PHYSICAL, CHEMICAL AND BIOLOGICAL ASPECTS OF NUTRIENT EXCHANGE BETWEEN THE MARINE BENTHOS AND THE OVERLYING WATER

by

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ABSTRACT

Nutrient exchange between the marine benthos and the overlying water was studied over a two-year period at a station located on a slightly sloping, fine-sand bottom in 18.3 m of water (at mid-tide level: tidal range of spring tide about 3 m) off the Scripps Institution of Oceanography pier. The site was located between two submarine canyons in a region known as the La Jolla Bight. Nutrient exchange was studied *in situ* using acrylic plastic boxes. Both transparent and darkened boxes were employed. When inserted 5 cm into the sediment, the boxes isolated 30 cm x 30 cm of sediment and 9 liters of overlying water. Water samples taken from within the boxes and sediment cores taken outside of the boxes were analyzed for various nutrients (ammonia, nitrate, nitrite, phosphate, dissolved organic carbon, nitrogen and phosphorus, sediment inorganic and organic carbon content) and biological properties (bacterial numbers, chlorophyll *a*, phaeopigments, respiration and photosynthesis). The difference between the nutrient concentration inside the box at the beginning and at the end of an experiment (4-6 hr duration) was used to calculate the exchange rate. Controls consisted of water samples incubated and treated in the same manner as the boxes but containing no sediment. Water samples taken from inside the boxes, after the initial samples, introduced no outside water to the inside of the boxes. Other parameters measured were: sediment incident irradiation, organic macro-detritus input, fallout of fine organic debris from the water column, temperature, relative sediment height, relative surge strength, and sediment porosity. These other

parameters were measured to determine what physical, chemical and/or biological factors influence the rate of nutrient exchange.

The results show that nitrate is taken up by the benthos at an average net rate of 77 $\mu M/m^2$/day (range: 720 $\mu M/m^2$/day taken up to 647 $\mu M/m^2$/day produced). The exchange of nitrate was, by multiple regression analysis, significantly correlated with the initial nitrate and ammonia concentrations and with oxygen changes in the light box. Nitrite exchange had an average net production of 34 $\mu M/m^2$/day (range: 5 $\mu M/m^2$/day taken up to 97 $\mu M/m^2$/day produced). The factors which affect nitrite exchange appear to also affect ammonia exchange. In addition, the activities of the benthic algae are of importance with regard to ammonia exchange and perhaps to a slight extent with nitrite exchange. Phosphate exchange had an average net production of 77 $\mu M/m^2$/day (range: 438 $\mu M/m^2$/day taken up to 502 $\mu M/m^2$/day produced). Phosphate exchange showed, by regression analysis, a significant relation to the phosphate concentration in the bottom water. The results indicate that the benthos is usually not phosphorus limited (exchange of phosphorus resulted in an average net production). However, phosphorus production does not yield a large surplus over the needs of the benthos and the exchange of phosphorus is highly dependent upon the diffusive gradient across the sediment-sea water interface and the activities of both the sediment surface algae and bacteria.

The uptake of dissolved organic carbon averaged 7 mg C/m^2/day (range: 370 mg C/m^2/day taken up to 285 mg C/m^2/day produced). The exchange of dissolved organic nitrogen had an average net uptake rate of 75 $\mu M/m^2$/day (range: 1326 $\mu M/m^2$/day taken up to 1280 $\mu M/m^2$/day produced). Dissolved organic phosphorus had an average production rate of 12 $\mu M/m^2$/day (range:

28 $\mu M/m^2$/day taken up to 59 $\mu M/m^2$/day produced).

The interdependencies of the other physical, chemical and biological parameters were also examined.

TABLE OF CONTENTS

LIST OF FIGURES

Figure Page

Figure Page

LIST OF TABLES

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I INTRODUCTION

Life in the ocean is largely dependent upon the production of organic matter by the phytoplankton. Phytoplankton growth and production is influenced by many factors such as; light, temperature, nutrients, grazing pressure, etc. The quantity and quality of these numerous factors varies seasonally, areally and with depth in the ocean. Of the above factors the critical role of nutrients in limiting primary productivity is well established (Eppley et al, 1973; Ryther and Dunstan, 1971; Strickland, 1965; Thomas, 1969). Productivity and growth models such as those of Dugdale (1967), Riley (1963) and Steele (1958) all incorporate nutrient terms.

The photosynthetic processes of phytoplankton produce organic matter from the inorganic carbon, water and inorganic nutrients found in sea water. This organic matter is the source of energy for the rest of the marine food chain. Since there is only a limited amount of biologically utilizable inorganic minerals present on the earth, organic production could not proceed indefinitely without the regeneration of organic matter into its inorganic constituents.

The ubiquity and phenomenal biochemical abilities of bacteria, even under the most adverse conditions, places the bacteria primarily in the trophic role of decomposer (Kim and ZoBell, 1972; Morita and ZoBell, 1955; ZoBell, 1934, 1946, 1968, 1973). Another trophic role of bacteria involves their ability to take up dissolved or otherwise unavailable organic matter and convert it into bacterial biomass which is available for consumption by other organisms (commonly referred to

as secondary production). ZoBell and Landon (1937) maintained the California mussel in the laboratory on nothing but bacteria. MacGinitie (1932) grew the worm Urechis caupo, which normally lives in mud-flats that have high bacterial densities, on a Pseudomonas species for 68 days. Controls, which were fed nothing, died by the end of 63 days. Johannes and Satomi (1966) found that the assimilable protein of shrimp fecal pellets was due to the presence of bacteria. DiSalvo's (1971) experiments suggest the assimilation of bacterial proteins by corals. Sorokin (1973) determined that Scleractinian corals assimilated 10-20% of their carbon content per day from bacteria. Luck et al (1931) reported that although most holozoic protozoans are not specific as to what they will ingest, some are. Gray and Johnson (1970) found that species of bacteria have varying levels of attractiveness to the gastrotrich, Turbanella hyalina. Chet et al (1971) determined that there may be a chemical detection of specific prey by bacterial predators. Seki (1966), Sorokin (1966), Zhukova (1963) and ZoBell (1954) discuss the nutritive role of bacteria in a more general manner, while Sorokin (1971) and ZoBell (1946) give an overview of bacteria as components of marine ecosystems.

The regeneration of nutrients in the ocean is not solely due to the activities of bacteria and other microorganisms. The release of ammonia (NH_3-N), nitrate (NO_3-N), nitrite (NO_2-N), urea ($CO(NH_2)_2$) and phosphate (PO_4-P) has been shown to be a regenerative function of the entire plankton community. Depending upon the nature and the degree of the physiological stress, phytoplankton will take up nitrate and release it back into the environment as nitrite (Carlucci et al, 1970; Vaccaro and Ryther, 1960), as well as oxidize organic matter during their

metabolism. The excretion of urea by zooplankton and its uptake by marine phytoplankton is discussed by Eppley et al (1973) and McCarthy (1971). The regeneration of nitrogen and phosphorus by zooplankton was studied by Conover and Corner (1968), Hargrave and Geen (1968), Johannes (1964) and Pomeroy et al (1963). The relationship between nutrient cycling, primary production and zooplankton regeneration of nutrients has been discussed by Corner and Davies (1971), Eppley et al (1973), Harris (1959), Ketchum (1962) and Martin (1968). Dugdale (1967) and Dugdale and Goering (1967) provide a mathematical model for phytoplankton growth under nutrient limiting conditions. In this model, productivity is closely coupled with the regeneration of nitrogenous nutrients by the zooplankton.

The upper water layers, where both phyto- and zooplankton are most abundant, has been shown to be most critical in the overall cycling of nutrients. Redfield et al (1963) and Riley (1951) state that the bulk of organic matter produced by the phytoplankton in the euphotic zone is recycled in these upper water layers. Craig (1971) emphasizes this fact in his study of oxygen consumption in abyssal waters. Williams et al (1969) state that only 0.51% of the carbon fixed in the upper waters enters the deep sea in a dissolved form.

Since the production of organic matter occurs mainly in the upper 500 meters of water, the concentration of organic matter is higher in these waters than in the deeper waters. In the surface waters the average estimates of POC (particulate organic carbon) and DOC (dissolved organic carbon) are 0.1 mg and 1.0 mg C/l respectively, while in the deeper waters their concentrations fall to an average of 0.01 mg C

(POC)/l and 0.5 mg C (DOC)/l (Williams, 1971). The distinction between these two forms (POC and DOC) is merely one of experimental convenience of size separation by filtration. The organic carbon which passes through a filter of pore size 0.5 μm to 1.0 μm is DOC and that which is retained on the filter is POC (Sharp, 1973). However, as the volume of ocean water above 200 m is only 2.1% of the total ocean volume of 1.4×10^{21} liters (Sverdrup et al, 1942), the total amount of organic carbon is greater in the deeper waters than in the shallow waters.

