Fecal Pellet Production
By *Macoma balthica*
And Pellet Transport
In Cobequid Bay, Nova Scotia

Fecal Pellet Production
By _Macoma balthica_
And Pellet Transport
In Cobequid Bay, Nova Scotia

By

James Stephen Moffat

A Thesis
Submitted to the Faculty of Arts and Science
In Partial Fulfilment of the Requirements
for the Degree
Bachelor of Science

McMaster University
May, 1975

Bachelor of Science (1975)
(Geology)

McMaster University
Hamilton, Ontario

TITLE: Fecal Pellet Production by Macoma balthica and Pellet Transport in Cobequid Bay, Nova Scotia.

AUTHOR: James Stephen Moffat

SUPERVISOR: Dr. M. J. Risk

NUMBER OF PAGES: vii, 41.

Abstract

Large high density populations, up to $3,000/m^2$ of the bivalve Macoma balthica inhabit the muddy intertidal areas in the Bay of Fundy, Nova Scotia. The fecal pellets produced by Macoma b. are resistant to breakdown. Off Spencer's Point, the pellets are transported via small intertidal channels away from the shore onto a sand bar, at low tide. At high tide the channels act as traps for fecal pellets. The pellets breakdown over the sand bar at high tide, but a large proportion of the pellet remains in suspension as a mucous bound mud agglomerate. In an area of 2000 Macoma $b./m^2$, the rate of fecal pellet production is approximately 1 Kg dry $wt/m^2/yr$.

The rate of pseudofecal production increases with water turbidity. The rate of sediment reprocessing is approximately 9 Kg dry wt. of $sediment/m^2/yr.$, or a layer of wet sediment approximately 3.3 cm. deep.

The Macoma b. in Cobequid Bay are largely deposit feeding. In areas of high population density and coarser sediment, this depletes the surface of sediment mud and fine sand. The influx of sediment necessary to sustain such a population is, in part, pseudofecal material from Macoma b. populations higher on the mud flats.

Acknowledgements

The author wishes to thank Dr. M. J. Risk for his valuable guidance and enthusiasm throughout the course of this study. The author also appreciates the assistance and helpful suggestions provided by Mr. Douglas Craig and Miss Verena Tunnicliffe. Special thanks go to Miss Nancy Bourdon for deciphering my cryptogrammatic handwriting and typewriting the manuscript.

Table of Contents

List of Figures

List of Plates

Introduction

The large intertidal mud areas in Cobequid Bay, Bay of Fundy, Nova Scotia, are characterized by high population densities of the tellinid bivalve, *Macoma balthica*, the amphipod *Corophium voltator*, and localized populations of *Mya arenaria*. In some areas of the bay, population densities of *Macoma balthica* exceed 3,000 individuals/m^2. The population density of *Macoma balthica* is, in part, controlled by the bacterial population of the surficial sediments (Newell, 1965). *Macoma balthica* is the most significant producer of copious amounts of resistant fecal pellets in the muddy intertidal areas.

Macoma balthica has a wide geographical range, extending from the Arctic, to both sides of the boreal North Atlantic and as far south along the Eastern North American coast as Chesapeake Bay. Coan (1971) synomized the species with *Tellina inconspicua* Broderip and Sowerby, extend *Macoma balthica*'s range through the North Pacific, as far south as San Francisco Bay.

Study Area

The bulk of the observations and data in this report were taken along a transect across the intertidal area off Spencer's Point during the summer of 1974. The area lies off a small headland, but is nevertheless typical of Cobequid Bay mud flats.

The transect off Spencer's Point begins on the well-sorted narrow sand beach at the base of a Triassic red bed cliff (Station 1). Offshore 50 meters is a slightly elevated juvenile salt marsh. The density of grass on this salt marsh is quite low and it is not characteristic of the typical large salt marshes in Cobequid Bay.

STUDY AREA

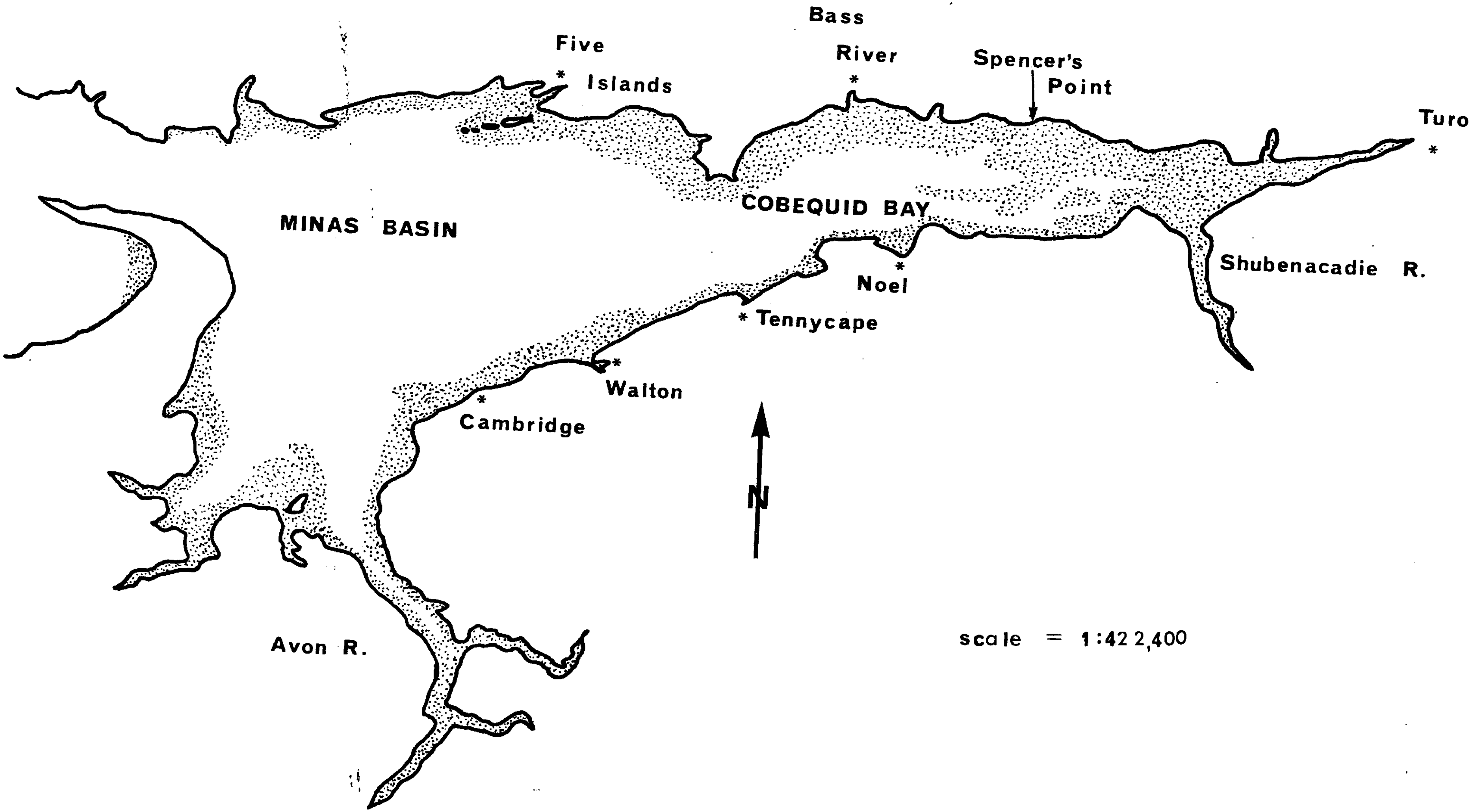
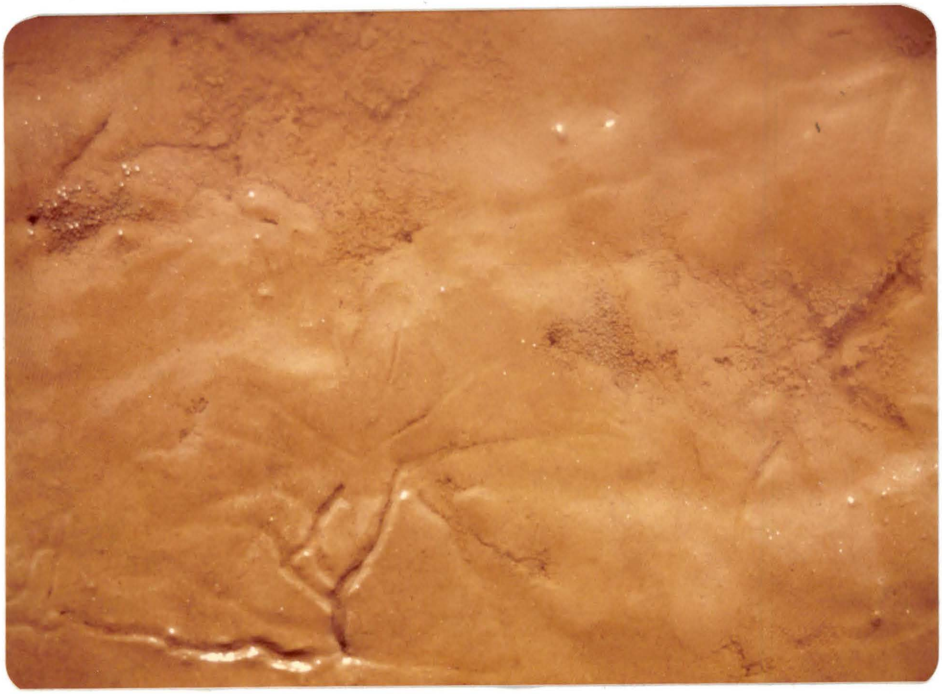

Five Islands
Bass River
Spencer's Point
Turo
MINAS BASIN
COBEQUID BAY
Shubenacadie R.
Noel
Tennycape
Walton
Cambridge
N
Avon R.
scale = 1:422,400

Plate I: Spencer's Point transect



x2

Plate II: *Macoma balthica* feeding traces and fecal deposits

The transition from salt marsh to mud flat is sharp along the transect. The very fine muds on the upper portion of the mud flat have a high fluid content, and a loose consistancy. The muds derive their characteristic red colour from the Triassic red bed source rocks. The mud becomes firmer going farther offshore, as the sand proportion in the sediment increases. Ripples first appear 450m. from shore (Station 10), marking the near shore edge of a sand bar. Fifty meters offshore from Station 10, megaripples appear. The only organism found living in these highly mobile sands was the small polychaete Scoleolepis, which feeds upon the mud drapes in the troughs of the megaripples. The Macoma population extends from the salt marsh to the near shore edge of the sand bar.

Slightly meandering shallow channels about 40cm. deep and 50cm. wide transect the mud flats. During periods of low rainfall, the channels are silted up with highly fluid muds. A heavy rainfall during low tide flushes the silt from the channels, and causes slight channel migration. Other than rainfall, there appears to be no fresh water source for these small streams. Salt water drains off the upper mud flats via these channels during low tide. In winter, new channels are created by ice gouging the mud surface as the ice floats onshore with the rising tide, or offshore with the retreating tide.

