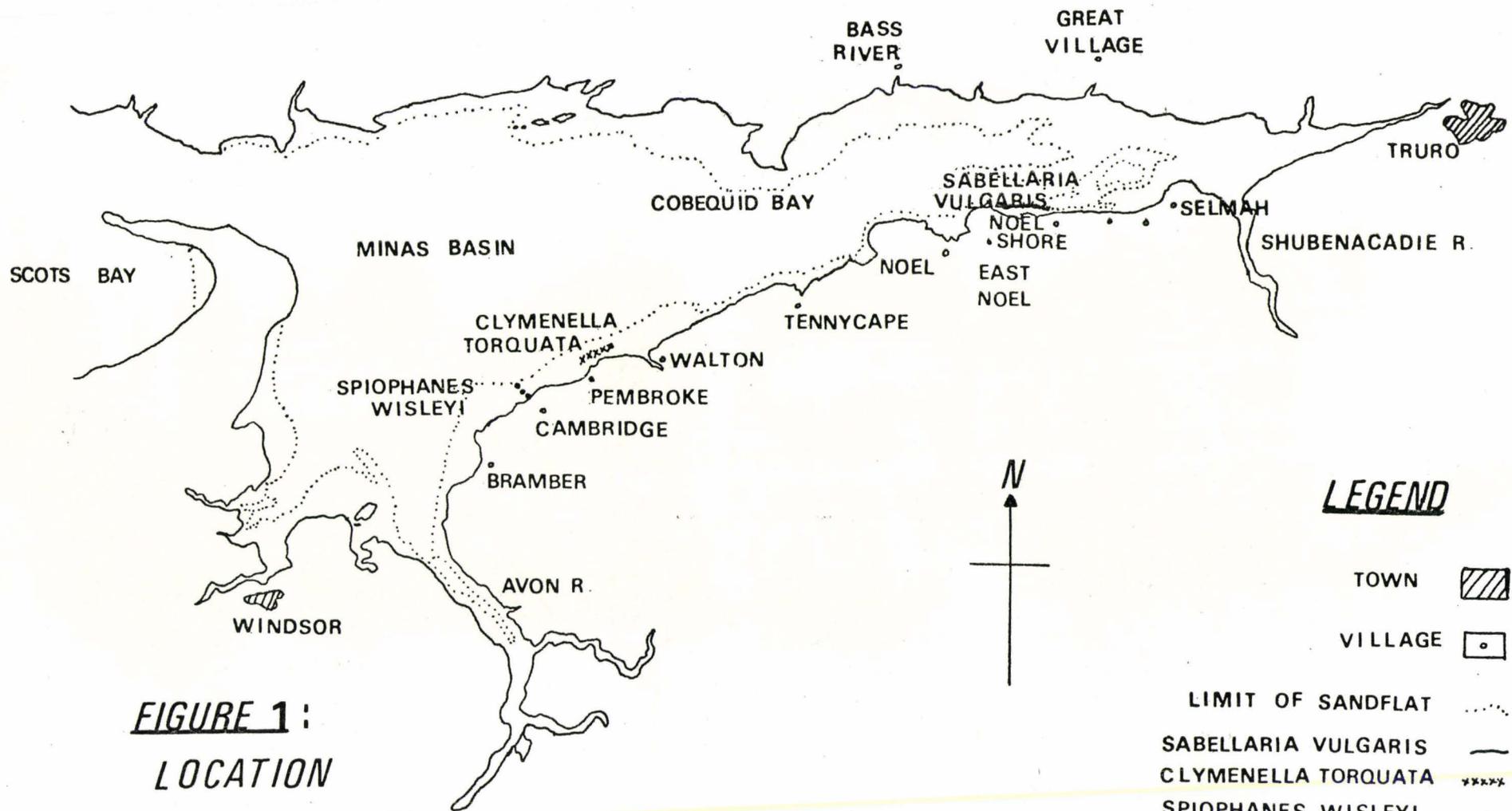


FIGURE 1:
LOCATION
MAP OF SAMPLED POPULATIONS OF
THE THREE TUBICOLOUS POLYCHAETES,
BAY OF FUNDY, NOVA SCOTIA.

bedded conglomerate and arkose (Klein, 1963) and Horton slates and shales (Mississippian in age) exist in varying proportions from East Noel Head westward, producing the forest supratidal zone eight to ten metres above the intertidal zone. East of East Noel Head, saltmarsh supratidal zone predominates as a result of the presence of Pleistocene till outcropping. There are local variations where this is reversed (parts of Noel Shore, for example).

Tidal range varies along the coast: at Cambridge, tidal range is little more than nine metres; at Burncoat Head (just west of Noel), tidal range is often fifteen metres, due to the funneling effect of Burncoat Head and Economy Point (just west of Bass River) on the north side of Cobequid Bay. During periods of spring tide, the saltmarsh is inundated whereas the forest zone is not.

The substrate in the intertidal zone comprises four types of sediment (on a broad scale): muddy silt, fine to medium-grained sand, gravel lag and rock outcrop (predominantly Triassic redbeds). The Cambridge and Pembroke transects were composed of dominantly fine-grained sand and silt; there occurred Spiophanes wisleyi and Clymenella torquata respectively. Sabellaria vulgaris was collected in areas of coarse gravel lag in the lower intertidal zone off Noel Shore and East Noel.

Species Descriptions

Clymenella torquata, diagrammed in Figure 2, is a tubicolous maldanid polychaete (Barnes, 1968). The species builds a straight vertical tube, open at both ends, approximately 20 cm. long and 0.3 cm. in diameter (Rhoads and Stanley, 1965) (Figure 3). Feeding occurs in an upside down

position (all life processes do in fact); the worm feeds at the base of its tube, choosing grains only finer than 1.0mm. (Rhoads and Stanley, 1965) and periodically voiding fine-grained unconsolidated coiled feces from the top of its tube (Craig, 1974). This species was found in relatively large densities in the sandier parts of the Pembroke transect (Plate 1), just north of a rock ledge (Horton shale outcrop) which separates the siltier Macoma and Mya intertidal faunal zone from the sandy Clymenella torquata faunal zone. Population densities measured were $425/m^2$, $436/m^2$, and $415/m^2$; a typical population is exhibited in Plate 2. Sanders et al. (1962) reports populations of C. torquata in densities up to $615/m^2$ in Buzzards Bay, Massachusetts; Mangum (1964) states that the species occurs in densities between $200/m^2$ and $600/m^2$ from Florida up to the Gulf of St. Lawrence. Populations are generally clumped: this may reflect induced larval settling by established populations of adult worms.

Tube construction has been studied in the field (Sanders et al. 1962) and in the laboratory (Mangum, 1964; Rhoads, 1967 and Kenny, 1969). Sanders et al. (1962) report that grain selection was apparently random. Large grains unsuitable for digestion are manipulated into position by the lips where they are cemented to the tube with mucus from mucus glands located in the mouth region. The tubes collected did not have any conical appearance which would imply sequence of construction; by reason of the worm's mode of life, the top of the tube is probably built first and the tube is added to as the worm burrows down into the sediment. Tube construction starts ten days after hatching (Newell, 1951). Kenny (1969) and Mangum (1964) state that differences in grain size between the tube sediment and substrate sediment do not occur within the settled area, but

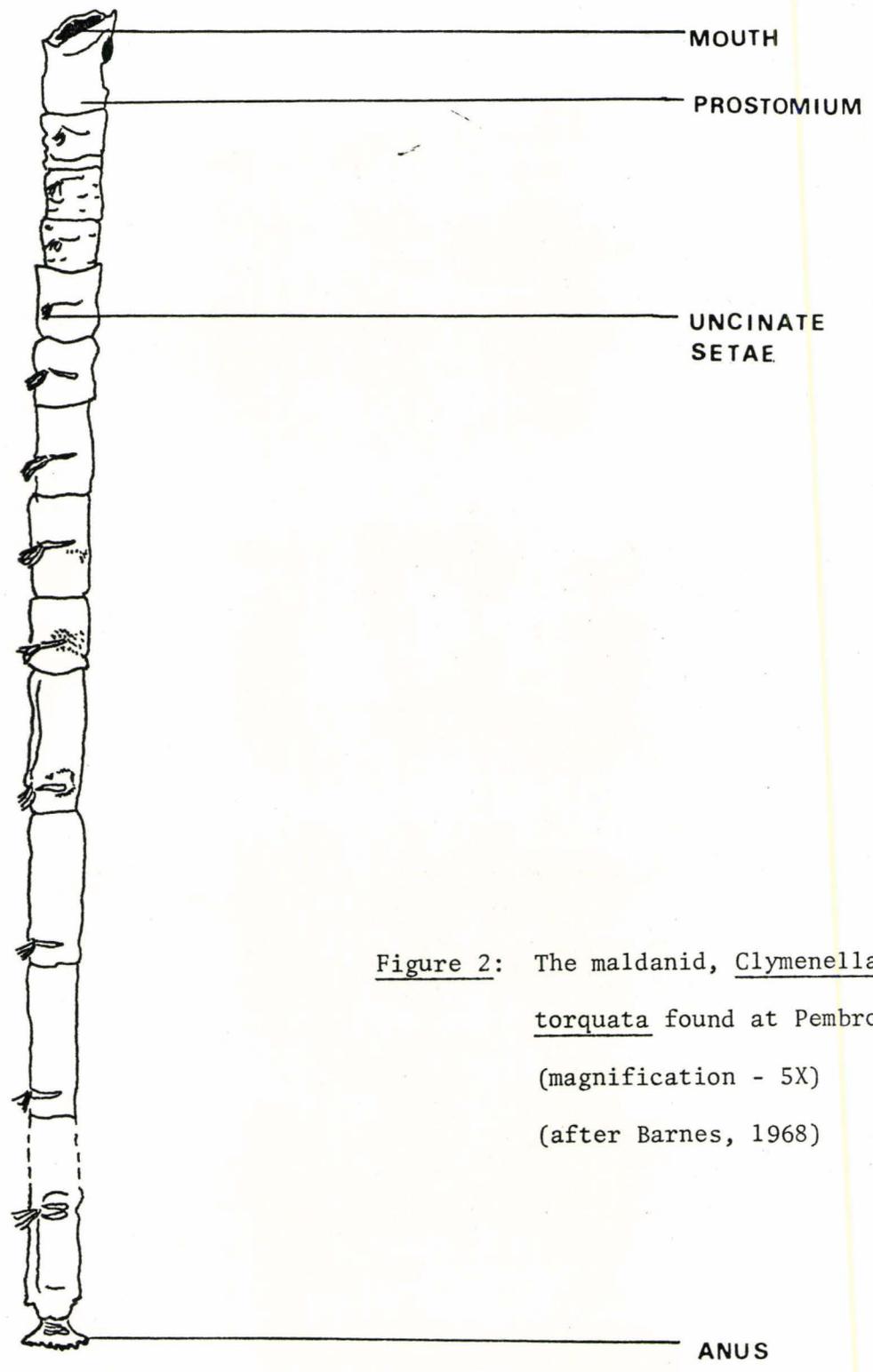


Figure 2: The maldanid, Clymenella
torquata found at Pembroke.
(magnification - 5X)
(after Barnes, 1968)

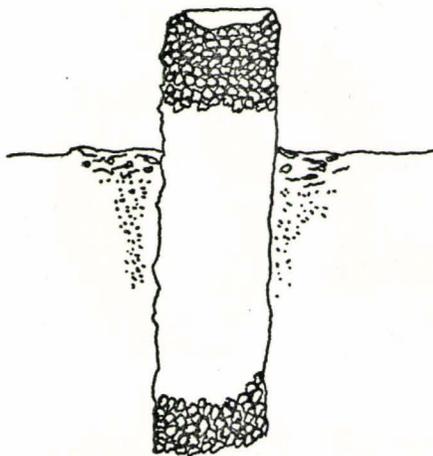


Figure 3: Anterior portion of sand-grain tube of
Clymenella torquata (after Barnes, 1968).
(magnification - 8X)



Plate 1: Pembroke transect.

