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Sediment – animal – water interaction, Buzzards Bay, Massachusetts

by Egbert G. Driscoll¹

ABSTRACT

Four stations in the northwestern part of Buzzards Bay, Massachusetts, were monitored from October, 1971 to November, 1972. Nitrogen, non-carbonate carbon, total organics and carbonate of the sediment were examined. Dissolved oxygen, salinity, temperature and pH of the bottom water were determined concurrently.

Characteristics of sediments, benthic animals and bottom water are all interrelated in Buzzards Bay. Seasonal variations in the organic content of the sediment are due largely to variations in the standing crop of benthic microorganisms. The standing crop of deposit feeders is, in part, controlled by the abundance of microorganisms. Bioturbation and fecal formation by deposit feeders result in increased surface area for colonization by microorganisms. Biodeposits further represent a readily available nutrient source for such organisms. It is suggested that a feedback relationship exists, increasing microorganisms resulting in increasing deposit feeder abundance. The latter, through bioturbation and biodeposition, produce an environment suitable for increasingly abundant microorganisms. The rate of this feedback is temperature dependent.

Both the dissolved oxygen and the pH of the bottom water are, in part, dependent upon characteristics of the sediment. Lower pH and dissolved oxygen values occur over fine grained, organic rich sediments than above coarse grained, organic poor sediments. This is, presumably, due to the higher biological and chemical oxygen demand of fine sediments and to the fecal deposition by deposit feeders which is associated with such sediments.

1. Introduction

Interactions between bottom water, sediments and the benthos have been investigated by many workers. Such efforts have been reviewed by Mare (1942), Trask (1955), Hayes (1964), Jørgensen (1966), Thorson (1966), Postma (1967), Newell (1970), Rhoads (1974) and others. In Buzzards Bay, Massachusetts, a considerable effort has been devoted to studies of various aspects of the benthic fauna (Sanders, 1958, 1960; Weiser, 1960; Driscoll, 1967; Rhoads and Young, 1970; Levinton and Bambach, 1970, 1975; Driscoll and Brandon, 1973; Driscoll and Swanson, 1973), the water column (Peck, 1896; Fish, 1925; Anraku, 1964; Pearce, 1969), and the sediment (Hough, 1940; Moore, 1963; Rhoads and Stanley, 1965; Rhoads, 1970). The present effort involves an examination of certain interactions between the benthic

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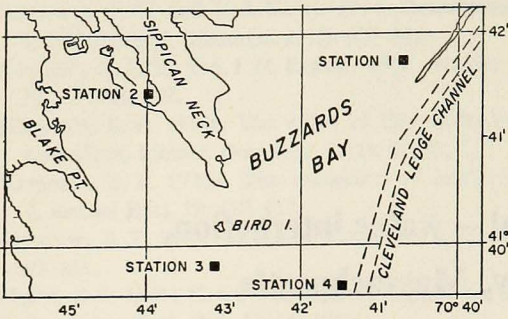


Figure 1. Index map of northwestern Buzzards Bay.

The four monitored stations are indicated.

fauna, the bottom water and the sediments of Buzzards Bay. In particular, the origin and annual variation of organic material in the sediment is investigated. The effect of increases in sedimentary organics upon deposit feeder abundance during the summer is discussed. It is suggested that bioturbation of sediments and fecal production by deposit feeding infauna are both involved in important feedback mechanisms determining benthic organic production. Organic content of the sediment is indicated to be a significant factor in the control of dissolved oxygen concentration and pH of bottom water immediately overlying the sediment. The results of a seven month study of the biodeposition of four selected invertebrate species are utilized to interpret the importance of feces and pseudofeces in the annual variation of sediment organic content.

2. Study area

Four stations characterized by diverse sediment types and depths from 0.9 to 12.5 m were selected in northwestern Buzzards Bay (Fig. 1). Stations 1, 2 and 3 were identical to those examined by Driscoll and Swanson (1973) in a study of the structure of epifaunal communities colonizing dead bivalve shells. Station 4 was selected in fine, offshore sediments to provide a larger spectrum of sediment types. Various physical and chemical parameters are indicated in Table 1.

Stations 1 and 3 are located in sediments typical of the *Ampelisca* spp. community of Sanders (1958, 1960) and the open bay facies of Driscoll and Brandon (1973). Stations 2 and 4 are in sediments which support the *Nucula proxima-Nephtys incisa* community (Sanders' 1958, 1960). Station 2 represents the nearshore facies, and station 4, the offshore facies of Driscoll and Brandon (1973).

The textural, mineralogical and geochemical classification of Moore (1963) defines four major facies types in Buzzards Bay. Three of these are represented by the stations examined here. Stations 2 and 4 are located in protograywacke, station 3 in feldspathic sand, and station 1 in sediments intermediate between quartzose sand and mixed rock type gravels (Moore, 1963).

Return to station was accomplished through land fixes. Divers commonly encountered evidence of experimental work carried out earlier by Driscoll and Swanson (1973) at stations 1, 2 and 3. It is estimated that a single station includes an area not exceeding 50 m in diameter.

Table 1. Various physical and chemical parameters of the substrate and bottom water at four stations in northwestern Buzzards Bay, Massachusetts. Mean annual values refer to the data points indicated in figures 2, 3 and 4. Mean ranges of replicate samples are indicated in parentheses.

	Station number			
	1	2	3	4
Mean Grain Diameter (phi)	0.91	3.38	1.66	4.26
Standard Deviation of Grain Diameter	1.45	1.37	0.94	0.96
Mean Annual Total Organics (%)	0.48 (0.14)	2.20 (0.49)	0.58 (0.16)	3.20 (0.65)
Mean Annual Organic Carbon (%)	0.11 (0.08)	0.90 (0.30)	0.13 (0.05)	0.97 (0.24)
Mean Annual Organic Nitrogen (%)	0.027 (0.027)	0.060 (0.022)	0.026 (0.023)	0.147 (0.019)
Mean Annual Carbonate (%)	3.91 (0.90)	6.61 (1.81)	4.12 (1.00)	11.44 (2.04)
Depth (m)	4.6	0.9	7.0	12.5
Mean Annual Dissolved Oxygen (mg l^{-1})	9.18 (0.08)	9.20 (0.06)	8.66 (0.05)	8.33 (0.09)
Mean Annual pH	7.91 (0.08)	7.87 (0.09)	7.89 (0.02)	7.84 (0.07)

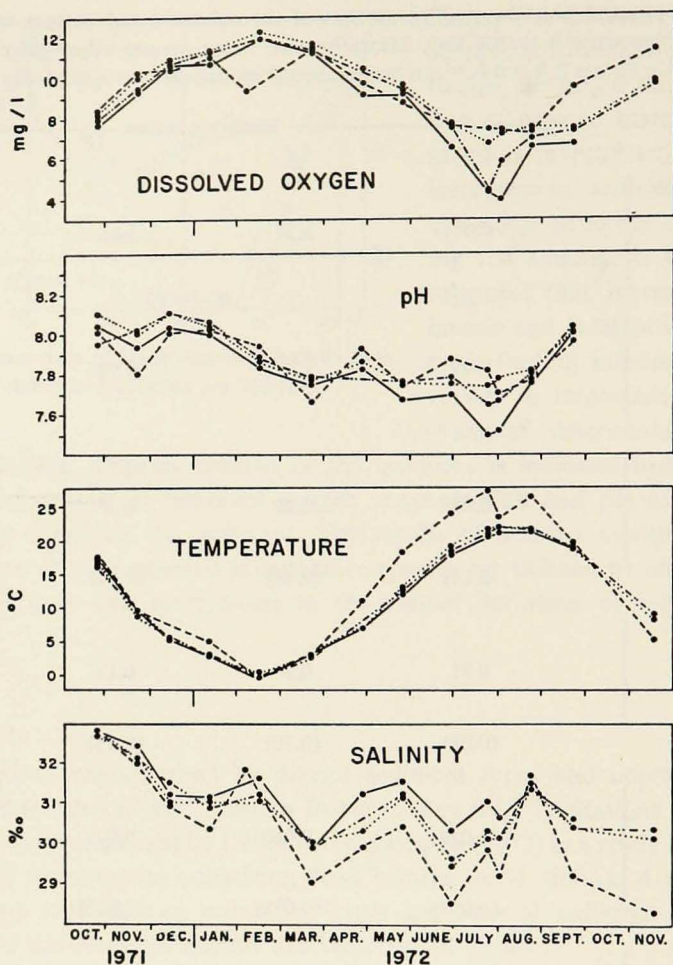


Figure 2. Bottom water characteristics at four stations in northwestern Buzzards Bay from October, 1971 to November, 1972. Dashes indicate sta. 2 (depth = 0.9 m); dots indicate sta. 1 (depth = 5.6 m); dots and dashes indicate sta. 3 (depth = 7.0 m); solid line indicates sta. 4 (depth = 12.5 m).