Egestion and Pellet Description

Macoma balthica feeds on the surface sediments using a long flexible incurrent siphon which undergoes a rotating motion, sucking up mud as the siphon comes into contact with the surface, and extending the siphon

Plate III: Macoma balthica fecal pellets

Plate IV: Macoma balthica in situ

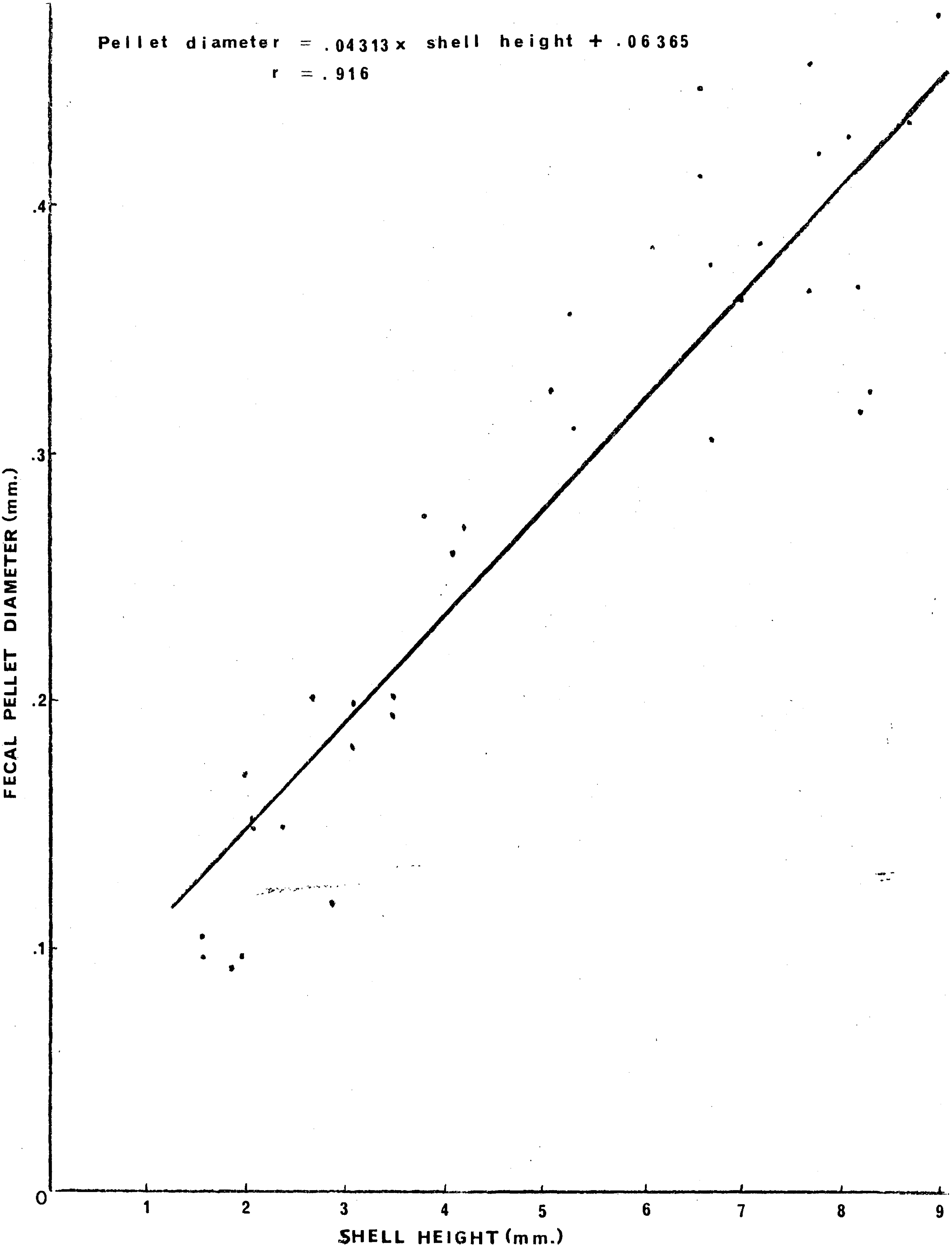
upwards, allowing the sediment to slide down the tube. Fine particles which are rejected are voided through the incurrent siphon as pseudofeces, loose coils or blobs, without passing through the gut. Material which is ingested is subsequently compacted and subdivided by a periodic contraction of the pyloric sphincter (Arakawa, 1970), after the bacterial population has been cropped off the sediment in the gut. This moulding action produces a series of oblate, cylindrical pellets with an average height (length) to diameter ratio of 0.563. Arakawa (1970) notes similar pellets are produced by <u>Macoma incongrua</u>, <u>Macoma tokyoensis</u> and <u>Macoma praetexta</u>. Pellets are voided on the surface through the excurrent siphon. Occasionally, pellets are ejected within the burrow as well. The top or bottom of a pellet commonly exhibits either a small boss, or a depression.

Pellets are held together by mucus secreted by the animal, and consist of an outer, bound mud layer surrounding a sand core. Elongated sand grains are aligned parallel to the height axis of the pellet.

To define the relationship between animal size and pellet size, the shell heights and lengths of 37 <u>Macoma balthica</u> specimens were measured and each specimen dissected. The diameters and heights of an average of 9 pellets per specimen from the midgut area, were measured. There is a linear relationship between the size of <u>Macoma balthica</u> and pellet diameter (Figure 1, Appendix I).

The volume of an average pellet in a sample of 4,242 pellets was calculated by measuring the diameters and heights of 40 randomly-selected pellets, and assuming cylindrical shapes. The average dry weight was determined by drying the sample. By assuming a specific gravity of 2.6 for the solid portion of the pellets, a wet density of 1.68 g/cm^3 was

Figure 1


Pellet diameter = .04313 x shell height + .06365
r = .916
FECAL PELLET DIAMETER (mm.)
.4
.3
.2
.1
0
1
2
3
4
5
6
7
8
9
SHELL HEIGHT (mm.)

calculated.

Pellet resistivity

An experiment was conducted to demonstrate the resistant nature of the fecal pellets.

Method

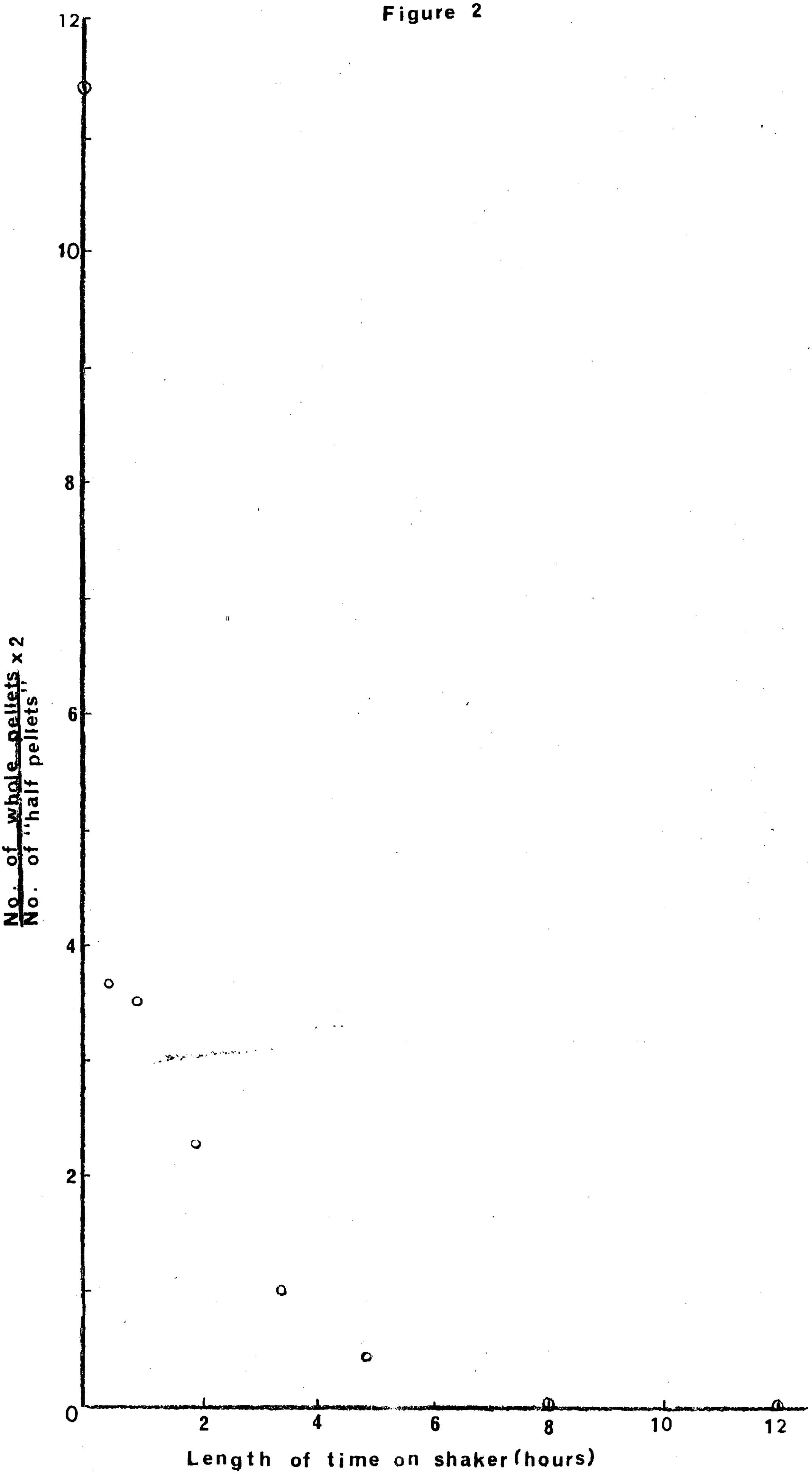
Six 2.3ml. samples of Macoma balthica fecal pellets collected from small intertidal channels off Spencer's Point and preserved in formalin, were placed in 300ml. Erlenmyer flasks and filled with distilled water. The pellets averaged 0.396mm. in diameter (1.33ɸ), with a standard deviation of 0.0455mm.. Ten percent of each sample was non-pelletal sand and silt. Each sample held approximately 75,400 pellets.

The flasks were shaken on an Ederbach biological culture shaker at 184 cycles/min., with a horizontal displacement of 4.2cm.. The motion of the shaker set up a vigorous, turbulent, to and fro motion in the flasks. The length of time that a flask was shaken, determined the degree of pellet destruction. The latter was determined by randomly sampling the material in each flask following settling, counting the number of whole pellets, dividing by the number of "half pellets" and multiplying by two. A "half pellet" was counted when enough material was seen under the microscope to be visually pieced together into a volume roughly equivalent to that of half a pellet. As the pellets were well sorted, the ideal half pellet volume could be estimated by visual comparisons of whole pellets with pellet remains.

Results

The rate of pellet destruction decreased as the experiment progressed

Figure 2


No. of whole pellets x 2
No. of "half pellets"
12
10
8
6
4
2
0
2
4
6
8
10
12
Length of time on shaker (hours)

(Figure 2). As pellets are destroyed into their constituent sand and mud particles, forceful interpelletal collisions become less and less frequent. After twelve hours of shaking, 99.9% of the pellets were destroyed.