A clumped population of Clymenella
torquata. Note planar surface.

(book is 20 cm. long)



Plate 2: Pembroke transect.

A single Clymenella tube surrounded by
coiled, unconsolidated feces. (coil is

0.8 cm. in diameter)

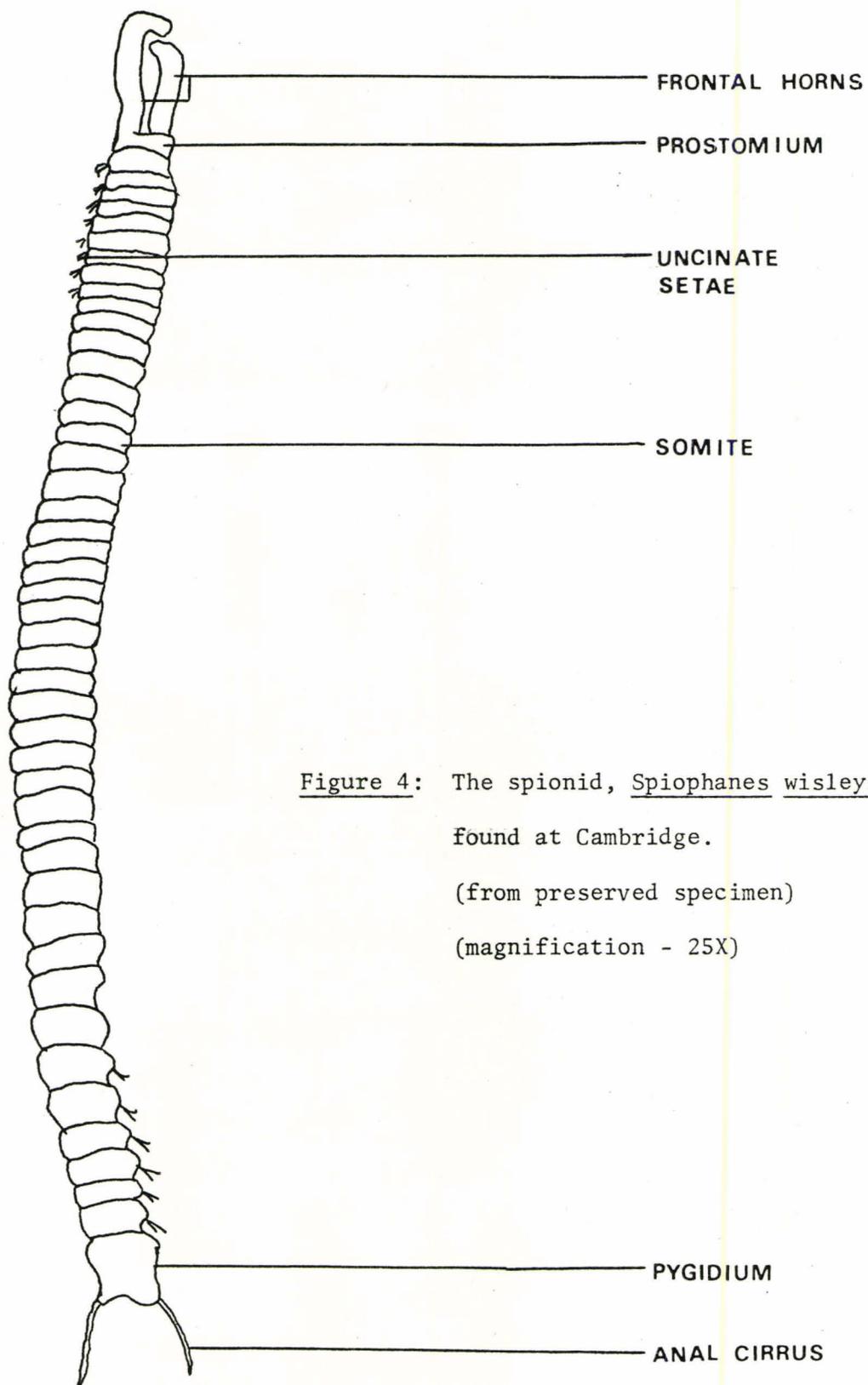


Figure 4: The spionid, Spiophanes wisleyi
found at Cambridge.
(from preserved specimen)
(magnification - 25X)

large populations are found in areas of grain size 0.25 mm. (Kenny, 1969).

Spiophanes wisleyi is a little known species of the order Spionidae. It is a non-selective deposit feeder, using two frontal horns to drag the detritus surrounding the tube into the top of the tube. Such a feeding process leaves a surface trace, but the preservation potential is low as the worms are small (2 cm. in length, 0.15 cm. in diameter. - see Figure 4). Feces are also excreted from the top of the tube as the worm moves down its tube, turns around and moves to the top again voiding unconsolidated rod-like fine-grained feces. Spiophanes wisleyi was found exclusively at Cambridge (Plate 3); population densities varied from 4000/m² to more than 90,000/m². Population counts by the author and a co-worker yielded the following data:

(stations are 100 m. apart)

W2 (approximately 150 m. from the cliff face) - 98,000/m²

W3 - 87,000/m²

W4 - 71,000/m²

W5 - 54,000/m²

W6 - 31,000/m²

W7 - 32,000/m²

W8 - 12,000/m²

W9 - 13,000/m²

W10 - 4,000/m²

A population density of 71,000/m² is illustrated in Plate 4.

This species existed in sediment ranging in grain size from coarse silt to medium-grained sand lower down in the intertidal zone. The tubes are constructed from the surrounding sediment; tubes average 4 cm. in length and slightly less than 0.3 cm. in diameter (Figure 5). The tubes are open at both ends which allow oxygen down to the anoxic zone thereby oxidizing the sediment at depth in some areas. Discussion among the author and co-workers has led to the hypothesis that the tubes are added

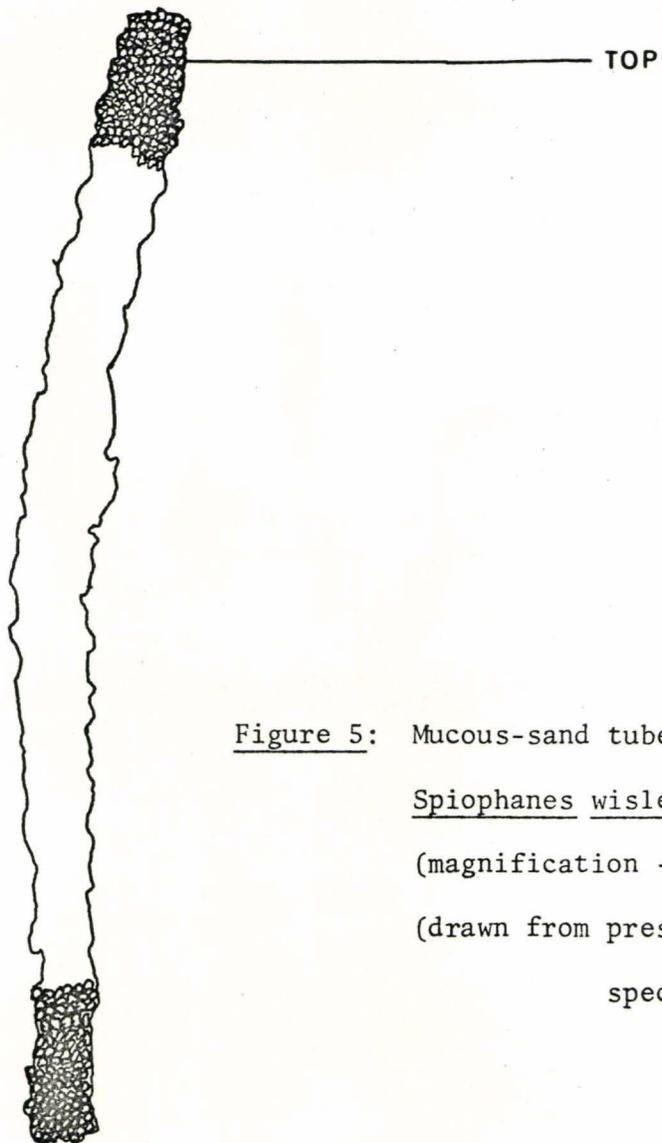


Figure 5: Mucous-sand tube of
Spiophanes wisleyi.
(magnification - 5X)
(drawn from preserved
specimen)

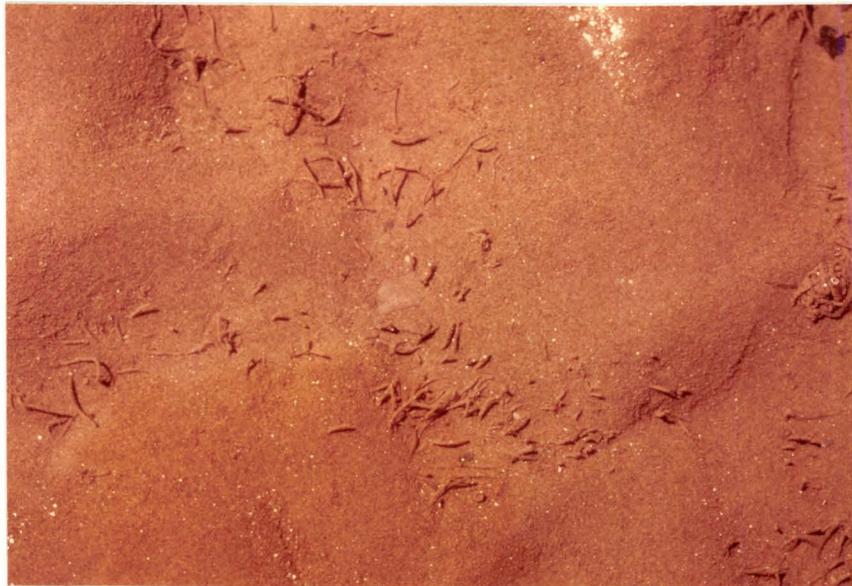


Plate 3: Cambridge transect.