3. Materials and methods

Data were derived from: 1) periodic bottom water samples, 2) periodic sediment samples, and 3) laboratory experiments concerning the biological oxygen demand and fecal production of selected invertebrates. Stations were sampled as indicated in Figs. 2, 3 and 4.

a. Bottom water samples. Techniques for obtaining water samples immediately adjacent to the bottom have been discussed by Smith (1971), Kemp *et al.* (1971), and Joyce (1973). The present samples were collected by divers utilizing a simple

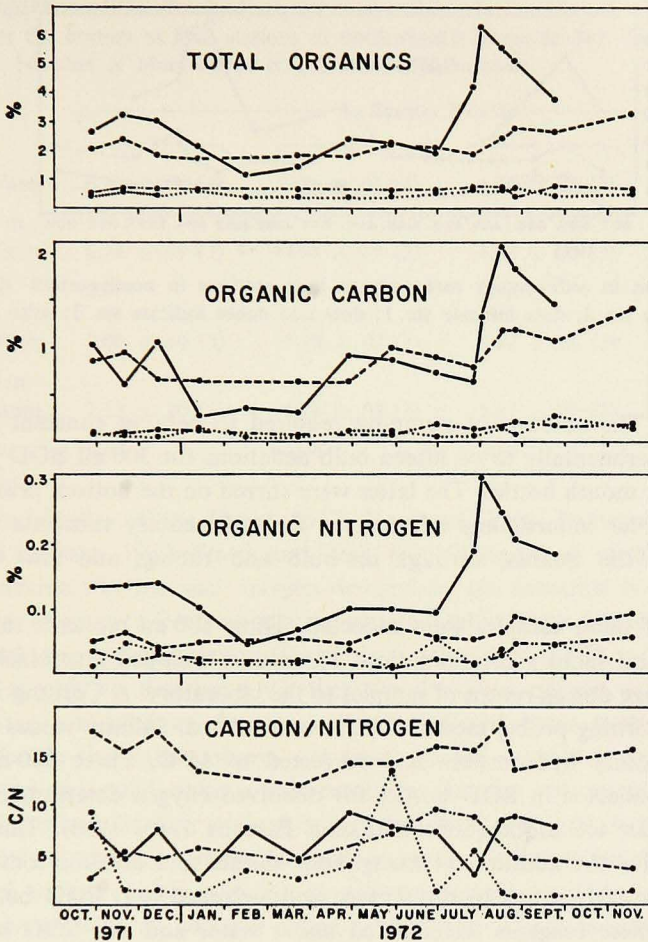


Figure 3. Sediment characteristics at four stations in northwestern Buzzards Bay from October, 1971 to November, 1972. Dashes indicate sta. 2 (depth = 0.9 m); dots indicate sta. 1 (depth = 5.6 m); dots and dashes indicate sta. 3 (depth = 7.0 m); solid line indicates sta. 4 (depth = 12.5 m).

and inexpensive hand operated device (Driscoll, 1972). This sampler consists of two 30 cm² boards separated by a distance of 1 cm. Rubber tubing extends from a hole in the center of the upper board to a hand operated bulb pump equipped with two one-way valves. Additional tubing leads from the bulb to the sample bottle.

In operation, the diver placed the device on the sediment surface and exercised care not to disturb the bottom. The diver maintained himself in a down current direction, so as not to disturb the sediment. The hand bulb was pumped several times to replace water trapped between the boards during descent. Rubber tubing was fed into the mouth of a sample bottle which had been filled previously with surface water, and pumping was continued until all surface water was replaced by

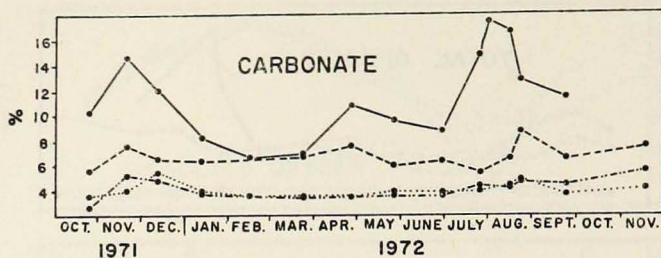


Figure 4. Variation in sedimentary carbonate at four stations in northwestern Buzzards Bay. Dashes indicate sta. 2; dots indicate sta. 1; dots and dashes indicate sta. 3; solid line indicates sta. 4.

bottom water. The amount of pumping required to achieve constant values was determined experimentally to be fifteen bulb deflations for 300 ml BOD bottles and for 500 ml wide mouth bottles. The latter were stirred on the bottom prior to pumping. Bottom water immediately adjacent to the sedimentary substrate was drawn gently between the boards, through the bulb and tubing, and into the sample bottle.

Two types of water samples were collected. Three 500 ml replicate samples were taken for pH and salinity determination. These were pumped into black bottles to inhibit pH change during return of samples to the laboratory. A Corning model 7 pH meter with a Corning probe, model 476051, was utilized. Salinity values were determined with salinity hydrometers and corrected to 15°C. Three 300 ml replicate samples were collected in BOD bottles for dissolved oxygen determinations by the modified Winkler technique (Strickland and Parsons 1965, 1968). This technique normally requires the addition of manganous sulfate and alkaline iodide reagents after the sample is returned to the surface and siphoned into BOD bottles. In the present study these reagents were added under water and the BOD bottles were sealed prior to return to the surface. Measured amounts of the reagents were carried in disposable hypodermic syringes. Leakage was avoided by insertion of the syringe points into rubber tubing which was attached to a sample carrier similar in design to that of Fager *et al.* (1966). The latter was used for the transport of sample bottles by the diver. Both reagents are heavier than water and do not escape from BOD bottles following injection on the bottom. Comparison of this technique with the standard practice of adding manganous sulfate and alkaline iodide reagents on the surface after the sample has been siphoned into a BOD bottle was undertaken. Utilizing boiled sea water the present technique resulted in a mean value of 2.06 ml l⁻¹ (s = .03) whereas standard techniques applied to the same water yielded a mean of 2.21 ml l⁻¹ (s = .04). Techniques utilized here avoid atmospheric contamination.

It has been demonstrated by many workers that the biological and chemical oxygen demand of various sedimentary substrates can be measured in closed systems

Table 2. Comparison of the dissolved oxygen concentration in the bottom water and in water 0.5 m above the bottom at four stations in northwestern Buzzards Bay. Dissolved oxygen is in mg l^{-1} . Number of observations is indicated in parentheses.

