FACTORS INFLUENCING THE DISTRIBUTION OF THE BIVALVE *MACOMA BALTHICA* OF THE INTERTIDAL MUDFLATS OF COBEQUID BAY, NOVA SCOTIA

FACTORS INFLUENCING THE DISTRIBUTION OF THE BIVALVE *MACOMA BALTHICA* OF THE INTERTIDAL MUDFLATS OF COBEQUID BAY, NOVA SCOTIA

By

Verena J. Tunnicliffe

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ABSTRACT

Population studies on the bivalve Macoma balthica L. in the intertidal mudflats of Cobequid Bay, Nova Scotia show some of the highest recorded densities; maximum density was 3492/m^2. Direct bacterial counts of 40 surface sediment samples gave an average bacterial density of 5.9 X 10^9 bacteria/g. dry wt. sediment. Macoma densities correlate significantly with bacterial densities (r = .880). The organic carbon contributed by the bacteria represented an average of one-third of the organic carbon in the sediment; organic carbon was found at an average of .4% by weight in the sediment. Calculations of daily protein requirements of Macoma balthica show that there is insufficient protein present in the sediment. The bivalve probably filter feeds to supplement its diet. No correlation was found between Macoma densities and either organic carbon distribution or vertical position on the mudflat.

ACKNOWLEDGEMENTS

This study would have been impossible without the support and encouragement from the entire Geology Department for such an interdisciplinary undertaking. My special thanks to Dr. Michael Risk whose enthusiasm was boundless and supervision of this project very valuable. Marika Karolyi provided me with endless assistance, ideas and good cheer in the field. I especially appreciated the assistance provided by Dr. Jean Westermann in terms of both her laboratory equipment and her advice. Without the help of Dr. Alena Mudrock and the services of Canada Centre for Inland Waters, the analysis for carbon and nitrogen would have been impossible. My additional thanks to Mr. Joseph Lambiase for the computer plots of the data and his encouragement and to Miss Maureen Dickson for her typing skills.

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INTRODUCTION

The survival of any organism in an environment is a function of the severity of environmental factors and the organism's resistance. The intertidal environment is of particular interest because of its exposure to both high-energy marine and exposed terrestrial conditions. The infauna of the intertidal sediment is influenced by many factors, but broad classifications of the organisms are usually made on the basis of nutrition. Food is often a major limiting factor in both terms of quantity present and the process by which the population acquires it. This study undertakes to understand the important factors determining the distribution of an intertidal organism particularly from the nutritional aspect.

The lamellibranch Macoma balthia Linnaeus is a common inhabitant of boreal intertidal mudflats of the east coast of North America (Figure 1). It achieves a maximum length of 30 mm. and may live 10 years. Macoma has a strong foot enabling rapid vertical and horizontal movement. A long motile incurrent siphon serves for ingestion; filtration of the overlying water layer has been observed but direct feeding on the substrate is preferred (Bubnova, 1972). The topmost flocculent layer of the sediment is sucked up by the siphon which also may reject sediment by reversal of flow. Ingested material passes through the alimentary canal, and faeces are voided onto the sediment by the shorter excurrent siphon. Vassallo (1971) observed Macoma to

Figure 1 -- Macoma balthica in situ
Trace of incurrent siphon is
toward top of photograph.

feed only at high tide. As the incurrent siphon moves across the mud surface it loosens the surrounding sediment and the combined action of the siphon and water currents gradually scours out a small pit (Figures 2 and 3). This pit may serve as a trap for fines and organic debris. The siphons leave a star-shaped trace on the sediment surface with scattered pelletized faeces (Figure 4).

Considerable work has been done to investigate the relationship between submergence time and organism distribution (Beanland, 1940; Newell, 1970; Vassallo, 1969) indicating distribution is related to feeding time. Macoma distribution also appears to be related to sedimentary characteristics. Driscoll and Brandon (1973) and Boyden and Little (1973) found that Macoma is associated with a muddy sand or mud in both the subtidal and intertidal environments. Associated with sediment size of the deposits is water content and compaction, current strength and amount of deposited organic material.

As a deposit feeder Macoma picks up organic debris that is present on the surface. Mann (1972) estimated a large organic input by marsh grasses in Georgia but a large variety of other sources is also possible. Bader (1957) reports a linear relationship between pelecypod populations and non-refractory organics. Gilbert (1969) found that organic content is more influential than sediment particle size in determining occurrence of Macoma. A number of studies are cited by Newell (1970) that relate Macoma density to organic nitrogen and carbon content. Much of the organic matter occurs as refractory compounds such as lignin and cellulose which cannot be digested by most

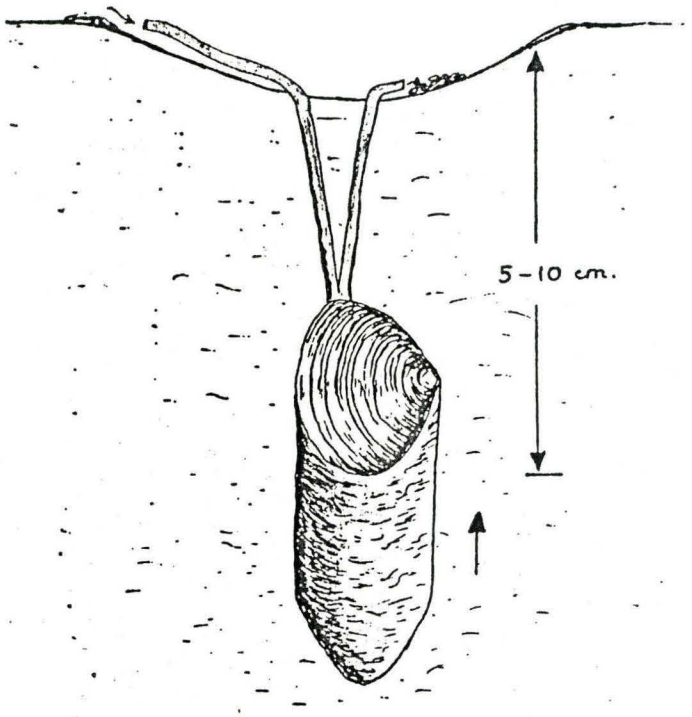


Figure 2 -- Action of Macoma balthica in situ.

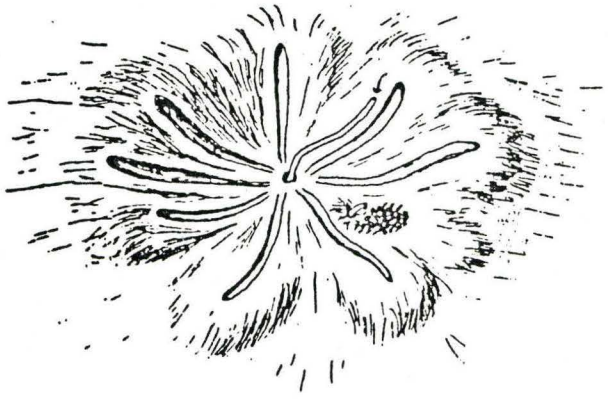


Figure 3 -- Pit caused by actions of Macoma siphons.