Example of erosion of Spiophanes wisleyi tubes in ripple trough. Population density is low, hence mobile substrate occurs. (picture is 20 cm across)



Plate 4: Cambridge transect.

Example of Spiophanes wisleyi exposed by eroding tidal creek. (pencil is 10 cm. long)

to in length during periods when the tubes are covered by shifting sediment (as in Plate 3). Gosner (1971) states that many spionids possess tubes of membranous and mud covered nature - this is probably the case for Spiophanes wisleyi. Such mucous tubes actually disturb the sediment laminae very little, the laminae meeting the tubes at right angles (Schafer, 1972). During periods of erosion, the sediment is washed away but the tubes remain; the tubes however, lose support and lie horizontally (in tidal creeks parallel to the direction of current - see Plate 4). At this time, the worms move down in the tubes to below the erosional surface.

Sabellaria vulgaris, a tubicolous sabellariid polychaete, builds its tubes on the gravel lags of the lower intertidal zone. It is a filter feeder, feeding necessarily only when submerged with specialized parapodia shaped like fans (see Figure 6 (a) for species, Figure 6 (b) for food gathering organs). Feces are voided from the tubes with the aid of a ciliary current moving from anterior to posterior on the dorsal side (for respiration) around the pygidium to the ventral side where it leaves the tube anteriorly to the worm (Schafer, 1972). As stated previously, Sabellaria vulgaris was found in the lower intertidal gravel lag deposits ranging from East Noel (Plate 5) to the extreme eastern part of Noel Shore. Populations are sporadic (Plate 5), being dependant on the existence of gravel lag (stable substrate) in a zone of low evaporation rates. The genus is typified by lack of spacing within populations (Figure 7) (Newell, 1970). The more massive the colony, the greater its surface area and hence the food collecting ability of the colony. Apparently, settling is induced by the presence of turbulence, turbidity and other recently settled larvae.

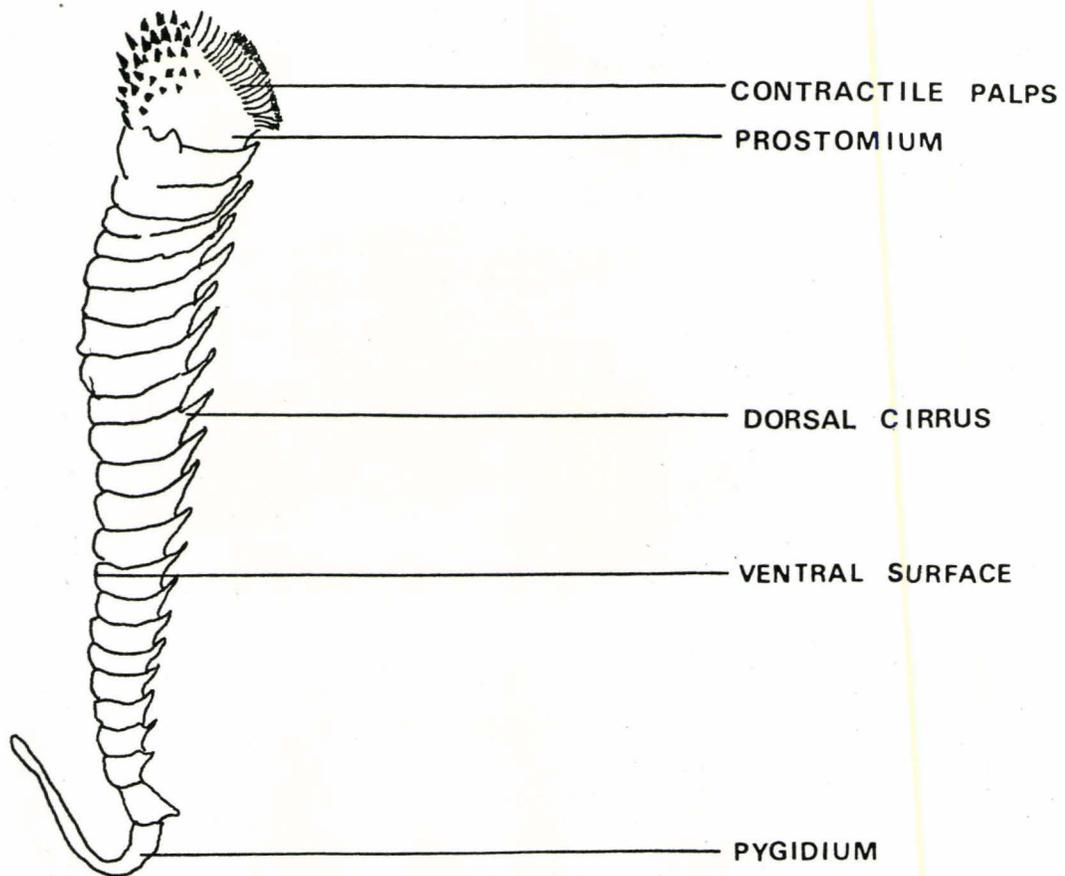


Figure 6 (a): The sabellariid, Sabellaria vulgaris found at East Noel and Noel Shore.

(magnification - 5X)

(taken from Gosner, 1971)

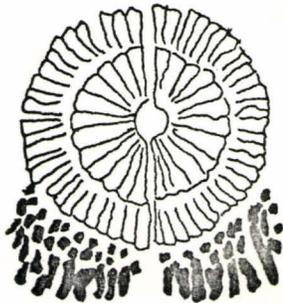


Figure 6 (b): Operculum or contractile palps opened for catching suspended sand grains.

(magnification - 10X)

(taken from Gosner, 1971)



Plate 5: East Noel II transect.

Occurrence of Sabellaria vulgaris tubes
at extreme low tide.

(bottle is 12 cm. tall)



Plate 6: East Noel transect.

Sinuuous tubes are built parallel to the
rock surface. (knife is 9 cm. long)

Newell (1970) reports that the larvae respond strongly to some component of the organic fibre binding recently constructed tubes. The stability of whole, stable tubes is also important to larval settling. Wilson (1970 (a), 1970 (b)) has demonstrated these causal relationships for two generic relatives in the lab. Bleakney (personal communication, 1973) reports the presence of sabellariid reefs exposed only during spring tides off Kingsport in the Avon R. estuary (Nova Scotia); reefs of sabellariids are reported in the North Sea (Sabellaria alveolata, S. spinulosa - Schafer, 1972) and along the northern coast of Florida (Phragmatopoma lapidosa, S. vulgaris - Gram, 1968). Population densities vary from ten per square metre to more than five hundred per square metre along East Noel and Noel Shore; populations exist in the thousands in reef colonies.

The sinuous tubes are parallel to the surfaces of the pebbles or cobbles they are build on (Plate 6). The tubes range in width from 0.3 cm. to 0.7 cm. and vary in length also, from 3 cm. to as much as 10 cm. (Figure 7). The tube is built right from the juvenile adult stage - the grains are smaller and the diameter of the tube is smaller at the oldest end because of this. Grains are caught with two rows of contractile palps which when opened are a circular fan shape (see Figure 6(b)). The grains are passed down to the mouth by way of a ciliary tract along the centre of the palps. The lips manipulate the grains into an area of the mouth where mucus is secreted onto them (from ventral oesophageal glands); the lips in the final act, place the grain into place on the tube as more mucus is secreted to cement the grain to the tube wall. The mucus is insoluble in sea water (Newell, 1968) but breaks down readily without constant renewal; a worm secretes mucus from ventral glands while manoeuvring in the tube, laying a fresh layer of mucus with every ascent and descent

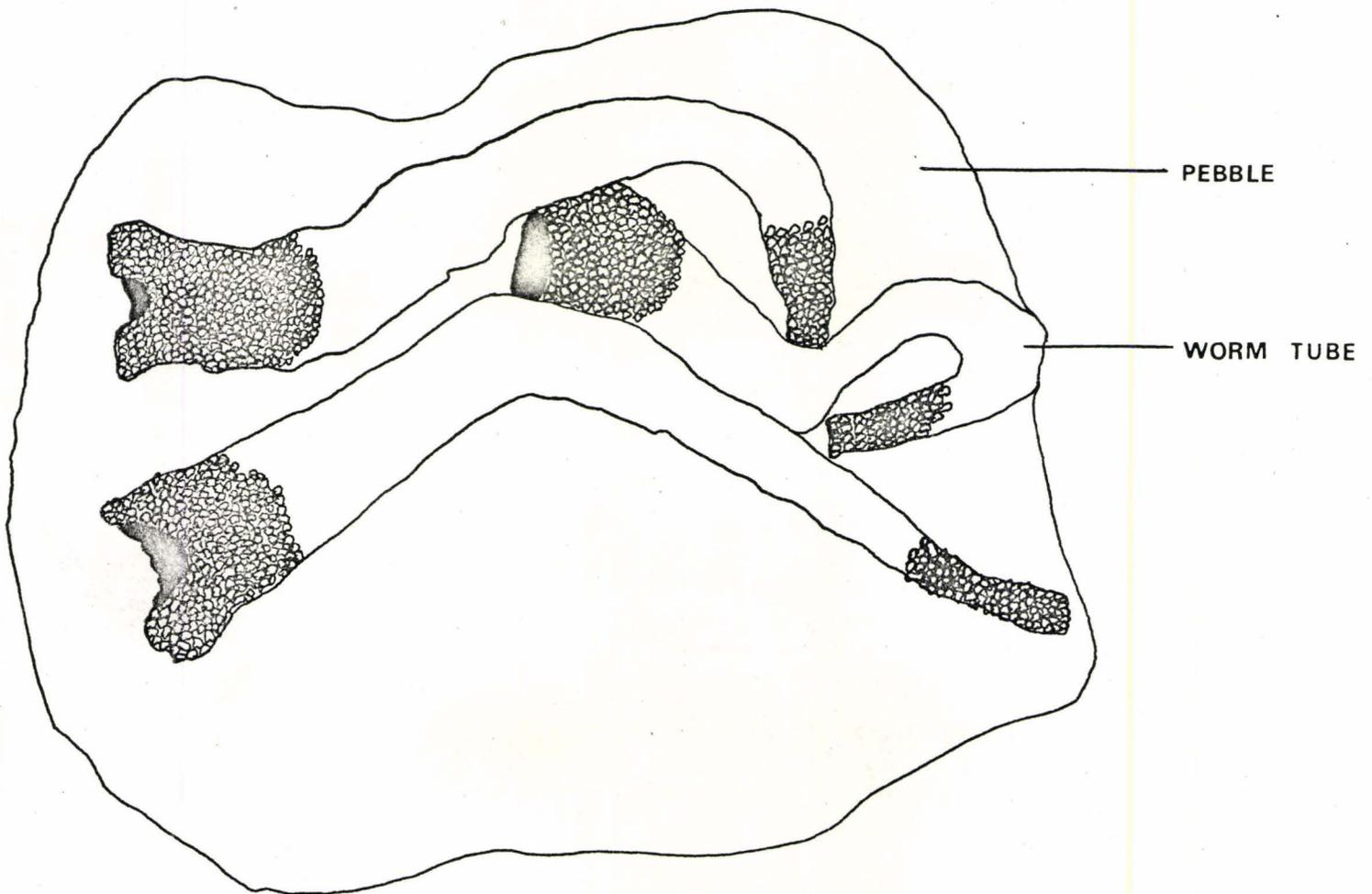


Figure 7: Sinuous sand-grain tubes of Sabellaria vulgaris
cemented to a pebble.

(magnification - 4X)

(drawn from collection specimen)

(Schafer, 1972).

Sample Collection

Clymenella torquata was collected near the Pembroke transect. Station 16 of the transect (just beyond the rock ledge of Horton shale) was redesignated C1 for thesis purposes. At station C1, a core tube 2.5 inches in diameter was used to take a sediment sample 25 cm. in depth. The sample core was then extruded from the tube using a fitted plunger and split into two lengths 15 cm. and 10 cm.. Each fraction was bagged and sprinkled with formalin to kill any deposit feeding fauna which could affect the grain size of the sample. Tubes within a radial distance of two metres of the station were collected: collection was best performed when a pit was dug by shovel (pit was approximately 30 cm. deep, 0.5 m. wide) and the sides of the pit washed with water from the pit. The tubes became well exposed and complete tubes could be picked away from the eroded walls. Twenty-five to thirty Clymenella tubes were collected and placed in a plastic bottle containing formalin. Six other stations were sampled with the same techniques along a line roughly east of station C1 at intervals of 50 metres. Sampling halted when sand was replaced by rock outcrop.

Sediment cores at stations 17 and 21 of the original transect (50 m. and 250 m. north from station C1) where Clymenella were rare were taken by D. Craig for grain size measurements of the top 10 cm. to compare with the areas of high Clymenella populations.

Spiophanes wisleyi was sampled on the Cambridge transect at stations 100 m. apart starting at the rock ledge-muddy silt interface. The stations

were labelled W1 through W10. Sediment cores were taken, ranging in depth from 17 cm. to 40 cm.; however, only the top 20 cm. were analyzed. The cores were split into lengths of 10 cm., bagged and treated with formalin. The best method for collecting Spiophanes tubes was to take trowelfuls of tubes and surface sediment and sieve them through a spaghetti strainer. Upwards of several hundred tubes were taken from a 1 metre radius around each station, placed in plastic bottles and preserved with formalin.

Sabellaria vulgaris tubes, because of their dependance on the presence of lower intertidal gravel lags, were collected where they could be found. Station locations were the lower intertidal zones at East Noel (transects II and I designated stations R1, R2 respectively), at Mungo Brook (east side of Noel Shore - not shown on Figure 1) where stations R3 and R4 existed and below the McLellan farm (R5) in the central part of Noel Shore. For each of the five stations, two sediment samples were taken; one was of the presumed intermittently suspended sand (Middleton, personal communication, 1973) in the lee of boulders adjacent to the sites of worm tubes and the other was of the gravel lag upon which the Sabellaria built their tubes (both sampled with a shovel). Tubes were collected by picking up small pebbles and cobbles bearing worm tubes (Plate 6) and placing them in plastic bags, then cloth bags for protection. Ten to thirty worm tubes were taken at each station.

Analytical Procedure

Sample Preparation for Grain Size Measurement

Each of the tube samples were washed gently in water to separate

detritus and non-tube sediment from the tubes. Washing also removed the odour of formalin to allow more comfortable handling of the samples. The tubes were then soaked in bleach to promote disaggregation; times for the disaggregation process varied from one day (Sabellaria vulgaris tubes) to three and four days with vigorous agitation required (Spiophanes wisleyi). Such variable durations are related to mucus-sediment ratio and tube type: the more mucus in existence, the longer the duration of the disaggregation process. The resultant sediment was then washed and filtered through Whatman no. 3 filter paper and dried in the oven (below fume hood - SS124) in plastic petri dishes at a temperature of 80 degrees Centigrade. After drying, the samples were split into subsamples (about 0.5 gm.) adequate for loose grain size measurement with the Shadowmaster. The fractions of the samples remaining were placed into labelled plastic bottles and stored in SS/B119.

The sediment samples were dried, split into subsamples similar to those of the tube subsamples, washed of the formalin, dried and placed into vials. The fractions of the samples remaining were placed back into their plastic and cloth bags and stored. In a few cases, the samples were dried, washed of the formalin and salt, dried, then split and placed into vials and bags; however, this process was found to be less efficient. Splitting was done using the Humboldt mechanical splitter and microsplitter located in SS124.

Sample Preparation for Mineralogical Determination

Each of the reserve samples for Clymenella and Spiophanes were coned and quartered (method after Carver, 1971) to subsamples of

approximately 0.8 gm. in weight.

The tube subsamples of Clymenella torquata were mixed together to produce one sample labelled CT; the sediment samples were similarly mixed into one sample labelled CS.

The reserve tube and sediment samples of Spiophanes wisleyi were mixed in analogous fashion to the C. torquata samples to produce mineralogy samples WS (sediment) and WT (tubes).

The tube samples of Sabellaria vulgaris, because of their small total volumes, were measured directly for mineralogical content - without splitting or mixing. The sediment samples (of presumed intermittent suspension origin) were similarly measured. The gravel lag samples were not analyzed for mineralogy.

Analysis - Grain Size

For Clymenella torquata, there are seven tube samples and fourteen sediment samples.

Each sample of 0.5 gm. was sprinkled on a clean glass slide located under the lens of the Shadowmaster. The slide was moved across the screen in a grid pattern, the grid points being farther apart than the mean grain size (as suggested in Carver, 1971). The grain size was measured by fitting each grain's largest apparent diameter within a circle inscribed on a piece of acetate - the acetate being easily transferable across the screen of the Shadowmaster. The acetate circles were at half phi intervals. This method is a modified version of Faber's method outlined in Mabeoone's paper (1962).

The grains were chosen by using the ribbon method (outlined in

Carver, 1971). Two hundred or three hundred grains were measured per station.

This method was also used on the twenty sediment samples and ten tube samples of the Spiophanes wisleyi collection.

The Shadowmaster was inappropriate for the gravel lag of the Sabellaria vulgaris samples. The intermittently suspended sand samples and the tube samples were measured using the Shadowmaster, while the gravel lag was sieved.

Analysis of Mineralogy

For Sabellaria vulgaris, each of the ten samples (five tube samples, five intermittent suspension samples) were examined under the binocular microscope at a magnification of 20X. The mineralogy was divided into two broad categories: heavy minerals and light minerals. Heavy minerals were amphibole, pyroxene, epidote, iron oxides and rock fragments; light minerals were clays, micas, quartz and feldspars. Identification was made by colour, habit and cleavage.

Two samples each, one sediment and one tube sample had been taken for the other two species, Clymenella torquata and Spiophanes wisleyi. For each of these samples, one thousand grains were examined under the mineral categories of heavy minerals, light minerals. Grains were chosen randomly while on a 9X9 grid with the table of random numbers in Snedecor and Cochran (1967).

Results

Grain Size Analyses

After graphing the data (stations 17 and 21 for Clymenella are in

Figures 8 and 9), Inman statistics were calculated and t-tests performed on the Inman statistics. The grain size data are in Tables A1, A2 and A3 in Appendix I. The Inman statistics, sorting and mean grain size (Inman, 1952), were calculated for each station of each species; the data are compiled in Tables A4, A5 and A6 in Appendix II. Student's t-tests were carried out on the differences of the means of the sorting and mean for each species: the test was an attempt to define the significance (yes or no) at a confidence level of 95% between the substrate grains and tube grains. The t-test (method after Snedecor and Cochran, 1967) values are drawn up in Tables 1, 2 and 3. As well, the critical "Inman percentiles" were averaged (Tables A4, A5 and A6) for each species to compare an average cumulative curve of the tube sediment with an average cumulative curve of the substrate sediment. The generalized curves are presented in Figures 10, 11 and 12.

Mineralogy Analyses

Data are presented in Tables 4 and 5.

Discussion

Clymenella torquata

The t-tests showed significance at the 95% confidence level for the difference between the means. The difference in the sorting, however, was not significant. These two results are obvious in the generalized curves (Figure 10) for Clymenella torquata. Kenny (1969) and Mangum (1964) discovered no preference for grain size in tube construction for Clymenella torquata. Rhoads and Stanley (1965) described the occurrence

Figure 8: Cumulative curve of grain size data
for station 21, species Clymenella torquata.
Worm population is very low.