		Station Number			
		1	2	3	4
July 25, 1972	Bottom Water	$6.70 \pm .09$ (3)	$7.29 \pm .02$ (3)	$4.03 \pm .07$ (3)	4.33 — (2)
	Water 0.5 m above bottom	$6.77 \pm .09$ (3)	$7.28 \pm .07$ (3)	$4.15 \pm .05$ (3)	$4.46 \pm .03$ (3)
	Difference	0.07	0.01	0.12	0.13
Aug. 1, 1972	Bottom Water	$7.09 \pm .10$ (3)	$7.20 \pm .02$ (3)	$5.87 \pm .08$ (3)	$3.97 \pm .09$ (3)
	Water 0.5 m above bottom	$7.13 \pm .10$ (3)	$7.28 \pm .03$ (3)	$5.97 \pm .09$ (3)	$4.03 \pm .10$ (3)
	Difference	0.04	0.08	0.10	0.06

(Edwards and Rolley, 1965; Carey, 1967; Hargrave, 1969; Pamatmat, 1971, 1973; Edberg and Hofsten, 1973; Smith and Teal, 1973). One aspect of the present study was to determine whether such oxygen demand by the substrate is reflected in the bottom water of an open freely circulating system. Only a limited effort has previously been directed toward this question (Richards and Redfield, 1953).

It was desirable to determine whether the dissolved oxygen concentrations of bottom water, collected as described above, differed from such concentrations slightly higher in the water column. On two separate occasions, comparisons were made between dissolved oxygen concentrations on the bottom and those 0.5 m above the bottom at the four stations being considered (Table 2). In all but one case, bottom water values were lower. The single exception indicates equal concentrations of dissolved oxygen above and at the sediment-water interface. Comparison of oxygen concentrations on the two different sampling occasions indicates a lack of uniformity. At station 2, for example, the difference between values obtained above, and at, the sediment surface, is only .01 mg l^{-1} on July 25 but is .08 mg l^{-1} on August 1. Other stations show comparable variations on different days.

This inconsistency led to examination of the possibility that dissolved oxygen concentrations in the bottom water vary through a tidal cycle. The presence of such variation could account for the data in Table 2.

A single station was chosen for examination. For logistical reasons this station is not one of those which were monitored throughout the year. The new station, located in Great Harbor, adjacent to Woods Hole, Massachusetts, is approximately 2.5 m deep and is characterized by a mud bottom with a high organic content. Data collected at various intervals for eleven hours indicate that the dissolved oxygen concentration in the bottom water may vary in excess of 1.0 mg l^{-1} during this period of time (Fig. 5). The mean dissolved oxygen concentration of the bottom water throughout this eleven hour period was .04 mg l^{-1} less than that of water

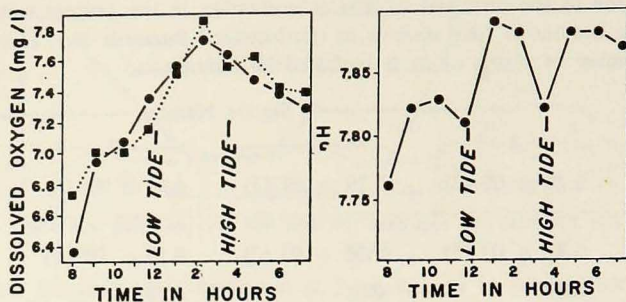


Figure 5. Variation in dissolved oxygen and pH of bottom water and water 0.5 m above the bottom in Great Harbor, Massachusetts, during an eleven hour period. Squares indicate values 0.5 m above the bottom. Note that the pH values of the bottom water are reduced during the periods of slack water associated with high and low tide.

0.5 m above the bottom. However, the concentration of dissolved oxygen in the bottom water occasionally exceeds that of water 0.5 m above the bottom.

Variation in the pH of bottom water was also examined during this tidal cycle study. The range of values is in excess of 0.1. The pH of the bottom water decreased during periods of slack water associated with high and low tides (Fig. 5).

Detailed examination of hourly variations in dissolved oxygen and pH of the bottom water is beyond the scope of the present study. Factors such as photosynthetic activity, turbidity, wave action and composition of the substratum are probably involved. The present effort indicates only that short term changes may account for the differences in the variation between bottom water 0.5 m above the bottom observed on separate days (Table 2).

b. Sediment. Three replicate disposable petrie dish samples (Howard and Henry, 1966) were collected by divers at each station at the same times as the water samples. These were dried at 105°C and homogenized prior to analysis. No attempt to remove the macrofauna was undertaken prior to homogenization.

Per cent carbonate was determined by weight loss following digestion in dilute HCl. Seisser and Rogers (1971) have evaluated various methods of carbonate analysis and conclude that this technique yields only rough approximations of the true carbonate value in marine sediments, particularly if small sample sizes are utilized. Roberts *et al.* (1973) indicate that a portion of the organic carbon is lost in solution utilizing this technique. All of the present samples were large and were analyzed for carbonate at a single time. Identical acid concentrations and solution intervals were used for all samples. The carbonate and organic data presented here are internally consistent.

Total organic content of the sediment was determined on carbonate free samples by combustion to constant weight at 550°C. Carbon and nitrogen analyses were carried out on a Coleman Carbon-Hydrogen Analyzer, Model 33, and a Coleman

Nitrogen Analyzer, Model 29B. Such carbon and nitrogen values are considered to represent organic carbon and organic nitrogen (Russel-Hunter, 1970; Winberg, 1971). Stevenson (1962) has suggested that nitrogen measurements of this kind may, in part, reflect ammonia contained in the lattice structure of clay minerals.

c. Oxygen demand and fecal production. The goal of this aspect of the work was to examine changes in the oxygen demand and biodeposition rates by selected invertebrates throughout the year. The data indicates the general magnitude of such changes under conditions of temperature, food supply and salinity which approximate conditions in the study area at any given time. Evaluation of the individual significance of changes in the various environmental parameters which affect oxygen demand and biodeposition was not attempted.

Four suspension feeding species were examined on five separate occasions between the coldest and warmest water temperatures of 1972 (Feb.-Aug.). On each occasion approximately twenty individuals of *Mya arenaria*, *Mytilus edulis* (bivalves), *Crepidula fornicata* (gastropod) and *Ciona intestinalis* (Ascidian) were acclimated for forty-eight hours to circulating salt water tanks at the Marine Biological Laboratory, Woods Hole, Massachusetts. Equal current flow over different parts of the $1.3 \times 0.7 \times 0.1$ m (90 l) tanks was maintained by a series of baffles in order to ensure comparable food supply and oxygenation to all specimens. A constant flow rate in excess of 250 l per hour was maintained. Single determinations of oxygen demand were made during the morning, afternoon and evening of a single day on all specimens. Such determinations involved enclosing specimens in 16 oz. water filled jars resting in a submerged position in the circulating tanks for one hour. Water samples were removed from the jars and modified Winkler titrations (Strickland and Parsons, 1965, 1968) were employed in the determination of dissolved oxygen concentration. Oxygen consumption by the invertebrates was estimated by difference from blanks which were run concurrently.

Fecal production (including the production of pseudofeces) was evaluated during three separate twenty-four hour periods utilizing the same specimens which were employed in the oxygen demand studies. Individuals were placed in open, two liter bowls which were submerged in the circulating salt water tanks. Biodeposits produced during each twenty-four hour period were collected with a suction device, filtered, dried and weighed. Initially, controls were run to determine the amount of non-fecal sedimentation from the water column. However, because the biodeposits were concentrated in small piles within bowls, they and natural sediments could be separated mechanically. Tissue weights were determined following drying at 100°C for twenty-four hours.