However, even though marine bacteria will grow at very low concentrations of organic matter (ZoBell and Grant, 1943), the observation, made by Keys et al (1935) and many others, that the principal limitation to bacterial growth in the sea is the availability of organic matter is well founded. This is because, besides being in very low concentration, the bulk of the organic matter which is present in the sea is refractory and not readily decomposed (Barber, 1968; Duursma, 1965; Krogh, 1934a, 1934b; Menzel, 1964, 1968, 1970; Williams et al, 1969; Williams and Gordon, 1970).

The decomposition of organic matter and nutrient cycling in the water column has been examined extensively by many investigators. Waksman and Renn (1936) used oxygen uptake in a laboratory study on the rate of decomposition of organic matter added to sea water. Cooper (1935) looked at the liberation of phosphate when planktonic organisms decomposed. Hoffman (1956) studied the regeneration of phosphorus in the planktonic community. Strickland and Austin (1960) took a larger view of the various chemical forms of phosphorus and their cycling in oceanic waters. Confer (1972) used a laboratory ecosystem to study the interactions existing among plankton, attached algae and the phosphorus cycle.

The decomposition of nitrogenous organic matter in sea water was elucidated by von Brand et al (1937, 1939, 1940, 1941, 1942). Jorgensen (1955) and Lewin (1961) looked at the dissolution of silica from diatom walls in sea water.

Grill and Richards (1964), using a 200 liter polyethylene drum, followed simultaneously the regeneration of phosphorus, silicon and nitrogen from decomposing phytoplankton. They added a natural phytoplankton population, caught in a net haul, to the 200 liter drum which had been enriched with inorganic plant nutrients. After a month the container was darkened and the decomposition of the phytoplankton was initiated by the natural population of microorganisms present. The chemical forms and concentrations of phosphorus, silicon and nitrogen were followed during this regenerative period.

Although the decomposition of organic matter and nutrient recycling through the food chain is almost completely within the upper several hundred meters of water, some organic matter sinks or is otherwise transported to the deeper waters. This fallout of organic matter accounts for most of the organic input to the deep-sea benthos. Other sources of organic input to the benthos are: secondary organic production by bacteria, chemosynthesis by bacteria, photosynthetic processes in shallow waters, DOC uptake by benthic organisms, turbidity currents and by the migration phenomenon, whereby shallower living organisms are eaten by deeper living animals and so on until the benthic animals are eating those that are just above the sediment (Deuser, 1971; Heezen et al, 1955; Menzies et al, 1967; Sanders and Hessler, 1969; Shoener and Rowe, 1970). The rate of supply of food to the deep-sea

benthos is so slow that it limits the biomass of the organisms present (Sanders and Hessler, 1969).

Even though the organic matter content of marine sediments is between 0.1% (by weight) in some abyssal plains to 25% in some fjords (Boysen-Jensen, 1914; Gross, 1967; Trask, 1939), much of it may be unavailable as a food for the benthos. One of the reasons for this, as has already been alluded to, is that the biologically reactive organic matter in the upper waters is rapidly decomposed and, therefore, only the more refractory organic matter sinks to the bottom. Another factor limiting the quantity of available organic matter for the benthos is the interaction of organics with clay minerals (Bader, 1962; Hamilton and Greenfield, 1965; Pinck, 1962). Erdman et al (1956) found that organic scavenging by clay minerals can result in the survival of amino acids, intact, for several thousand years.

The organic matter that does reach the sediment surface is altered mainly at the site of deposition. With increasing depth of burial in the sediment the organic matter decreases in concentration and consists of more refractory molecules (Degens et al, 1964; Volkmann and Oppenheimer, 1962). The sedimentary organic matter of shallow or nearshore regions is less refractory than that from deep-sea sediments. Anderson (1940) states that while 4.5% of the organic matter from nearshore regions was available for decomposition, only 0.5% of the organic matter from the deep sea was available for decomposition by organisms. Anderson (1940) and Pamatmat and Banse (1969) found no correlation, however, between the amount of organic matter and the availability of the organic matter for biological decomposition. Waksman and Hotchkiss (1938) also

found that the organic matter of deep-sea sediments is less readily available for decomposition than the organic matter from nearshore sediments. They also found that the organic matter in basins was more readily oxidized than that in the deep sea.

Much of the organic matter present in the sediment is a complex, refractory material called humic acid. Humic acids make up approximately 30-60% of the total organic matter of sediments (Degens et al, 1964). Humic acids found in the marine environment are ultimately derived from organisms living in the ocean or from terrestrial organic debris (Degens et al, 1964; Nissenbaun and Kaplan, 1972). Humic substances are formed from the residual organic matter remaining after the decomposition of plant and animal matter by microorganisms. They are likewise slowly decomposed by the activities of microorganisms. The biochemical processes leading to humic acid formation and decomposition, selectively remove nitrogen, phosphorus, sulfur and oxygen leaving a residue proportionately richer in hydrocarbons (ZoBell, 1949). The hydrocarbons produced are also susceptible to microbial degradation (Ahearn and Meyers, 1973). Humic acids have recently been found by Prakash et al (1973) to have a stimulatory effect on the growth of some marine diatoms. The humic substances used in their study were from marine sources and the stimulatory effect was greatest with low concentrations of low molecular weight humic substances.

The degradation of organic matter in the marine sediments and the concomitant release of its decomposition products has been a neglected field of study. This can be attributed to several factors. The main problem is that this is a process that has to be studied <u>in situ</u>. Most

sediment samplers in use today disturb the sediment-sea water interface to a degree which alters the dynamics of exchange. Also, in the deep sea where the organic matter in the sediment is refractory, the amount of time necessary to perform in situ experiments would create additional problems for ship positioning. Remote placing of sampling systems also has inherent engineering problems. In shallow water these problems can be overcome. The organic matter concentration is generally greater and more reactive. Measurements can also be done in situ, without a remote sampling apparatus, by using diver operated equipment. The advent of self-contained underwater breathing apparatus (SCUBA) has made possible the in situ study of microbial transformations in the sediments of shallow water.

A few studies have been done of benthic nutrient regeneration. these were done by analyzing nutrient gradients within and/or above the sediment. From these gradients the rate of nutrient flux across the sediment-sea water interface was calculated (Johannes, 1972; Okuda, 1960; Rittenberg et al, 1955). Recently, however, investigators have attempted to obtain these rates by direct in situ measurement (Hallberg et al, 1973; S. Hale, University of Rhode Island, personal communication).

As stated above, most investigations on nutrient regeneration have been done in the laboratory. Laboratory conditions can accelerate and/or retard one or more of the regenerative processes. Acceleration is desirable in an organically-impoverished system such as sea water where in situ rates of regeneration are so low as to be virtually undectable. For the present study, a sediment system was chosen to

investigate nutrient regeneration. In this sediment environment, nutrients (organic and inorganic) were more concentrated than in the overlying waters. This, plus the greater density of benthic microorganisms, would naturally accelerate the regenerative transformation rates.

II NATURE OF THE PROBLEM AND DESCRIPTION OF STUDY AREA

The objectives of the present study were three-fold: 1) to design an *in situ* experimental methodology that would allow the quantification of the rates of exchange of nutrients between the sediments and the overlying water in the nearshore environment; 2) to quantify such rates over a period of time; and 3) to determine those physical, chemical and biological factors which might influence the rates of exchange.