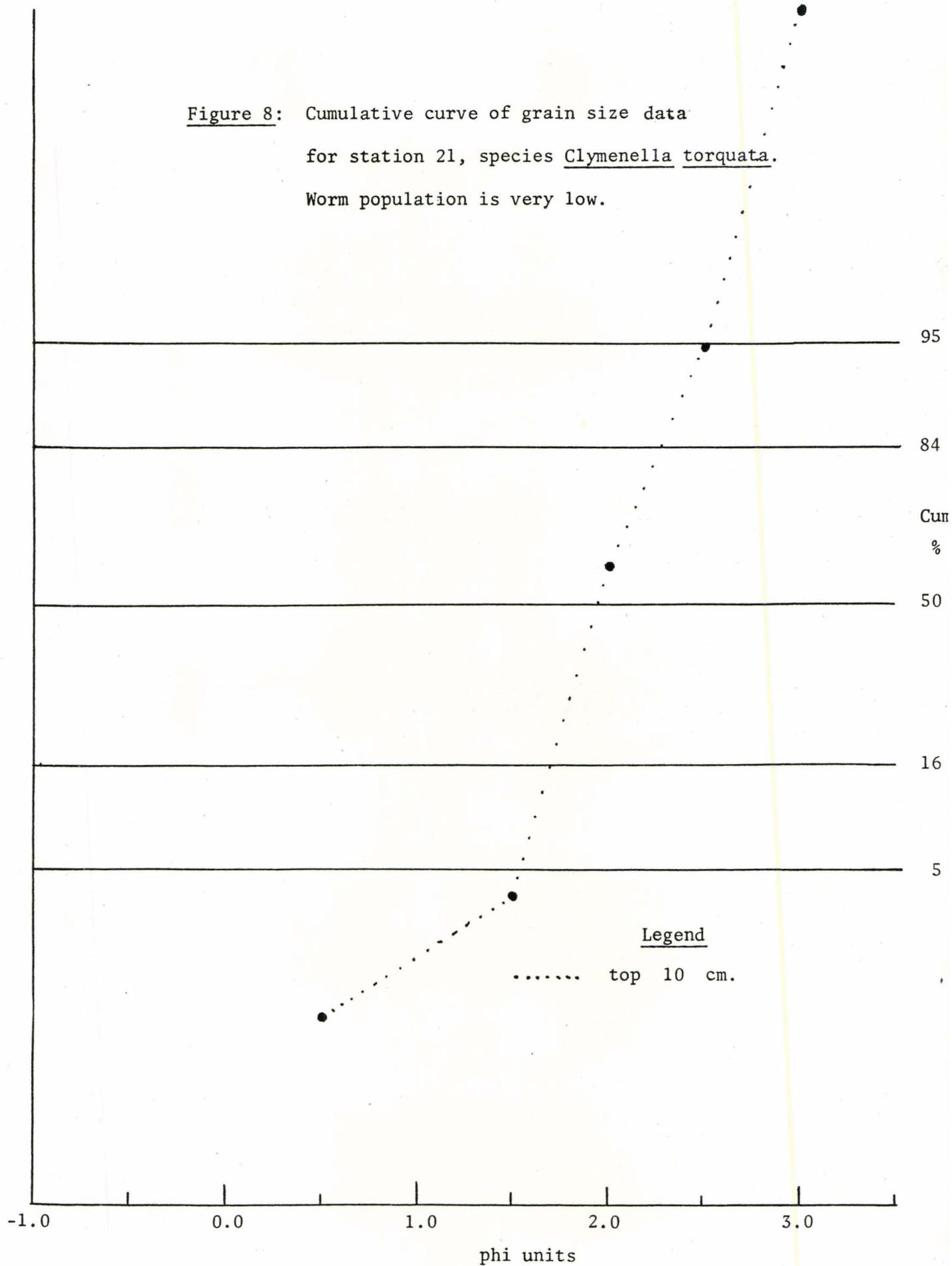


Figure 9: Cumulative curve of grain size data
for station 17, species Clymenella torquata.

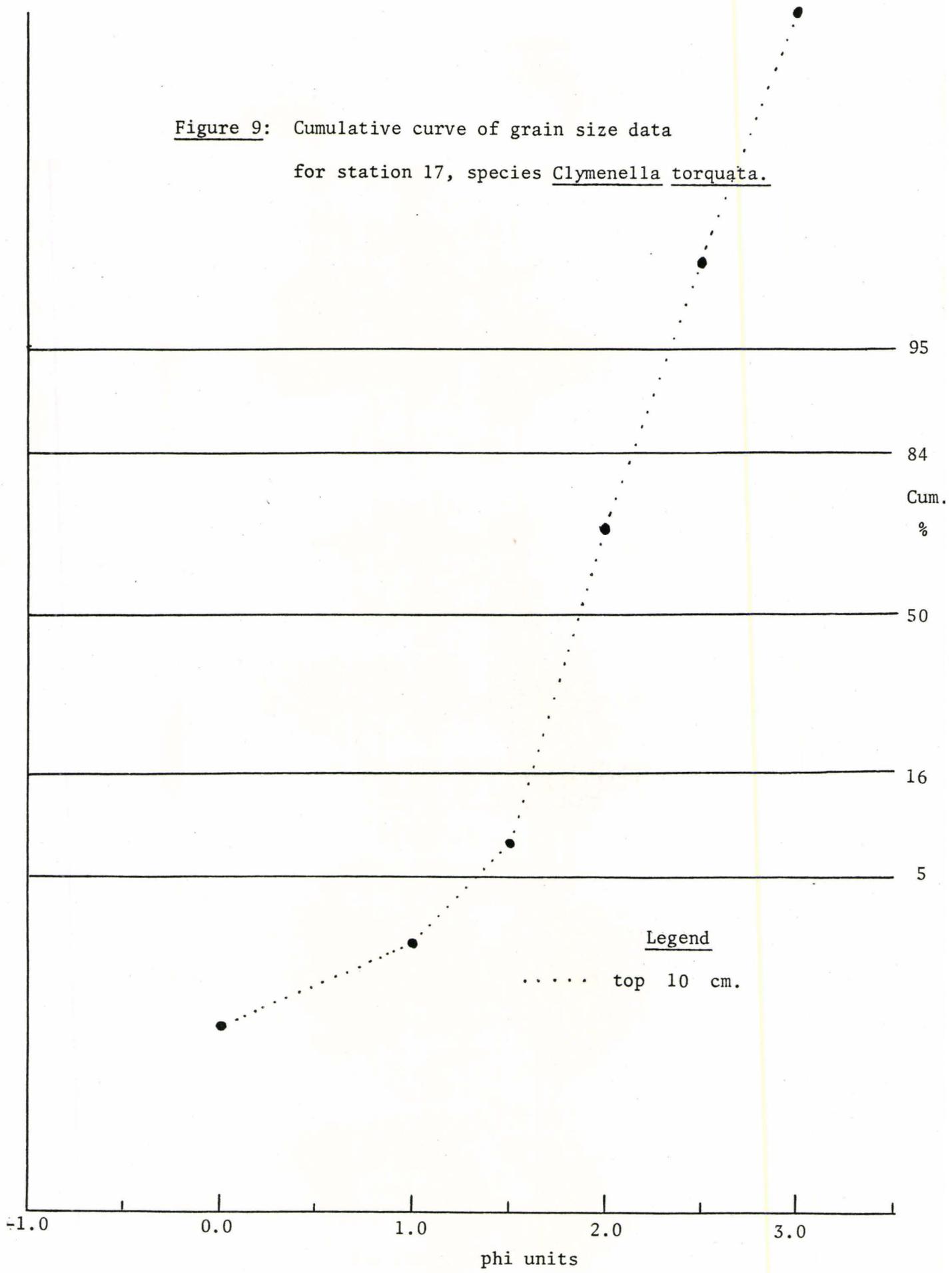


Figure 10: Generalized cumulative curves of grain size data for the species Clymenella torquata.
(data from Table A4)

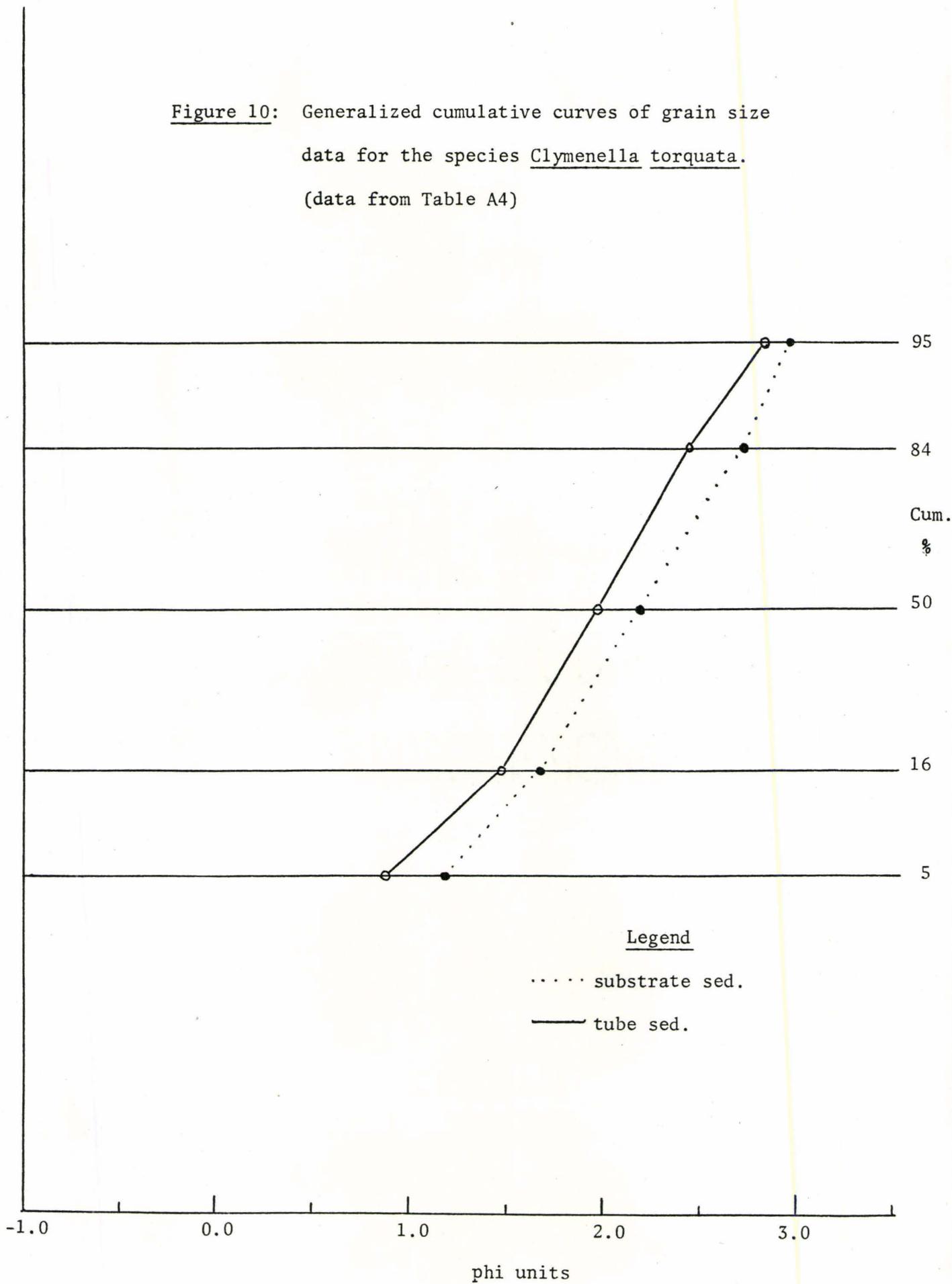


Figure 11: Generalized cumulative curves of grain size data for the species Spiophanes wisleyi.
(data from Table A5)

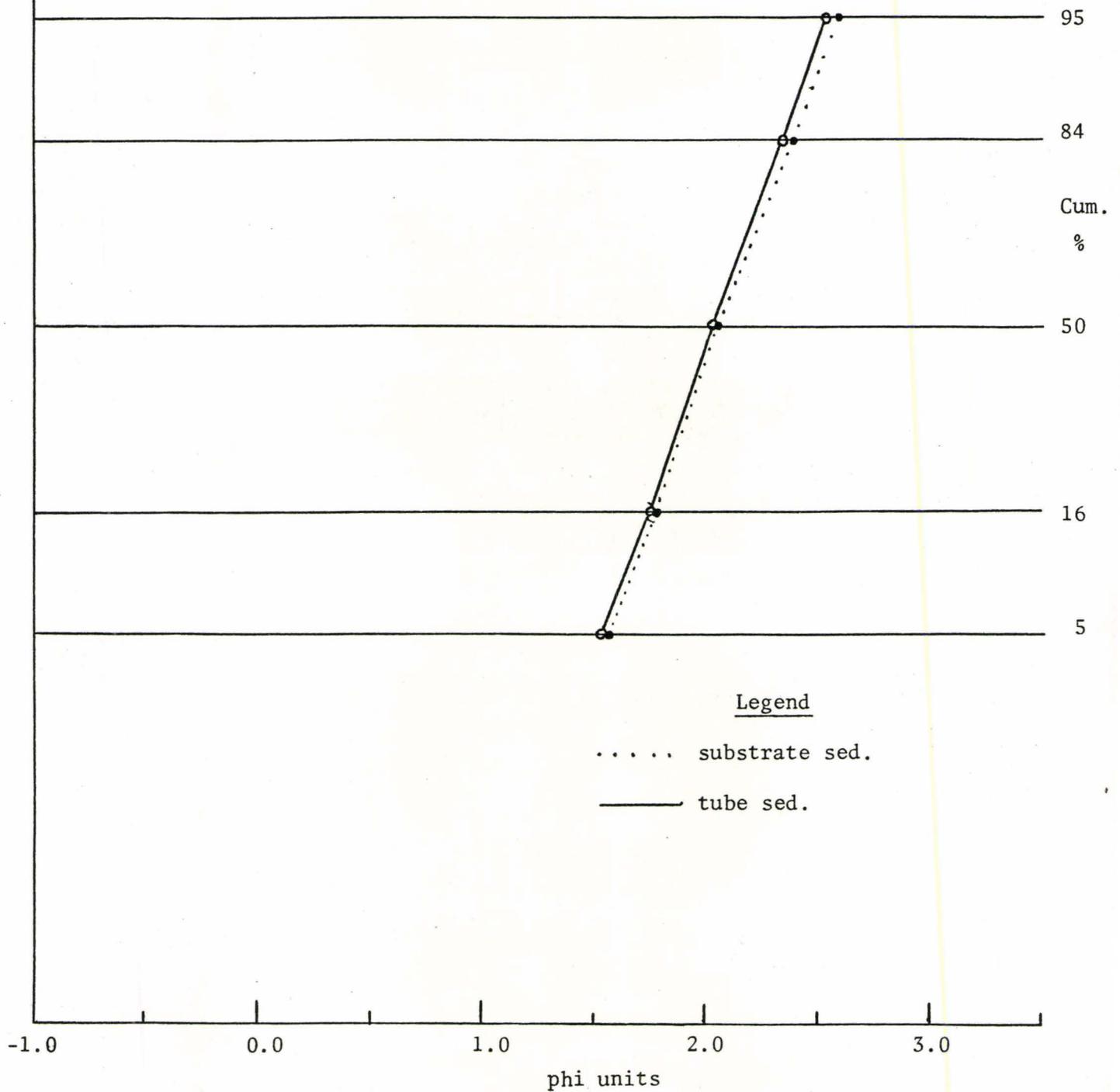


Figure 12: Generalized cumulative curves of grain size data for the species Sabellaria vulgaris.
(data from Table A6)

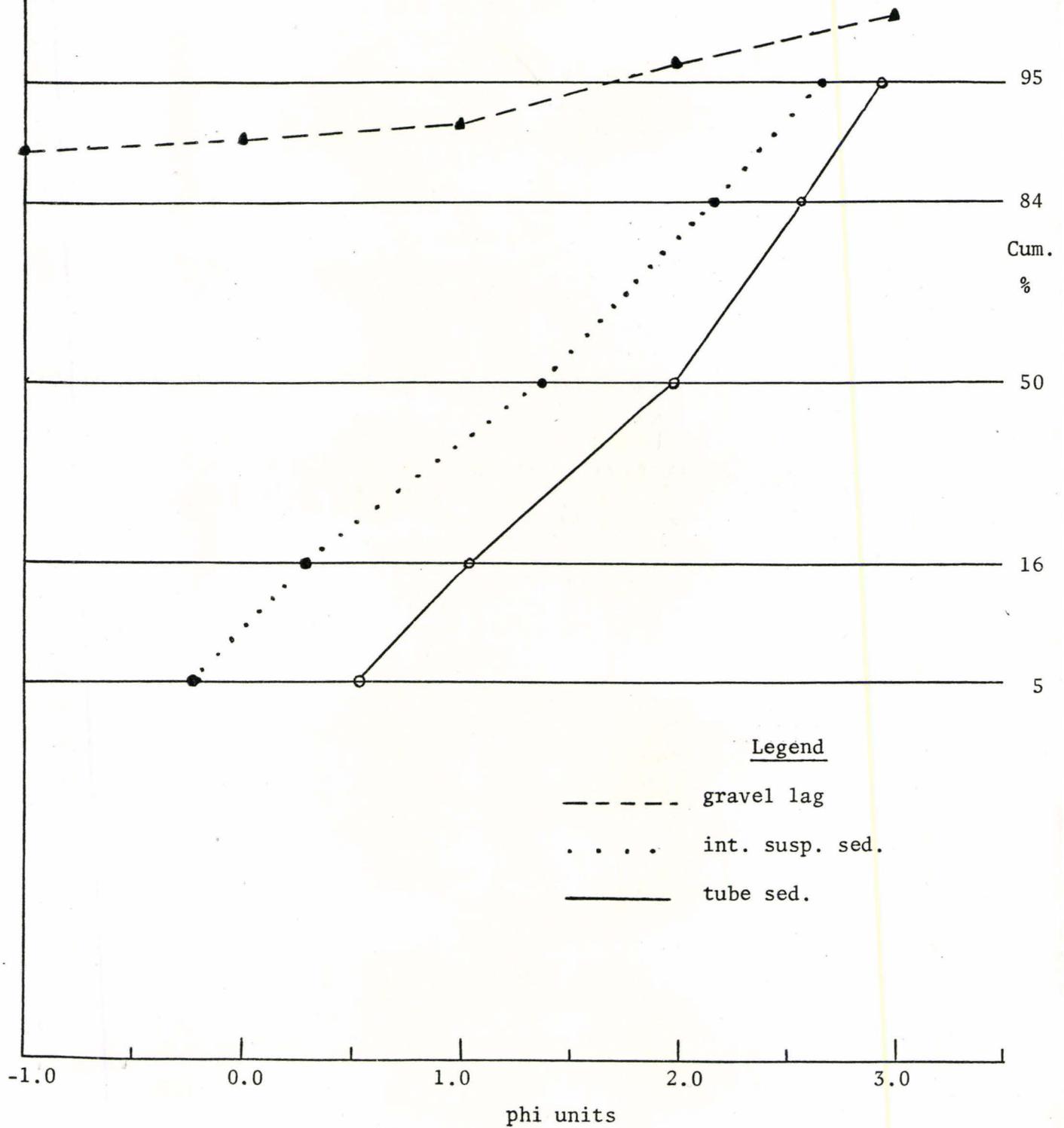


Table 1: Tests of significance in the differences in the mean grain sizes and sorting coefficients for the Clymenella torquata collection.

tested statistic	calculated t	table t
sorting	0.7058	2.8087
mean	5.2008	2.4450

Calculated t value was found using the formula associated with Table 3.

Calculation of the table t value was carried out using this formula:

$$\text{table } t = \frac{\left(\frac{s_1^2}{n_1} t_1 + \frac{s_2^2}{n_2} t_2 \right)}{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}$$

where: t_1 is value t for $n_1 - 1$ d.f. from table

t_2 is value t for $n_2 - 1$ d.f. from table.

(after Snedecor and Cochran, 1967)

Cochran, 1967)

Table 2: Tests of significance on the differences in the mean grain sizes and sorting coefficients for the Spiophanes wisleyi collection.

tested statistic	calculated t	table t
sorting	0.8868	2.5811
mean	0.4367	2.5974

Calculated t value was found using the formula associated with Table 3.

Calculation of the table t value was carried out using this formula:

$$\text{table } t = \frac{\left(\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2} \right)}{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}$$

(after Snedecor and Cochran, 1967)

Table 3: Tests of significance on the differences in the mean grain sizes and sorting coefficients for the Sabellaria vulgaris collection.

tested statistic	calculated t	table t
sorting	1.2868	3.495
mean	2.1620	3.495

Table t value is from t table in Snedecor and Cochran, 1967.

Calculation of the calculated t value was carried out using this formula:

$$t = \frac{|\bar{X}_1 - \bar{X}_2|}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}}$$

where \bar{X}_1, \bar{X}_2 are means of the tube and substr data.

s_1, s_2 are std. dev.

n_1, n_2 are nos. of samples
(after Snedecor and

Cochran, 1967)

Table 4: Mineralogical data of the substrate and tube sediment samples of Clymenella torquata and Spiophanes wisleyi.

Sample	heavy mineral count	%	light mineral count	%
CS	191	19.1	809	80.9
CT	126	12.6	874	87.4
WS	128	12.8	872	87.2
WT	96	9.6	904	90.4

Table 5: Mineralogical data of the substrate and tube sediment samples of Sabellaria vulgaris.

Sample	heavy mineral count	%	light mineral count	%
RS1B	29	14.5	171	85.5
RT1	12	6.0	188	94.0
RS2B	34	17.0	166	83.0
RT2	14	7.0	186	93.0
RS3B	14	7.0	186	93.0
RT3	21	10.5	179	89.5
RS4B	32	16.0	168	84.0
RT4	12	6.0	188	94.0
RS5B	16	8.0	184	92.0
RT5	12	6.0	188	94.0

of biogenic graded bedding as a result of reworking by Clymenella torquata populations; this would be plausible at Pembroke but for the constant flushing by the tides. The spongy texture described by Sanders et al. (1962) was present in the field; the sand was more porous compared to adjacent areas lacking in significant population densities of Clymenella torquata. The feces produced are easily suspended by the incoming (or outgoing) tide producing a source of removal of fines to enhance the spongy texture and lack of biogenic graded bedding. Some stability is lent to areas where populations reach densities of $500/m^2$ as such areas were not ripple marked but flat. Lower populations ($200/m^2$) did not prevent ripple marks from forming - the tubes existed both in the troughs and at the crests inferring the stability of the tubes but not the substrate.