From this experiment, it can be inferred that in the system, so long as the mucous coating does not undergo rapid biodegradation (which it probably does not, judging by the length of time the pellets last in the laboratory in water) the pellets are sufficiently resistant to withstand transport off a mud flat. Once the pellets reach the more energetic lower tidal flat-sand bar environment, the rate of pellet destruction probably increases dramatically. The collisions with sand in suspension and bedload break up the pellets. Since the mucous binding is persistent, clumps of finer clay and silt particles would be expected to remain agglomerated. Even though any sand size particles will break away from the pellet over a sand bar, a large proportion of the pelleted material remains bound, though in unrecognizable shapes.

Transport of fecal pellets

Using Shields'diagram (Blatt, Middleton, and Murray, 1972), the critical shear velocity required to move a pellet of diameter 0.367mm. is 1.327cm/sec. Therefore, Macoma fecal pellets are easily transported at low current velocities. The hydrodynamic equivalent of such a pellet is a quartz grain 0.1mm. in diameter (3.33ϕ).

When a small wave hits a shallow intertidal channel at right angles, during tidal retreat, fecal pellets are washed towards and eventually into the channel from distances up to 4m. away from the channel. When the mudflat is covered by water, currents parallel to shore move the pellets into the channels where they become concentrated. Pellets are also con-

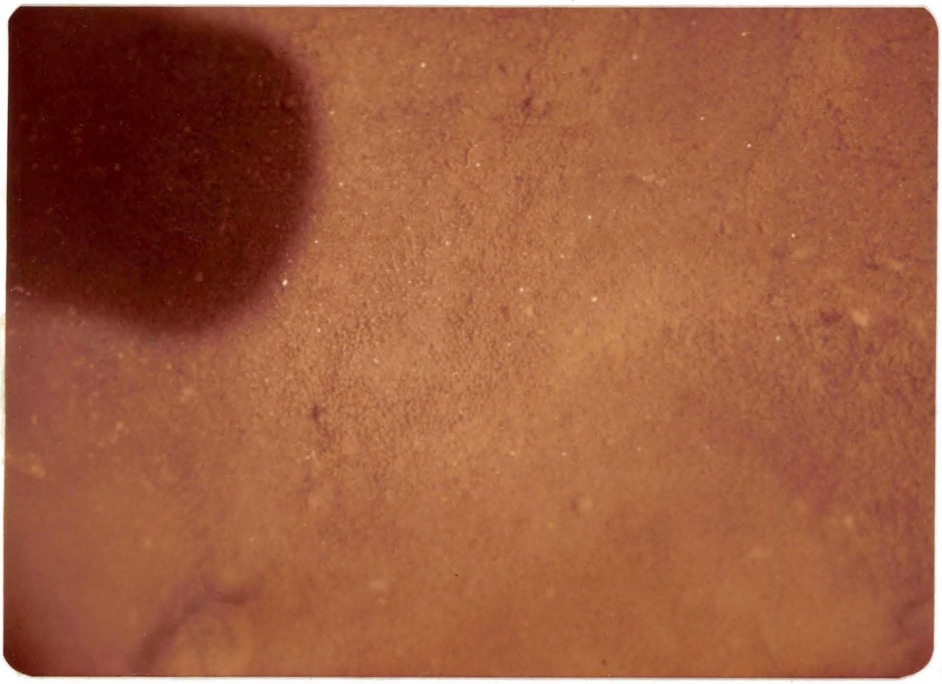


Plate V: Stream deposit of Macoma balthica fecal pellets

Plate VI: Macoma pelletal cone, Five Islands, N.S.

concentrated in sand windrows in the flood lee of small boulders on the lower portion of the mud flat. Movement of the pellets away from the shore off the mud flat takes place in the streams at low tide.

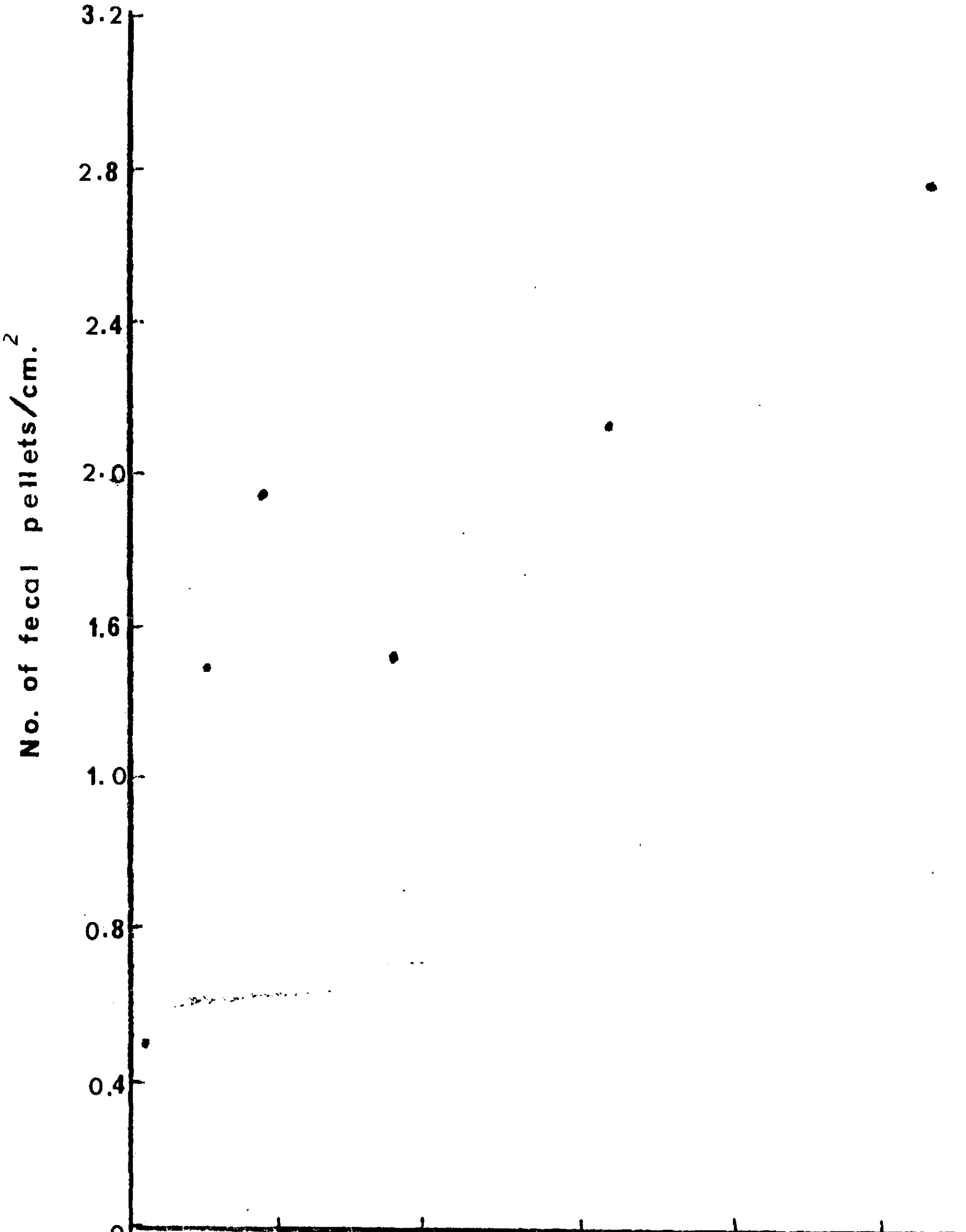
To demonstrate the funnelling effect produced by these channels, a series of surface counts of fecal pellets was taken along a short transect parallel to the shore at right angles to a small intertidal channel about half a meter across. The surface density of Macoma pellets decreased towards the channel from a distance of 21m. (Figure 3).

A surface count of pellet densities was also taken along the Spencer's Point transect from the near shore margin of the mud flat, to a distance of 350m. from shore. Beyond this, pellets could not be distinguished due to the abundance of sand particles on the sediment surface.

Station	Population density of Macoma balthica	Number of pellets/cm^2
1	0	0
2	143	
3	143	0.542
4	430	1.386
5	562	1.833
6	1253	2.849
7	1631	9.882
8	2142	3.937
9	1339	?

The Macoma population peaks at Station 8. From Stations 3 to 7, there is a visible relationship between the number of pellets on the surface and population density (Figure 4). Pellet transport beyond Station 7 is therefore more significant than in the upper mud flat.

Figure 3


3.2
2.8
2.4
2.0
1.6
1.0
0.8
0.4
0
4
8
10
16
20
No. of fecal pellets/cm.^{2}
Dist. to shallow intertidal channel (m.)

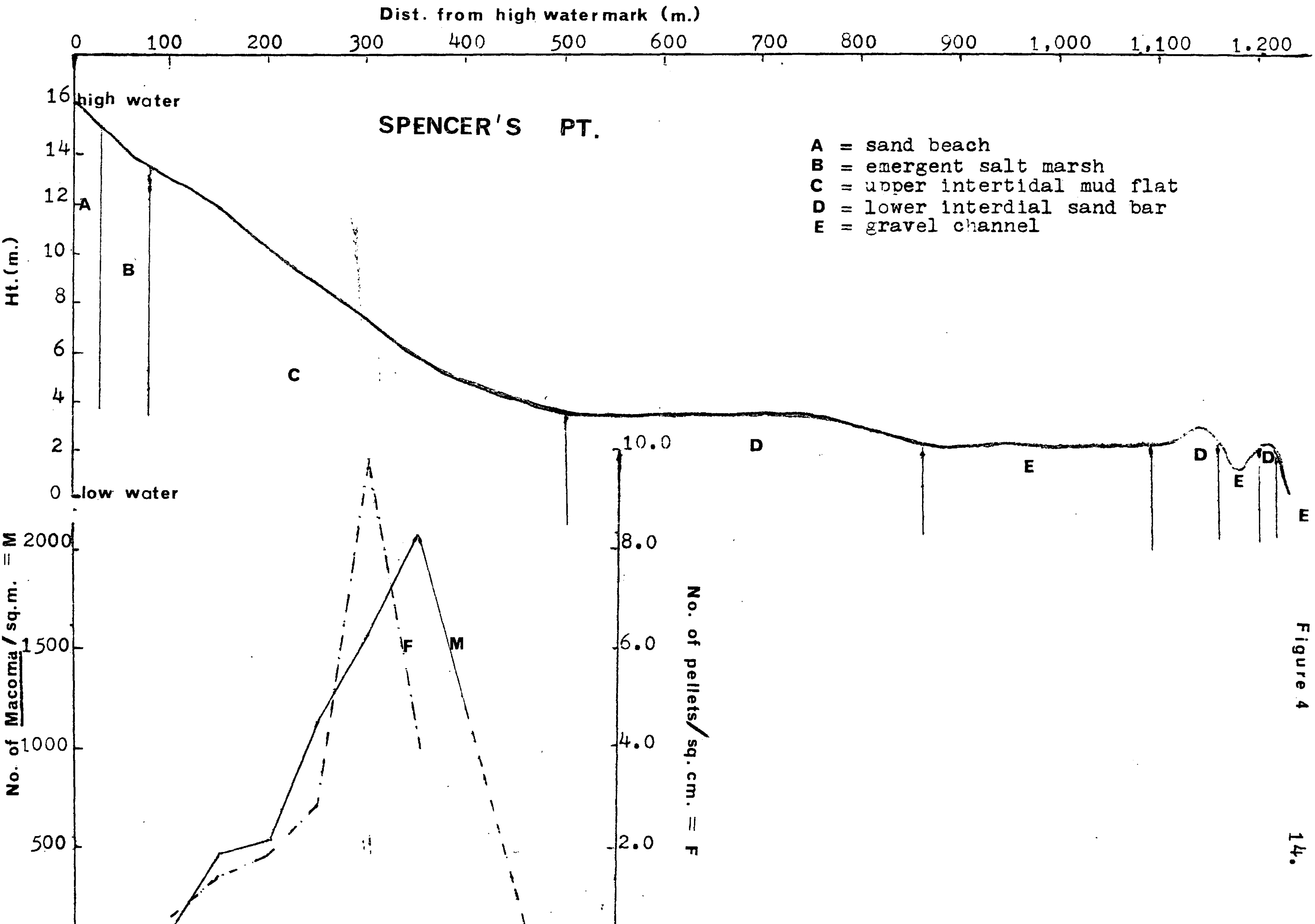

Dist. from high watermark (m.)
0
100
200
300
400
500
600
700
800
900
1,000
1,100
1.200
Ht. (m.)
16
14
12
10
8
6
4
2
0
high water
low water
SPENCER'S PT.
A = sand beach
B = emergent salt marsh
C = upper intertidal mud flat
D = lower interdial sand bar
E = gravel channel
A
B
C
D
E
D
E
D
E
No. of Macoma / sq.m. = M
2000
1500
1000
500
No. of pellets / sq. cm. = F
10.0
8.0
6.0
4.0
2.0
F
M

Figure 4

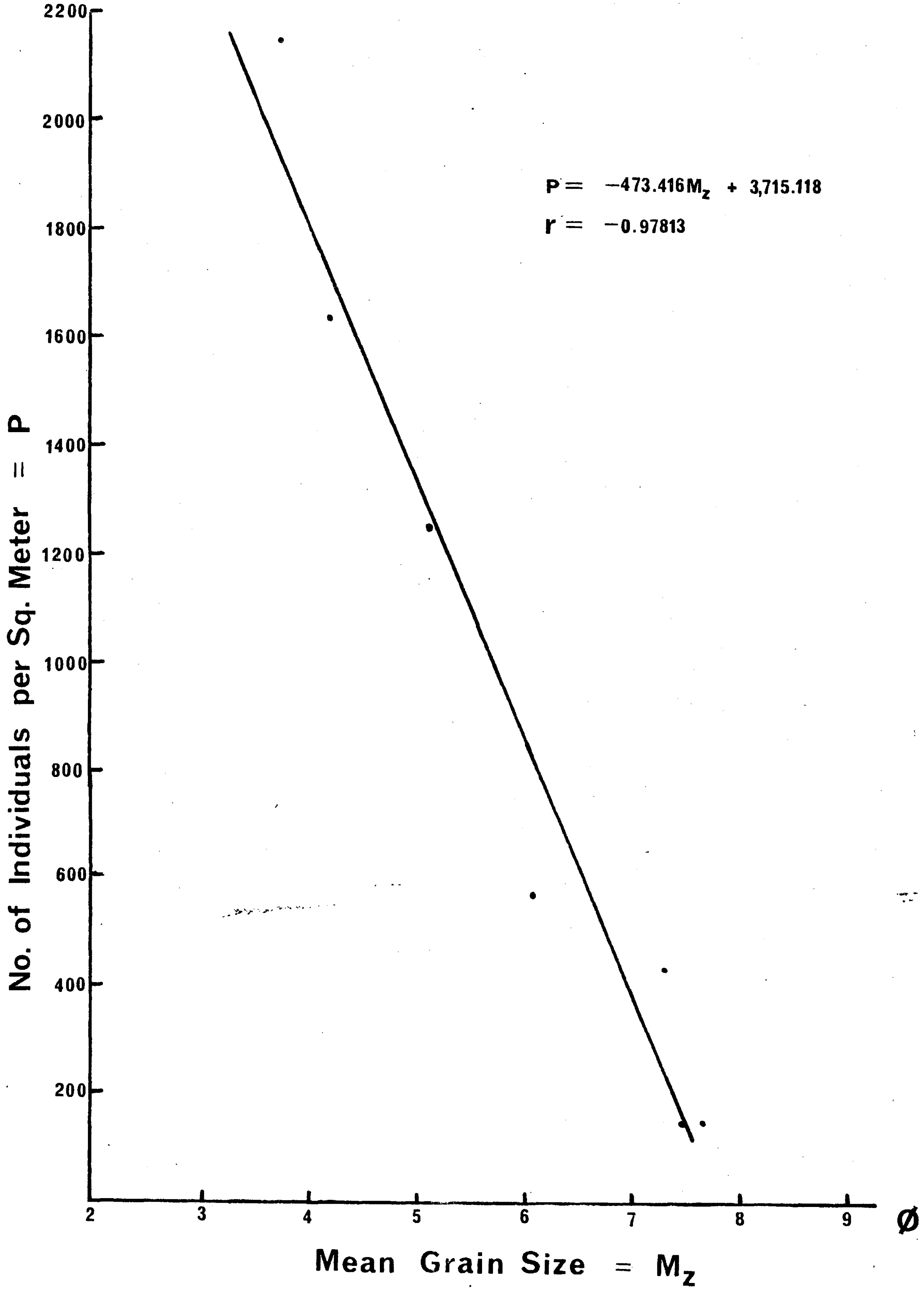
Grain Size and Macoma Population Density

Using the pipette and dry seive methods, the mean grain sizes of samples, collected 50m. apart along the Spencer's Point transect from the beach to the lower edge of the mud flat, were calculated. (Appendix II)

Newell (1965) reported a linear relationship between decreasing grain size of the sediment and increasing populations of Macoma balthica and Hydrobia ulvae, and organic carbon and nitrogen in the sediment. (Longbottom (1970) reported a similar relationship to Newell's, between grain size and populations of Arenicola marina and organic carbon and nitrogen.) Figure 5 illustrates that the opposite correlation occurs in the area studied, between Macoma population density and grain size of the sediment. The sediment which Newell and Longbottom studied was generally coarser than the muds off Spencer's Point. The highest population density of Macoma balthica, reported by Newell, occurred in the finest sediment he studied, which had a median diameter of 5.65ϕ. The coarsest sediment he studied had a median diameter of 2.05ϕ.

The highest population density of Macoma balthica on the Spencer's Point transect (2142/m^2, Station 8) occurs in sediment with a median diameter of 4.185ϕ, roughly compatible to the grain sizes corresponding to Newell's maximum population densities. At Station 9, (50m. offshore from Station 8) the population density drops to 1339/m^2 and the median grain size of the sediment increases to 2.59ϕ. The population density drops off even fruther in the coarser sediment at Station 10, but since the box core could not be pushed deep enough into the sediment to sample the Macoma population, the density at this station could not be measured. Beyond Station 10, the population density of Macoma drops to zero, since Station 10 marks the near shore edge of a megarippled sand bar.

Figure 5


P = −473.416M_z + 3,715.118
r = −0.97813
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
2
3
4
5
6
7
8
9
Ø
No. of Individuals per Sq. Meter = P
Mean Grain Size = M_z

It is suggested that in deposits of the Spencer's Point area finer than 3.75ϕ, the factor limiting Macoma populations is feeding time, rather than the organic carbon and nitrogen content of the sediment. Feeding time increases with distance from the shore, due to the decrease in aerial exposure time, and an increase in surface rugosity, other than the surface effect caused by the presence of feeding pits. As the surface rugosity increases, the number of small puddles in which Macoma b. can deposit feed at low tide increases.

Another factor which might be limiting the populations of Macoma b. in the finer muds, is the water content of the sediment. The muds on the upper portion of the Spencer's Point mudflat have a very high fluid content which could inhibit the ability of a large Macoma to maintain a stable position in its burrow. The limiting factor beyond Station 8, might be increased mobility of the coarser substrate. Small ripples give way to megaripples 25m. offshore from Station 10.

Feeding by Macoma balthica

In order to estimate the rates of turnover of sediment by Macoma b., a feeding experiment was conducted on a group of large individuals.

Method

The animals were partly buried posterior end up in beakers partly filled with sand and gravel. A shallow cup with a small elongate hole in the middle was secured over the clam. Only the top few millimeters of the clam's posterior protruded above the level of the cup.

Pre-dried and weighed aliquots of mud averaging about three grams each, were mixed with water and transferred to the cups using a pipette.

Thus both siphons were exposed to a mud film for a given length of time, while the clam remained partly immobilized. (In one case, only the excurrent siphon protruded above the cup.)

The Macoma did not immediately begin to feed and may only have begun to do so several hours after the start of the experiment. The length of exposure time varied, therefore, between two to three days. Fecal pellets were counted and measured and the area of reworking in each cup was measured. The water temperature during the experiment ranged between 8 - 10°C.

A second method used involved simply clearing the sediment above Macoma burrows in aquariums, and counting and measuring the pellets ejested during a period of twelve hours.

There were problems inherent in both methods. In the longer term experiment, some of the Macoma balthica in the laboratory suspension fed, thereby thwarting attempts to measure the amount of reworking due to the actions of deposit feeding. The animals in the short term experiment could have spent a large portion of their alloted feeding time reconstructing parts of their burrows disturbed when the surface sediment was cleared of feces. Feces could have been voided within the burrow, escaping the census at the end of the experiment.

Results

For the long term experiment, in the size range between shell lengths 22.0mm. and 29.3mm., the average dry wt. of pellets produced by a Macoma balthica in one day with six hours of non-feeding time, would be approximately 2.39mg. (Appendix III). Feeding activity is almost nil during the winter months. Therefore, it is assumed that Macoma balthica only actively feeds 200 days of the year in the Bay of Fundy. Therefore a Macoma in this size range may produce approximately 0.48g. dry weight of fecal pellets per year. Assuming population density of 2000/sq.m. of Macoma b. the rate of fecal pellet production would be approximately 1 Kg/m^2/yr.. The rate of pellet production obtained from the short term experiment was only 356g., which the author considers to be low due to the design of the experiment. Therefore the length of the experiment is crucial to these estimates. The available feeding time could not have been extended for the longer term experiment, since only a limited amount of sediment was available to the animal for reworking.

Bubnova (1972), using sets of smaller Macoma balthica, conducted similar experiments to determine assimilation and rates of reprocessing by Macoma balthica and Portlandia arctica. He developed an assimilation formula - $U^{-1} = \frac{R-H}{R} 100$

where U^{-1} = assimilation in percent (=21% for Macoma b.)
R = quantity of food consumed in mg. dry weight
H = quantity of pellets produced in mg. dry weight

From Bubnova's (1972) data, the amount of sediment reprocessed (all material taken up by the incurrent siphon), averaged over all the size groups that he studied, is approximately ten times the amount of sediment consumed. Therefore the rates of sediment reprocessing could be found knowing the amount of feces produced. Using the long term experimental data, the rate of reprocessing therefore is 6.14g. per year per individual. If the population density in this size range were 2000/m^2, this would amount to a rate of sediment reworking of 12.27Kg. of dry sediment per

Plate VII: Macoma pseudofecal coils

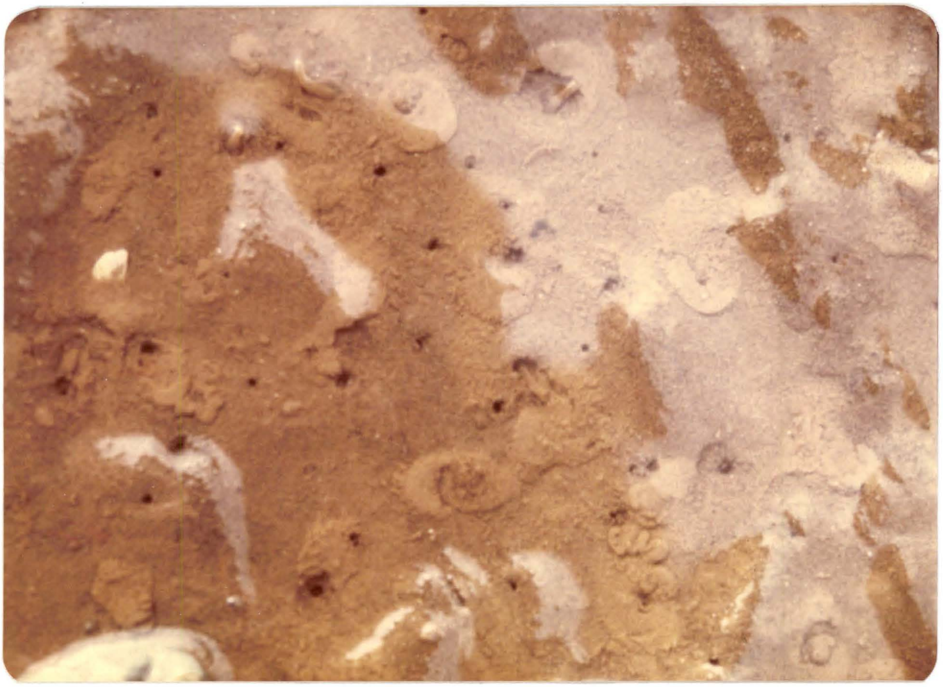


Plate VIII: Macoma producing amorphous pseudofeces sq. meter per year. Assuming that the sediment is 40% water, this would amount to a layer of sediment 4.47cm. deep. Using a hypothetical population distribution, and a reasonable extrapolation of reworking rates by smaller Macoma balthica, it is more realistic to expect a turnover of 9Kg. of dry sediment/yr., or a layer 3.3cm. thick. Therefore in areas of high population density of Macoma and high rates of discharge of pseudofecal material, large amounts of sediment are being reprocessed. The rate of pseudofecal production is just as an important factor in these estimates as it is difficult to estimate on a mud flat. The production of pseudofeces by Macoma was seen to increase dramatically when water turbidity was high. Pseudofecal production during the last stages of tidal retreat was nil when the water was calm. This may indicate that suspension feeding forms the bulk of the feeding activity of Macoma balthica.

The feeding pits on the Bay of Fundy mud flats are well developed. Macoma were not observed to deposit feed at low tide on the upper mud flats at Spencer's Point where Macoma feeding pits were the only visible dominant structure on the mud flat surface. Therefore Macoma must be deposit feeding at least in these areas and presumably all across the mud flats at high tide.

Conclusions

The deposit feeding actions of Macoma balthica, in areas of moderately high population densities, are capable of transforming copious amounts of fine sediment into more easily transportable forms. The bulk of the very fine sediment intake is rejected as pseudofeces which is readily taken into suspension. The mud and fine sand which is injested, is compacted into resistant easily transported fecal pellets. During the period when a mud flat is under water, intertidal channels act as pellet reservoirs, trapping pellets as they are moved by the currents parallel to the shore. At low tide the pellets are carried off the mud flat via these channels.

Since the diet of the animal is limited to fine sand and mud by the diameter of the incurrent siphon, and the siphonal suction gradient, continued deposit feeding will quickly remove fine sediment from a surface. Therefore, large regular influxes of fine sediment are needed to sustain large populations of *Macoma balthica*. A portion of this material is pseudofeces carried away from the shore from populations of *Macoma* higher on the mud flat.

In areas of high population density, *Macoma balthica* influences to a considerable degree, the rate of accumulation of fine sediment and sedimentary textures. The rate of sedimentation of fine material is decreased in areas where *Macoma* primarily deposit feed, and increased where they suspension feed.

References Cited

Arakawa, K. Y., 1970, Scatalogical studies of the Bivalvia (Mollusca). Adv. Marine Biol., Vol. 8, pp. 307 - 436.

Blatt, H., G. V. Middleton, and R. Murray, 1972. Origin of Sedimentary Rocks, Englewood Cliffs, N.J.: Prentice-Hall, Inc., 634pp.

Bubnova, N. P., 1972, The nutrition of the detritus feeding mollusks, Macoma balthica, and Portlandia arctica (Gray) and their influence on bottom sediments. Oceanology, 12, pp. 899 - 905.

Coan, E. V., 1971, The Northwest American Tellinidae. Veliger, 14 (Supplement), pp. 1 - 50.

Longbottom, M. R., 1970, The distribution of Arenicola marina (L.), with particular reference to the effects of particle size and organic matter of the sediments. Jour. Exp. Marine Biol., and Ecol., Vol. 5, pp. 138 - 157.

Newell, R., 1965, The role of detritus in the nutrition of two marine deposit feeders, the prosobranch Hydrobia ulvae, and the bivalve Macoma balthica. Proc. Zool. Soc. London, Vol. 144, pp. 25 - 45.

APPENDIX I

Shell Length (mm.)	Shell Height (mm.)	Mean $\frac{\text{Pellet D.}}{\text{Pellet Wt.}}$	Mean Pellet D. (mm.)
22.9	8.9	2.170	.478
21.6	8.0		
21.5	8.2	1.779	.324
18.0	6.5	2.376	.445
18.9	6.9	1.761	.361
20.3	8.1	1.409	.365
20.0	7.7	2.100	.420
21.7	9.2	1.067	.363
20.6	8.1	1.268	.315
14.6	5.2	2.509	.355
14.7	5.2	2.005	.309
23.0	8.6	1.615	.432
21.8	7.6	1.873	.455
10.3	4.0	2.128	.259
8.3	3.0	1.656	.181
11.8	4.2	2.225	.269
5.5	2.0	1.303	.148
3.8	1.5	1.055	.104
8.0	2.8	1.428	.117
14.4	5.0	2.004	.324
17.2	7.1	2.108	.383
19.5	7.6	1.843	.364
16.7	6.6	2.257	.375
11.1	3.7	1.762	.274
16.5	6.5	1.807	.409
16.5	6.6	1.350	.305

Shell Length (mm.)	Shell Height (mm.)	Mean Pellet D. / Pellet Ht.	Mean Pellet D. (mm.)
8.9	3.4	1.687	.202
7.8	2.6	1.679	.201
6.1	2.0	2.112	.152
9.2	3.4	2.350	.194
4.7	1.8	1.250	.091
5.2	1.9	1.746	.170
8.8	3.0	1.386	.199
11.4	6.0	1.930	.383
19.1	8.0	1.893	.426
3.4	1.5	0.919	.095
5.5	1.9	1.050	.095
6.0	2.3	1.359	.148

Pellet Resistivity Experiment

Sample #	Length of time on shaker (hours)	$\frac{\text{\# of whole pellets}}{\text{\# of "half pellets"}} \times 2$
Initial	0	11.396
1	0.5	3.620
2	1.0	3.487
3	2.0	2.222
4	3.5	0.971
5	5.0	0.394
6	8.0	0.011
7	12.0	0.002

Station #	Phi Percentile			Mean Grain Size (Phi units)	No. of *Macoma*/m^2
	$\phi 84$	$\phi 50$	$\phi 16$		
1	2.33	1.92	1.57	2.04	0
2	10.10	7.50	4.90	7.50	143
3	10.98	7.19	4.77	7.65	143
4	11.65	6.20	4.08	7.31	430
5	9.54	5.10	3.62	6.09	562
6	8.34	3.97	3.04	5.12	1253
7	6.40	3.43	2.78	4.20	1631
8	5.34	3.32	2.59	3.75	2142
9	4.06	2.75	1.15	2.65	1339
10					
11					0

Station 1 - beach

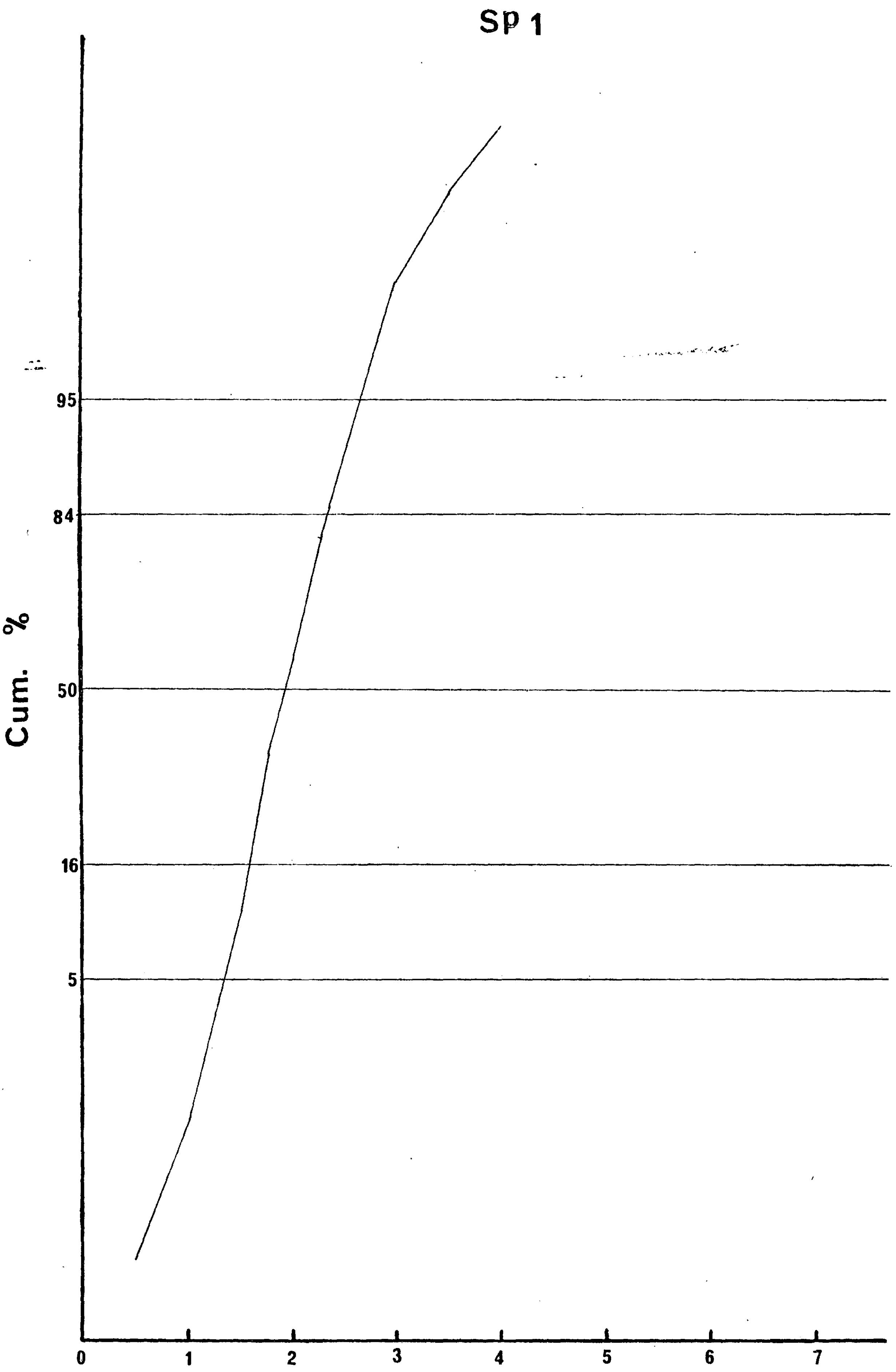
Station - emergent salt marsh

Stations 3 to 10 - mudflat

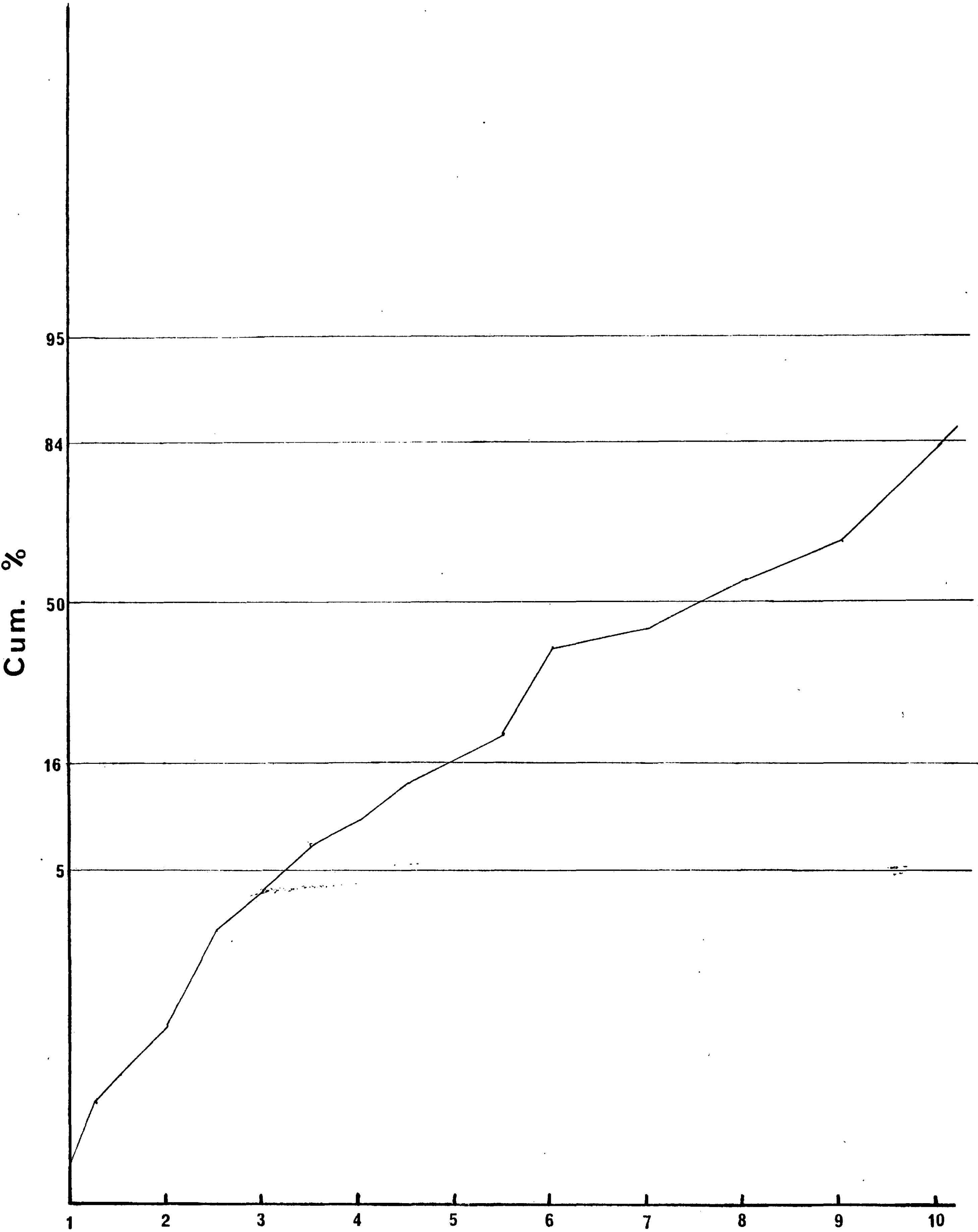
Station 11 - sand bar

$$\text{Mean Grain Size (Mz)} = \frac{\phi_{84} + \phi_{50} + \phi_{16}}{3}$$

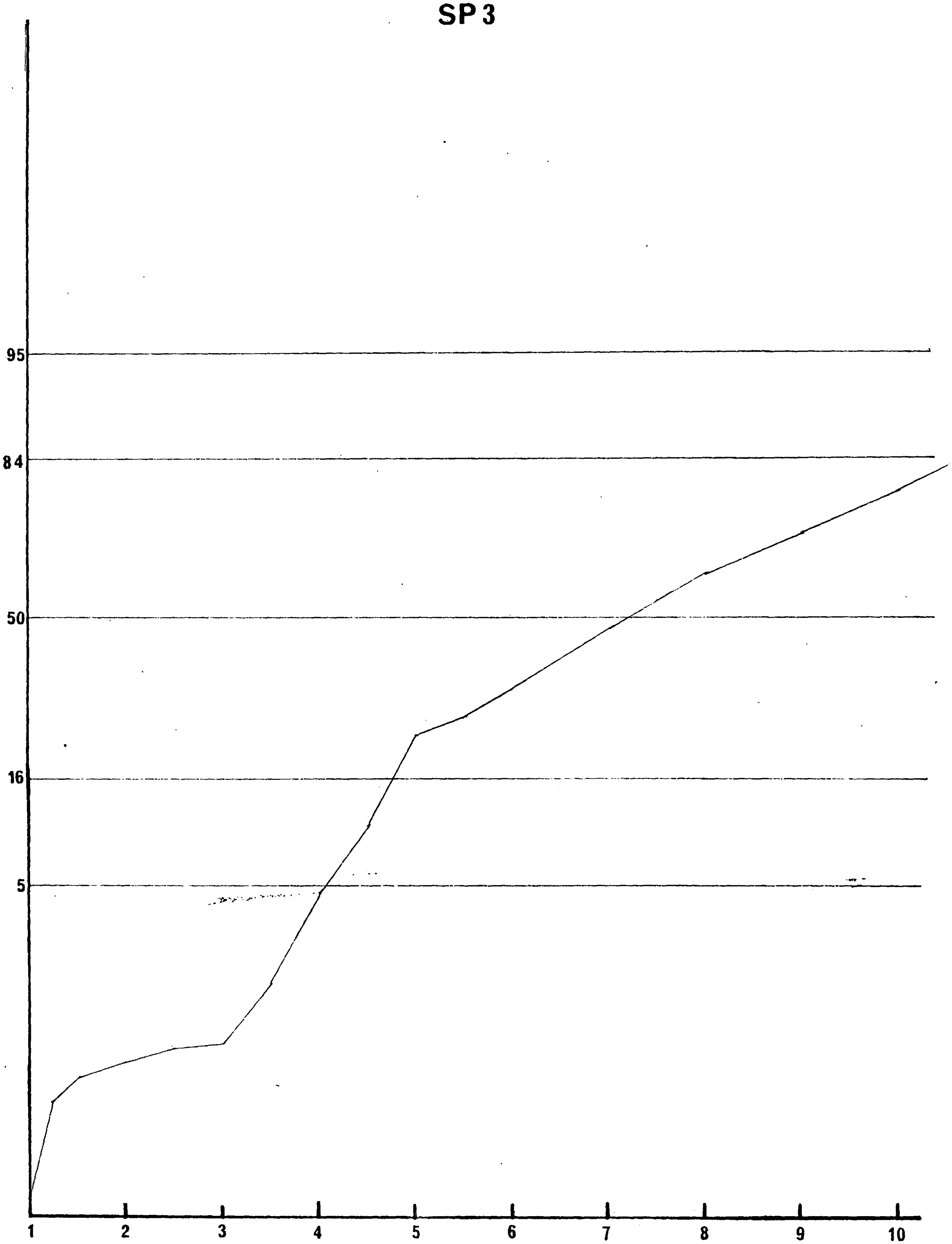
APPENDIX II


Sp 1
Cum. %
95
84
50
16
5
0
1
2
3
4
5
6
7

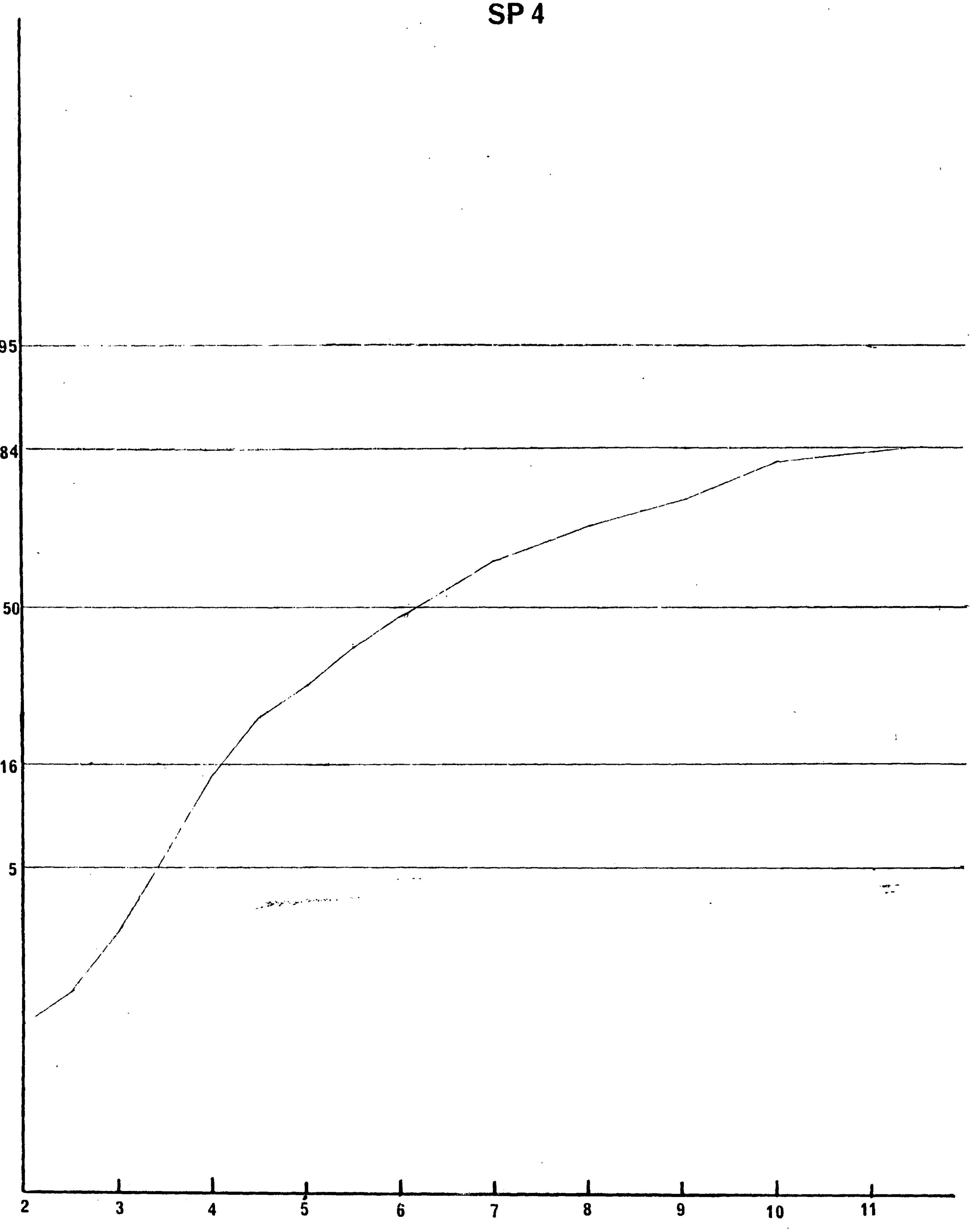
Sp 2

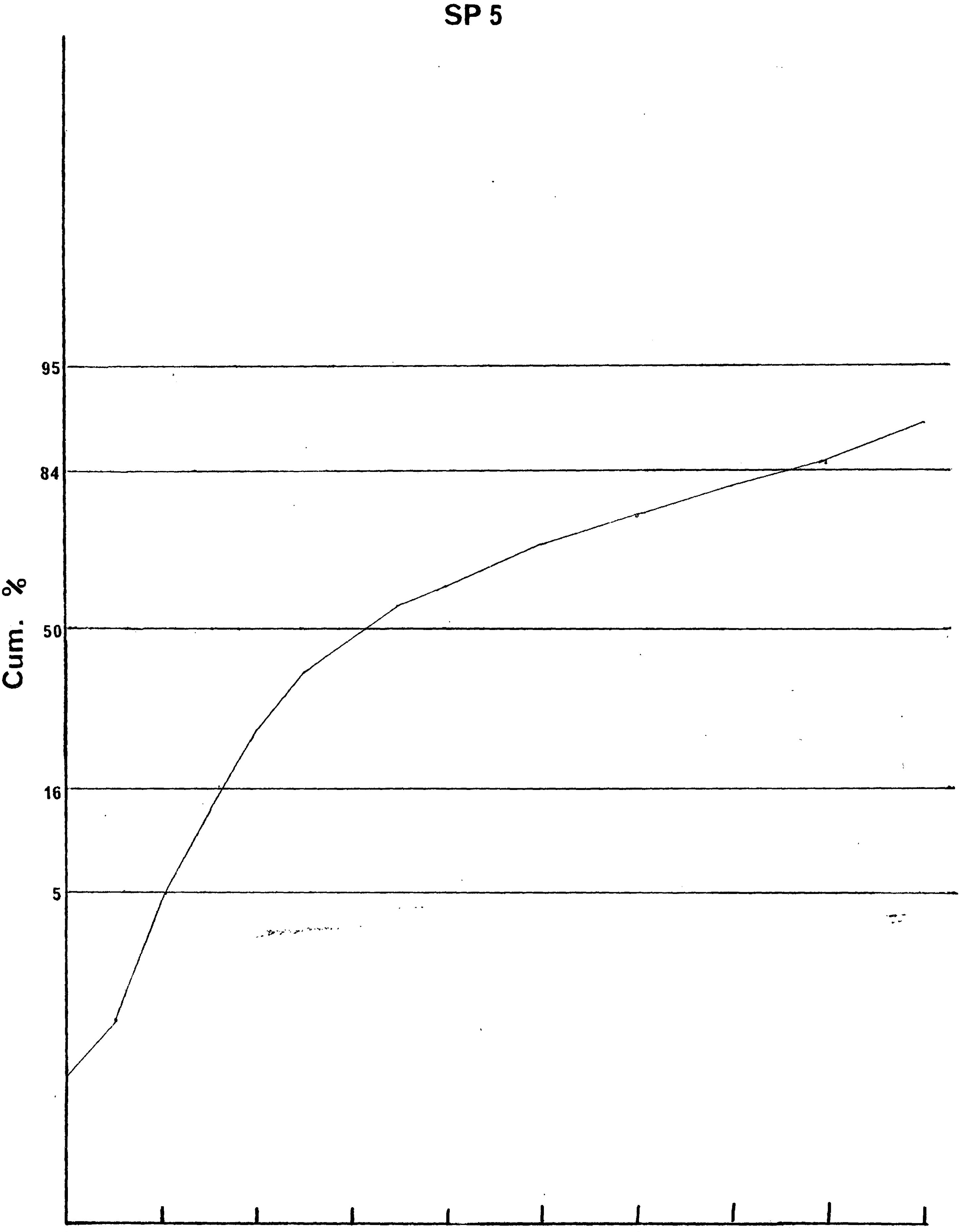


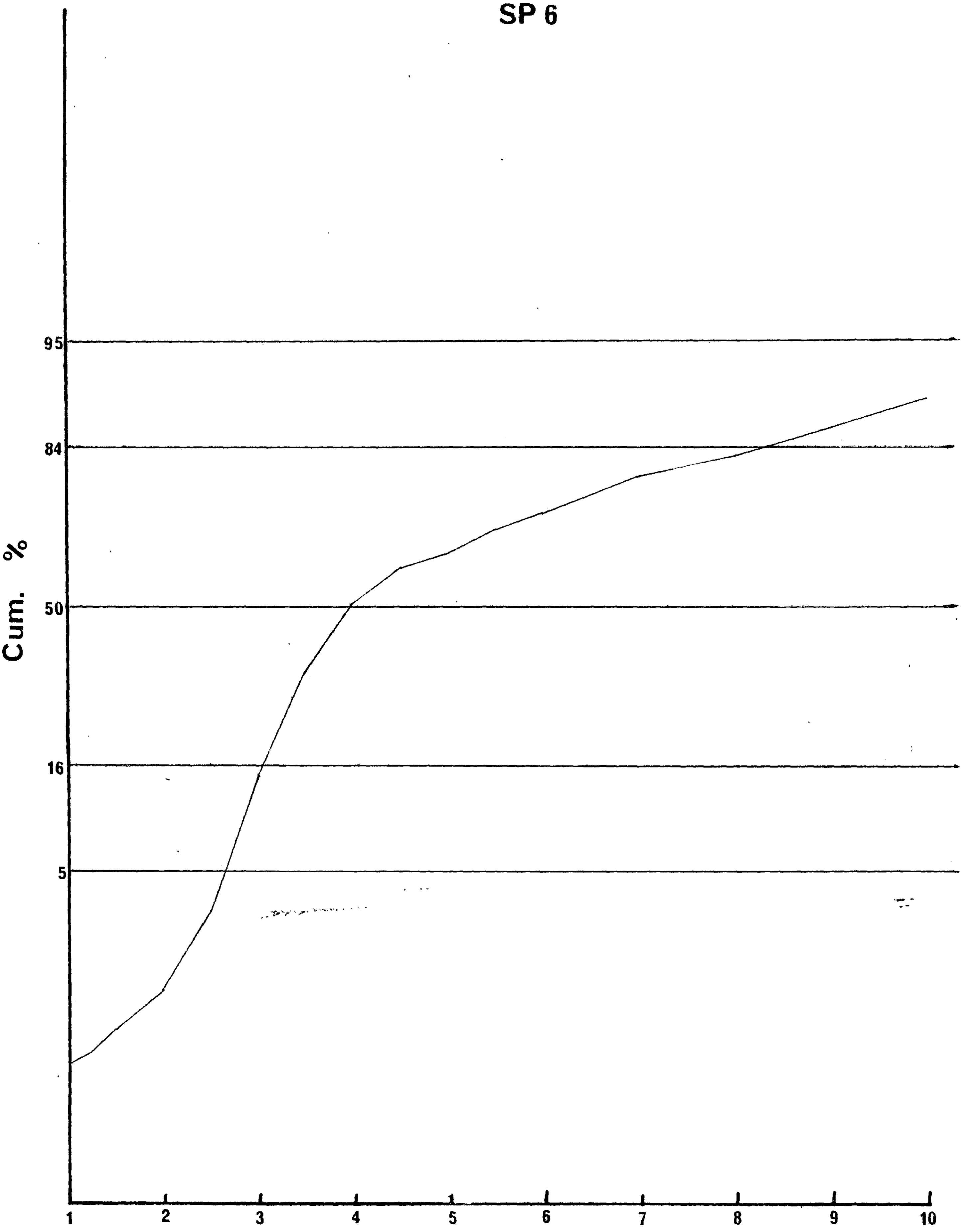
SP 3

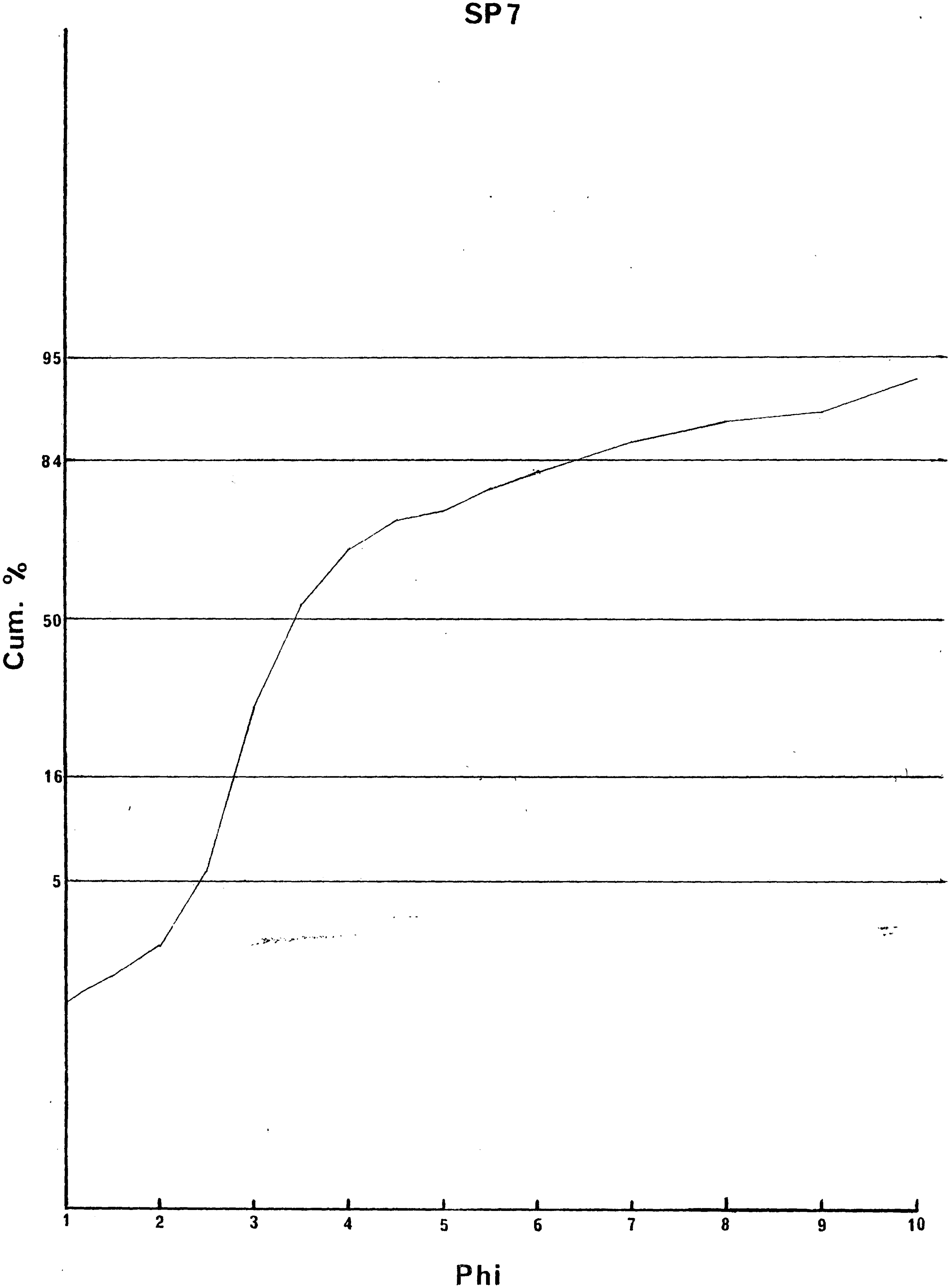


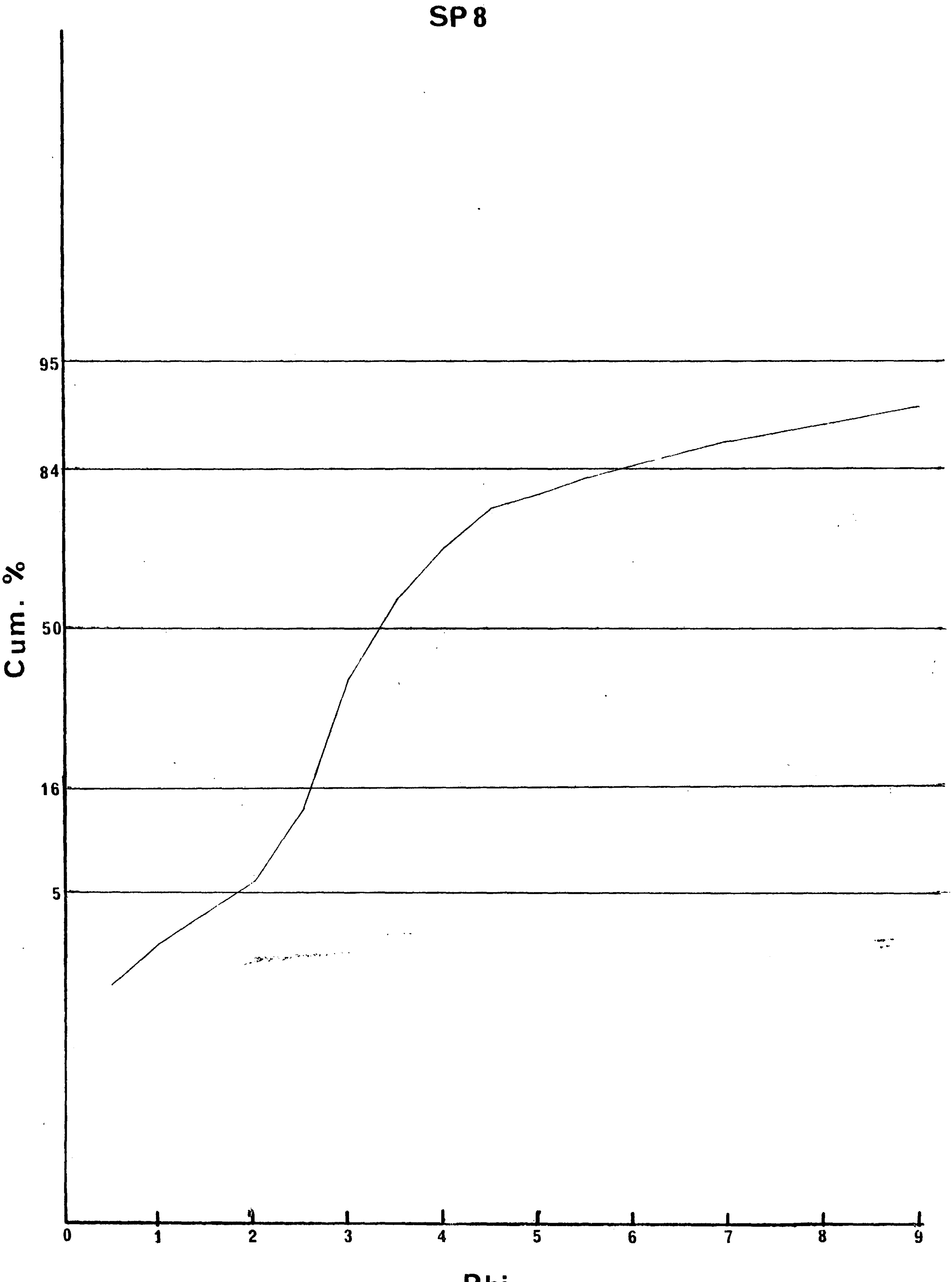
SP 4

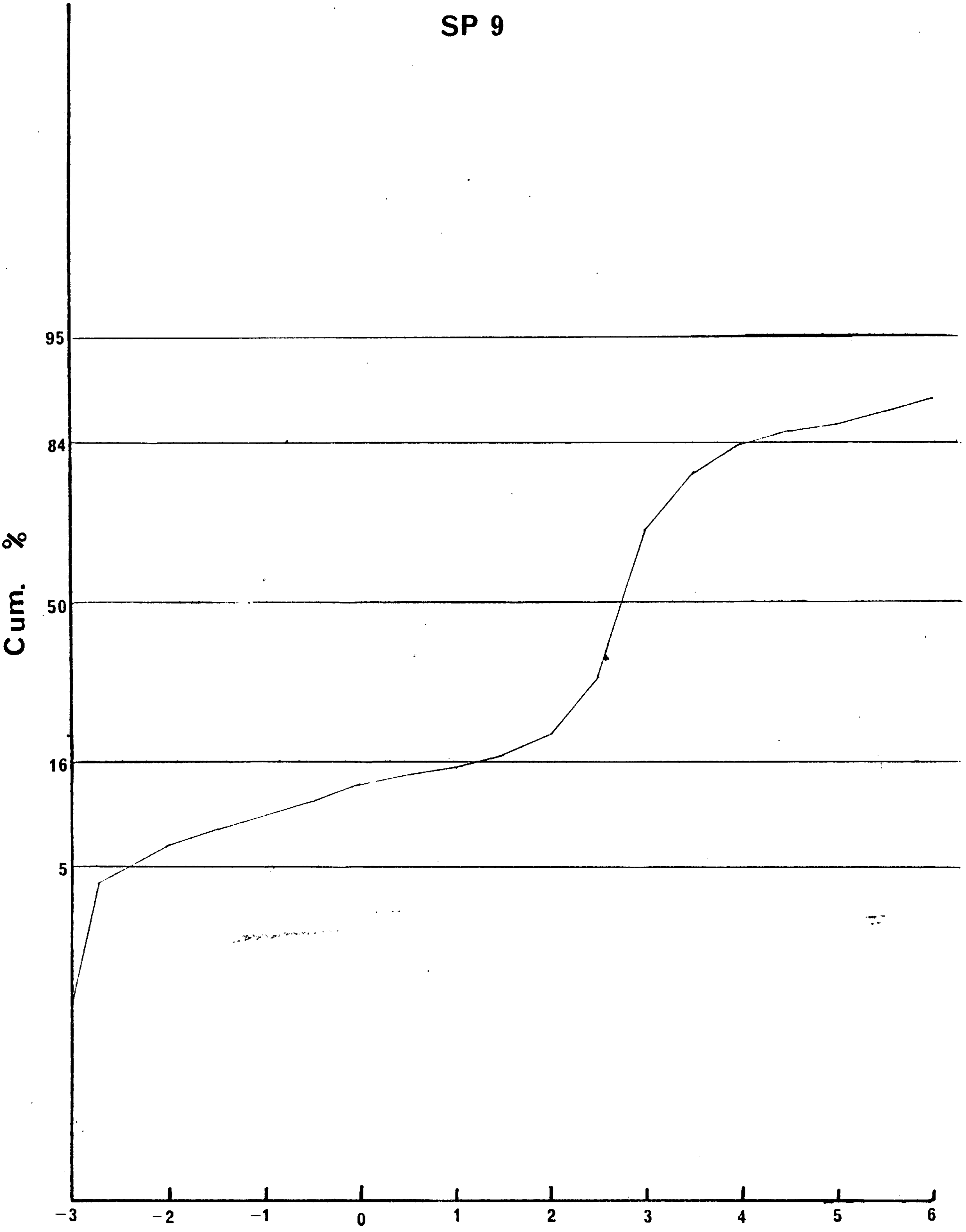



SP 5
Cum. %
95
84
50
16
5
2
3
4
5
6
7
8
9
10
11


SP 6
Cum. %
95
84
50
16
5
1
2
3
4
5
6
7
8
9
10


SP7
Cum. %
95
84
50
16
5
1
2
3
4
5
6
7
8
9
10
Phi


SP 8
Cum. %
95
84
50
16
5
0
1
2
3
4
5
6
7
8
9
Phi


SP 9
Cum. %
95
84
50
16
5
−3
−2
−1
0
1
2
3
4
5
6

APPENDIX III

Long term feeding experiment

	Shell Length (mm.)	Length of xperiment (hours)	Feces/day (mg dry wt.)	Feces/year (g dry wt.)	Sediment Reworked/day (mg dry wt.)	Sediment Reprocessed per day (mg dry wt.)	Sediment Reprocessed per year (g. dry wt.)
	26.1	39.5	3.350	0.667	1208.43	42.93	8.586
	28.0	66.0	Excurrent cup	siphon below level	32.57	32.57	6.514
	22.0	67.5	0.751	0.150	124.99	9.62	1.925
	29.3	47.5	2.613	0.523	463.20	33.49	6.697
	23.0	66.5	2.861	0.572	102.05	36.666	7.333
Average	25.68	57.4	2.394	0.478	386.25	36.68	6.136

$$U^{-1} = \frac{R - H}{R}$$

$$R = \frac{H}{.79}$$

R = quantity of food consumed (mg dry weight)
H = quantity of fecal pellets (mg dry weight)
U = assimiliation =.21 for *Macoma balthica* (Bubnova, 1972)

Sediment reprocessed = 10.124 × R

$$\text{Sediment reworked} = \frac{\text{Area of sediment reworked in cup}}{\text{Area of cup}} \times \text{Wt. of sediment film before experiment}$$

Short term fecal production experiment

	Shell Length (mm.)	Feces/day (mg dry wt.)	Feces/year (mg dry wt.)	Sediment Reprocessed per day (mg dry wt.)	Sediment Reprocessed per year (g dry wt.)
	28.2	0.417	83.43	5.346	1.069
	22.4	1.661	332.12	21.281	4.256
	20.2	0.882	176.46	11.307	2.261
	26.0	0.607	121.42	7.780	1.556
Average	24.2	0.892	178.36	11.428	2.286