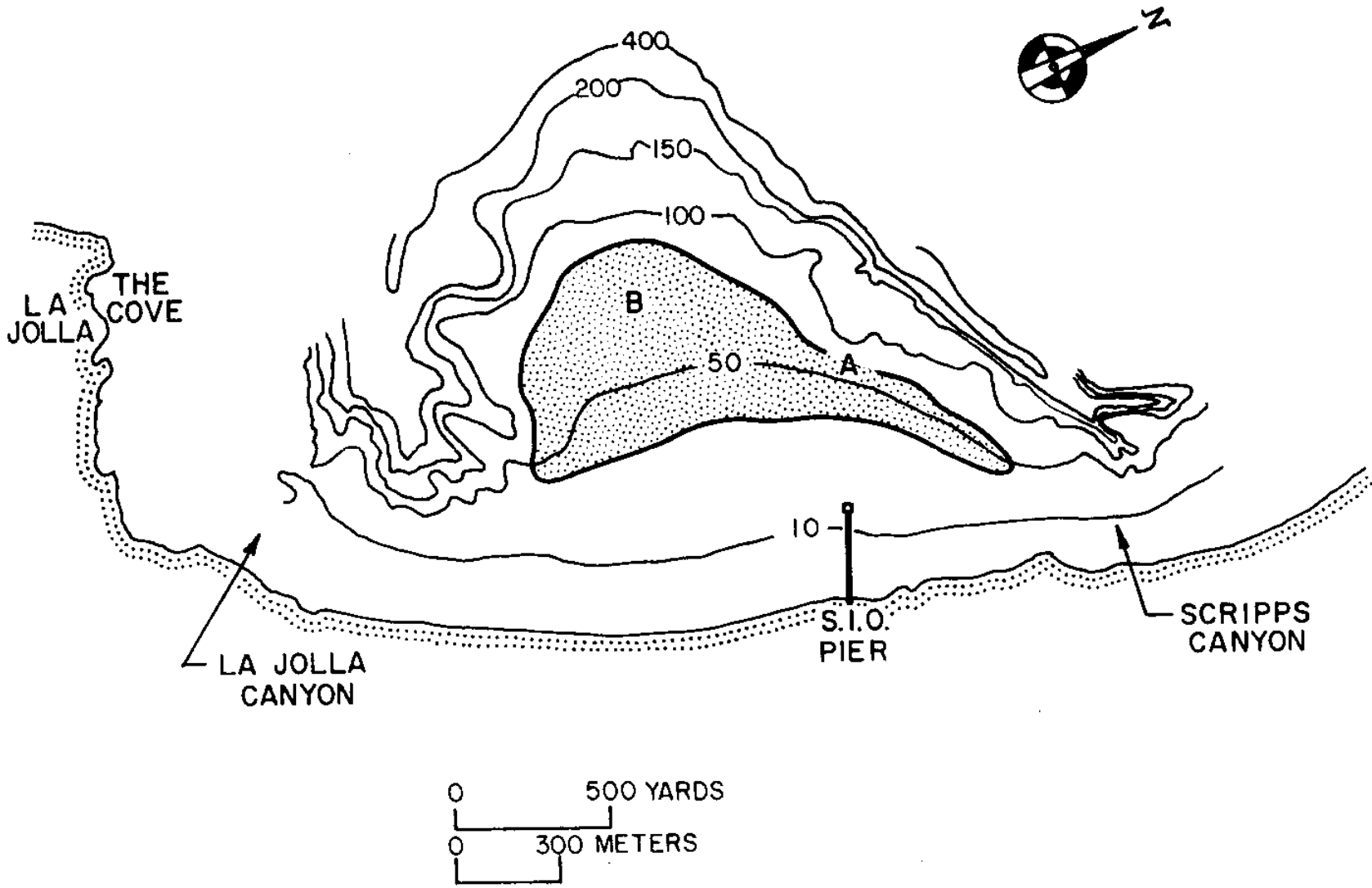
The sampling site for this study was chosen for the following reasons. The site is relatively stable and, therefore, would not change greatly during the course of the investigation. Also a great deal of information is known about the region in which the study was located. The sampling site was readily accessible from the Scripps Institution of Oceanography (SIO). Since these experiments were performed *in situ* using SCUBA, the depth of water was another critical concern. At the sampling site depth (about 18 m) a diver making the two 25 minute dives required for each experiment, did not have to worry about decompression. Also, another important factor concerning the selection of this site was that at this location and depth, it was relatively easy to obtain diving partners which are a necessary requirement for doing *in situ* SCUBA experiments.

The study site (see Fig. 1) was located in 18.3 m of water (at mid-tide level: tidal range of spring tide about 3 m), approximately 900 m off the beach in front of the SIO pier, on a slightly sloping fine-sand bottom in a region known as the La Jolla Bight (32° 42' N; 117° 15' W). The station was permanently marked with a spar buoy.

The La Jolla Bight region is characterized by its sedimentary

FIGURE 1

Study site (A) and extended study area (B:stipled area). Contour intervals are in feet.


400
200
150
100
50
10
B
A
N
THE COVE
LA JOLLA
LA JOLLA CANYON
S.I.O. PIER
SCRIPPS CANYON
0 500 YARDS
0 300 METERS

isobathyic similarity over broad reaches (Fager, 1968; Inman, 1953). This similarity in sediments varies in a systematic manner and in general is characteristic of the depositional environment (Inman, 1953). Therefore, the results of a study done at 18 m in one locality can be inferred as being generally valid for broad areas of the Bight. From my own observations and those of Inman (1953), it appears that the results from this sampling site would be valid for an area of sediment extending across the Bight region and from a depth of approximately 15 meters to 22 meters. In some parts of the Bight the upper depth limit is only 19 meters while in other sections it goes as deep as 25 meters. The stippled area in Figure 1 outlines this area.

The size distribution of the sediments and their variability in the La Jolla Bight was extensively studied by Inman (1953). The phi median diameter (Md ϕ = ϕ50th percentile) of the sediments at the experimental station was 3.50 to 3.25 phi units (88 to 105 μm). (All percentiles are cumulative percent). The phi deviation measure ($\sigma\phi$ = 1/2 [ϕ84th percentile - ϕ16th percentile]) for these sediments is between 0.3 to 0.5 phi units and is a measure of the sorting or spread of sizes of the sediments. The phi skewness measure ($\alpha\phi$), which is a dimensionless measure of the departure of the phi mean grain diameter (Mϕ) from the phi median grain diameter ($\alpha\phi = \frac{M\phi - Md\phi}{\sigma\phi}$), for the sediments at the experimental site was from between -0.15 to +0.05. The phi skewness measure is zero for a symmetrical size distribution, negative when skewed towards smaller phi values and positive when skewed towards larger phi values. At the experimental site the phi skewness values were usually slightly negative and therefore the distribution was skewed

towards smaller phi values (larger grain diameters).

Besides the common factors of waves and currents which affect the deposition of sediment in a shallow water region, in the La Jolla Bight the presence of two underwater canyons greatly affects the deposition of sand. This is not only due to their marked influence on currents and waves but also due to their being physical barriers to the transport of sediment particles. Longshore transport of sand into the Bight is effectively blocked by the canyons except for a narrow zone of shallow water at the head of the northern canyon (Inman, 1953). The canyons, therefore, act as traps for organic debris and inorganic particles moving into and out of the Bight on the sediment surface (Chamberlain, 1960).

The descriptive physical oceanography of this region is given by Reid et al (1958). There is an offshore south-flowing current (California Current) of cool, low salinity water and a subsurface counter current that at certain times of the year may affect the surface (Davidson Current). Closer to the coast the flow is generally southward, but the flow is affected by a large tidal component which moves the water clockwise at high tide yielding a northward component (Gaul and Stewart, 1960). In the La Jolla Bight the "near-surface waters" flow in a predominantly northerly direction with some counter-clockwise rotational motion associated with the La Jolla Canyon complex. There also is an onshore-offshore motion associated with the tidal cycle (Hirota, 1973). The Bight is affected by the passage of internal waves (Arthur, 1960; Kamykowski, 1972). These produce fairly rapid changes in both the physical and chemical makeup of the water. For example, a 4°C drop has

been observed at the sampling site of this study over a period of ten minutes. Kamykowski (1972) and references cited therein give a more complete description of internal waves and changes brought about by their presence.

The movement of water in the nearshore region is associated with wave action and consists of: 1) shoreward mass transport of water due to wave motion in the direction of wave propagation; 2) movement of this water as longshore currents; 3) seaward return of this water as rip currents; and 4) longshore movement of the rip current head outside of the breaker zone. Seaward return of water is also associated with a net drift of water along the bottom in the breaker zone (Inman and Quinn, 1952; Inman, 1953).

III FIELD METHODS

This section details the various procedures and samplers used in the field. The succeeding section gives the methods employed in the laboratory analyses of the field samples and the techniques used in a number of laboratory experiments.

Nutrient Exchange

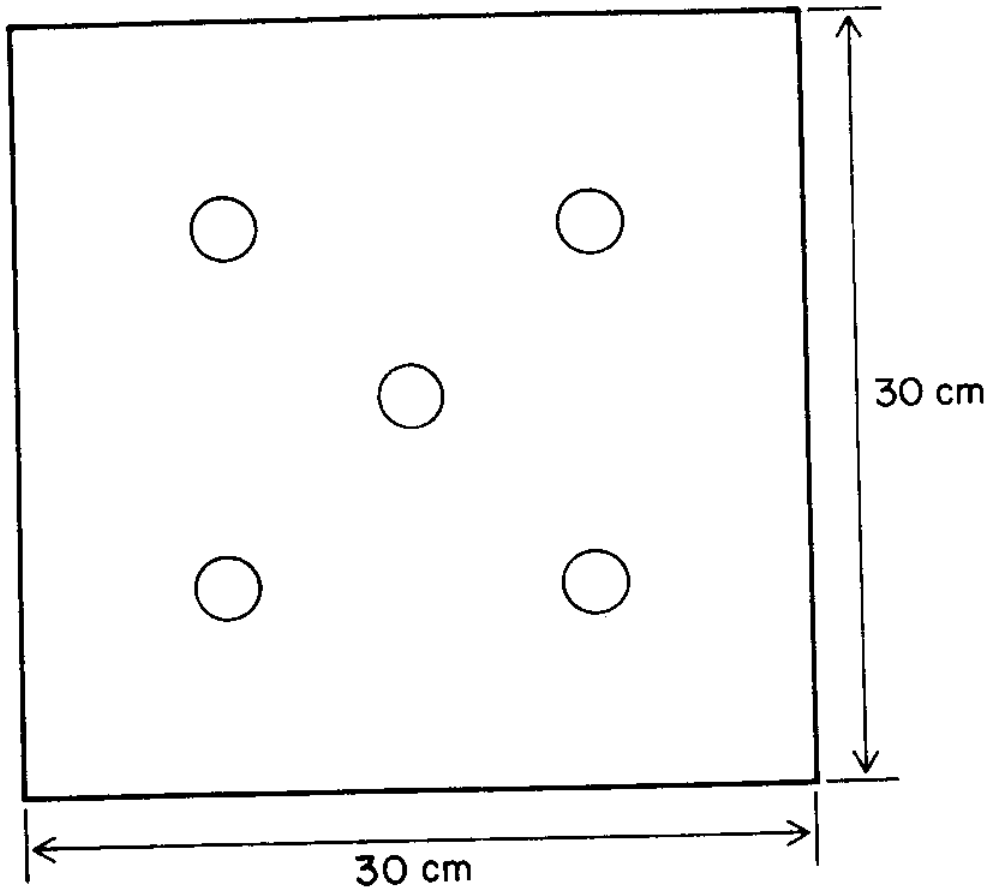
The method used to measure nutrient exchange between the sediments and the overlying water was basically the classic bell-jar technique. The "bell jar", however, was a specially designed acrylic plastic box (Figs. 2 and 3). The inside of the box was 30 cm long x 30 wide x 15 cm high. Light was excluded from the dark boxes by wrapping them with black electrical tape. When a box was inserted five centimeters into the sediment it enclosed 900 cm^2 of sediment and nine liters of overlying sea water. Box type #1 was used in the experiments of April 2, 1971, through December 8, 1971, and box type #2 was used in the experiments of January 3, 1972, thorugh February 20, 1973.

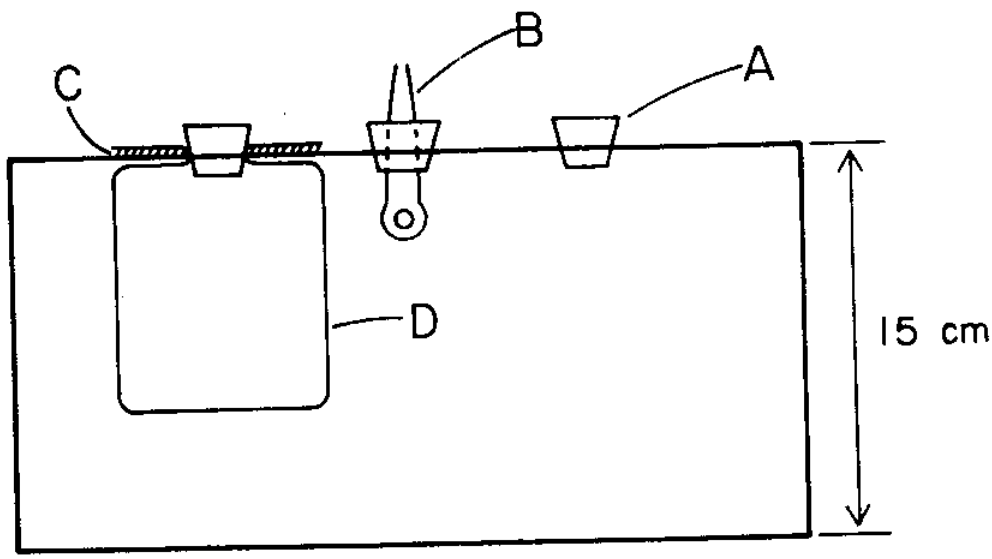
The procedure to insert the box into the sediment was to dive to the experimental site, remove several of the silicone stoppers from the top of the box, and then to carefully push the box into the sediment to a depth of five centimeters (depth permanently marked on the sides of the boxes). Great care was taken during this process not to disturb the surface layer of sediment; aroung the edges of the box disturbance was unavoidable. By taking water samples inside and outside of the box immediately after insertion, it was found that the insertion procedure did not affect the concentration of any of the nutrient parameters

FIGURE 2

Box type #1 showing silicone stopper (A), sample port (B) silicone sealant (C) and the two plastic bags (D) expanded to displace water removed by sampling. Box itself is made of 9.5 mm acrylic plastic.