The grain size analyses of the two stations seaward of the Clymenella populations (stations 17 and 21) produced interesting results. The mean grain sizes were coarser than the substrate sediment means for those regions inhabited by large populations of Clymenella. The sorting was excellent at both stations (Inman's classification, 1952) whereas sorting was only fair for the Clymenella stations' sediments. Such trends can be explained by the environments in which the two stations existed. Station 17 was in the middle of a tidal channel and sampling therefore occurred on very mobile, actively winnowed sand. Station 21 was on the opposite side of the tidal channel to the Clymenella populations, up out of the tidal channel. However, winnowing was still much more prevalent than in the areas inhabited by the Clymenella (less prevalent than in channel, though). These results imply that the feces are removed from the area

altogether; they are not deposited 100 metres seaward of the population. Population distributions of Clymenella are also affected by the degree of energy.

The analysis of the mineralogy showed a decrease in heavy mineral concentration in the Clymenella tubes; this must be due to the lesser desirability of heavy minerals as a result of a generally smaller grain size. Visual examination of intact tubes showed that the majority of the heavy minerals had been chosen for a flat side or flat habit; the flat side was placed on the inside of the tube. There appeared to be no change in mineralogy throughout the tube length; occasionally some tubes did possess granule sized grains at the top of the tube. Why this occurs is unknown - larger grains would be much more suitable on the bottom of the tube as anchors were it not for the upside down feeding habits of Clymenella. Perhaps the use of larger grains at the top of the tube reflect the imprecision of sorting by the young adult Clymenella as it starts to build the tube.

Spiophanes wisleyi

No significance could be attached to the differences between the means and sorting coefficients of the tube, substrate sediments. This is reflected in the generalized cumulative curves for the tube and substrate sediments, (Figure 11). This supports Schafer's statement that some spionids build mucus structures uniform in building material and shape. The construction of tubes occurs during times of burial by shifting sediment by picking grains with no preference. The sorting is so good in the substrate itself (average sorting coefficient is 0.31) that improvement

on it would prove very difficult for any organism.

The presence of large populations of this species prevents active erosion from occurring; intense matting rivals turtle grass in terms of stabilizing the sediment. Where tidal creeks do occur, the tubes are abandoned by the worms and erosion occurs. The tubes do remain in place while the surrounding sediment which is not mucus-bound is eroded. Intensive habitation of an area by Spiophanes wisleyi helps to oxidize the sediment at depths of 5 to 10 cm..

Heavy minerals seemed to be selected against in this case also (see Table 4) for tube building. For a non-selective deposit feeder, this is left unexplained. Visual observation of whole tubes left no impressions of preferred mineralogical selection in any part of the tubes. What heavy minerals did exist were apparently chosen for their flat habit.

Sabellaria vulgaris

Despite an obvious difference in the means of the substrate sediment and tube sediment, there was no significance at the 95% confidence level. The sorting coefficients' difference also displayed no significance. This is surprising in the light of the fact that Sabellaria vulgaris is a filter feeder and gathers grains for tube building by means of the same mechanism. Gram (1968) reports an improvement in sorting of the sediment behind Phragmatopoma lapidosa (sabellariid) reefs off the coast of Florida. He attributes this to the desirability of fines for food. This does not occur for the sampled populations which were sporadic and small and so had little effect on the local substrate. Grain size relationships are similar between this study and Gram's (1968) in that

the tubes are finer-grained than the surrounding substrate; this grain size difference is dependant on the ability of the currents (the competence) to suspend certain grain sizes.

The overall trend of the mineralogical analysis seems to be that the light minerals are preferred for tube building. This may reflect the ability of turbulence of the water to be unable to suspend heavy minerals despite their small size due to specific gravities. A traction fraction with a higher percentage of heavy minerals may have been included with the supposed intermittent suspension fraction. Sabellaria vulgaris does differ from Phragmatopoma lapidosa in that carbonate shell fragments are almost completely selected against. Gram (1968) reports that P. lapidosa uses carbonate shell fragments in the building of the tube because shell fragments despite coarser grain sizes are generally more buoyant than equant quartz and feldspar grains. Phragmatopoma lapidosa also concentrates heavy minerals (also reported by Gram, 1968). This author found some Sabellaria tubes that concentrated heavy minerals in the older parts of the tubes - this was not widespread. Again, heavy minerals were selected for habit - the classic example of this in the literature is Owenia fusiformis (an oweniid) (Fager, 1964). In that species heavy minerals are initially chosen for small grain size and flat habit. As the worm grows, the percentage of heavy minerals decreases and percentage of carbonate grains (shell fragments) increases.

Kirtley and Tanner (1968) report that in some parts of the sabellariid reefs off the north shore of Florida, where the worms had died, the protein cement has been replaced by carbonate dissolved from the shells. Such could not occur in the populations sampled in this study

as carbonate is generally lacking in S. vulgaris tubes found. The facts that the populations are scattered and do not form reefs infer low preservation potential.

Conclusions

Clymenella torquata in large population densities (400 - 500/m²) stabilizes the sediment by hindering the formation of ripples. Lower population densities do not prevent the substrate from becoming mobile. The substrate becomes spongy in texture as a result of increase in porosity through feeding by large populations. Biogenic graded bedding has been reported in the literature (Rhoads and Stanley, 1966) but was not observed here. This species does prefer the coarser grains from the substrate to build tubes (difference in means was statistically significant) but the sorting difference was not statistically significant; sorting varies very little between the two entities, one tube and substrate.

Spiophanes wisleyi builds tubes with no preference of grain size or range of grain sizes. It inhabits areas of fine-grained sand, coarse-grained silt that are well-sorted. Large population densities (up to 98,000/m²) stabilize the substrate and prevent ripple formation. Because of the finer grain size present in the substrate, one can associate the occurrence of this species with a low energy upper intertidal zone which accumulates detritus. Both Clymenella torquata and Spiophanes wisleyi tend to select against heavy minerals.

Sabellaria vulgaris builds tubes by catching grains suspended in the water column and glueing them to the tube wall. When in reef form, sabellariids are very significant: they cause the sediment behind them to

become better sorted (behind referring to position with respect to prevailing current); they concentrate heavy minerals and carbonate shell fragments. However, this author had access to sporadic populations of Sabellaria vulgaris and trends in mineralogy were reversed. Grain size appeared to be finer in the tubes compared with the presumed intermittently suspended sediment but no statistical significance was attached. Simultaneously, sorting appeared better in the tubes but was not statistically significantly different from that of the intermittently suspended fraction. Population densities were too low to stabilize the substrate in their high energy environment.

Geologic Significance

Each of the three species inhabits a different energy environment and presents unique characteristics to its environment.

Clymenella torquata inhabits a region of medium-grained sand and in large numbers initiates a stable substrate as well as a certain increase in porosity. In certain cases, biogenic graded bedding may result but did not appear to be present in the study area. In the geologic record, therefore, localized ripples and adjacent plane beds with increase in porosity may indicate the fossil presence of large populations of upside-down deposit feeding polychaetes. Biogenic graded bedding may or may not be present.

Spiophanes wisleyi inhabits a low energy area as indicated by accumulations of detritus and muddy silt. In such large populations as was discovered at Cambridge, the addition of organic matrix would be large - such an addition aids in binding the sediment. Tubes do not vary

in grain size or sorting as compared to the sediment and so any breakdown in the organic matrix of the tubes would deny the tubes the chance of being fossilized. Preservation potential is therefore low.

Sabellaria vulgaris occurring in sporadic populations has very low preservation potential. Sabellariids thrive on the existence of high energy and a stable substrate because they are filter feeders. Kirtley and Tanner (1968) feel that sabellariids may have played an important part in the formation of reefs in the geologic past. Certain trace fossils such as Sabellarifex (Cambrian to Lower Devonian of Germany and Sweden - Howell, 1962) and Sabellarites (Ordovician around Montreal - Howell, 1962) may be fossil sabellariid reefs; these make excellent palaeoecologic indicators being formed subtidally in high energy zones near beaches. Preservation increases with volume and increase in the concentration of carbonate shelly fragments (such as in Phragmatopoma lapidosa reefs) which may become sources of carbonate cement. The reef structures also affect the surrounding substrates by improving the sorting, decreasing the mobility and affecting the distribution of mineralogy.

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Appendix I: Grain Size Data of the Twenty-two Stations Sampled
for Tubicolous Polychaetes.

Table A1: Grain Size Data of the Seven Stations for Clymenella
torquata.

(a)

phi size	CSIA	count	%	Cum. %	CSIB	count	%	Cum. %	CTI	count	%	Cum. %
-1.0												
-0.5										1	0.5	0.5
0.0		1	0.5	0.5		2	0.7	0.7		1	0.5	1.0
0.5						1	0.3	1.0		2	1.0	2.0
1.0		3	1.5	2.0		8	2.7	3.7		7	3.5	5.5
1.5		1	0.5	2.5		14	4.7	18.3		13	6.5	12.0
2.0		36	18.0	20.5		75	25.0	33.3		87	43.5	55.5
2.5		76	38.1	32.5		98	32.7	77.3		64	32.0	27.5
3.0		65	32.5	41.0		58	19.3	96.7		22	11.0	98.5
3.0		18	9	100		1.0	3.3	100.0		3	1.5	100.0

(b)

phi size	CS2A	count	%	Cum. %	CS2B	count	%	Cum. %	CT2	count	%	Cum. %
-1.0												
-0.5												
0.0		2	0.7	0.7		2	3.0	1.0				
0.5		2	0.7	1.3		3	1.9	7.5		2	1.0	1.0
1.0		8	2.7	4.0		8	4.0	6.5		1	0.5	1.5
1.5		17	5.7	9.7		14	7.0	13.0		2	4.0	5.5
2.0		70	23.3	33.0		69	34.5	48.0		70	35.0	40.5
2.5		57	17.3	50.3		74	37.0	85.0		81	40.5	36.0
3.0		112	37.3	82.3		30	15.0	100.0		34	17.0	98.0
3.5		37	12.3	100.0						4	2.0	100.

(c)

phi units	CS3A	count	%	Cum. %	CS3B	count	%	Cum. %	CT3	count	%	Cum. %
-1.0												
-0.5												
0.0		1	0.5	0.5		1	0.5	1.0		4	2.0	3.5
0.5		1	0.5	1.0		8	4.0	5.0		8	4.0	7.5
1.0		7	3.5	4.5		14	7.0	12.0		17	8.5	15.5
1.5		7	3.5	8.0		13	6.5	18.5		12	6.0	21.5
2.0		79	39.5	47.5		62	31.0	49.5		84	42.0	63.5
2.5		77	38.5	86.0		57	28.5	78.0		58	29.0	92.5
3.0		21	10.5	96.5		18	9.0	87.0		8	4.0	96.5
3.5		7	3.5	100.0		26	13.0	100.0		7	3.5	100.0

(d)

phi units	CS4A	count	%	Cum. %	CS4B	count	%	Cum. %	CT4	count	%	Cum. %
-1.0		1	0.5	0.5								
-0.5												
0.0		3	1.5	2.0						1	0.5	0.5
0.5		2	1.0	3.0								
1.0		13	6.5	9.5		4	2.0	2.0		8	4.0	4.5
1.5		23	11.5	21.0		3	1.5	3.5		16	8.0	12.5
2.0		59	29.5	50.5		32	16.0	19.5		84	42.0	54.5
2.5		54	27.0	77.5		78	35.0	58.5		66	33.0	87.5
3.0		16	8.0	85.5		62	31.0	89.5		12	6.0	93.5
3.5		29	14.5	100.0		21	10.5	100.0		13	6.5	100.0

(e)

phi units	CS5A	count	%	Cum. %	CS5B	count	%	Cum. %	CT5	count	%	Cum. %
-1.0		1	0.5	0.5								
-0.5						1	0.5	0.5		2	1.0	1.0
0.0						1	0.5	1.0		6	3.0	4.0
0.5		3	1.5	2.0		7	3.5	4.5		8	4.0	8.0
1.0		7	3.5	5.5		11	5.5	10.0		12	6.0	14.0
1.5		13	6.5	12.0		19	9.5	19.5		20	10.0	24.0
2.0		86	43.0	55.0		53	26.5	46.0		64	32.0	56.0
2.5		50	25.0	80.0		86	43.0	89.0		55	27.5	83.5
3.0		24	12.0	92.0		15	7.5	96.5		28	14.0	97.5
3.5		16	8.0	100.0		7	3.5	100.0		5	2.5	100.0

(f)

phi units	CS6A	count	%	Cum. %	CS6B	count	%	Cum. %	CT6	count	%	Cum. %
-1.0												
-0.5												
0.0		1	0.5	0.5						3	1.5	1.5
0.5		1	0.5	1.0						2	1.0	2.5
1.0		3	1.0	2.5		2	1.0	1.0		9	4.5	7.0
1.5		4	2.0	4.5		1	0.5	1.5		5	2.5	9.5
2.0		47	23.5	28.0		26	13.0	14.5		86	43.0	52.5
2.5		72	36.0	64.0		66	33.0	47.5		71	35.5	88.0
3.0		34	17.0	81.0		91	45.5	93.0		19	9.5	97.5
3.5		38	19.0	100.0		14	7.0	100.0		5	2.5	100.0

Appendix II: Tables of Calculated Averages for General Curves

(Figures 10, 11 and 12) and Calculated Inman Statistics.

Table A4: Percentile Averages, Inman Statistics for *Clymenella torquata*.

Statistic/ Percentile							
	CS1A	CS1B	CS2A	CS2B	CS3A	CS3B	
(a) 5	1.20	1.64	1.11	0.85	1.10	0.50	
16	1.66	1.93	1.67	1.55	1.67	1.35	
50	2.07	2.41	2.48	2.02	2.07	2.00	
84	2.71	2.85	2.93	2.49	2.46	2.83	
95	2.90	3.06	3.10	2.71	2.82	3.11	
sorting	0.53	0.44	0.63	0.47	0.40	0.74	
mean	2.19	2.39	2.30	2.02	2.07	2.09	
Statistic/ Percentile	CT1		CT2		CT3		
5	0.95		1.45		0.30		
16	1.57		1.72		1.05		
50	1.95		2.12		1.85		
84	2.41		2.55		2.30		
95	2.75		2.82		2.75		
sorting	0.45		0.42		0.63		
mean	1.99		2.14		1.68		

(b)

Statistic/ Percentile		CS4A	CS4B	CS5A	CS5B	CS6A	CS6B
5		0.72	1.60	0.95	0.59	1.52	1.74
16		1.30	1.93	1.57	1.35	1.81	2.02
50		2.00	2.40	1.95	2.04	2.32	2.52
84		2.89	2.89	2.65	2.40	3.02	2.84
95		3.12	2.45	3.03	2.85	2.80	3.04
sorting		0.80	0.48	0.54	0.53	0.61	0.41
mean		2.10	2.41	2.11	1.88	2.42	2.43
Statistic/ Percentile		CT4		CT5		CT6	
5		1.03		0.15		0.84	
16		1.56		1.10		1.61	
50		1.97		1.94		1.98	
84		2.45		2.50		2.42	
95		3.02		2.84		2.80	
sorting		0.45		0.70		0.41	
mean		2.01		1.80		2.02	

(c)

Statistic/ Percentile		CS7A	CS7B	totals	avg.		CS17
5		1.44	1.40	16.36	1.17		1.34
16		1.67	1.73	23.21	1.66		1.62
50		2.01	2.17	30.41	2.17		1.87
84		2.65	2.50	38.11	2.72		2.15
95		3.06	2.61	41.36	2.95		2.34
sorting		0.49	0.38	2.48	0.53		0.27
mean		2.16	2.12	30.69	2.19		1.89
Statistic/ Percentile		CT7		totals	avg.		CS21
5		1.22		6.02	0.86		1.54
16		1.60		10.22	1.46		1.70
50		1.96		13.72	1.96		1.95
84		2.40		17.01	2.43		2.27
95		2.71		19.74	2.82		2.51
sorting		0.40		3.43	0.49		0.29
mean		2.00		13.65	1.95		1.99

Table A5: Percentile Averages and Inman Statistics for Spiophanes wisleyi.

(a)	Statistic/ Percentile	WS1A	WS1B	WS2A	WS2B	WS3A	WS3B
	5	1.75	1.58	1.75	1.71	1.75	1.36
16	2.11	1.78	2.10	1.90	1.94	1.68	
50	2.55	2.14	2.37	2.37	2.22	2.00	
84	2.82	2.53	2.70	2.68	2.51	2.31	
95	3.01	2.65	2.97	2.85	2.71	2.50	
sorting	0.36	0.38	0.30	0.39	0.29	0.32	
mean	2.47	2.16	2.46	2.29	2.23	2.00	
Statistic/ Percentile	WT1		WT2		WT3		
5	1.74		1.60		1.74		
16	2.02		1.81		1.97		
50	2.45		2.20		2.32		
84	2.69		2.60		2.65		
95	2.81		2.80		2.81		
sorting	0.34		0.40		0.34		
mean	2.36		2.21		2.31		

(b)

Statistic/ Percentile		WS4A	WS4B	WS5A	WS5B	WS6A	WS6B
5		1.61	1.69	1.51	1.39	1.44	1.41
16		1.80	1.87	1.65	1.61	1.65	1.62
50		2.07	2.17	1.87	1.86	2.00	1.85
84		2.39	2.50	2.13	2.12	2.41	2.12
95		2.67	2.75	2.35	2.30	2.70	2.38
sorting		0.30	0.32	0.24	0.26	0.38	0.25
mean		2.10	2.19	1.89	1.87	2.03	1.87
Statistic/ Percentile		WT4		WT5		WT6	
5		1.54		1.51		1.49	
16		1.67		1.74		1.66	
50		1.89		2.06		1.92	
84		2.15		2.31		2.25	
95		2.34		2.47		2.47	
sorting		0.24		0.29		0.30	
mean		1.51		2.03		1.91	

(c)

Statistic/ Percentile		WS7A	WS7B	WS8A	WS8B	WS9A	WS9B
5		1.55	1.45	1.56	1.55	1.63	1.58
16		1.71	1.65	1.72	1.68	1.78	1.75
50		1.98	1.91	1.51	1.88	2.04	2.00
84		2.30	2.20	2.45	2.17	2.73	2.40
95		2.50	2.40	2.72	2.40	2.76	2.67
sorting		0.30	0.28	37	0.25	0.48	0.33
mean		2.01	1.93	2.09	1.93	2.26	2.08
Statistic/ Percentile		WT7		WT8		WT9	
5		1.50		1.30		1.57	
16		1.66		1.63		1.72	
50		1.90		1.87		1.96	
84		2.24		2.21		2.25	
95		2.44		2.50		2.43	
sorting		0.23		0.25		0.27	
mean		1.93		1.92		1.99	

(d)

Statistic/ Percentile		WS10A	WS10B	totals	avg.
5		1.59	1.40	31.26	1.56
16		1.73	1.62	35.35	1.77
50		1.95	1.83	40.95	2.05
84		2.23	2.05	40.75	2.39
95		2.45	2.30	51.99	2.60
sorting		0.25	0.22	6.27	0.31
mean		1.98	1.84	41.62	2.08
Statistic/ Percentile		WT10		totals	avg.
5		1.53		15.35	1.53
16		1.68		17.56	1.76
50		1.87		20.44	2.04
84		2.10		23.41	2.34
95		2.20		25.27	2.53
sorting		0.21		2.94	0.29
mean		1.89		0.51	2.05

Table A6: Percentile Averages and Inman Statistics for *Sabellaria vulgaris*.

(a)	Statistic/ percentile	RSIA	RSIB	RS2A	RS2B	RS3A	RS3B
	5			-0.11		0.32	
16			0.20		0.66		0.57
50			0.68		1.19		1.73
84			1.35		1.85		2.16
95			2.00		2.50		2.89
sorting			0.58		0.60		1.30
mean			0.78		1.26		1.37
	Statistic/ percentile	RTI		RT2		RT3	
5		0.23		0.10		-0.20	
16		0.63		0.55		0.54	
50		1.57		1.81		1.65	
84		2.15		2.55		2.45	
95		2.60		2.95		3.06	
sorting		0.77		1.00		0.96	
mean		1.39		1.55		1.50	

(b)

Statistic/ percentile	RS4A	RS4B	RS5A	RS5B	Totals	Avg.
5		-0.25		-1.14	A(-1 ϕ) B-1.20	89.95 ^{wt} % B -0.24
16		0.25		0.00	A(0 ϕ) B 1.45	90.99 ^{wt} % B 0.29
50		1.61		1.70	A(1 ϕ) B 6.90	92.11 ^{wt} % B 1.38
84		2.48		3.00	A(2 ϕ) B10.85	95.99 ^{wt} % B 2.17
96		2.87		3.11	A(3 ϕ) B13.35	97.80 ^{wt} % B 2.67
sorting		1.12		1.50	B 5.10	B 1.02
mean		1.37		1.50	B 6.28	B 0.74
Statistic/ percentile	RT4		RT5		Totals	Avg.
5	1.76		0.75		2.65	0.53
16	2.22		1.52		5.20	1.04
50	2.73		2.13		9.95	1.99
84	3.02		2.67		12.85	2.57
95	3.15		2.95		14.70	2.94
sorting	0.40		0.58		3.70	0.74
mean	2.62		2.10		9.16	1.83