4. Results

Annual changes in dissolved oxygen, pH, temperature and salinity of the bottom water are illustrated in Fig. 2. Comparable values for total organics, carbon, nitrogen

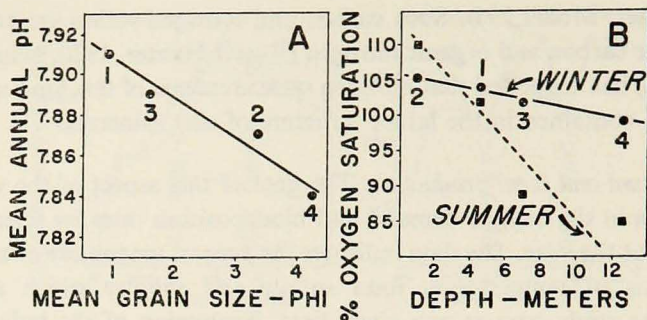


Figure 6. Relationship of bottom water parameters to grain size and depth at four stations. Station numbers are indicated. A, Relationship of mean annual pH of bottom water to mean grain diameter of the substratum. B, Relationship of mean per cent oxygen saturation of bottom water to depth. Winter values represent the mean of five monitoring occasions from December through May. Summer values represent the mean of six occasions from June through November.

and C:N ratios of the sediment are shown in Fig. 3. Fig. 4 illustrates variation in sedimentary carbonate.

a. Salinity. With a single exception, salinity variation did not exceed 5‰ at any station, with values falling between 28‰ and 33‰. The exception, not indicated in Fig. 2, occurred immediately following a rainfall of 16 cm in a 48 hour period during June of 1972. A salinity of 7‰ was recorded at station 2. Values recovered to near normal within two days.

b. Dissolved oxygen. Throughout the year dissolved oxygen concentrations in the bottom water ranged from a summer low of 3.97 mg l⁻¹ (sta. 4) to a winter high of 12.23 mg l⁻¹ (sta. 1). The greatest variation in dissolved oxygen at different stations was encountered during the summer months (Figs. 2, 6, 7).

Winter values were more uniform, excepting those marginal areas of the bay which were frozen over periodically. Dissolved oxygen values decreased significantly below the ice (sta. 2, Fig. 2). Presumably this was due to the absence of sea-air mixing. Reduction of dissolved oxygen in frozen marginal areas of the bay was not reflected at other, unfrozen, stations (Fig. 2, January-March data points). This was in contrast to the effects of freezing upon salinity, in which the salinity of all stations increased although only one of them was frozen over.

c. pH. The annual range in bottom water pH was from approximately 7.5 to 8.1 (Fig. 2). Lowest values were recorded during late July and early August, particularly over the fine grained organic rich sediments of station 4. High values occurred from September through January. After January they decrease, more or less regularly, to the summer lows. A more variable pattern was demonstrated by station 2, which was located immediately adjacent to the shore in a partially enclosed cove.

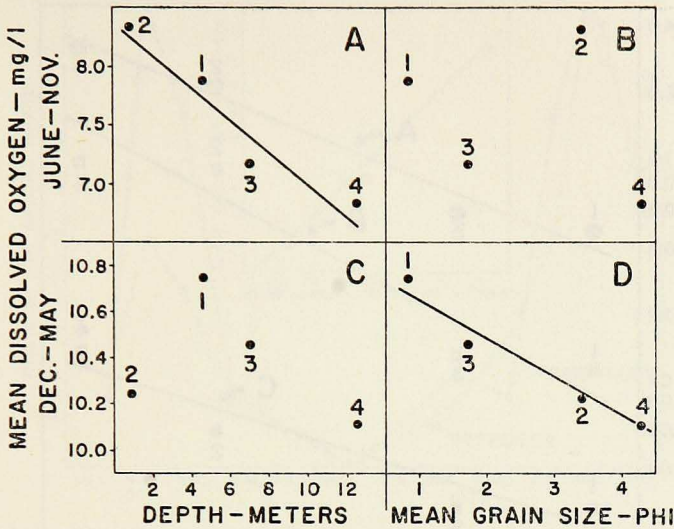


Figure 7. Relationship of dissolved oxygen of the bottom water to depth and mean grain diameter of the sediment during June-November, 1972 and December-May, 1972-73.

d. Organics. Seasonal variation in total organics, organic carbon, and organic nitrogen of the sediment is indicated in Fig. 3. Variations were small throughout the year at stations characterized by coarse sediments (1,3). Finer sediments (stas. 2 and 'particularly' 4) demonstrated marked parallel seasonal variations in all three parameters. All organic parameters measured are inversely related to grain size (Fig. 8).

Minimum values of the three organic parameters occurred in January and February. Maximum values, recorded in late July and early August, achieved levels approximately twice as high as those which were present throughout the remainder of the year. C:N ratios varied irregularly throughout the year and were generally low. Mean annual C:N values at stations 1, 3 and 4 were 4.0, 5.2 and 6.6 respectively. Station 2, located in a shallow restricted cove, bordered by private residences, demonstrated higher values, the annual mean being 15.1.

e. Carbonate. Annual variations of total sedimentary carbonate are illustrated in Fig. 4. The variations in coarse sediments (stas. 1, 3) were small, but significant peaks were present in finer sediments. The principal carbonate peak occurred in late July and early August. A secondary peak was observed in November-December. These maxima coincided with those noted for total organics, organic carbon and organic nitrogen (Fig. 3). Carbonate content of the sediment was generally greater in finer sediments. A good correlation exists between mean annual per cent carbonate and mean annual per cent nitrogen (Fig. 9).

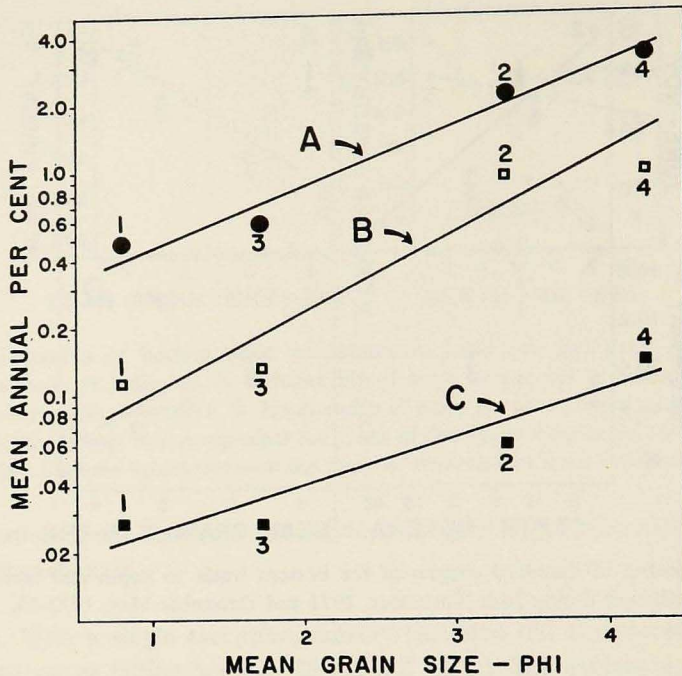


Figure 8. Relationship between mean annual per cent organics and mean grain diameter at four stations in northwestern Buzzards Bay. Station numbers are indicated. A, total organics. B, organic carbon. C, organic nitrogen. N = 11 for each data point.

f. Biodeposition. The possibility that increase in the metabolic rates of benthic invertebrates may result in substantial additions of feces and pseudofeces to the sediment during late July and early August has been examined.

Biodeposition (fecal and pseudofecal production) and the rate of oxygen consumption for four suspension feeding invertebrates were found to be positively correlated. A single example is illustrated for *Crepidula fornicata* (Fig. 10, a). This is typical of the relationships observed between maximum fecal production and maximum (active) BOD for *Crepidula fornicata*, *Mytilus edulis* and *Ciona intestinalis*. Results for *Mya arenaria* are less satisfactory, possibly due to deviations from normal behavior of this infaunal species in the glass containers utilized in the experimental work. Minimum fecal production and minimum (standard) BOD also showed fairly high correlations for *C. fornicata*, *M. edulis* and *C. intestinalis*. Newell (1970) has reviewed differences between active and standard BOD.²

Biodeposition in all species examined was body weight specific and may be treated in the same way as active and standard oxygen demand. Fig. 10, B-F illustrates the

2. Active BOD refers to oxygen demand of an organism during periods of peak activity. Standard BOD refers to the reduced oxygen demand during periods of quiescence. These values are approximated here by the maximum and minimum of three BOD determinations on twenty specimens made over a twelve hour period.

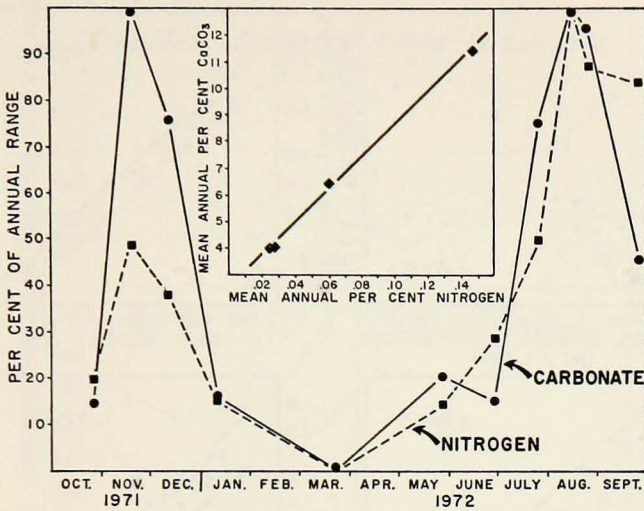


Figure 9. Relationship between mean carbonate and organic nitrogen in northwestern Buzzards Bay from October, 1971 to September, 1972. Correlation is indicated in the upper central part of the figure. Data points in the correlation diagram are annual mean values obtained throughout the year at each of four stations. The lower portion of the figure indicates variation during the year. Data points represent the mean values of all four stations and are plotted as a percentage of the maximum annual range of each variable.

relationship between dry tissue weight and biodeposition of *C. fornicata* on five occasions. Data for *M. edulis* and *C. intestinalis* are comparable. From graphs of this kind one may evaluate the active and standard rates of biodeposition at various temperatures for a hypothetical individual of any given size. Fig. 11 presents such data for the four species examined here.

5. Discussion

Salinity of Buzzards Bay bottom water is controlled by rainfall, depth (as an expression of mixing of the water column), distance from shore and freezing of marginal portions of the bay. Reduced salinities at all stations during June reflect heavy spring rains typical of the area. The effects of rainfall and runoff are reduced, but not eliminated in offshore and deeper stations (Fig. 2). In February, increases in salinity reflect freezing of peripheral portions of the bay. The resultant removal of water by freezing is shown most strongly at station 2, which was frozen over, but is evident at all stations examined.

Annual salinity ranges conform to the equation:

$$\ln S = -0.168 \ln D + 1.487$$

where S = mean annual salinity range in ‰ and D = depth in meters. The maximum deviation of values predicted by this equation from observed values is 0.1‰.

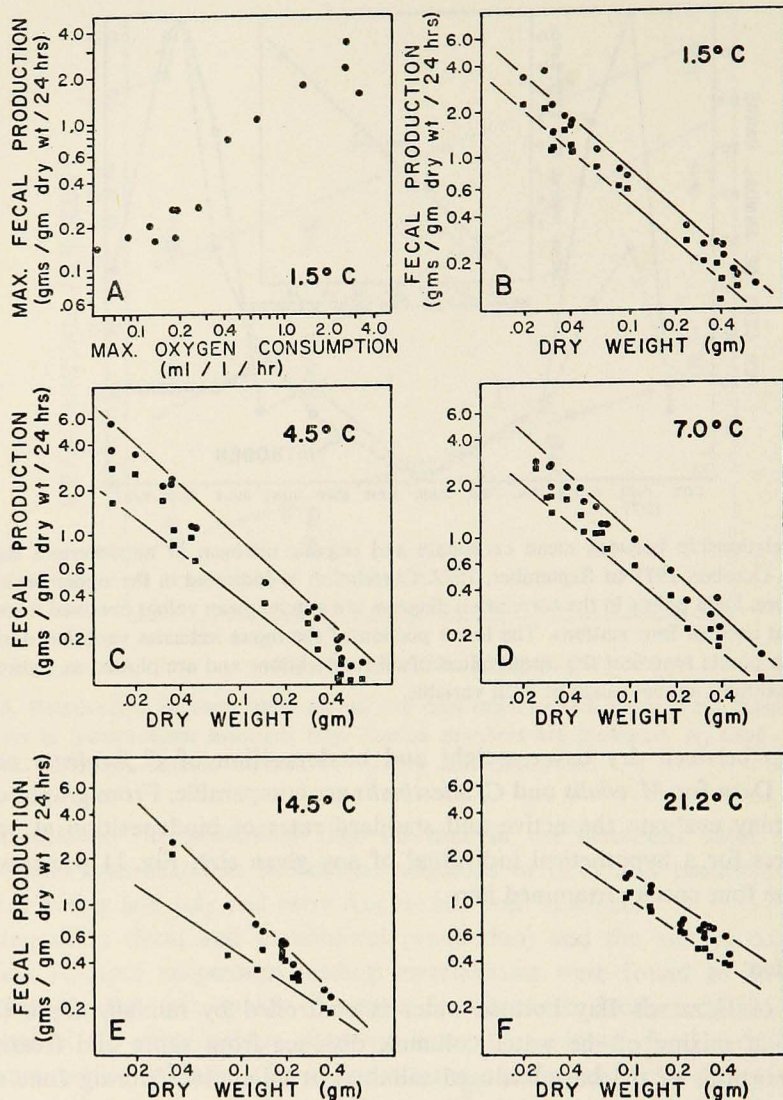


Figure 10. Oxygen demand and fecal production of *Crepidula fornicata*. A, Correlation of maximum fecal production and maximum oxygen consumption at 1.5°C. B-F, Maximum and minimum biodeposition per dry weight biomass at various temperatures during 1972. A, B, Feb. 18-22; C, Mar. 29-31; D, Apr. 25-27; E, May 30-June 2; F, Aug. 9-11.

Because deeper areas are commonly further from shore in Buzzards Bay, it is difficult to evaluate these variables separately.

Dissolved oxygen concentrations in the bottom water are related to temperature, mixing of the water column and uptake at the bottom. Figure 2 provides data on dissolved oxygen in bottom water. The stations range in depth from 0.9 to 12.5 m.

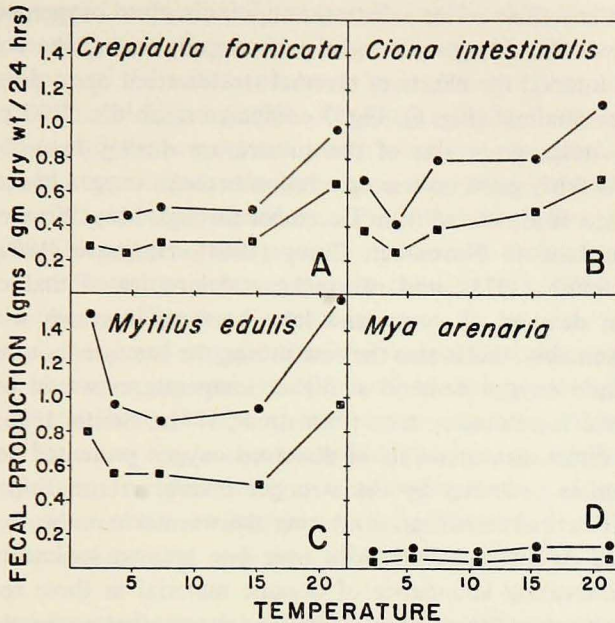


Figure 11. Relationship of temperature to maximum and minimum fecal production rates for 0.2 gm individuals of four species. The graphs are constructed from data like that shown for *Crepidula fornicata* in Fig. 10, B-F. Note that the scope of fecal production does not vary markedly with temperature and that maximum fecal production per gm dry weight occurs at the highest temperature examined. The accuracy of results for *Mya arenaria* is questionable. Poor results for this infaunal species may reflect the unnatural conditions in the experimental glass bowls.

It appears (Fig. 2) that the thermal characteristics of the bottom water at a given station are characteristic of that depth throughout the geographically restricted study area. Weak thermal stratification of the water of northwestern Buzzards Bay is first evident in late April and is well established by late May. Such stratification is reduced in late September and absent by late October.

Data are treated here over two time periods; June-November and December-May. Fig. 6 illustrates the relationship of mean annual per cent oxygen saturation of the bottom water to depth during these time intervals. Saturation values, at different temperatures and salinities, were obtained from the monogram of Green and Carritt (1967). Bottom waters of the bay were supersaturated to an average depth of approximately 12 meters from December through May and to approximately 5 meters from June through November. The mean per cent saturation varied significantly with depth in the warmer months. From December through May values were more nearly constant. Oxygen saturation of the bottom water is related to the degree of thermal stratification.

As a result of the relationship between stratification and dissolved oxygen, one

would expect that any effect of the substratum upon dissolved oxygen concentrations would be most evident, though not most pronounced, during the colder months. During this time interval the effects of thermal stratification upon dissolved oxygen concentrations are minimal (Fig. 6). Fig. 7 compares mean dissolved oxygen values to depth and to mean grain size of the substratum during June-November and December-May. A fairly good inverse correlation between oxygen concentration and mean grain diameter is illustrated from December through May. No such correlation is apparent from June to November. Carey (1967), Hargrave (1969), Pamatmat (1971a, 1971b), Smith (1973), and others have demonstrated that chemical and biological oxygen demand of ocean and lake bottoms increases with increasing temperature. Presumably, this is also the case during the summer months in Buzzards Bay. Such increased oxygen demand at higher temperatures would be reflected in measurements involving closed systems (Pamatmat, 1971a; Smith, 1973; and others). However, in the direct measurements of dissolved oxygen presented here, the effect of the substratum is obscured by the stronger inverse relationship of dissolved oxygen to depth (thermal stratification) during the warmer months.

Lower dissolved oxygen concentrations over fine grained sediments (Fig. 7, D), may reflect the increasing abundance of organic material in these sediments (discussed below). However, a variety of investigations suggest that no simple relationship exists between substrate oxygen demand and substrate organic content (Edwards and Rolley, 1965; Pamatmat, 1971b; Edberg and Hofsten, 1973).

Mean annual pH values at the different stations demonstrate a fairly good positive correlation with the mean grain diameter of the sediment (Fig. 6, A). However, the maximum range between mean values was only 0.07. A Kruskal-Wallis H-test (Wolf, 1968) does not indicate significant difference at the .05 probability level. However, the probability of difference is well above the .10 level.

Lower pH values during late July and early August correspond to maxima of temperature (Fig. 2) and maxima of total organics, non-carbonate carbon, and nitrogen in the sediment (Fig. 3). Furthermore, the mean annual pH of the bottom water is lower over fine grained stations characterized by higher organic concentrations (Fig. 6, A). Both of these observations suggest that the pH of the bottom water is being affected by sedimentary parameters. It is possible that the production of varying quantities of organic acids or respiratory carbon dioxide at the sediment-water interface is reflected in the bottom water.

The origin and kind of particulate organic matter in sediments is of importance inasmuch as this comprises the food supply of deposit feeding animals. Newell (1970) reviewed the origin of organics in sediments collected by Longbottom (1968, 1970) from the North Kent coast. He argues that, if the annual maxima of sedimentary organic carbon corresponded to phytoplankton blooms, and if such maxima were not accompanied by nitrogen maxima, it could be concluded that the variation was due to organic debris falling onto the sea floor, rather than to variation in the standing crop of benthic microorganisms. In the fine sediments of Buzzards Bay organic

nitrogen and organic carbon exhibited parallel variation patterns throughout the year (Fig. 3), maxima occurring in late July and early August.

The productivity of the water column in this area has been examined by Peck (1896), Fish (1925), and Lillick (1937). Rhoads, *et al.* (in Press) concluded, on the basis of this work, and their own eleven month monitoring program, that the principal phytoplankton blooms in Buzzards Bay are in December-January and September-October. A subordinate bloom occurs from April to June. Although a slight increase in the various sedimentary organic parameters occurs in early summer (April-June), the maxima of sedimentary organics do not coincide with either of the principal phytoplankton blooms (Fig. 3).

Rhoads *et al.* (in press) suggest that the inverted nutrient stratification of the water column may dampen out the effects of surface productivity cycles. Under such conditions the bottom acts as a nutrient reservoir. Although this would appear to be the case, it does not explain the late July-early August organic maxima reflected in the sediments. It is conceivable that an unusually early plankton bloom peculiar to 1972 resulted in unique sedimentary organic maxima during late July and early August of that year. However, an alternate possibility must be considered.

Several lines of evidence suggest that these carbon, nitrogen, total organic maxima are the result of the increasing abundance of benthic microorganisms. (1) High nitrogen values indicate that a substantial fraction of the organic portion of the sediment is living, rather than being composed of dead particulates deposited from the water column. (2) It seems unlikely that the July-August organic maxima are due to detrital input from marsh and seagrass. Station 4, located in an offshore area is virtually devoid of larger plants but demonstrates the most significant July-August increase in sedimentary organics. Station 2, located in a small shallow cove bordered by marshes and supporting a crop of *Zostera marina*, is characterized by a relatively small July-August increase in organics. The sediments of both of these stations are fine-grained. (3) The highest summer water temperatures in the area occur in late July and August. Such peaks are associated with maximum fecal production by benthic invertebrates (discussed below). Although feces and pseudofeces are initially low in nitrogen, colonization by bacteria elevates this value within a few days (Newell, 1965; Johannes and Satomi, 1966; Frankenberg and Smith, 1967). Bacterial reduction of detritus is high during June, July and August (Rhoads *et al.*, in press).

These lines of argument suggest that both benthic bacteria and benthic diatoms are important constituents of the organic fraction of the fine grained sediments in Buzzards Bay. As early as 1933, Reuszer noted a correlation between the bacterial abundance and the carbon content of the sediments in the Woods Hole region. Monitoring of benthic diatoms at station R (Sanders, 1958) by E. Moul indicates that these are also significant contributors to the summer organic maxima (personal communication H. L. Sanders). It is suggested that the late July and early August

organic maxima are related to increases in the standing crop of these benthic micro-organisms.

Mean annual organic nitrogen, organic carbon and total organic concentrations all increase logarithmically as the sediments become finer in Buzzards Bay. The slopes of the regression lines demonstrate a fair degree of parallelism (Fig. 8). This is in agreement with the results of a variety of marine and freshwater studies (Bramwell and Cole, 1939; Wood, 1964; Newell, 1965; Buchanan, 1966; Thomas, 1969). Somewhat higher nitrogen and carbon values are reported here than those reviewed by Newell (1970). However, it is of interest that the slopes of the present regression lines are very nearly the same as those reported by Wood (1964), Newell (1965) and Longbottom (1968) in which these workers excluded semi-liquid muds.

The higher concentration of total carbonate in fine grained sediments is evident in Fig. 4. The annual mean per cent carbonate at the four stations was strongly correlated with the phi mean grain diameter ($r = .83$, Woolf, 1968). In a previous study of this area fifty-four stations exhibited no such correlation (Driscoll and Brandon, 1973). Calculated from their data, $r = -.17$. However, Driscoll and Brandon collected their samples during the period June-September. It is evident from Fig. 4 that the summer season is characterized by significant changes in sedimentary carbonate. The high correlation between carbonate and mean grain diameter is apparent only if stations are sampled concurrently, as in the present effort.

Carbonate is not commonly considered as a seasonal variable in the examination of shallow marine sediments. However, if sediments do not manifest an annual net carbonate gain, then as much carbonate is returned to the water column via solution as is removed from it, excepting that amount which accrues to the sediment as a function of the sedimentation rate. In Buzzards Bay there is no indication of a significant net gain of carbonate by the sediment. Carbonate values, recorded from the muds of Buzzards Bay more than thirty years ago (Hough, 1940), are similar to those of the present. Presumably, this balanced carbonate budget is maintained on an annual basis.

It is reasonable to believe that seasonal fluctuations in sedimentary carbonate should be characteristic of many environments similar to Buzzards Bay. Well documented seasonal variations in shell accretion, water temperature, pH of the bottom water, organic content of the sediment and the activity of shell destructive organisms all indicate that this should be the case.

Because we have no evidence of direct chemical precipitation of calcium carbonate in Buzzards Bay the bulk of the sedimentary carbonate would appear to be contributed by shell-bearing benthic invertebrates. The local distribution of deposit feeders and suspension feeders is related to grade of deposit, organic content of the sediments, and resuspension of the sediment by tidal currents (Sanders, 1958; Rhoads and Young, 1970; Driscoll and Brandon, 1973). Deposit feeding benthos are more abundant in fine grained sediments characterized by high organic content. Of particular importance in such sediments are the bivalves *Nucula*, *Yoldia* and *Macoma*. These,

Table 3. Coefficients of correlation and coefficients of determination for organic nitrogen and carbonate at four stations in northwestern Buzzards Bay. *N* = 11. Mean grain size is indicated.

Station Number	Coefficient of Correlation	Coefficient of Determination	Mean Grain Size (Phi)
1.....	.06	.00	0.91
2.....	.59	.35	3.38
3.....	.30	.09	1.66
4.....	.83	.69	4.26

and various foraminifera, constitute the only abundant shelled species which might contribute significant quantities of carbonate to the fine grained sediment.

One may examine the possibility that the standing crop of deposit feeding molluscs, as represented by sedimentary carbonate, is partially controlled by the food supply, represented by the standing crop of benthic microorganisms. If such were the case the seasonal correlation between organic nitrogen (benthic microorganisms) and carbonate would be high in fine grained deposits in which such deposit feeders are abundant. Comparable correlations in coarse grained sediments, characterized by suspension feeders relying upon the water column as a source of nutrition, would be low. Coefficients of correlation and coefficients of determination for nitrogen and carbonate are presented in Table 3. Correlation is high in the fine grained sediments and virtually nonexistent in the coarse grained deposits. In the finest sediments (sta. 4) approximately seventy per cent of the variation in carbonate is due to the regression of carbonate on organic nitrogen. This interpretation implies a marked seasonal difference in bivalve growth rates with the maximum growth rates occurring in July and August. Data concerning growth of the important deposit feeding bivalves is not available but Panella and MacClintock (1968) have demonstrated that daily summer growth increments of *Mercenaria mercenaria* from this area may be as much as twenty times thicker than daily winter growth increments. It is difficult to separate the effects of food resources and temperature upon deposit feeding bivalve growth utilizing the present data. However, the importance of food is indicated in Figs. 3, 4 and 9. There is a secondary peak of total sedimentary carbonate during October-December. This peak is paralleled by an increase in the total organics and nitrogen of the sediment, but is associated with steadily decreasing water temperatures (Fig. 2). Inasmuch as the carbonate analyses included both living and dead shells, this October-November peak suggests an increase in total deposited carbonate rather than an increase in dead shells only.

If the shells of living deposit feeding molluscs constitute a major source of carbonate at fine-grained stations, it is necessary to examine the possibility that the soft parts of such species may contribute significantly to the organic nitrogen values in these areas. It could be argued that the correspondence of nitrogen and carbonate peaks in the summer (Figs. 3, 4) simply reflects a larger standing crop of deposit feeding molluscs during this season, rather than increased molluscan abundance controlled by an increased abundance of microorganisms in the sediments.

It appears unlikely that macrofaunal tissue contributed significantly to the nitrogen values determined for the sediment. The correlation between nitrogen and carbonate becomes progressively better in finer sediments (Table 3). This correlation indicates a relationship between carbonate and nitrogen in fine sediments which is not present in coarser sediments. Absolute amounts of either carbonate or nitrogen are irrelevant. Numerous epifaunal and infaunal suspension feeding molluscs and bryozoa are present in the coarse sediments of Buzzards Bay (Driscoll and Brandon, 1973). Consequently, it is unlikely that carbonate-nitrogen correlations would be so clearly related to grain size if nitrogen values represented only macrofaunal tissue. Furthermore, large living individuals of the macrobenthos which were incorporated in the sediment samples would be reflected by large variations in nitrogen values between replicates. These are not present (Table 1).

This argument also assumes that the living and dead shells and shell fragments of deposit feeding molluscs are a reasonable reflection of their living abundance at any given time. The long term accumulation of large amounts of dead shell in fine sediments would preclude the use of carbonate as an indicator of the deposit feeder standing crop. The cyclic nature of carbonate concentrations (Fig. 4) indicates in itself that shell material is rapidly removed from fine grained sediments. However, it should be further noted that the species concerned are characterized by small, thin shells, that they inhabit a zone of only a few cms near the sediment-water interface, that the sediment is rich in organic matter, and that the pH of the overlying bottom water is somewhat reduced. All of these factors, in association with bacterial decomposition of the shell matrix, argue for rapid solution of shell material in fine-grained sediments.

A final consideration involves the possible effects of experimental error on the correlation coefficients of nitrogen and carbonate at the various stations. Such error will be more important at stations 1 and 3, characterized by small seasonal variation in these parameters, than at stations 2 and 4, where seasonal variation is large. If values for carbonate and nitrogen are selected from the three replicate samples so as to yield the highest possible coefficient of correlation at stations 1 and 3, the resultant coefficients are 0.73 and 0.59 respectively. These values are less than that obtained by utilizing mean carbonate and nitrogen values at station 4 (0.83). If station 4 values are selected in order to yield the lowest possible correlation, then $r = .62$ at that station. This is a significantly higher value than is obtained with mean values at stations 1 and 3 (Table 3). A real trend in the coefficient of correlation between stations appears to be present, despite the possibility that values at stations 1 and 3 may be somewhat underestimated.

The substantial contribution of feces and pseudofeces to bottom deposits has received attention from many workers (Moore, 1931; Damas, 1935; Fox and Coe, 1943; Verwey, 1952; Ito and Imai, 1955; Rhoads (1974). Rates of biodeposition depend upon a variety of factors, including pumping rate (Jørgensen, 1966), food supply (Tenore and Dunstan, 1973), and several others.

Fig. 11 illustrates changes in the biodeposition rates of *C. fornicata*, *M. edulis*, *C. intestinalis* and *M. arenaria* under ambient conditions in the laboratory from February to August. The present data conflicts with that of Loosanoff (1958) and Haven and Morales-Alamo (1966) at temperatures approaching 0°C. These workers report little measurable fecal production at temperatures of less than about 3°C. In the present experiment both *C. intestinalis* and *M. edulis* produced surprisingly large amounts of biodeposits at these temperatures. The cause of this discrepancy is not known.

The highest active and standard rates of biodeposition for all four species occurred at maximum experimental temperatures in August. These temperatures correspond to those occurring in Buzzards Bay in late July and early August. Furthermore, changes in the rates of biodeposition of *C. fornicata*, *C. intestinalis* and *M. edulis* were greater between 15° and 20°C than at most other comparable 5° ranges (excepting changes near 0°C in *Mytilus*). This is in accordance with temperature dependent changes in the rate of oxygen consumption of a variety of invertebrates. Newell and Northcroft (1965) have illustrated that the standard and active rates of oxygen consumption by *Littorina littorea*, *Cardium edula*, and *Balanus balanoides* are more or less independent of temperature changes below 15°C but that the active rate increases markedly at higher temperatures.

From Fig. 11 one may calculate that 0.2 gm individuals of *C. fornicata*, *C. intestinalis* and *M. edulis*, at temperatures of approximately 20°C will produce their own weight in biodeposits in 25, 22 and 16 hours respectively. Smaller individuals produce larger quantities of feces per gram tissue, and much of the Buzzards Bay macrofauna is composed of small individuals. This evidence indicates that very substantial amounts of feces and pseudofeces are added to the sediments of Buzzards Bay in late July and early August, and that lesser quantities are contributed during the remainder of the year. Young (1971) has documented increased fecal production at summer temperatures in the deposit feeder, *Nucula proxima*, (Probably *N. annulata*, see Hampson, 1971) from Buzzards Bay.

6. Summary and conclusions

Selected interactions between the sedimentary substratum, benthic organisms and characteristics of the bottom water in Buzzards Bay have been examined. Relationships existing here provide insight concerning sediment-animal-water interactions in other typical shallow water situations. Fig. 12 is a qualitative diagrammatic outline of some of these relationships as indicated by the present investigation as well as by the efforts of other workers.

a. Interactions within the sediment. In Buzzards Bay variations in the organic content of the sediment appear to be primarily due to the abundance of benthic microorganisms. A number of lines of evidence support this conclusion. (1) The peak concentrations of carbon, nitrogen and total organics occur in late July and August.

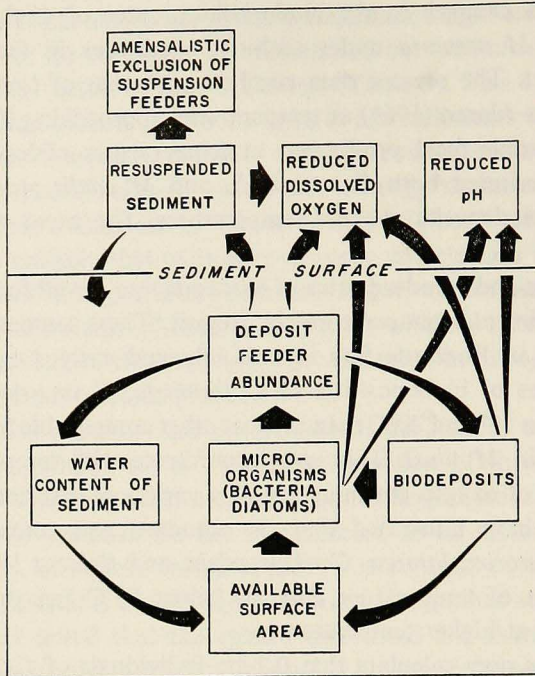


Figure 12. Diagram of selected interactions between the sediment, animals and bottom water in the muds of Buzzards Bay.

If such organic maxima were determined by sedimentation of dead planktonic organisms from the water column one would expect temporal correspondence with the fall and winter phytoplankton blooms documented by Rhoads, *et al.* (in press). (2) The July-August carbon peak is paralleled by a nitrogen peak. The occurrence of this nitrogen peak infers that the sedimentary organics represent living material rather than dead and decomposed remains of planktonic microorganisms. (3) Mean annual carbon, nitrogen and total organic values demonstrate a strong correlation with the phi mean grain diameter of the sediments. If detrital organic material, derived from the shore, were of significance, one would expect higher concentrations of organics in nearshore muds than in offshore muds. This is not the case. (4) The correlation of organics with mean grain size infers that grain surface area may be a controlling factor on microorganism abundance (Newell, 1970; Hargrave, 1972). Mare (1942) has pointed out that, assuming an adequate nutrient supply, generation time of bacteria and benthic diatoms is not a limiting factor on population density.

Sedimentary carbonate is largely a reflection of the living and dead shells of benthic organisms. In fine grained sediments these organisms are largely deposit feeders. It appears that seasonal fluctuations in the abundance of microorganisms may act as a control upon the abundance of deposit feeding molluscs in these fine

grained sediments. This is indicated by increasingly high correlation between nitrogen and carbonate in the finer sediments.

If microorganism abundance is related to sediment surface area (Newell, 1970; Fenchel, 1970) and if infaunal deposit feeder abundance is, in part, dependent on microorganism abundance, a feedback mechanism exists within this system (Fig. 12). Rhoads and Young (1970) have demonstrated seasonal changes in the water content of the fine sediments in Buzzards Bay. Water content of the surface sediments is greater during the summer due to increased bioturbation by the deposit feeding benthos. Such bioturbation by locally abundant species has been examined in more detail by Rhoads (1963) and Gordon (1966). In Chesapeake Bay Harrison and Wass (1965) have indicated a correlation between water content of the sediment and the distribution patterns of *Ensis directus*, *Nephtys incisa* and *Retusa canaliculata*. Schumacher (1963) related the oxidation depth in freshwater sediments to the abundance of tubificids. Seasonal variations in sedimentary water content appear to be a widespread phenomenon.

Several aspects of bioturbation may affect the abundance of microorganisms. These include physical breakdown of the sediment, increased depth of the aerobic habitat, the vertical transport of nutrients, the breakdown of flocculated grains in the digestive tracts of certain animals (Fenchel, 1970) and pelletization by other species (Rhoads, 1974). Not all of these result in increased surface area within the sediment. However, increased porosity and permeability in association with increased depth of the aerobic habitat may well produce a net gain in the surface area available for colonization by microorganisms. Such new surface area, becoming available for bacterial colonization during the deposit feeder maxima of July and August, would result in a further increase in microorganism abundance. The difficulties inherent in the estimation of the pore space available to microorganisms has been examined by Crisp and Williams (1971) and Williams (1972).

A second suggested feedback mechanism involves fecal production by deposit feeding animals in the fine grained sediment. It has been demonstrated that substantial amounts of feces and pseudofeces are produced during the July-August period by benthic invertebrates. Such biodeposits provide new surfaces for colonization by bacteria and diatoms as well as a readily available nutrient supply. The fecal pelletization of fine sediment may result in a decrease of the total surface area. However, such biodeposits have been purged of most microorganisms in the digestive tracts of invertebrates and present a significant amount of new surface available for microbial colonization.

The interactions illustrated in Fig. 12, below the sediment-water interface, are active in fine grained sediments throughout the year but appear to be substantially increased during the higher temperatures of summer.

b. Interaction between sediment and bottom water. Certain effects of sedimentary parameters upon the overlying bottom water are illustrated in Fig. 12. In Buzzards

Bay, greater oxygen depletion and lower pH values were observed in bottom water overlying fine grained, organic rich substrates than above coarse grained, organic poor substrates. pH and dissolved oxygen values above fine sediments were lower than those observed 0.5 m above the bottom. More than thirty years ago Waksman and Hotchkiss (1938) observed that substrate oxygen demand was inversely related to grain size in this area.

Bacterial and macrofaunal respiration are indicated as factors of significance in the biological depletion of dissolved oxygen in Buzzards Bay bottom water (Fig. 12). It is also reasonable to suggest that the July-August introduction of substantial amounts of feces is an important factor influencing the chemical oxygen demand of the substrate and acts to remove significant quantities of dissolved oxygen from the bottom water. Supporting evidence for this possibility is found in Fig. 2 in which July-August bottom water oxygen values are shown to drop substantially, particularly at station 4 (offshore mud). Hargrave (1972) has demonstrated that newly voided feces of the fresh water snail *Limnaea* are characterized by an oxygen demand approximately six times as great as older material. It should be further noted that the introduction of substantial quantities of feces to this system may provide new surface area for colonization by microorganisms; which in turn results in increased biological oxygen demand on the overlying water column.

An additional factor influencing the increased depletion of bottom water oxygen during the summer involves resuspended sediment. Rhoads and Young (1970) have documented the amensalistic exclusion of suspension feeders from fine grained sediments in Buzzards Bay. Such exclusion is caused by the resuspension of bioturbated fine grained sediment by tidal currents. Maximum turbidity of the bottom water occurs during mid-ebb tide (Rhoads, *et al.*, in press). In puget Sound Pamatmat (1971) reported a decrease in oxygen concentration during the ebbing tide and ascribed it, in part, to oxygen consumption by resuspended sediment. Because bioturbation is more active during the high temperatures of summer, and because resuspended sediment is subject to chemical oxidation processes (Edwards and Rolley, 1965), it is reasonable to suggest that such sediment contributes to depletion of dissolved oxygen from the bottom water.

Reduction in the pH of the bottom water over fine grained, organic rich sediments is illustrated in Fig. 6, A. Particularly low pH values were recorded in late July and early August (Fig. 2). One possibility is that these low pH values reflect the reduction of increasingly abundant complex organic compounds, and the resultant increase in organic acids in the bottom water.

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