TOP VIEW



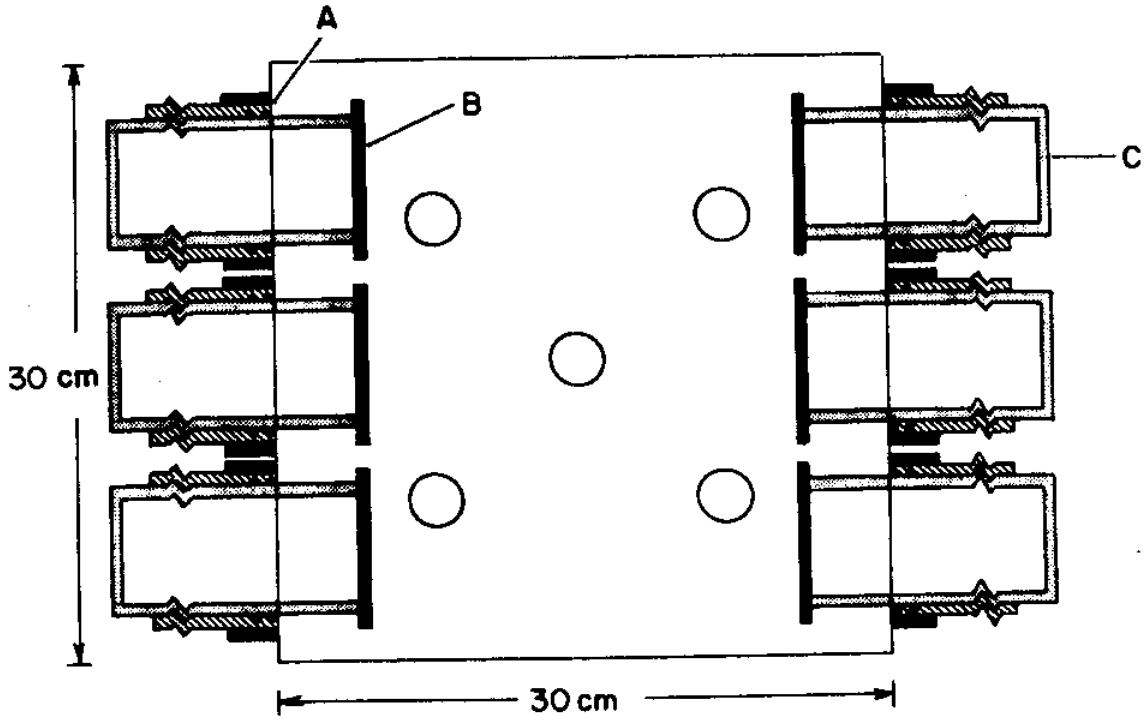


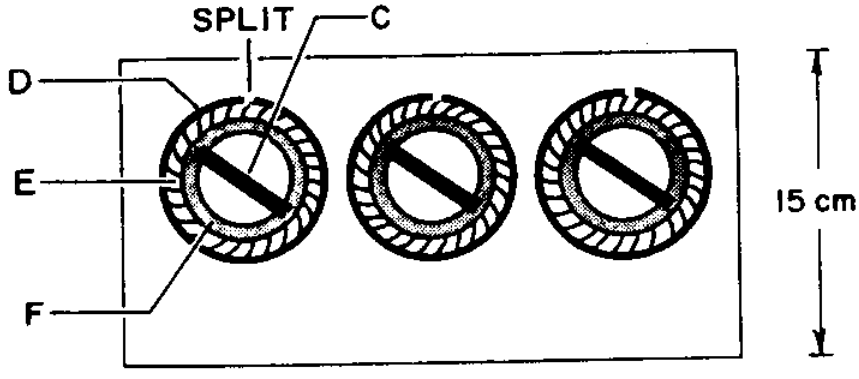
SIDE VIEW

FIGURE 3

Box type #2 showing "O" ring (A), end stop (B; 7.6 cm diameter clear-acrylic disc, 3.2 mm thick), plunger handle (C; 6.35 mm clear-acrylic rod), outer plunger support (D; clear-acrylic tubing 6.95 cm O.D. x 7.3 cm I.D. x 2.5 cm high, split at a point to allow for O.D. of "O"-ring support), "O"-ring support (E; clear-acrylic tubing, 7.6 cm O.D. x 6.35 cm I.D. x 9.5 cm high) and plunger (F; 6.35 cm O.D. x 5.1 cm I.D. x 19.0 cm long, is made of clear-acrylic tubing; outside machined to allow it to pass through "O"-ring support and to be water-tight with use of "O" rings; end stop glued to plunger). Outer support and "O"-ring support glued to box which is made of 9.5 mm clear-acrylic plastic. Silicone stoppers and sample port are not shown.

TOP VIEW





SIDE VIEW

which were measured. However, if the surface layer was disturbed there was an increase in nutrient concentrations inside of the box compared to the amounts found in the waters immediately outside the box.

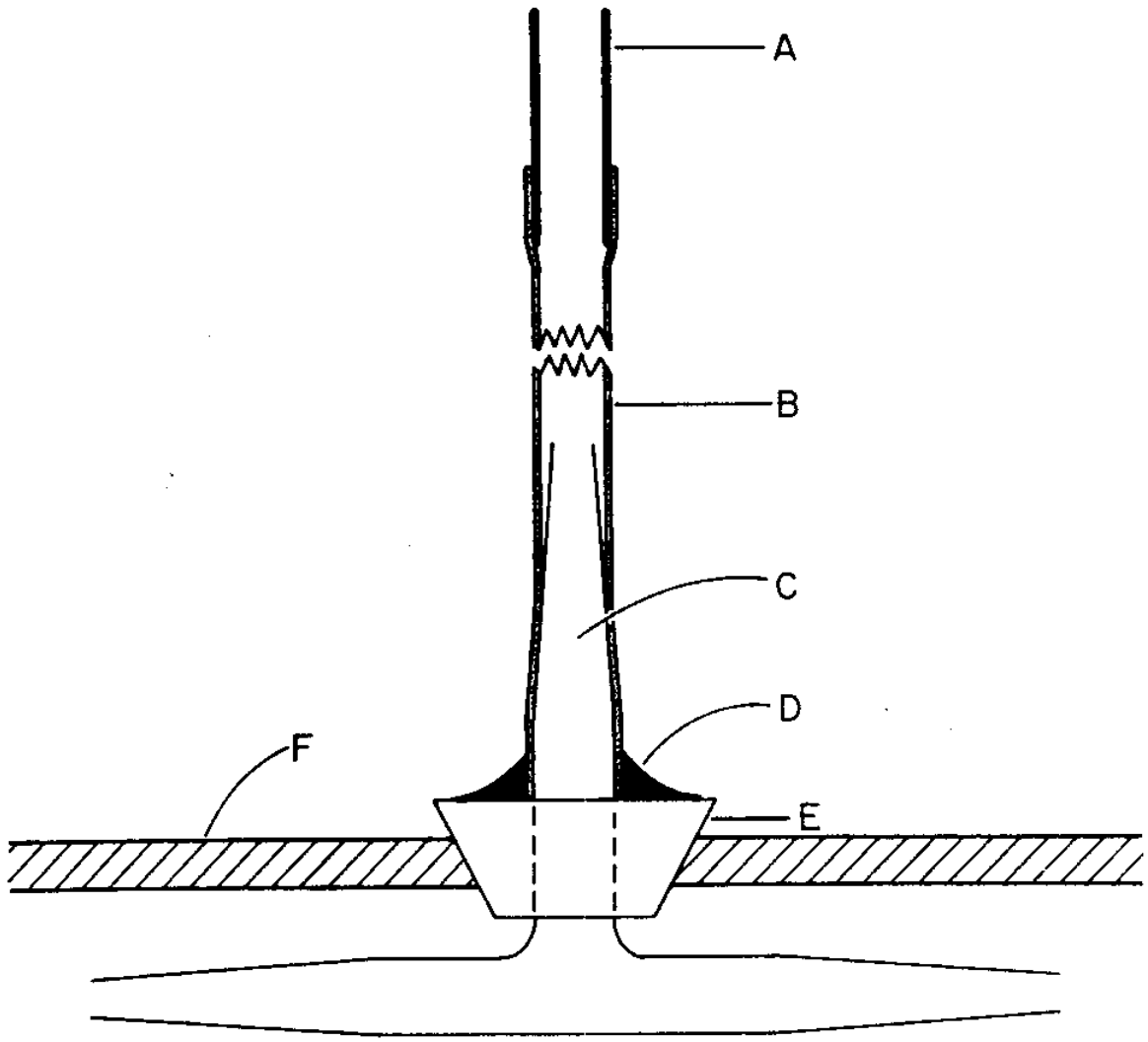
Once inserted the boxes were ready to be sampled for initial or zero time (Ot) nutrient concentrations. The nutrients considered were ammonia (NH_3-N), nitrate (NO_3-N), nitrite (NO_2-N), phosphate (PO_4-P), dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP). The sampling bottle used in all experiments, except for Ot samples in the experiments before June 21, 1972, consisted of a one-liter polyethylene bottle. In the mouth of the bottle was cemented a #6 silicone stopper which had a silicone tube (16 mm O.D x 9.5 mm I.D.) cemented into it. This tubing protruded out from the mouth of the bottle by 15 cm. A spring clamp was used to close off the tube opening. On the bottom of the sample bottle a small hole was made and plugged with a #00 silicone stopper. The cement referred to above was in all cases a silicone sealant.

The sampling port on the box consisted of a polyethylene T-tubing connector pushed up through a #6 silicone stopper inserted in the middle of the box (Fig. 4). The connector was oriented with its opening projections inside of the box running parallel to the top of the box and the surface of the sediment. The silicone stopper had a silicone tube (same size as given above) inserted into it and was cemented to the stopper with silicone sealant. The tubing extended about eight centimeters outside of the box, and contained at the end a short piece (5-8 cm) of glass tubing. The silicone tubing was closed off with a spring clamp.

The Ot samplers used in the experiments of June 6, 1972, and before were of several kinds. Both larger and smaller volume polyethlene bottles

FIGURE 4

Box Sampling Port showing glass tubing (A), silicone tubing (B), plastic T-connector (C), silicone sealant (D), silicone stopper (E) and top of box (F).


A
B
C
D
E
F

were tried, and in the experiment of January 14, 1972, the Ot water samples were taken outside of the box with a Van Dorn sampler. In all other instances the water samples were obtained from the inside of the box.

To obtain a water sample from inside of the box the following procedure was used. The silicone tubing protruding from the polyethylene bottle was pushed over the glass tubing of the sample port. The clamps on both pieces of tubing were removed. The sample bottle, which had been flushed and filled with nitrogen in the laboratory, was compressed due to the almost two atmospheres of pressure at 18.3 meters and began to fill slowly when the clamps were removed. In order to fill the bottle completely the residual nitrogen in the bottle was voided by removing the #00 silicone stopper from the bottom while gently squeezing the bottle which was in an inverted position. Since the density of polyethylene was less than the density of sea water, the sample bottle floated upside down during this procedure which expedited the process of removing the residual nitrogen. When the bottle was completely filled, the stopper was replaced. Both pieces of tubing were then clamped and the sample bottle removed.

While taking the water samples at Ot, the stoppers, which had been removed from the box during insertion, were not replaced. Therefore, as the Ot water samples were taken, new bottom water would enter the box. By being sunk five centimeters into the sediment there was little probability of sea water moving from the outside of the box to the inside and vice-versa once the boxes were stoppered. This is because water, being virtually incompressible, could not be forced into the box

unless the box itself was concurrently pushed out of the sediment and this did not occur. Actually, even if the boxes were inserted just below the sediment surface there would be little or no water forcefully exchanged between the inside and the outside. They were inserted five centimeters to assure against diffusive exchange, and also to assure they were firmly anchored to the bottom.

Since the box was slightly flexible there was the possibility of a forceful pushing of water out of the box if enough pressure were applied to the top of the box. While this was never observed in the field, it could be forced to occur if a diver applied sufficient pressure to the top of the box. When this was done the turbulence generated was great enough to disturb the fine material lying at the sediment-sea water interface. Since experiments were not performed when the swell, or pressure head, was greater than approximately one meter, the possibility of this magnitude of turbulence being generated inside of the boxes were remote.

No new water was introduced into the boxes after Ot. In box type #1 (Fig. 2) this was accomplished by placing two collapsed polyethylene bags (one inside of the other) through one of the holes in the top of the box. The lips of the bags extending outside of the box were cemented to the box with silicone sealant to prevent leakage around the edges. The opening into the box was plugged with a #6 silicone stopper. As a water sample was being taken, the stopper in the mouth of the bags would be removed, and the bags in the box would fill with sea water replacing that removed by the water sampler. The volume of water the bags displaced was a maximum of 1500 ml. In box type #2

the procedure was simplified by placing "O"-ring sealed plastic plungers into the sides of the box. This modification not only simplified the sampling routine, but also allowed multiple samples to be taken. To compensate for the water being removed by the sampler, one or more of the plungers was simultaneously pushed into the box. Each plunger could displace approximately 400 ml of sea water. With six plungers in each box a total of 2400 ml of sea water could be sampled from the box. This total volume could be taken at one time or smaller samples could be taken a number of times.

Mixing of the water inside the boxes to assure representative samples was examined using methylene blue dye in the oxidized (blue) state. Two to three milliliters of concentrated dye was injected with a syringe into an inside corner of a sealed box. The dye began to spread and within 20 minutes was uniformly dispersed inside of the box. The spreading of the dye was not entirely a diffusive process. The box was not rigid and pressure gradients caused by passing waves agitated the water inside the box. Using the same dye injection procedure, it was established that the taking of a one-liter water sample would mix the water inside the box. The most thorough way found to take a mixed water sample was to suck up about 500 ml of water into the sample bottle, then gently squeeze the bottle and force about 200 ml back into the box and then to continue taking the sample. In addition, in box type #2 (Fig. 3), the process of pushing the plungers into the box also helped mix the water. Therefore, even though the water inside the box was relatively stagnant, it was probably mixed by convection, slight turbulence, by the process of taking a water sample and by diffusion.

To serve as a control on the rate of nutrient flux caused solely by the water above the sediment enclosed in the box and to quantitatively determine this flux, light and dark bottle measurements were made in the experiments of May 12, 1971, through October 10, 1972. They were discontinued because the activity in the water was so low that it would not affect the results of the box experiments.

The procedure for these controls followed one of two routines. In the experiments of May 12, 1971, through June 6, 1972, several liters of bottom water were sampled as described previously. A sample was brought back to the surface, mixed, and poured into a two-liter, glass-stoppered transparent (light) bottle and into a darkened (wrapped with black electrical tape) bottle. These bottles were returned to the bottom and incubated next to the boxes. In the experiments of June 21, 1972, through October 10, 1972, the light and dark bottles were filled with surface water and brought to the bottom. The water inside the bottles was then displaced with air from a SCUBA tank. The bottles were then slowly rotated from an upside-down position to a right-side-up position, allowing the bottom water to slowly enter. The glass stoppers were then replaced and the bottles were incubated next to the experimental boxes.

In all subsequent treatments and analyses, the water from the bottles and boxes were treated in the same manner. These included pre-filtering, nutrient analyses and analyses for chlorophyll _a_, phaeopigments, and number of bacteria.

The experimental procedure described above had some inherent problems. A major problem encountered with the use of the boxes was scouring. Surge moving back and forth across the boxes, was accelerated

around the corners. If the flow was great enough, sand around the edges of the boxes would be carried away. A number of experiments were ruined when the sand at one or more of the corners was scoured away, allowing free interchange of the outside water with that inside the box. By sinking the boxes 5 cm into the sediment this problem was lessened but not eliminated. To further alleviate the problem, deflectors were placed around the boxes to slow down the rate at which the corners would be scoured. These deflectors were four rectangular pieces of clear acrylic plastic, 30 cm x 10 cm x 9.5 mm which were pushed into the sediment approximately 5 cm from the sides of the boxes. Two deflectors were placed on each of the two sides of the boxes that were directly in line with the water movement caused by the surge. The deflectors were not inserted perpendicular to the sediment surface but rather at a slight angle slanting back towards the box. All experiments in which one or more corners were scoured out completely were terminated. This occured mainly in the winter and early spring when the area was hit by large storm waves.

Several other experiments were terminated for biological reasons. In one experiment, a California Grey whale was seen to be acting strangely in the vicinity of the sampling site on the day of an experiment. It was later found that the whale had hit some stakes that protruded from the bottom at this site and had bent them. It also had hit the light and dark boxes, breaking them. On another occasion an octopus "attacked" the dark and light boxes, pulling out most of the stoppers and the sampling port. The octopus was later found using two of the stoppers to plug up the entrance to its shelter hole. In total, approximately 13 of 52

experiments were terminated. These did not include those which were set up and subsequently cancelled due to adverse weather conditions.

The nutrient exchange rate between the benthos and the overlying water could be obtained in two ways other than is given in this investigation. One way is to measure the nutrient gradient across a distance or depth z_1 to z_2, and simultaneously measure water movement. From these data the flux could be calculated. There are a number of problems with this approach. If the water were stagnant, then the concentration gradient across a distance (z_2-z_1) would be a good measure of exchange. If the flux were very low then the distance (z_2-z_1) would only need to be greater. Also, there could be no biological or chemical exchange of the nutrients in the water. However, in shallow coastal waters the nature of the water movement precludes gradient measurements. Immediately at and above the sediment surface a gradient measurement might be attempted but with (z_2-z_1) so small the flux would have to be high. Also, at the sediment-sea water interface there is a great deal of water movement caused by both surge and currents. Turbulent water mixing, therefore, prevents the measurement of a nutrient gradient across small distances close to the sediment surface where the nutrient gradient is the largest.

A second way would be to measure the nutrient gradient going down into the sediment and to assume that nutrient cycling within the sediment is non-existent or at a minimum and, secondly, to assume that the surface acts just as the deeper sediments. The first assumption is necessary if one believes that a nutrient gradient is actually a diffusive gradient and the nutrients are diffusing out of or into the sediment.

This appears to be a valid assumption for undisturbed sediments (Lerman and Brunskill, 1971; Mortimer, 1971; Okuda, 1960; Rittenberg et al, 1955). However, the second assumption is clearly not valid. The disturbance of surface sediments, the presence of a photosynthetically active benthic flora, and the input of organic matter to the surface layer of sediment at the experimental site used in the present study precludes the validity of the second assumption.

The method used in this investigation measures nutrient exchange directly and takes into account surface sediment conditions. The only assumption made is that isolating the sediments being examined does not alter the nutrient exchange. Over the short time intervals in which the boxes were in place this appears to be a valid assumption.

Replicate Nutrient Exchange

The methods used for these experiments were the same as discussed above. However, instead of a single light and a single dark box, several of either the dark and/or light boxes were used. In all cases the positioning of the boxes at the site was to insert the first box and then to insert the second and succeeding boxes 15 cm to 30 cm from each other, all in a straight line.

Sediment Cores

The sediment cores were taken for the following analyses: chlorophyll a/cm^3, phaeopigments/cm^3, number of bacteria/cm^3 and inorganic and organic carbon content, as percent of dry weight of sediment. All of the above analyses involved a subcoring of the original core. The subcoring technique is described in the section on Laboratory Methods.

The main corer used consisted of a piece of polyvinylchloride

(PVC) tubing (4.75 cm O.D. x 4.3 cm I.D.) approximately 13 cm long (Fig. 5). To take a core, the bottom plate and top stopper were removed and the corer was gently pressed about half its length into the sediment. The top stopper was then reinserted and the exhaust tube clamped shut. The bottom plate was slipped into place and secured to the corer by a piece of rubber tubing stretched over it, as the corer was removed from the sediment. The corer was then placed upright, in a carrying rack.

To obtain deeper sediment, a clear, acrylic plastic tube of the same diameter as the PVC corer but 30 cm long was used. It was plugged at the top and bottom with a rubber stopper. To obtain a core, both stoppers were removed and it was gently pushed and rotated into the sediment. With the corer almost entirely inserted, the top stopper was replaced and the corer slowly pulled out. As the corer cleared the surface of the sediment, the bottom stopper was put into place. As the bottom stopper was pushed in, the top stopper was removed to allow for the expulsion of water. When the bottom stopper was fully and securely in place, the top stopper was again replaced. This corer was then hand held in an upright position and brought back to the surface where it was placed in a holder.

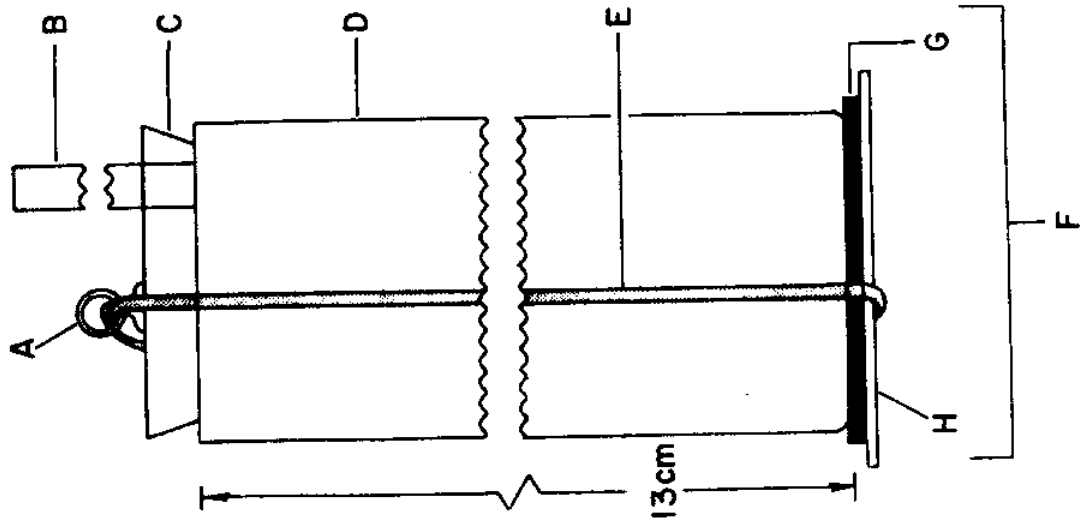
By using these techniques the sediment cores obtained were undisturbed except for a small region near the walls of the corer. Also, unlike remote corers, this technique allowed the operator to pick the exact sampling site desired. With this technique one is also able to discard any cores which are disturbed and, then with a minimum of effort, another core can be taken.

FIGURE 5

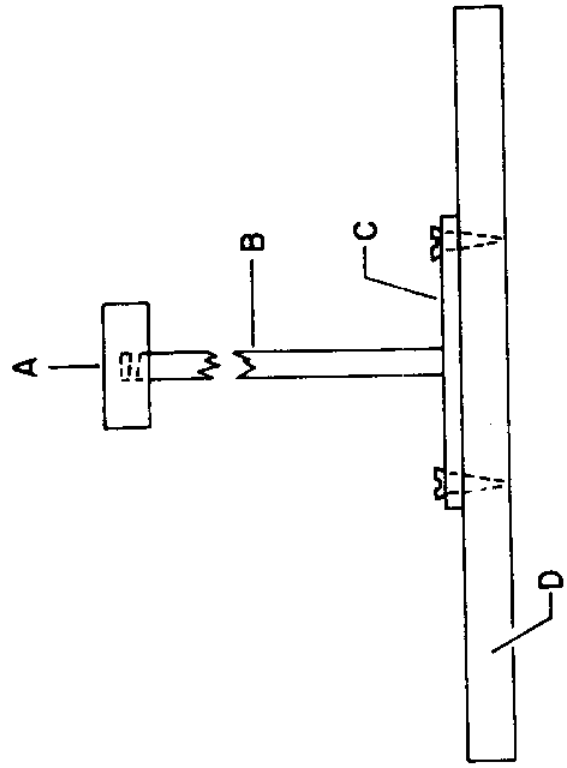
Core Extruder (left) showing PVC block machine to I.D. of corer (A), the PVC support (B), the base plate to which the PVC support is welded (C; 10 cm x 10 cm) and the wooden base of the extruder (D; 70 cm x 70 cm).

Corer (right) showing eye screw (A), exhaust tubing (B), #9 1/2 stopper (C), PVC pipe (D; 4.75 cm O.D. x 4.3 cm I.D. x 13 cm long), rubber tubing band (E), and the bottom plate (F) composed of 3.2 mm or 6.5 mm thick foam neoprene (G) plus the 7.6 cm x 6.35 cm x 1.6 mm thick aluminum plate (H) to which the neoprene is taped.

CORER



CORE EXTRUDER



Relative Sediment Height

The method used to measure relative sediment height was that of Inman and Rusnak (1956). Four stakes were driven into the sediment at the site of the experiments. The distance from the sediment surface to a permanent mark on each stake was recorded using a transparent T-square (Fig. 6). Sediment movement was determined by subtracting this height (zero level) from the height measured on the same stake at a later date. The average value, in centimeters for all four stakes was taken as the depth of sediment either gained or lost over the particular interval.

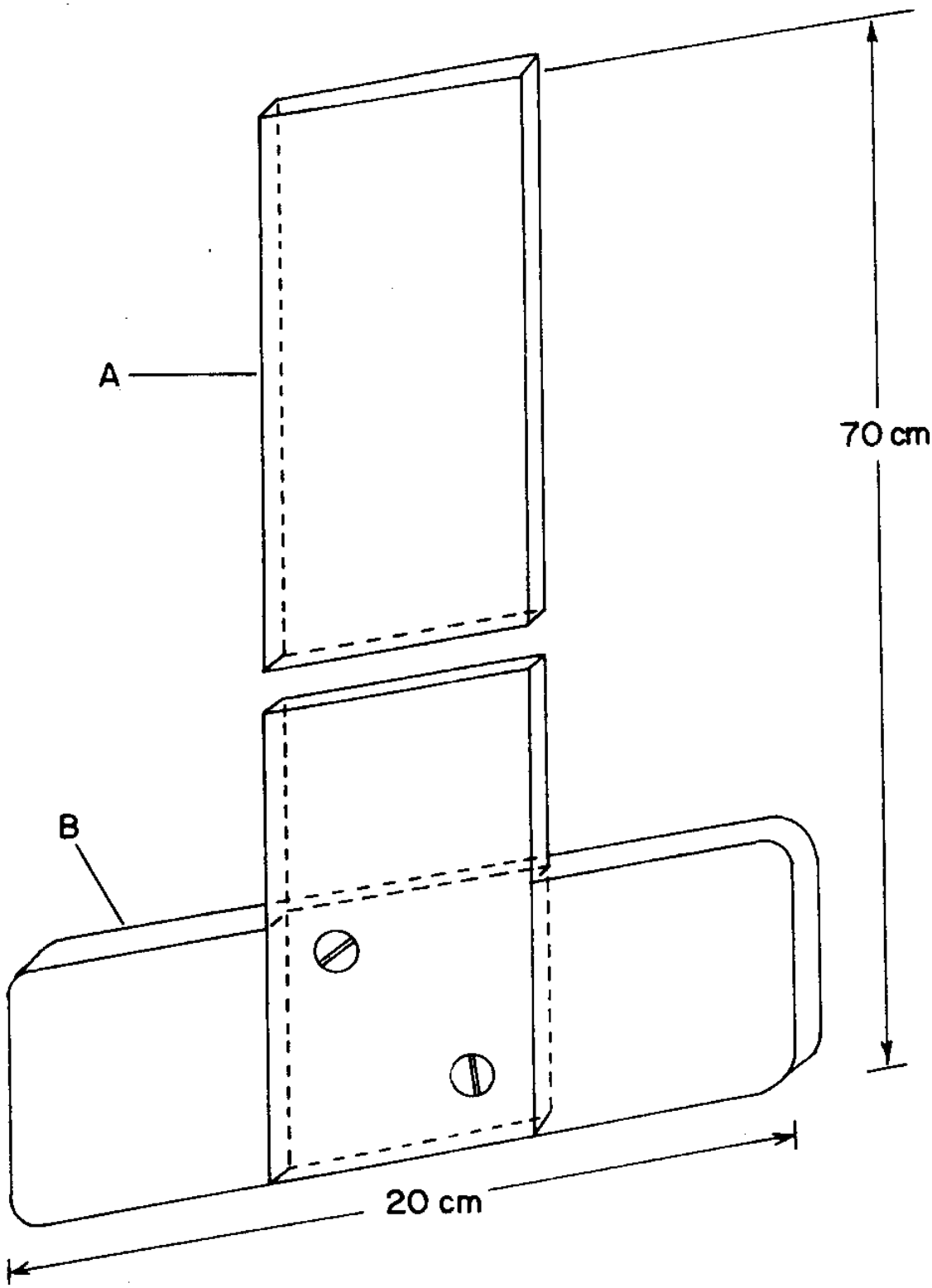
This is a measure of relative sediment height and not a measure of total sediment movement. The relative height change over an interval of time may be zero, but the amount of sediment movement may have been great. The problem is that the relative height may remain unchanged but the sediment at the experimental site may have been transported to another location and replaced by sediment from shallower or deeper waters.

Macro-Detritus Collections

The definition of macro-detritus is, for the purposes of this dissertation, all debris lying upon the surface of the sediment which is seen by a diver and can be picked up by hand and placed in a 4 mm bag. This material included mostly Phyllospadix blades and their living and nonliving attachments, e.g. sand, worm-tubes, periphyton and perifauna. The macro-detritus also contained Macrocystis debris, other algal fragments, wood, etc., as well as attached communities. None of the plant macro-detritus was indigenous to this study site so it must have entered the region by settling out of the water column or by being

FIGURE 6

Acrylic T-square showing the clear-acrylic measuring portion (A) and the wooden base plate in which it is secured (B).


A
B
70 cm
20 cm

transported across the sediment surface by water movement. To determine the quantity of material entering the study area, two four-square meter permanent quadrats (2 m x 2 m) were laid out at the experimental site. Initially all of the macro-detritus lying within the quadrats was removed. Input values for macro-detritus (as $g/m^2/day$) were thus derivable by subsequent collections of the material which had entered the quadrats during a given period of time. The storage of the macro-detritus and techniques used to analyze it are given in the section on Laboratory Methods.

Detrital Fallout

Detrital fallout consists of fine suspended material in the water column having a density greater than sea water and would, therefore, sink and fall into traps designed to catch this type of material. The traps were set on a long pipe stake (2.5 cm O.D.) driven into the sediment and protruding approximately two meters above the sediment. Twenty centimeters below the upper end of the stake a "stop" was made by securing a piece of neoprene to the pipe with a hose clamp. The purpose of the "stop" was to prevent the trap from falling below the 20 cm level.

Each trap consisted of two units. One unit was a baffle system with a number of attached 89-mm screw caps, from which the entire center section was removed leaving only the threaded portion. These caps were permanently attached to the underside of the baffles using a silicone sealant. The baffles were made of plastic, 12.5 mm, eggcrate-louvred flourescent light diffusers. They were designed to prevent surge and wave action from scouring out the trapped material. The basic design was suggested by Mr. Andrew Soutar of SIO. The second unit of the

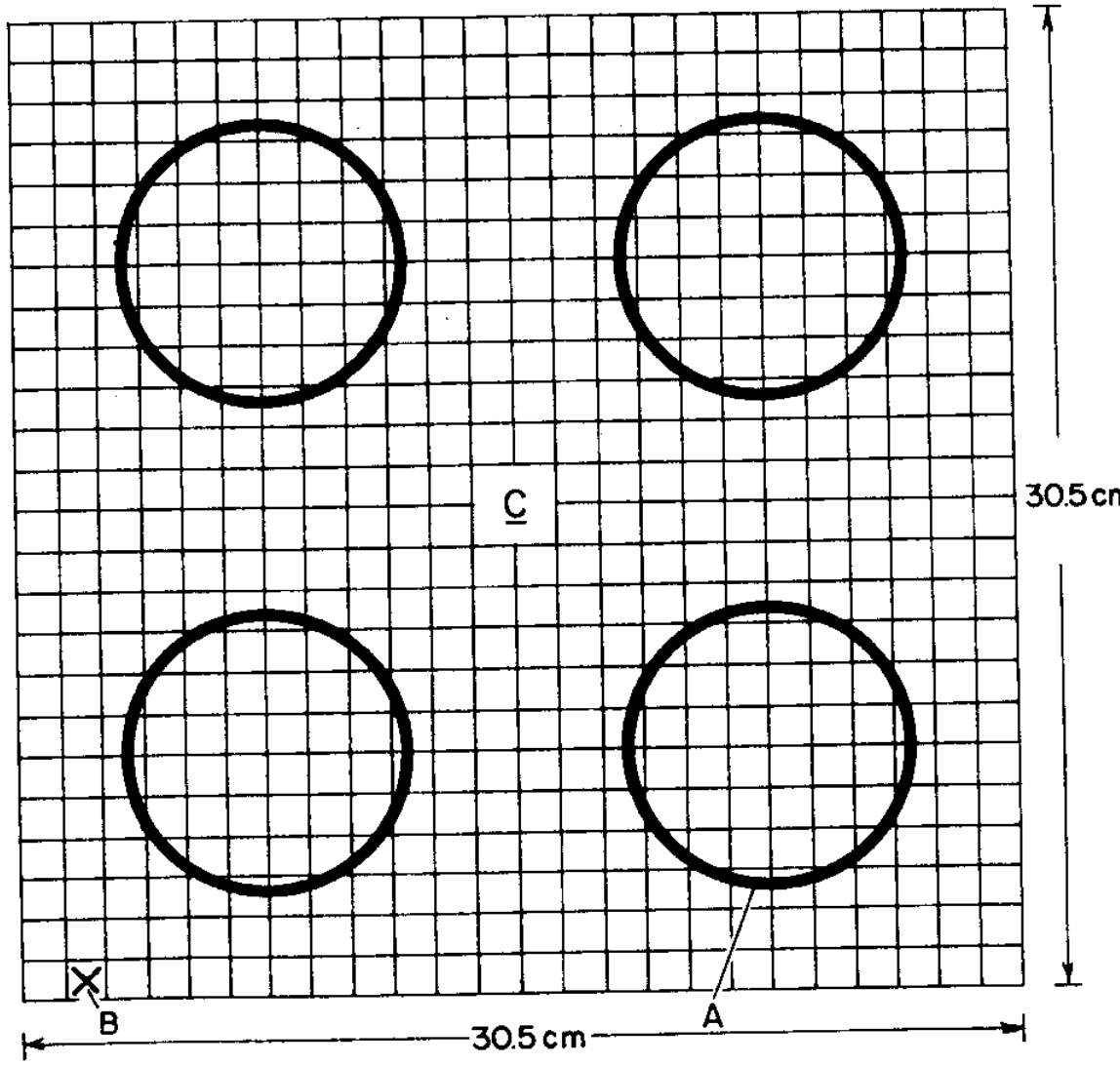
trap consisted of a number of 450 ml jars which were the actual collection vessels. The jars fastened into the screw caps mounted in the underside of the baffles. Inside each jar for the August 22, 1972 and subsequent collections, there was a 4-6 gm plastic vial with small holes in the sides. The vials were full of mercuric chloride ($HgCl_2$). When immersed in sea water the $HgCl_2$ in the vials would slowly go into solution and diffuse into the surrounding water in the jar. The purpose of this was to slow down and hopefully inhibit the growth of organisms that entered the jar and, thereby, arrest or decrease the rate of respiratory loss of organic carbon from the collection jars. (Entire trap minus collection jars and $HgCl_2$ vials is shown in Fig. 7.)

Visual inspection of the traps showed that the $HgCl_2$ did deter all macroscopic growth, as evidenced by the growth on all of the traps that did not contain $HgCl_2$. This growth was mainly bryozoans and algae. