THE ROLE OF ORGANIC MATTER IN DETERMINING THE DISTRIBUTION OF PELECYPODS IN MARINE SEDIMENTS[1]

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ABSTRACT

Sediments in the region of Mt. Desert Island, Maine, indicate that their organic content and its state of decomposition, as expressed by $L/R_n \times$ T.O. (where L = refractory organics, R_n = nonrefractory organics, and T.O. = total organics), are primary factors in controlling the distribution of sediment-dwelling pelecypods. The relationship of pelecypod population density to the physical characteristics of the sediments and the depth of overlying water are apparently secondary in importance.

INTRODUCTION

Statement of Problem. This research was undertaken to study the relationships of the physical sedimentary characteristics, the organic content of the sediments, and the pelecypod populations of a present-day near-shore marine environment. From the samples collected and from the data obtained during analysis, an attempt is made to show that the relationship between the bottom-dwelling pelecypods and the sedimentary environment is one of dynamic interdependence between physical sedimentary factors, chemical factors, and microbiology, the latter two being of primary importance. The factors quantitatively considered for this project are: water temperature, salinity, and depth, the median diameter of sedimentary particles, the coefficient of sedimentary sorting, the organic content of sediments, the amount of decomposition of organic material, and the total density of the pelecypod population.

Description of Sampling Areas. The relatively shallow waters of bays and sounds in five areas in the region around Mt. Desert Island, Maine, were selected for study. A total of 27 samples from this general region (see Fig. 1) was examined.

Somes Sound (Area I) is a small but typical fjord about 4.5 miles long and 0.8 of a mile wide at its widest point. It gradually deepens

[1] Data taken from a portion of Ph.D. Dissertation, Univ. of Chicago, 1952.

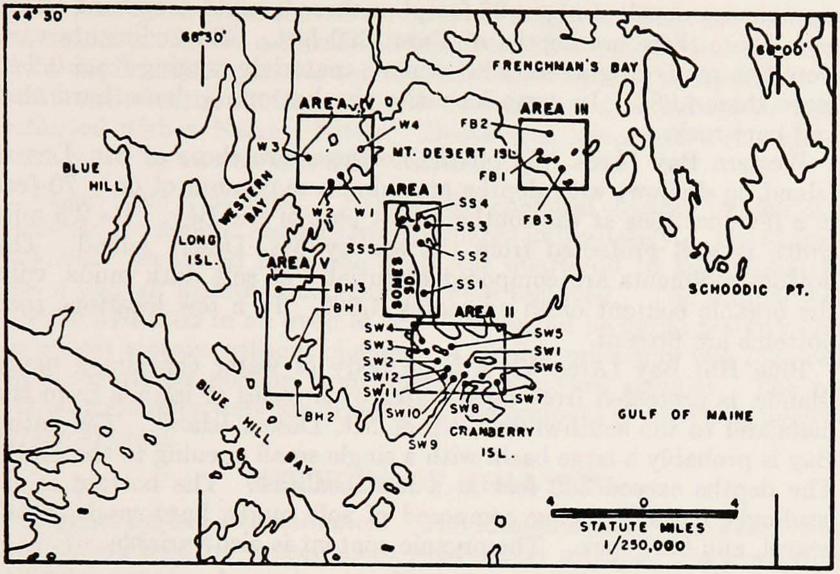

Figure 1. Map of the region of Mt. Desert Island, Maine. The five sampling areas are indicated by the rectangular outlines, the sample locations by the black dots.

southward to a maximum of about 190 feet, then shallows slightly for 0.8 of a mile; the water then shoals from 145 to 30 feet at the sill in 0.6 of a mile. The sides of the Sound are exceedingly steep and at many places the water exceeds 100 feet only a few yards from the western shore. The bottom sediments, except for some rocky and gravelly locations near shore, are essentially dark muds with variable amounts of organic matter ranging from about 1.0 to 8.0%.

Somes Sound opens into a protected bay north of the Cranberry Islands (Area II). Here the water has a maximum depth of about 90 feet, but in most of the bay it ranges between 25 to 50 feet. The deepest portion, probably a small basin, is about one mile southeast of the fjord entrance and 0.2 of a mile south of the northern shore. This bay is protected from open water on the south by the Little and Great Cranberry Islands and a shallow rocky bottom. Eastward it opens into the Gulf of Maine, where the depth gradually increases to 190 feet in about 5 miles. The sediments range from fine muds to gravels, and the organic matter varies from less than 1.0 to more than 3.0%. Many locations have a hard rocky bottom.

Area III, in Frenchman's Bay on the northeastern shore of Mt. Desert Island, is protected from the open part of the Bay by five small islands (Porcupine Islands). In the area sampled, the water attains a maximum depth of about 95 feet, but there is rapid deepening to the east where there are depths of about 300 feet. The sediments vary from fine muds to gravels, with organic materials ranging from 0.5 to more than 4.0%. In some localities the bottom is dense hard clay and bare rock.

Western Bay (Area IV), off the northwestern shore of Mt. Desert Island, is shallow, with depths attaining a maximum of only 70 feet in a few locations at the southernmost part of the Bay. Its 2.5 mile width is well protected from the sea by Mt. Desert Island. The bottom sediments are composed essentially of soft dark muds, with the organic content often exceeding 4.0%. In a few locations rock bottoms are present.

Blue Hill Bay (Area V), a large body of water containing many islands, is protected from open water by a series of islands from the mainland to the southwestern tip of Mt. Desert Island. The entire Bay is probably a large basin with a single small opening to the south. The depths exceed 330 feet in a few localities. The bottom is exceedingly variable, being composed of soft muds, hard muds, sand, gravel, and bare rock. The organic content is also variable.

Field Investigation. Field investigations from July 15 to November 15, 1950 consisted essentially of a general survey of the area, including the collection of samples and their preparation. From the initial survey it became evident that the great abundance of pelecypods would allow a quantitative consideration of population density. Of the 16 species of pelecypods represented, *Nucula proxima*, *Yoldia limulata*, *Y. sapotilla*, *Vernicardia borealis* and *Astarta undata* were the most numerous and widespread.[2]

Methods of Sampling. A box drag was used to obtain samples of the pelecypod populations. This is a rectangular rigid drag (24″ wide, 48″ long, 6″ high) with five sides enclosed by ⅛-inch mesh wire. The drag, towed slowly over the bottom for a period of one minute at a relatively constant speed, proved most effective in both sands and muds since it collected a sample of adequate size and still prevented the loss of smaller mollusks. Upon completion of each drag, one pint of the sediment was separated for sedimentary analysis. The fauna was then removed from the remaining sediment.

A clamshell bucket and an orangepeel bucket were also used. These two samplers of different capacities retrieved smaller amounts of sedi-

[2] The remaining species were: *Crenella decussata*, *Astarta subaecquilatera*, *Pandora glacialis*, *Cerastoderma pinnulatum*, *Huculana tenuisulcata*, *Desinia discus*, *Macoma balthica*, *Laevicardium mortoni*, *Lyonsia hyalina*, and *Salemya velum*.

ment and fewer animals. Two or three samples from each of these instruments allowed a check on the biological sampling technique and gave duplicate samples for sedimentary and chemical analysis.

At each location water samples for salinity determinations were collected with a Nansen bottle. Depth and temperature recordings were made by means of a bathythermograph.

Preparation of Samples. To minimize chemical changes, the samples collected for organic analysis were prepared immediately. The sample originally separated from the drag was quartered to approximately 200 *g* and all macrofaunal remains were removed. The sample was then dehydrated in an oven at 50° C to curtail bacterial activity and to permit storage without change. A similar procedure was followed for a quartered portion from one of the bucket samples. The remaining samples were air-dried after the removal of all living macroscopic animals.

METHODS OF ANALYSIS

Organic Carbon Determination. The total amount of organic carbon was determined by a semimicro combustion method. In general, a weighed sample of powdered sediment was treated with 2% HCl to remove calcium carbonate, after which it was combusted in a measured volume of oxygen under controlled pressure. The carbon dioxide was determined gravimetrically, and the total amount of organic carbon was then computed. The combustion train, with some minor modifications, was constructed on the principles suggested by Pregl (Roth, 1937), Niederl and Niederl (1942), and Piper (1942).

Proximate Organic Analysis. A quantitative determination of the organic suites present in the sediment samples was obtained by running a series of extractions. The first extraction was accomplished by using ether in a soxhlet apparatus to remove nitrogenous fats and waxes, as well as resin-like materials, ethereal oils and fatty oils from both plant and animal material. The sample was then refluxed in 95% ethyl alcohol to remove the alcohol solubles such as waxes, resins, alkaloids, plant pigments, tannins, and phlobophenes. Then the extract was ignited, and the loss in weight represented the amount of alcohol solubles. The temperature of ignition was about 350 to 400° C, but in spite of this low temperature, some inorganic changes probably occurred. A second extraction was achieved with boiling water to remove compounds such as glucose, mannose, sucrose, other sugars, amino acids, some proteins, some organic acids, starches, and pectins. The extract was ignited and the loss in weight represented the water soluble organic matter in the sediments.

Hydrolysis of various portions of the remaining organic constituents in the sediments was performed with hot and cold concentrated acids. The samples were treated with approximately 100 ml of 2% boiling HCl, which hydrolyzed the hemicellulose. The reducing sugars obtained were determined by volumetric analysis with copper sulphate solution (Scales, 1915; Jackson, 1928). The sediment sample was then treated with 80% H_2SO_4 and autoclaved at 15 pounds pressure, thus hydrolyzing the cellulose portion to glucose. Barium chloride was added to the hydrolyzed filtrate in order to precipitate the sulphate. The extract and barium sulphate were dried to constant weight and combusted in the forementioned combustion train to

TABLE I. Sample Data

	Water			*Sediments*			
Sample	*Water depth (ft.)*	*Bottom Temp. (°F)*	*Salinity (°/oo)*	*Median Diameter (mm)*	*Coeff. of sorting (log)*	*Total Organic matter (%)*	*Pelecypod Density*
SS1	85	55	32.5	0.135	0.239	2.30	291
SS2	75	54	32.5	0.017	0.577	0.99	85
SS3	30	54	32.6	0.009	0.620	7.36	0
SS4	33	55	32.6	0.009	0.578	8.85	0
SS5	22	54	32.6	0.007	0.493	7.52	0
SW1	57	54	32.6	0.060	0.631	1.91	470
SW2	27	54	32.6	0.049	0.683	3.55	5
SW3	20	54	32.5	0.105	0.283	1.18	165
SW4	40	54	32.5	0.113	0.476	2.27	21
SW5	52	54	32.5	0.024	0.671	1.89	203
SW6	20	55	32.6	0.275	0.109	0.92	40
SW7	14	54	32.5	0.260	0.094	0.98	48
SW8	35	55	32.6	0.150	0.589	1.28	290
SW9	30	54	32.5	16.800	0.318	1.81	24
SW10	25	54	32.5	0.220	0.093	0.88	142
SW11	20	54	32.5	0.245	0.089	0.74	139
SW12	55	54	32.5	0.078	0.438	3.52	209
FB1	85	50	32.5	0.012	1.260	4.01	72
FB2	87	50	32.5	0.425	0.501	0.51	19
FB3	95	50	32.6	0.055	0.668	2.86	390
W1	8	51	32.5	0.170	0.756	4.18	0
W2	18	50	32.5	0.056	0.812	3.64	0
W3	30	51	32.6	0.009	0.634	3.85	22
W4	70	50	32.5	0.150	0.090	4.26	38
BH1	140	50	32.6	0.227	0.221	0.71	148
BH2	150	51	32.6	0.210	0.141	0.62	32
BH3	75	52	32.6	0.006	1.000	3.49	43

determine the amount of carbon. The cellulose content of the sediment was then computed by applying a factor of 2.49. The steps outlined thus far removed from the sample essentially all of the easily decomposable organic matter.

The final step in the proximate analysis was the determination of the lignin content (the remaining organic matter). Since there is no quantitative method for lignin determination, samples were combusted in the previously mentioned combustion train, and the carbon evolved was multiplied by 1.52 to obtain the amount of lignin or refractory organic matter (Waksman, 1933; Norman, 1937). The total amount of organic matter in each sedimentary sample was then determined by the sum of all of the proximate parts.

Sedimentary Size Analysis. Since all of the bottom samples contain particle sizes ranging from sand to fine clay, the size of the sand particles was determined with sieves while the silt and clay sizes were determined by pipette analysis of a dispersed suspension of the sediment in water (Krumbein and Pettijohn, 1938).

Salinity Determination. The salinity of the water overlying the sediments was determined volumetrically by standard methods (Oxner, 1920; Furman, 1939).

THE PHYSICAL, CHEMICAL, AND BIOLOGICAL RELATIONS

In the 27 samples considered, the water depth ranged from 8 to 150 feet and the median diameter of the sedimentary particles varied from 0.006 to 4.250 mm; one sample had a median diameter of 16.80 mm. The log of the coefficient of sorting[3] ranged from 0.089 to 1.260, and the organic content fluctuated from 0.51 to 8.85%. There was also a wide range in the pelecypod densities, from 0 to 470 individuals per sample. Temperature and salinity exhibited only slight differences.

The pelecypod population, as used in this discussion, refers to the total density of pelecypods, including all species. This procedure was followed because the species of pelecypods which are abundant enough to consider individually show the same general trends as the total pelecypod population. The investigation did not show any major ecological hiatus to the exclusion of one or more species.

Water Depth, Sedimentary Characteristics, and Organic Matter. Before we consider the biological aspects, it is first necessary to consider briefly the various physical relationships and organic content of the

[3] "Coefficient of sorting" is a sedimentary expression for the geometric quartile deviation, i.e., $QD_g = \sqrt{Q_3/Q_1}$ (Krumbein and Pettijohn, 1938).

sediments (see Table I). The median diameter of the sediments and the depth of overlying water gave evidence of a gross decrease in median diameter with increase in water depth.

There was a decrease in the coefficient of sorting with an increase in the median diameter, i.e., the greater the particle size the better the sorting. There were no sediments that had a median diameter of less than 0.10 mm and a sorting coefficient of less than 0.40. Only two samples displayed a median diameter of 0.20 mm or greater with a sorting coefficient that exceeded 0.22.

A poor relationship exists between the total organic content of the sediments and the depth of the water. Despite the wide scatter of points, the median diameter of the sediment generally decreased as the amount of included organic material increased. Only three samples with a median diameter of more than 0.135 mm contained more than 1.50% organic matter, and one sample with a median diameter of less than 0.05 mm contained only 0.99% organic matter. In general, of the size ranges encountered in the samples, the extremely small-size sediments had large amounts of organic matter, the extremely large-size sediments smaller amounts.

Pelecypod Density, Water Depth, Temperature, and Salinity. Fig. 2A shows water depth and total pelecypod density for each sample, and it is apparent that there is no significant linear correlation. It does seem possible, however, that there may be at least a gross increase in the populations per sample as the depth increases. If this is so, it is not consistent, since the group of five points at a water depth of about 80 feet have pelecypod densities of under 100 individuals.

When considering the work of Verrill (1874) and the literature summarized in Allee, *et. al.*, (1949), one expects to find a relationship between animal density and depth of water. If such a relationship does exist in these samples, it is a vague one and is strongly affected by some other significant factor or factors. Because of the small variations in salinity (0.2 $^{\circ}/_{\circ\circ}$) and temperature (4° F), no relationship is apparent between these two factors and the pelecypod populations. Probably the tolerance limits for salinity and temperature have not been surpassed.

Pelecypod Density and Physical Character of the Sediments. The relationship between pelecypod density and median diameter of the sedimentary particles is shown in Fig. 2B. Except in one instance, samples with pelecypod densities greater than 200 individuals fell within a median diameter range of 0.05 to 0.15 mm. Pelecypod densities of less than 100 (with one exception) were correlated with particles of exceedingly small median diameters (less than 0.025 mm), essentially

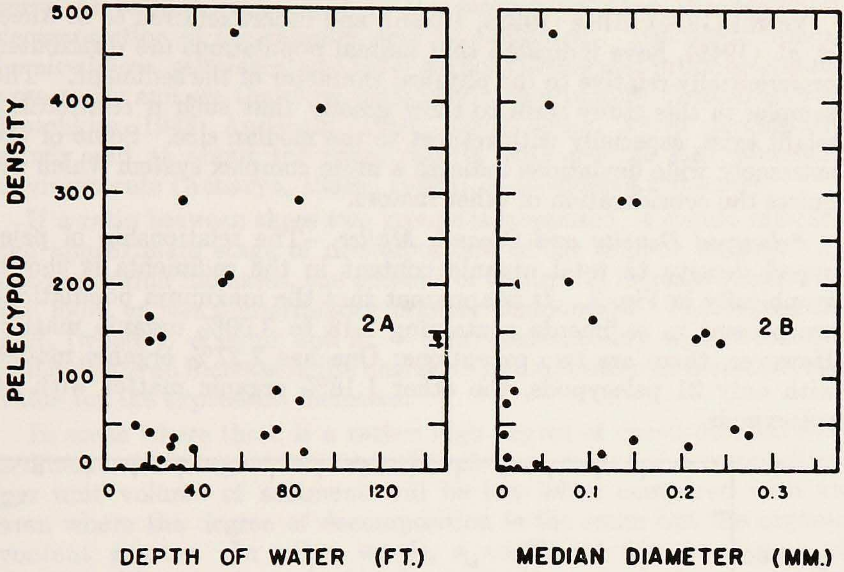

Figure 2A. Relationship between density of pelecypod populations in the sediments (from 0 to 500 individuals) and depth of water at the sample locations. 2B. Relationship between density of pelecypod populations and median diameter of sedimentary particles.

silt and clay. When the median diameter exceeded 0.20 mm, all samples had less than 150 pelecypods. It must be noted, however, that two samples with median diameters of about 0.05 mm contained 0 and 5 individuals, while the two samples containing the greatest number of pelecypods (over 350) also had median diameters of about 0.05 mm. Despite this wide discrepancy, there appears to be an over-all potential toward an increase in pelecypod density as the median diameter decreases and approaches the range of 0.15 to 0.05 mm; beyond this, and toward the extremely fine sizes, there is a sharp drop in the densities. Granted there is an extremely wide scatter of points, but such a relationship is apparent.

There is no obvious correlation between the coefficient of sorting and the pelecypod population. Samples with coefficients between 0 and 0.2, indicating good sorting, had pelecypod densities from 0 to 139. Samples with coefficients of 0.2 to 0.4 (normal sorting) had pelecypod densities between 0 and 291 individuals. When the sorting coefficient increased to 0.6 and 0.8 (poor sorting), the pelecypod density varied from 0 to 470 individuals. The above data suggest that the range in pelecypod densities may increase as the sorting of the sediment gets poorer.

Verrill (1874), Allee (1923a, 1923b), and others referred to in Allee, *et. al.* (1949), have indicated that animal populations are distributed preferentially relative to the physical character of the sediment. The samples in this study seem to show grossly that such a relationship might exist, especially with respect to the median size. Some of the extremely wide deviations indicate a more complex system which requires the consideration of other factors.

Pelecypod Density and Organic Matter. The relationship of pelecypod density to total organic content in the sediments is shown graphically in Fig. 3. It is apparent that the maximum populations are present in sediments containing 1.18 to 3.00% organic matter. However, there are two exceptions: One has 2.27% organic matter with only 21 pelecypods, the other 1.18% organic matter with 24 pelecypods.

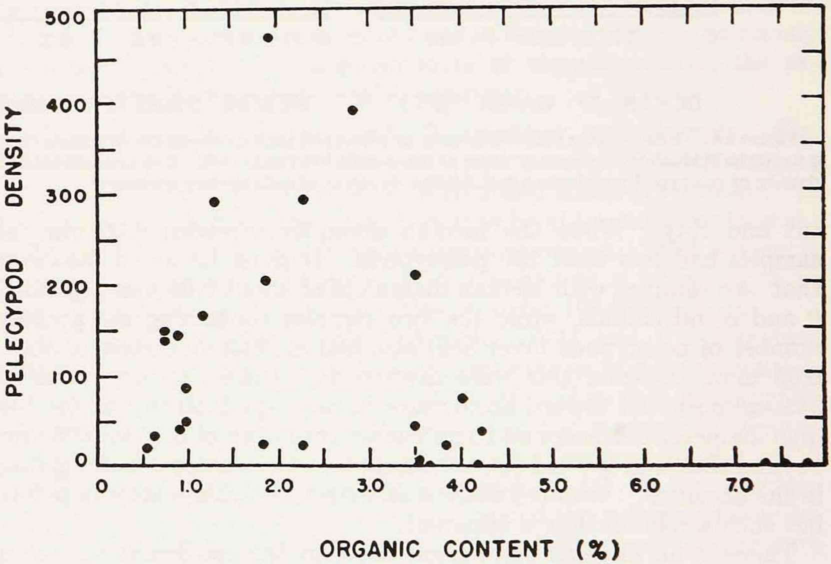

Figure 3. Relationship between density of pelecypod populations and organic carbon content (wt. %) of the sediments. (Note the curvilinear character of the plots when the two samples at about 2% organic material and 20 pelecypods are not considered.)

The next point to consider is the decomposition of the organic matter in the sediments. If the type of organic material is known (Norman, 1937), then it is possible to determine the stage or degree of decomposition. If it is assumed or known that the supply of organic matter in various locations contains the different types of suites of organic compounds in the same ratio, then the degree of decomposition of the samples may be compared. The lipids, resins, hemicellulose, celluloses, and other carbohydrates and proteins decompose easily and are therefore considered nonrefractory (Waksman and Hotchkiss, 1938; Anderson, 1940), while lignin, which decomposes slowly and at about the same rate in both aerobic and anaerobic environments (Acharya, 1935a, 1935b), is considered refractory.

If a ratio between these two groups is computed, it should indicate the approximate stage of decomposition of the organic matter. As decomposition increases, the amount of lignin will increase relative to the more or less nonrefractory organic compounds. The expression L/R_n (where L = lignin and R_n = total nonrefractory organic matter) will indicate an increase in the degree of decomposition as the numerical value for the expression increases.

In areas where there is a rather high degree of decomposition in a sediment of low organic content, the relative amount of decomposition per unit volume of sediment will be low when compared with an area where the degree of decomposition is the same but the organic content greater. In other words, a coefficient for the degree of decomposition is dependent only upon the actual decomposition, while a coefficient for the amount of decomposition is dependent also upon how much organic matter is available. Therefore, the expression L/R_n, representing the degree of decomposition, has been altered to take into consideration the total amount of organic matter present. The coefficient of the amount of decomposition which has gone on in a unit volume of sediment is represented by the expression $L/R_n \times$ T.O. (where T.O. = total organic content of sample).

Before use can be made of the determined value of the coefficient for the amount of decomposition in each sample, it must be assumed that the over-all ratio of refractory to nonrefractory organic compounds in the organic supply must remain relatively constant though the total amount of organic matter being supplied to the sediments (from whatever source) may vary greatly. If this assumption is fulfilled, then the decomposition coefficient for each sample may be compared with that of other samples. In Fig. 4A the relationship of the decomposition coefficient of organic matter in the sediment is plotted against the pelecypod density. Except for one sample, all of those with a coefficient exceeding 1.0 have pelecypod densities of less than 48 individuals. In view of the sharp break shown in Fig. 4A at a decomposition coefficient of 1.0, a comparison is made between the pelecypod density and the organic content of sediment having a coefficient of 1.0 or less. Fig. 4B clearly indicates an increase in pelecypod density with an increase in organic content. It is also worth noting here that, upon consideration of this decomposition factor, the two exceptions of low pelecypod density in samples of optimal organic content have been eliminated (see Fig. 3).

TABLE II. Coefficient of Decomposition

Sample No.	*Nonrefractory organic matter** (%)	*Refractory organic matter†* (%)	*Coefficient of amount of decomposition‡*
SS1	1.71	0.59	0.79
SS2	0.74	0.25	0.34
SS3	3.14	4.22	9.86
SS4	5.08	3.77	6.57
SS5	3.62	3.90	8.10
SW1	1.32	0.59	0.85
SW2	2.54	1.01	1.42
SW3	0.90	0.28	0.36
SW4	0.98	1.29	2.96
SW5	1.28	0.61	0.90
SW6	0.64	0.28	0.41
SW7	0.67	0.31	0.53
SW8	0.80	0.48	0.78
SW9	0.70	1.11	2.88
SW10	0.54	0.34	0.55
SW11	0.62	0.12	0.14
SW12	2.45	1.07	1.53
FB1	3.51	0.50	0.57
FB2	0.36	0.15	0.20
FB3	2.12	0.74	0.99
W1	2.55	1.63	2.68
W2	2.11	1.53	2.62
W3	1.89	1.96	3.98
W4	2.06	2.20	4.54
BH1	0.57	0.14	0.18
BH2	0.51	0.11	0.14
BH3	1.58	1.91	4.20

* Sum of ether, alcohol, and water extracts plus hemicellulose and cellulose.
† Lignin and lignoproteins.
‡ $L/R_n \times$ T.O. (L = refractory organics; R_n = nonrefractory organics; T.O. = total organics).

DISCUSSION AND CONCLUSION

Consideration of the organic material in the sediments permits a clarification of the interdependence of environmental factors as related

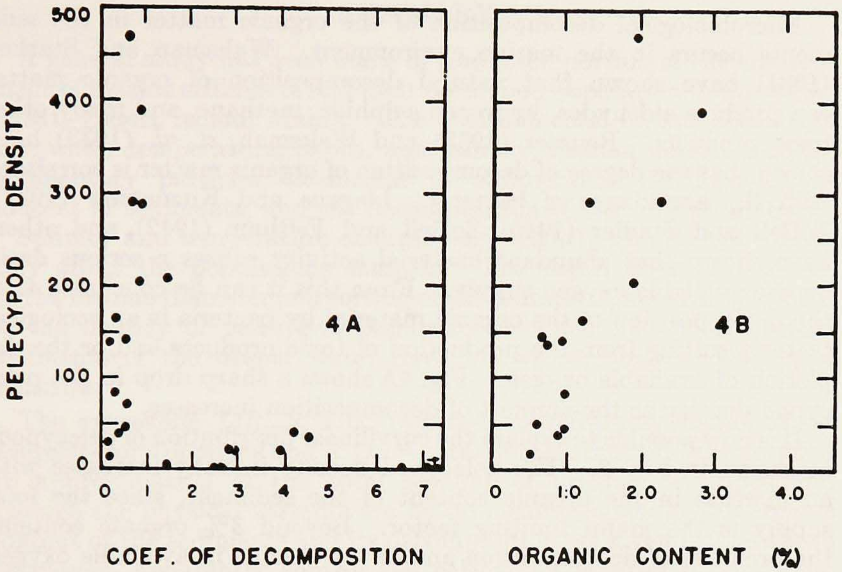

Figure 4A. Relationship between density of pelecypod populations and decomposition coefficient as determined by $L/R_n \times$ T.O. 4B. Relationship between density of pelecypod populations and organic carbon content (wt. %) of the sediments in samples having a decomposition coefficient of less than one.

to pelecypod densities. In undertaking any explanation of the apparent curvilinear distribution of pelecypods in relation to organic matter, it is necessary to consider (1) the feeding habits of the animals, (2) the abundance of food, and (3) the state of decomposition of the food supply.

According to the work of Petersen (1913), Blegvad (1915), and Jensen (1915), many pelecypods use the organic matter in the sediments as a food source. Mitsukuri (1881) and Drew (1899) showed that the palp appendages of the genus *Nucula* and *Yoldia* are functional in scooping up sedimentary detritus during the process of ingestion. In view of this it shall be considered that the organic matter in the samples studied is a primary source of pelecypod nutrition.

The abundance of food naturally affects the potential pelecypod population. If the food supply increases, the population has the potential to increase so long as the food supply is the major limiting factor. Fig. 4B shows an unmistakable increase in pelecypod population as the food supply (i.e., organic matter) increases.

Microbiological decomposition of the organic matter in the sediments occurs in the marine environment. Waksman and Starkey (1931) have shown that natural decomposition of organic matter can produce aldehydes, hydrogen sulphide, methane, and many other toxic products. Reuszer (1933) and Waksman, *et. al.* (1933) have shown that the degree of decomposition of organic matter is correlated with the abundance of bacteria. Liagena and Kuznetzow (1937), ZoBell and Stadler (1940), ZoBell and Feltham (1942), and others have shown that abundant bacterial activity causes a serious drain on the available oxygen supply. From this it can be concluded that the decomposition of the organic material by bacteria is an ecological factor resulting from the production of toxic products and/or the depletion of available oxygen. Fig. 4A shows a sharp drop in the pelecypod density as the amount of decomposition increases.

It is now possible to explain the curvilinear distribution of pelecypods as shown in Fig. 3. The pelecypod density initially increases with an increase in the organic content of the sediment, since the food supply is the major limiting factor. Beyond 3% organic content, the products of decomposition and/or the decline in available oxygen become the limiting variables, and the population decreases. The two exceptions to the curvilinear distribution as shown in Fig. 3 (those with optimum organic contents and low pelecypod densities) support the above contentions; they have decomposition coefficients of 2.88 and 2.96. The rest of the samples in the optimal range of organic content (1.18 to 2.86%) have decomposition coefficients of less than 1.00. The organic matter in these two samples is decomposed to a far greater extent and the population is thus kept at a minimum.

In reality the apparent curvilinear distribution of pelecypod densities represents a composite of the controlling aspects of physical, chemical and microbiological environmental factors. It has been shown that there are some gross correlations between organic content and the physical factors considered. The pelecypod density and the physical characteristics also show some gross relationships. The obvious correlation between pelecypod density and organic considerations makes it apparent that the most important pair of variants is the organic content and its state of decomposition.

The data obtained during this study indicate that greater detail in the determination of ecological variants may be exceedingly profitable. The consideration of micro variants such as bacterial flora, the specific organic chemical compounds, the source of these compounds, the type, rate and amount of decomposition, and many others may develop a clearer understanding of the over-all environment and its relationship to the animal population.

SUMMARY

A general study has been made of a selected portion of the environment of marine sediments and their pelecypod population in the region of Mt. Desert Island, Maine. The environmental factors considered are: water temperature, depth, and salinity, median diameter of the sedimentary particles, coefficient of sedimentary sorting, organic content of sediments, and the decomposition of the organic material.

Salinity and temperature changes vary slightly and do not noticeably affect the populations sampled. The depth of water, as well as the median diameter and sorting of the sediments, are grossly related to the density of pelecypod populations. Finer and poorly sorted sediments of the deeper water have the widest range of pelecypod densities.

The expression $L/R_n \times$ T.O. (where L = refractory lignin, R_n = nonrefractory organics and T.O. = total organic matter) is considered an approximation of the total amount of organic decomposition. Though the physical variants are by no means negligible, the organic content of the sediments and its decomposition, as given by the above expression, apparently control the pelecypod densities of any area. As the organic content (food supply) increases, the pelecypod population increases until bacterial decomposition of the organic material becomes the major limiting factor; then the population decreases.

ACKNOWLEDGEMENTS

The writer is indebted to Dr. H. A. Lowenstam for his suggestions, cooperation, material aid, and interest in this project. Drs. E. C. Olson, F. J. Pettijohn, J. M. Weller, and R. L. Miller gave freely of their time for suggestions and constructive criticism. Appreciation is also extended to Drs. H. C. Urey, S. Epstein, J. L. Hough, B. R. Speicher, and to Mr. N. T. Allen. Thanks are due Messrs. A. Bunker, J. Somes, T. Higgins, and C. Brown of Mt. Desert Island, Maine, and Mrs. M. Bader.

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