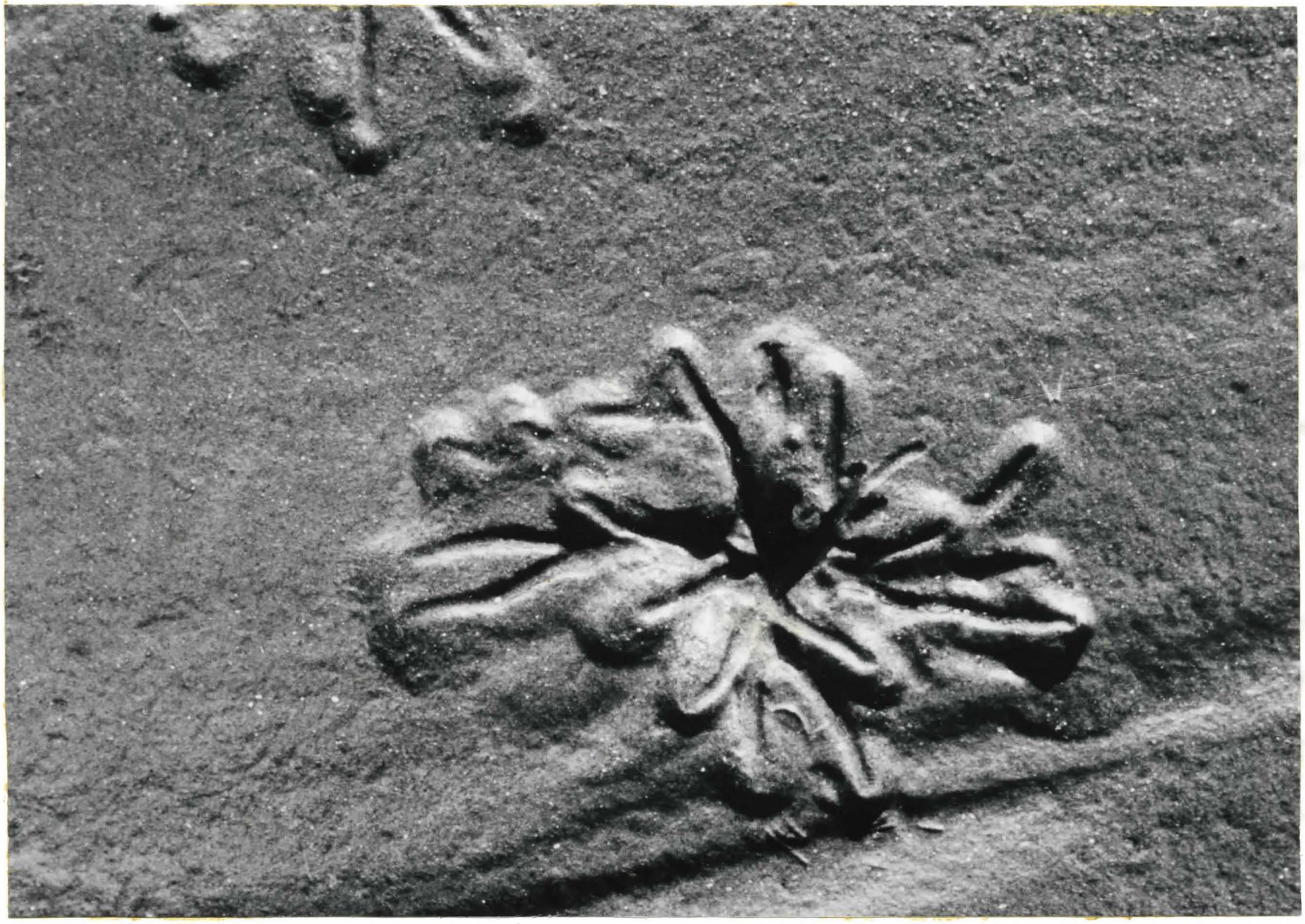


Figure 4 -- Surface trace showing the action of Macoma siphons.

invertebrates. This carbon can be mobilized through the food chain by chitinoclastic bacteria that actively decompose these compounds (ZoBell, 1946) and can survive under a variety of environmental conditions. Gooselink and Kirby (1974) describe microbial build-up on organic tissues and the subsequent conversion of the refactory compounds to high-protein microbial biomass.

The possible importance of these bacteria was demonstrated by MacGinitie (1932) and Newell (1965), who showed that certain invertebrates may live and thrive when fed only on a diet of bacteria. ZoBell (1938) extracted a ferment from bivalves that lyses most bacteria; Zhukova (1963) proved that digestion of bacterial cells in various invertebrates does occur, by taking cell counts in different regions of the intestine. The extent to which bacteria are important remains unknown. ZoBell and Felthan (1942), Wood (1965) and Newell (1970) maintain that bacterial biomass is sufficient to provide a considerable amount of carbon and nitorgen to benthic grazers. Hargrave (1970) calculates that less than 10% of daily microflora production is sufficient to satisfy the caloric requirements of a deposit feeding amphipod. On the other hand, Dale (1974) calculates that bacteria biomass is too low to satisfy the nutritional needs of macrofauna. As yet, no studies have attempted to correlate distributions of bacteria with those of a consumer invertebrate. Newell (1970), Mann (1973), and Dale (1974) have all shown that bacterial populations are related to organic content of the sediment. ZoBell (1938), Meadows and Anderson (1966), and Hargrave (1972) have described increasing bacterial

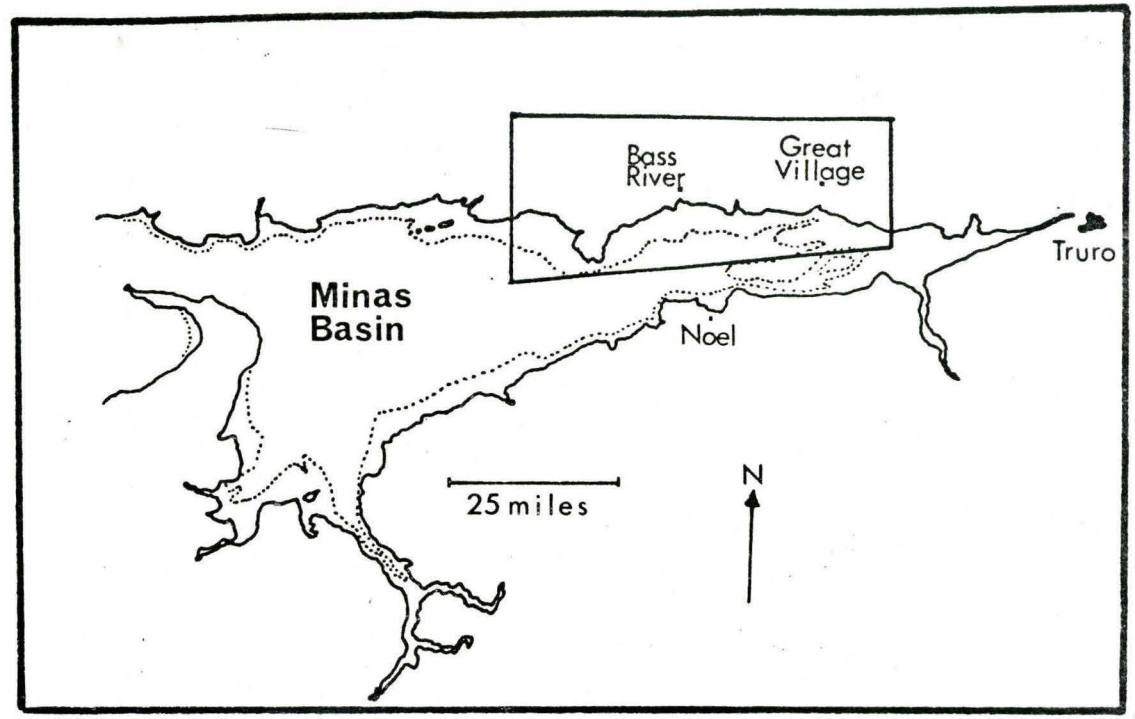
populations with decreasing sediment particle size. The process of breakdown of the marsh grass Spartina alterniflora by microbes has been studied by Mann (1973) and Gooselink and Kirby (1974).

This study proposes to: i) determine the population distribution of Macoma balthica on an intertidal mudflat, ii) examine the distribution of epipsammic bacteria in the upper few millimetres of sediment, iii) determine organic carbon and nitrogen content of the sediment on which the bivalves feed, iv) determine the effects of vertical position on the mudflats, and v) attempt an explanation of pattern of Macoma distribution in terms of the above factors.

Study Area

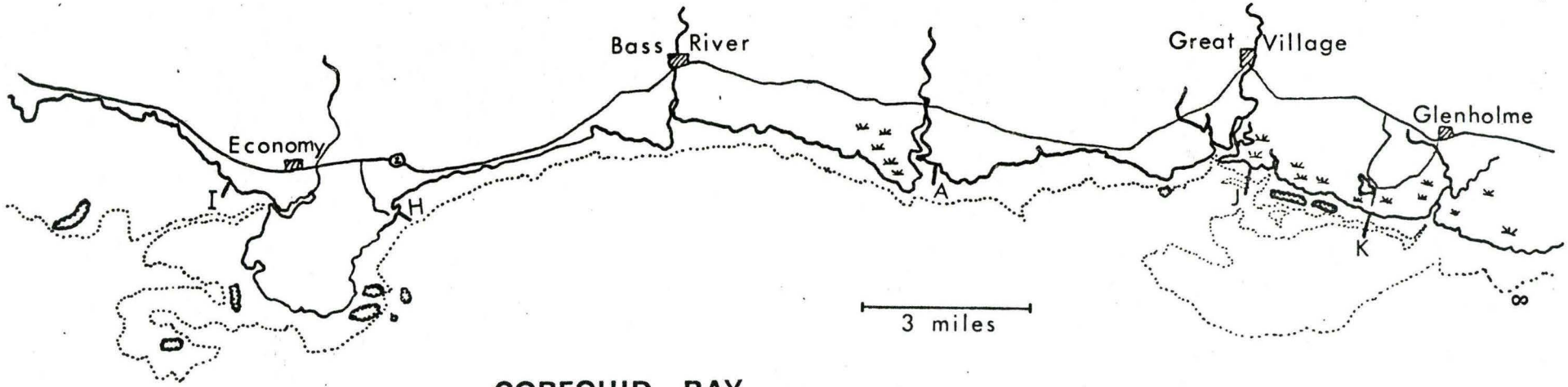
The Bay of Fundy (Nova Scotia) is characterized by very large tides: the largest are over 17 m. (55 ft.) in Minas Basin. Samples and data for this study were obtained from the north shore of Cobequid Bay, the southeast arm of the Bay of Fundy (Figure 5). Tidal currents of 2.5 knots have been recorded over the sand bars, but the mudflats develop in areas protected from wave and current action. Continual water action suspends sediment, so light penetration is reduced to the top few centimetres of water. The Bay is underlain by Triassic bedrocks and coastal exposure is usually Triassic outcrop or Pleistocene tills. Much of the supratidal zone is salt-marsh that is periodically (i.e., spring tides) inundated by the tide. Spartina alterniflora predominates the shore grasses: debris derived from it is abundant on the intertidal flats. The macrophytic algae Fucus and Ascophyllum are

Figure 5 -- Location of sampling transects on the north shore of Cobequid Bay.



LEGEND

high tide
low tide
outcrop
marsh



COBEQUID BAY

common on intertidal bedrock outcrops. Their detrital contribution by wave erosion is probably small due to their restricted distribution.

The sediments of the mudflats range from clay to fine sand; water content varies. Often a well-developed anoxic zone is found below about 7 cm. Biofacies distributions in this area have been studied by Craig (1975). The only other mollusc of abundance on the flats is the gastropod Nassarius obsoletus although Mya arenaria appears sparsely. Corophium volutator (an amphipod) is abundant locally, as are the infaunal polychaetes Neanthes and Nephthys. Macoma balthica occupies a dominant position in certain zones of the flats and is eaten by moon snails, shore birds, bony fishes,and rays.

METHODS

Five transects with 50 m. sample intervals were run perpendicular to the shore. The transects were spread out over a 20 mile range along the north shore of Cobequid Bay (see Figure 5). The height of each station was calculated with respect to the high mark of one cycle on the date surveying; all data were corrected to a common level using the mean tidal range of 11.6 m. for the area in 1974. Error is estimated as .5 - 1 m., and values presented in this report are considered to give at least relative tidal elevations.

The five transects were sampled at each station to give a total of 40 samples. A range of sediment types was seen from clay base to gravel base; however, an overlying mud layer was present on each transect. The sedimentary characteristics and number of samples taken at each transect are shown in Table 1.

At each station of transects A, H, I, J and K a 1 $m.^2$ quadrat was placed on the mud surface. Three plastic core jackets were haphazardly placed within the quadrat and sunk to a depth of at least 20 cm. The area of the three cores constituted $\frac{1}{16}^{th}$ of the square metre. The cores were extruded and sieved on the spot to collect and count all the Macoma larger than one millimetre. Counts were converted to individuals per $metre^2$. Most of the sampling was done in August by which time the May spatfall had grown to a countable size.

Sediment samples for counting the associated bacteria were

Table 1

Sampling characteristics of the five transects on north shore Cobequid Bay

Transect	Station Interval	Sedimentary Characteristic	Number of Samples
A	50 m	mud to sand	5
H	50 m	gravel in the mud	8
I	50 m	mud to fine sand	9
J	50 m	mud with gravel base	9
K	25 m	mud	9

collected at the same transect stations. Sampling was carried out at low tide in August. Using a sterile spatula, the top few millimetres of mud were lifted off and placed in a petri dish. The dish was covered, sealed and promptly frozen in a household freezer. The 40 samples were transported on dry ice and stored in a freezer in Hamilton, Ontario for five months.

Bacteria were enumerated by direct microscopic count using fluorescent light techniques, for the most part as described by Dale (1974). About 2 grams of sediment were weighed and diluted in 100 ml. of filtered seawater. This suspension was homogenized in a Waring Blender for 5 minutes at top speed ('purify') in order to shake the bacteria off the grains. 1 ml. of homogenate was pipetted into 100 ml. of filtered seawater and shaken for 30 seconds; 1 ml. and 10 ml. of this suspension were filtered separately through 45 mμ pore Millepore filter paper. (25 mμ was tried but it was difficult to see the bacteria in a much denser clay coverage.) The filter paper was then treated with 1:30,000 solution of acridine orange fluorescent stain. 1:5,000 or less as suggested by Wood (1965) and Strugger (1973) tended to stain too many of the sediment particles; in the 1:100,000 solution as used by Batoosingh and Anthony (1971), bacteria cells often did not pick up enough of the stain. The paper was dried, cleared with immersion oil and mounted on a slide. All utensils and glassware were kept in a 70°C oven between usage.

Counting of bacterial cells was done using a Zeiss fluorescent light. Different arrays of filters were required depending on how much

light was scattered by the filter paper and sediment particles. An oil condenser was used to achieve a dark background effect. Considerable problems were encountered, due to scattering of the light by the filter paper; this made distinction between bacterial cells and sediment particles difficult. The acridine orange stain reacts specifically with the charge on RNA molecules (Strugger, 1973). The stain thus reacts differently in live and dead cells: in the latter, the RNA molecule is degrading and upon staining the fluorescence is orange, while in the live or nondegraded cells, fluorescence is green. The clay particles, however, seemed to have a variety of surface charges and often fluoresced orange and green. Organic material was bright orange (Figure 6).

Because of confusion with sediment particles, only recognizable coccus and rod bacterial shapes were counted. Fields were chosen at random across the filter paper and bacteria counted until at least 500 were ennumerated. This method follows the recommendation of Lebedeva and Shumakova (1969) to reduce variation in cell counts. The filter had to be search at all levels due to bacterial penetration. Successive counts of the same sample differed by less than 10%. Operator bias was, however, not investigated, and may represent a considerable error.due to the subjective nature of the bacterial identifications. Wet-to-dry ratio of the sediments was determined using the same samples, and numbers of bacteria per gram dry weight were calculated by Dale's (1974) formula:

$$n = \frac{n \times A}{a} \times d.f. \times \frac{r}{w}$$

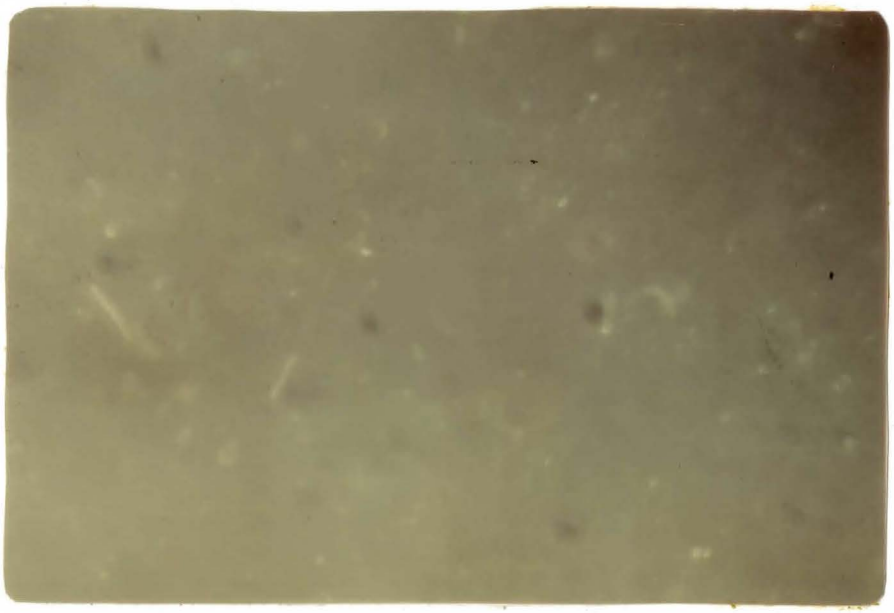


Figure 6 -- Average spread of bacteria on the filter paper. Resolution is poor due to the drifting of focus and fading of fluorescence due to exposure time. Two rod bacteria can be seen to the left in the photograph (each about 1μ in length).

where N is number per gram, n is mean count per microscopic field, A is filtration area, a is field area, d.f. is dilution factor, W is weight of sample and r is wet-to-dry ratio.

Bacterial numbers were converted to numbers per gram dry weight of sediment and thus are comparable to other studies. Luria's (1960) value of 2.2×10^{-13} g. dry weight was used for cell mass. (This represents an average value for coccus cells.) The results represent only bacterial populations on the surface where Macoma feeds. Micro-organisms also occur in large numbers at considerable depth of sediment (ZoBell and Feltham, 1942; Oppenheimer, 1960; Dale, 1974).

In order to analyze these sediments for organic carbon and nitrogen, about 10 gm. of each of the 40 samples were freeze-dried for 4 days. Each was then ground for 3 minutes in a Siebtechnik sediment grinder. For carbon analysis, 400 mg. of sediment were measured out for combustion in a Leco Carbon IR-12 autoanalyzer in which all inorganic carbon is excluded. Similarly, a few milligrams of sediment were subject to gas analysis in a Leco UO-14 modified nitrogen determinator.

Results were analyzed using multivariate statistical methods.

RESULTS

A data summary is presented in Table 2; complete field data for the Macoma census are given in Appendix A. Macoma balthica populations range from total absence near high tide level and at the bottom of transects to a maximum of approximately 3500 clams per square metre. The clams were found in all size ranges, although the 2 mm. to 7 mm. sizes were often lacking. Macoma was never found in the salt marsh and rarely in mobile sands.

Pearson correlation coefficients were calculated for all relationships between the variables (Table 3). Except for Macoma and bacterial numbers, none of the variables were significantly correlated. Macoma population density is not significantly correlated with tidal elevation; it is therefore considered unlikely that time of coverage by water is a significant parameter. Figure 7 shows how the Macoma population of each transect approaches a normal distribution with decreasing elevation, but it also shows that population maxima are neither of equal magnitude nor occur at the same tidal elevation. The relationship between Macoma and bacterial densities is significant at $P > .05$ (Figure 8).

Appendix B presents all the variables used to calculate bacterial numbers per gram dry weight of sediment. Area of filtration was 984.4 mm^2 and field of view of the microscope was .0154 mm^2 (100 X magnification fluorescent oil immersion lens). Bacteria were not

Table 2

Results of survey, bivalve population, organic carbon and microbiological analysis.

Transect	Station	Vertical drop from mean high tide (m.)	Macoma #/m^2	C (org) % dry wgt. sed.	Bacteria/gm. dry wgt. sed. X 10^6
A	2	3.25	306	.403	3879
	3	3.68	934	.268	8383
	4	3.93	805	.283	6165
	5	4.58	789	.214	4653
	6	5.03	225	.210	2053
H	3	7.6	193	.132	1867
	4	8.0	16	.147	985
	5	8.4	499	.199	8876
	6	8.5	16	.210	1249
	8	8.9	145	.225	1695
	9	9.3	225	.132	1785
	10	9.7	81	.077	1164
	11	10.0	81	.105	1061
I	2	4.8	0	.771	966
	3	7.3	2061	.993	16,761
	4	7.7	1691	.670	12,222
	5	7.9	1546	.300	4713
	6	8.1	531	.241	3266
	7	8.4	209	.284.	3838
	8	8.5	0	.208	3982
	9	8.7	0	.143	1940
	10	8.9	0	.150	961

continued ...

Table 2 (continued)

Transect	Station	Vertical drop from mean high tide (m.)	Macoma #/m^2	C (org) % dry wgt. sed.	Bacteria/gm. dry wgt. sed. X 10^6
J	2	3.5	0	.978	1283
	3	4.7	467	.820	1393
	4	7.3	274	.490	275
	5	8.6	741	.508	4390
	6	10.1	2383	.550	19,577
	7	11.9	1868	.445	14,477
	8	12.9	2254	.554	14,212
	9	13.6	1256	.480	9386
	10	13.3	32	.520	409
K	1.5	2.2	16	.630	1706
	2	3.4	16	.657	2154
	3	4.2	556	.280	5134
	4	5.1	1238	.620	13,022
	5	6.1	2141	.320	12,491
	6	7.2	2335	.520	17,025
	7	8.3	3494	.360	16,600
	8	9.3	2512	.300	9007
	9	10.3	1336	.410	930

Table 3

Pearson Product. Moment correlation coefficient matrix of measured parametres.

T.D. -- tidal drop; Mac -- Macoma numbers; C -- organic carbon; B -- bacterial numbers.

	T.D.	Mac	B	C
T.D.	1.0000	.247	-.235	.181
Mac		1.000	.234	.880*
B			1.000	.296
C				1.000

* significant at P > .01

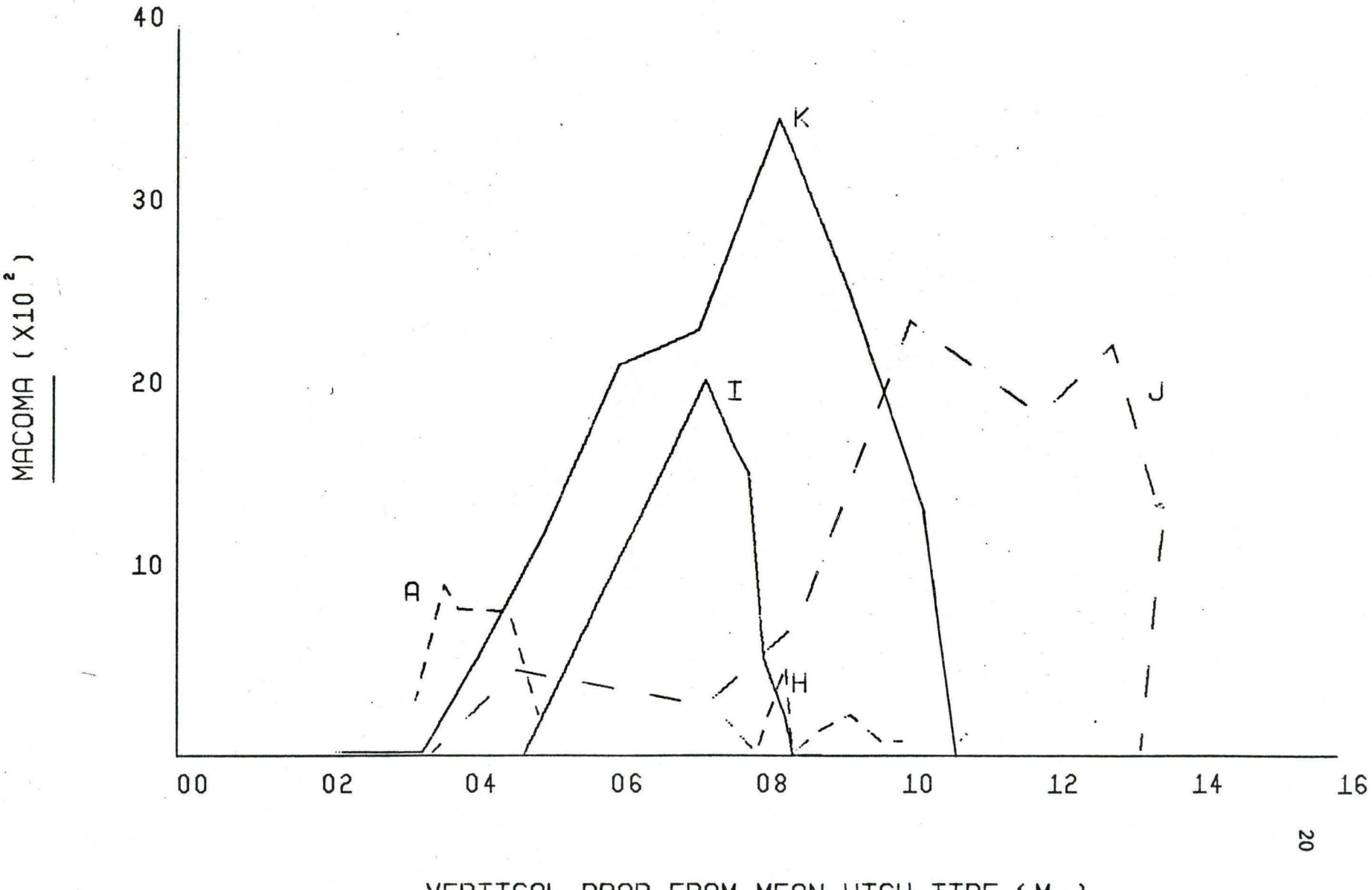


Figure 7 -- Distribution of Macoma balthica along each transect

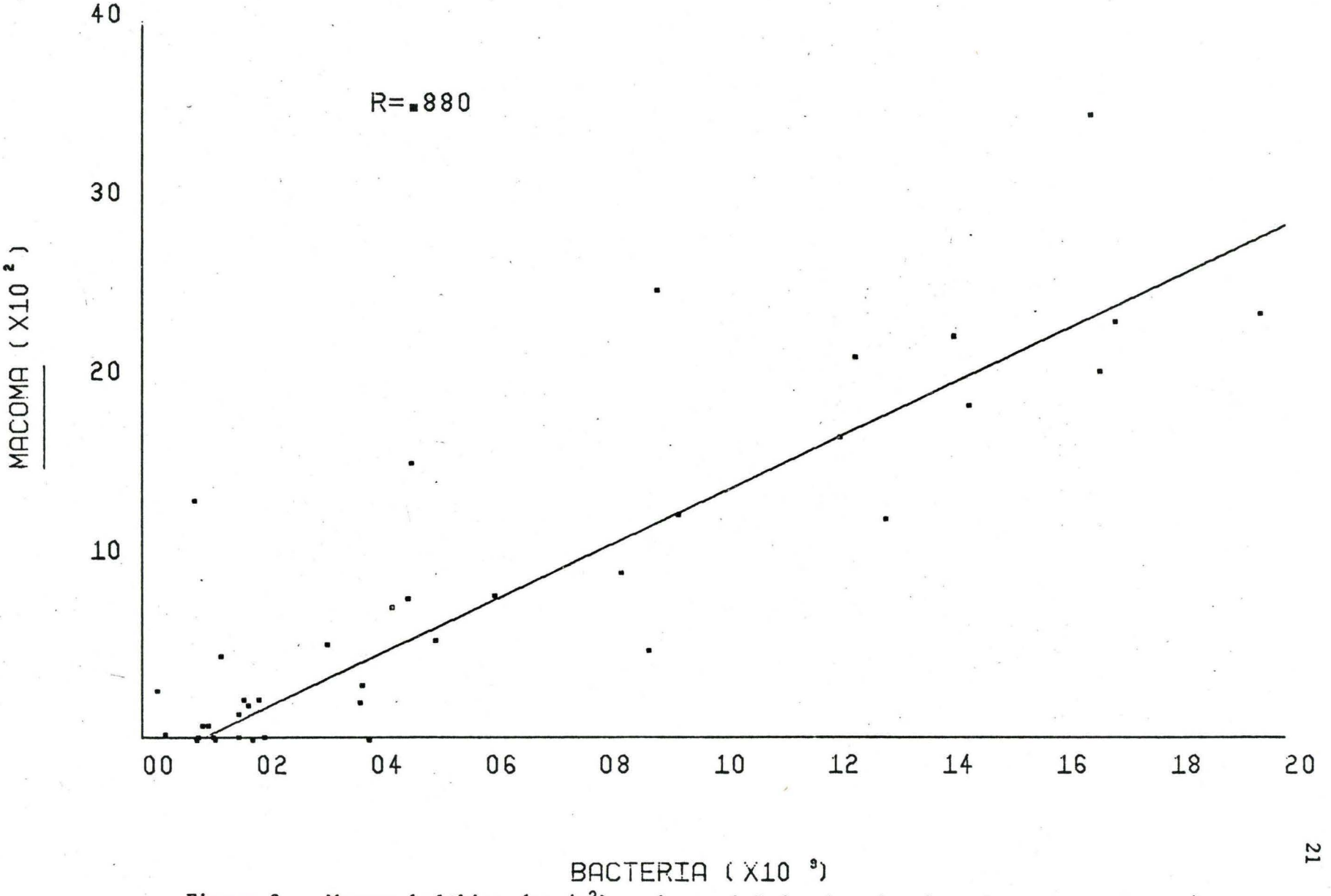


Figure 8 -- Macoma balthica (no./m^2) vs.bacterial density (no./gm. dry wt. sed.)

identified during counting but shape was distinguishable. Coccus bacteria predominated in all samples; long and short rods consisted of less than 10% of the population (Figure 6). For the most part, the bacteria were released into suspension by homogenating action, but occasionally bacteria adhered to sediment grains, appeared as the bright spots seen in Figure 9. Similarly, organic material had numerous attached bacteria (Figure 10). Closer examination of stems or veins showed the bacteria to be actually inside the vessels that often appear to be hollow. An examination of the filtrate from suspensions filtered through 45 mμ paper revealed very few bacteria that had passed through the pores.

Values of organic carbon (Table 2) range from .077 to .978% dry weight of sediment. These values are surprisingly low as considerable detritus from rockweeds and marsh grasses was observed on the exposed flats. Only the top few millimetres of sediment were analyzed; green and blue-green algal slicks develop in this layer and appear as a green haze on the mud surface (most pronounced on sunny days) about 3 to 5 hours after the water has receded. At each recession of the water the algal mat has disappeared. No significant correlation is present between either Macoma populations and organic content or bacterial populations and organic content (Figure 11). Possibly, at low carbon levels, other parameters are more important in determining population distribution, or the carbon distribution is a transient one varying from one tidal cycle to the next.

No significance was found in the relationships of tidal

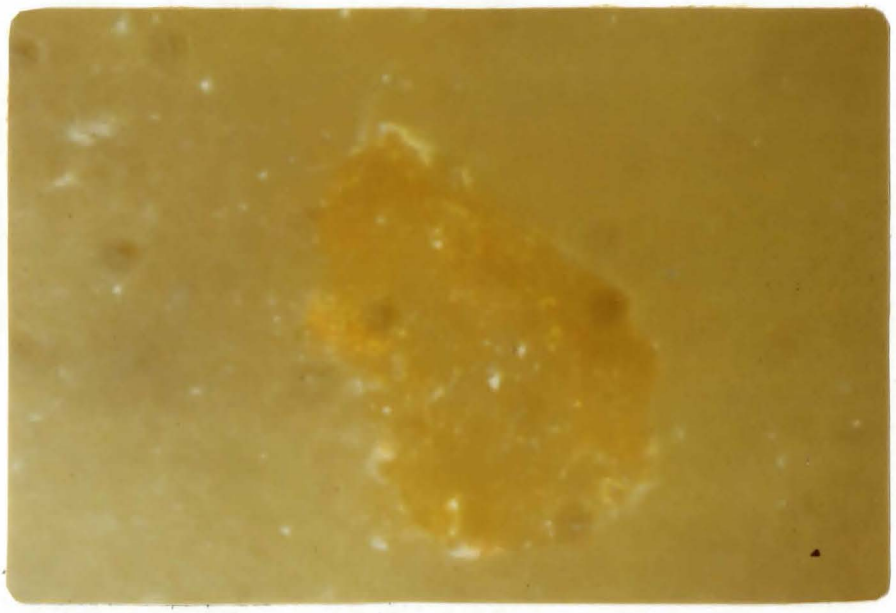


Figure 9 -- Bacteria (bright spots) attached to a sediment grain. Grain is about 9μ in length. (Ultraviolet light).

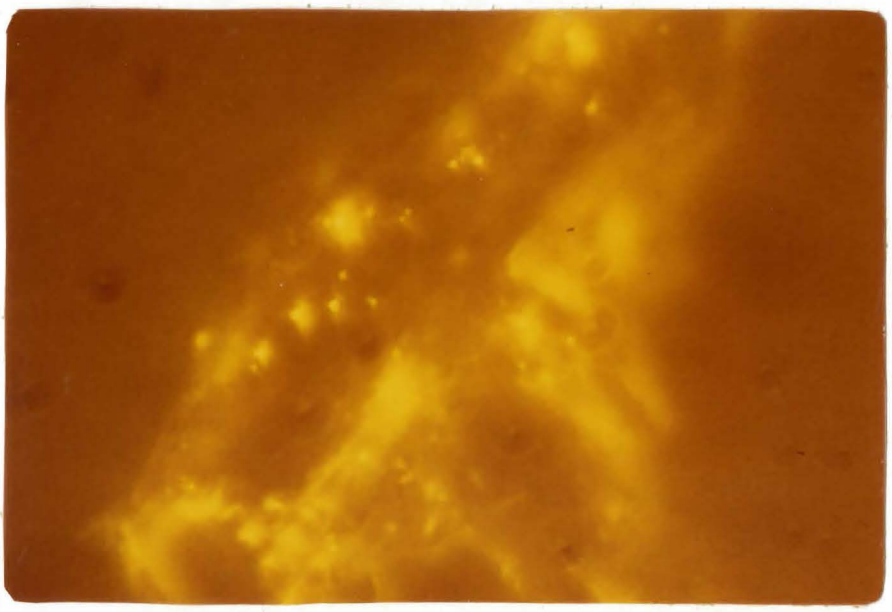


Figure 10 -- Bacteria attached to inner and outer walls of an organic 'stem'. Stem is about 6μ wide. (White light).

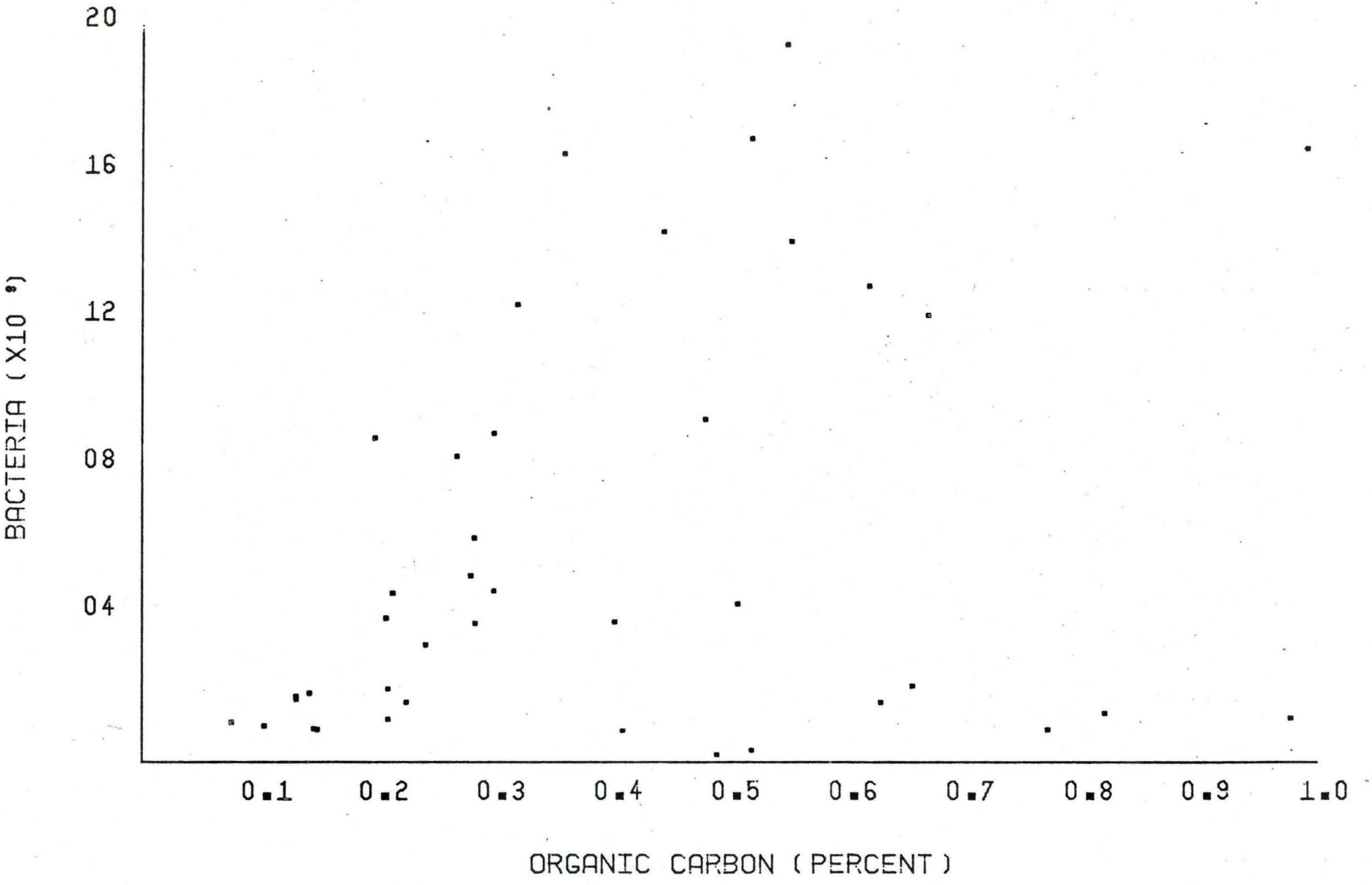


Figure 11 -- Bacterial density (no./g. dry wt. sed.) vs. organic carbon content (% dry wt. sed.).

elevations with either organic content or bacterial populations. This suggests that the deposition of organic material or bacteria from suspension is not related to water level.

Organic nitrogen values were too low to be accurately measured (roughly 0.02 - 0.05% dry weight of sediment) and were not included.

DISCUSSION

Macoma populations measured in this study are high compared to those of other studies (Table 4). Even the mean population of 832 individuals/m^2 on the Cobequid flats is greater than many maximal populations in other areas. Samples from both the north and south shores of Cobequid Bay show maximum populations over 2500/m^2.

The importance of microbes to food chains lies in their ability to utilize low protein detritus, refractory compounds and dissolved organic matter. Newell (1965) shows that epipsammic bacteria must be fixing atmospheric nitrogen and/or inorganic nitrogen from the sea. Gooselink and Kirby (1974) report a rapid efficient conversion (66%) of less refractory marsh grass compounds; the remaining refractory compounds require considerably more time for decomposition.

Values for bacterial counts lie in the middle of the range reported in the literature (Table 5). The plate technique usually represents 10% of the microbial population (Wood, 1965) but a comparison of methods showed direct microscopic count to be far more consistent (Anthony, 1963). The method, however, involves many hours of preparation. Counting procedure is difficult, as bacterial bodies, especially the cocci, are difficult to distinguish. The sediment samples used for bacterial counts in this study were stored at sub-zero temperatures for five months. To discover whether bacterial populations change during storage, Anthony (1963) held samples of Nova Scotia

Table 4

Maximum Macoma balthica populations from other studies.

Macoma/m^2	Location	Source
5928	Mersey Estuary	Fraser, 1932
3492	Bay of Fundy	This study
1600	Whitstable, Eng.	Newell, 1966
1200	Falmouth, Mass.	Gilbert, 1969
1200	San Fransisco	Vassallo, 1972
750	White Sea. USSR	Bubnova, 1972

Table 5

Densities of microorganisms from other studies.

#/gm. dry wgt. sed.	Technique	Location	Source
6.3 - 17.2 X 10^9	Fluores. microsc.	Azov Sea	Zhukova & Fedosov, 1963
14 X 10^9	Fluores. microsc.	Halifax	Anthony, 1963
.9 - 20 X 10^9	Fluores. microsc.	Fundy	This study
.12 - 10 X 10^9	Fluores. microsc.	Nova Scotia	Dale, 1974
2 X 10^9	Fluores. microsc.	Fundy	Anthony, 1963
200 - 450 X 10^6	Plate	California	ZoBell & Feltham,1942

Table 6

Organic carbon content of sediments from other studies.

Percent	Location	Source
1.8 - 7.6	Nova Scotia	Dale, 1974
3.9	White Sea, USSR	Bubnova, 1972
2.0	Whitstable, Eng.	Newell, 1966
1 - 8	average near shore	Trask, 1955
.13 - .98	Bay of Fundy	This study

sediments at -20°C for six months. No significant change in counts was found after this time. A similar study by Batoosingh and Anthony (1971) on Bay of Fundy sediments detected no such change. The latter authors report the presence of Bacillus (rod), Pseudomonas (rod) and Aeromonas (coccus) species. Bacterial populations in this study were less than 10% rods. Although Wood (1965, p. 28) estimates 65% of marine bacterial populations should be rods, he finds high coccus counts in areas proximal to land.

This study has found a significant correlation between bacterial and bivalve numbers. ZoBell and Feltham (1942) and Zhukova (1963) calculate biomass/volume of sediment and claim bacteria represent a large food source for deposit feeders. Dale (1974) calculated bacterial biomass in terms of per cent of available carbon and found it contributed only 2.5%. How important, then, is bacterial biomass to the nutrition of Macoma balthica? Using the value of bacterial biomass as calculated by Luria (1960) of 2.2×10^{-13} gm. dry weight, bacterial biomass in this study has a mean value of:

2.2×10^{-13} gm. $\times$ 5.9×10^{9} bacteria/gm. sediment

= 1.3 mg. bacterial biomass/gm. dry weight of sediment.

This study finds an average of about .395% carbon in the Cobequid Bay sediments (or 3.95 mg. of carbon/gm. dry sediment). Bacterial biomass, therefore, comprises about one-third of the organic carbon present. Values were found at Station K7 of 6.6×10^{9} bacteria/gm. sediment and organic carbon of .360%. Estimates of bacterial biomass are a little over 100% of the organic carbon. This station also has the

greatest Macoma density. Bacteria must represent a very significant part of the diet the clam retrieves from the sediments.

Considerable dependence on bacteria for a food source for Macoma is likely. Hargrave (1970) demonstrated a possible interdependence when he found that the greatest abundance of amphipod fecal pellets lead to the greatest bacterial density. Newell (1965) found Macoma balthica faeces served as a favourable microbial substrate, and a marked increase in nitrogen content was measured. Newell suggested that Macoma reingests the faeces to crop the bacteria. It is also possible that Macoma larvae may be induced to settle on sediments of high bacterial content, in a fashion similar to that found by Wilson (1955) for the opheliid polychaete. Ophelia bicornis.

The sediments from Cobequid Bay show very low values of organic carbon content in comparison with other studies (Table 6). Despite these low values, the sediments support large populations of Macoma balthica. The lack of correlation between Macoma and organic carbon contrasts with Gilbert (1969) who stated that organic content is more crucial than sediment size to Macoma density. The low carbon values and lack of significant correlation with bivalve distribution suggest that it is unlikely that Macoma exists entirely by deposit feeding.

Bubnova (1972) derived the following relationship for Macoma balthica nutrition:

$$R = pW^m$$

where R is daily requirement in mg. of organic matter or protein; p

is a coefficient defining level of food consumption in unit time for W = 1; W is the dry weight of a molluscan body; and m is a coefficient indicating the rate of change in the requirement with increasing body weight. For an arbitrary length of 12-14 mm., Bubnova estimates W = 14.3 mg., p = .36 and m = .57. The daily requirement of organic matter is estimated as:

$$R = .36 \times 14^{.57}$$

$$= 2.44 \text{ mg. organic matter/day.}$$

Trask (1955) uses a factor of 1.8 to convert to organic carbon. The requirement is, therefore, 1.35 mg. carbon/day. Bubnova reports that a Macoma 12-15 mm. in length processes about 0.6 gm. (dry weight) of sediment per day. Tunnicliffe (unpublished) reports 0.52/gm./da. for a similarly-sized Macoma. As Cobequid Bay sediments are .395% (average) carbon, there are 2.37 mg. carbon present in 0.6 gm. Macoma is able to assimilate 70% of the organic matter presented to it (Bubnova, 1972). Thus Macoma in Cobequid Bay is able to take in 1.66 gm. organic carbon deposit-feeding which approximately satisfies its requirements.

To satisfy metabolic needs, protein is vital. Bubnova finds Macoma ingested 23.4 mg. carbon, presumably to satisfy the protein demand. Application of the requirement equation with parameters for protein as indicated by Bubnova yields a daily protein requirement of .78 mg. Estimates of nitrogen content in this study were .02 to .05% of the sediment. So in .6 gm. sediment there is only .24 mg. nitrogen. Macoma assimulates 62% of protein ingested. The clam would have to

process over 5 times as much sediment than it does to satisfy its requirements.

Macoma balthica probably does not rely solely on deposit-feeding to survive. The bacterial contribution is great; even with multiplication rates of 1 to 6 time a day (Hargrave, 1970), however, requirements could not be satisfied. This contribution is not considered by most authors, although Newell (1965) suspects part-time filtration due to lack of nutritive material. Filtering has been observed by Macoma occasionally in this laboratory. Filtering on the mud-flats allows the ingestion of salt-marsh debris suspended by tidal currents. The vast amount of sediment in suspension probably results in low plankton productivity, but this suspended sediment may sustain epipsammic bacteria. Suspension feeders such as Balanus (Crustacea), Mytilus, Zyrphaea and Mya (Mollusca) are relatively abundant in the area (the latter up to 1200/m^2). ZoBell and Feltham (1942) sustained Mylitus edulis solely on suspended bacteria. Crawford et al. (1974) found the input of dissolved organics sufficient to support bacterial production at 30 µgC/l/hr. or about 10% of the suspended algal production in his area. Bacteria serve as intermediaries, producing particulate organic matter. Fraser (1932) found Macoma balthica populations near 6000/m^2 in an area that is characterized by a large input of industrial and human waste, and very turbid water.

The low values of carbon are surprising: a regular monthly inundation at spring tides of the salt-marsh would be expected to carry detrital Spartina into the Bay. Gooselink and Kirby (1974) find 56% of

the marsh grass readily breaks down to 67μ, a size fraction probably easily suspended by the tide. Minas Basin is a highly turbulent body of water and it is likely that detrital particles are kept in suspension and possibly continue decomposition in the water column. Odum (1959) finds an initial value of 10% protein in Spartina which increases to 24% upon decomposition. The easily degradable marsh-grass detritus would provide a good protein source for herbivores (Gooselink and Kirby, 1974) able to extract it from sediment or water.

Bacterial numbers do not correlate signifiantly with organic carbon distribution in contrast to the correlation found by Dale (1974). Although bacteria use carbon, this lack of correlation suggests that the detrital carbon is transient, perhaps unpredictably suspended and deposited. Newell (1965) finds that when organic debris is low, the limiting factor on microbial population size is not the organic content but the grade of the deposit.

Sediment size was not examined in this report but its limiting effect on bacterial and bivalve population size has been substantiated by many authors. ZoBell (1938) and Oppenheimer (1960) found an abundance of bacteria in finer grain sizes due to increased surface area and greater adsorption of organic material by surface attraction. Studies show maximum values of bacteria occuring at 8ø. The bacteria-sediment relationship may also be a two-way interaction. The excretion of polysaccharides is in quantities sufficient to act as a binding agent on the top sediment layer. Rhoads (pers. comm.) finds a considerable increase in shear stress is required to induce sediment

movement when silt-sized particles are inoculated with bacteria. Coarse sediments limit Macoma's ability to burrow and are low in organic carbon (Newell, 1965). Highly thixotropic muds inhibit secure positioning in the mud and may well clog a filtering siphon.

Macoma balthica appears to act as both a deposit- and suspension-feeder. Beanland (1940) proposed that zonation of Macoma is dependent upon time of immersion. Suspension-feeders can only filter when they are covered with water, and deposit-feeders require a layer to lubricate their incurrent siphons. Macoma occurs in subtidal (Thorson, 1957; Driscoll and Brandon, 1973) and intertidal muds. Stephen (1930) and Vassallo (1969) report maximum Macoma populations at the top of the intertidal. Beanland (1940) and Ress (1940) find Macoma maxima at the base of the intertidal zone. This study finds no correlation of intertidal position and Macoma density: populations peak in a variety of positions on the flat.

The Cobequid Bay flats seem to retain a considerable amount of water within the sediment at low tide. Poor drainage of the extensive flats may be responsible for the wide variance of zonation of maximum populations of Macoma.

Physical stresses of the subaerial environment during periods of exposure can be severe. The overlying sediment undoubtedly provides considerable protection to infaunal species. However, even this protection is probably insufficient in the face of severe factors such as ice flow effects. Signs of large areas of displaced sediment and ice-rafted sand and gravel are evident on the flats. Death for

many bivalves is inevitable in such local areas. Further study is necessary to develop all the factors that affect the distribution of Macoma populations.

SUMMARY

1. Populations of Macoma balthica L. on the north shore of Cobequid Bay are among the highest recorded with a maximum of 3492 Macoma/m^2.
2. As determined by direct fluorescent microtechniques, average bacterial populations in the study area are 5.9 X 10^9 bacterial/ gm. dry weight of sediment.
3. The correlation coefficient between bacterial and Macoma balthica densities is .880. Bacterial biomass constitutes 33%, on the average, and up to 100%, of the organic carbon in the sediment.
4. Daily requirement calculations for organic carbon and nitrogen indicate that there are insufficient quantities in the sediment Macoma ingests to sustain it by deposit feeding.
5. Macoma balthica's diet is probably supplemented by nutrients derived from suspension-feeding. High bacterial densities in the water column and suspended organic particles may supply these nutrients.
6. Low levels of organic carbon in the sediments may be due to low input or to a high degree of suspension by turbulent water. No correlation between bacterial distribution and organic carbon is present.
7. Macoma distributions do not correlate significantly with vertical position on the mudflat, probably because poor drainage allows deposit-feeding at low tide.

APPENDIX A

Transect	Station	* Number of *Macoma* in core			Total *Macoma*/m^2
		#1	#2	#3	
A	2	4	5	10	306
	3	24	18	16	934
	4	20	17	13	805
	5	21	17	11	789
	6	1	7	6	225
H	3	2	4	6	193
	4	1	0	0	16
	5	9	12	10	499
	6	1	0	0	16
	8	3	4	2	145
	9	0	4	10	225
	10	2	2	1	81
	11	1	2	2	81
I	2	0	0	0	0
	3	36	49	43	2061
	4	37	34	34	1691
	5	24	36	36	1546
	6	10	10	13	531
	7	10	0	3	209
	8	0	0	0	0
	9	0	0	0	0
	10	0	0	0	0

* Conversion factor: total no. of *Macoma* in cores X 16.1 = *Macoma*/m^2.

Appendix A (continued)

Transect	Station	* Number of *Macoma* in core			Total *Macoma*/m^2
		#1	#2	#3	
J	2	0	0	0	0
	3	8	9	12	467
	4	3	8	6	274
	5	15	18	13	741
	6	46	49	53	2383
	7	40	42	34	1868
	8	51	42	47	2254
	9	22	28	28	1256
	10	1	1	0	32
K	1.5	0	0	1	16
	2	0	1	0	16
	3	9	5	9	556
	4	23	28	26	1238
	5	41	45	47	2141
	6	60	31	54	2335
	7	66	72	79	3494
	8	38	52	66	2512
	9	16	24	43	1336

* Conversion factor: total no. of *Macoma* in cores X 16.1 = *Macoma*/m^2.

APPENDIX B

Transect	Station	No. of bacteria	No. of fields*	Weight of sample (g).	Wet-to-dry ratio of sediment
A	2.5	518	58	2.0524	1.3878
	3	508	31	1.6955	1.3478
	4	500	34	2.0923	1.3726
	5	510	42	2.1918	1.3187
	6	510	110	1.8511	1.2919
H	3	534	110	2.1210	1.2637
	4	507	190	2.1476	1.2255
	5	500	23	2.0449	1.3085
	6	534	180	1.9797	1.2605
	8	493	120	2.0034	1.2953
	9	505	100	2.0464	1.2045
	10	514	170	1.9769	1.1997
	11	497	180	2.0500	1.2150
I	2	510	280	2.2300	1.8706
	3	500	20	2.0942	2.1959
	4	504	17	2.3718	1.5639
	5	504	48	1.9800	1.3904
	6	500	70	1.8787	1.3440
	7	520	68	2.0900	1.6962
	8	500	55	1.9300	1.3216
	9	503	110	2.0885	1.3777
	10	496	180	2.1424	1.2388

* For 1 ml. of filtrate

Appendix B (continued)

Transect	Station	No. of bacteria	No. of fields*	Weight of sample (g.)	Wet-to-dry ratio of sediment
J	2	506	170	2.2817	1.5783
	3	511	170	2.0755	1.5086
	4	536	840	2.0744	1.4629
	5	605	60	2.0889	1.4203
	6	520	12	2.0714	1.4470
	7	482	14	2.1515	1.4165
	8	501	16	2.1234	1.5686
	9	520	22	1.9564	1.2173
	10	488	40	2.0099	1.0698
K	1.5	500	170	2.0154	1.8565
	2	512	110	2.2515	1.6140
	3	507	50	1.9607	1.5595
	4	490	18	1.9683	1.4742
	5	550	18	2.0965	1.3388
	6	376	10	1.8597	1.3212
	7	490	11	2.3418	1.2546
	8	528	24	1.9566	1.2532
	9	544	200	2.1273	1.1235

* For 1 ml. of filtrate

REFERENCES

Anthony, E.H., 1963. Regional variability of bacteria in north Atlantic sediments. In C.H. Oppenheimer (ed.), Marine Microbiology. Thomas; 730 p.

Batoosingh, E. and E.H. Anthony, 1971. Direct and indirect observations of bacteria on marine pebbles. Can. J. Microb., 17; 655-664.

Beanland, F.L., 1940. Sand and mud communities in the Dovey estuary. Journ. Mar. Biol Assoc. U.K., 24; 589-611.

Boyden, C.R. and C. Little, 1973. Faunal distributions in soft sediments of the Severn Estuary. Estuarine and Coastal Marine Science; 1; 203-223.

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

Craig, H.D., 1975. M.Sc. Thesis (unpublished). McMaster University.

Crawford, C.C., J.E. Hobbie and K.L. Webb, 1974. The utilization of dissolved free amino acids by estuarine microorganisms. Ecology, 55; 551-563.

Dale, N.G., 1974. Bacteria in intertidal sediments: factors related to their distribution. Limnol. Oceanogr., 19; 509-518.

Driscoll, E.G. and D.E. Brandon, 1973. Mollusc-sediment relationships in north-western Buzzards Bay, Massachusetts, U.S.A. Malacologia, 12; 13-46.

Fraser, J.H., 1932. Observations on the fauna and constituents of an estuarine mud in a polluted area. Journ. Mar. Biol. Assoc. U.K. 22; 69-85.

Gilbert, M.A., 1969. Environmental and interspecific interactions of Gemma gemma. Mya arenaria, and Macoma balthica as revealed by density and abundance patterns. M.Sc. Thesis (unpublished), University of Massachusetts.

Gilbert, M.A., 1973. Growth rate, longevity and maximum size of Macoma balthica (L.). Bio. Bull., 145; 119-126.

Gooselink, J.G. and C.V. Kriby, 1974. Decomposition of salt-marsh grass, Spartina alterniflora Loisel. Limnol. Oceanogr., 19; 825-838.

Hargrave, B.T., 1970. The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. Limnol. Oceanogr., 15; 21-30.

Hargrave, B.T., 1972. Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. Limnol. Oceanogr., 17; 583-596.

Lebedeva, M.N. and G.V. Shumakova, 1969. Reliability of data obtained by the method of direct bacterial count of filters. Microbiology, 38; 293-298.

Luria, S.E., 1960. The bacterial protoplasm: Composition and organization, p. 1-34. In I.C. Gunsalus and R.Y. Stanier (eds.), The Bacteria, v. 1. Academic.

MacGinitie, G.E., 1932. The role of bacteria as food for bottom animals. Science, 76; 490-491.

Mann, K.H., 1972. Macrophyte production and detritus food chains in coastal waters. Mem. Ist. Ital. Idrobiol., 29 suppl.; 353-383.

Meadows, P.S. and J.G. Anderson, 1966. Microorganisms attached to marine and freshwater sand grains. Nature, 212; 1059-1060.

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. Lond., 144; 25-45.

Newell, R.C., 1970. Biology of Intertidal Animals. American Elsevier, New York; 555 p.

Odum, E.P., 1959. Fundamentals of Ecology, 2nd ed. W.B. Saunders, Philadephia.

Oppenheimer, C.H., 1960. Bacteria activity in sediments of shallow marine bays. Geochim. Cosmochim. Acta, 19; 244-260.

Rees, C.B., 1940. A preliminary study of the ecology of a mud flat. Journ. Mar. Biol. Assoc. U.K., 24; 189-199.

Stephen, A.C., 1930. Studies in the Scottish marine fauna; additional observations on the fauna of the sandy and muddy areas of the tidal zone. Trans. Roy. Soc. Edinb., 56; 521-535.

Strugger, S., 1973. Staining Procedures, 3rd ed. The Williams and Wilkina Co., Baltimore; 540 p.

Thorson, G., 1957. Bottom communities. In Treatise on marine ecology and paleoecology. J.W. Hedgpeth (ed.) Geol. Soc. Amer. Mem. 67, 1; 461-534.

Trask, P.D., 1955. Organic content of recent marine sediments. SEPM Sp. Pub. #4; 428-453.

Vassallo, M.T., 1969. The ecology of Macoma inconspicua [=balthica] in Central San Fransisco Bay. Part 1. The vertical distribution of the Macoma community. The Veliger, 11; 223-234.

Wilson, D.P., 1955. The role of microorganisms in the settlement of Ophelia bicornis Savigny. J. Mar. Biol. Assoc. U.K., 34; 531-543.

Wood, E.J.F., 1965. Marine Microbial Ecology. Chapman and Hall, London; 243 p.

ZoBell, C.E., 1938. Studies on the bacterial flora of marine bottom sediments. J. Sedim. Petrol., 8; 10-18.

ZoBell, C.E., 1946. Marine Microbiology. A monograph on Hydrobacteriology. Chromica Botanica Co. Waltham, Mass.; 240 p.

ZoBell, C.E. and C.B. Feltham, 1943. The bacterial flora of a marine mud flat as an ecological factor. Ecology, 23; 69-78.

Zhukova, A.I., 1963. Quantitative significance of microorganisms in the nutrition of aquatic invertebrates. In C.H. Oppenheimer (ed.), Marine Microbiology, Thomas; 730 p.

Zhukova, A.I., and M.V. Fedosov, 1963. The significance of microorganisms of the upper sediment layer in transformation of organic matter. In C.H. Oppenheimer (ed.), Marine Microbiology, Thomas; 730 p.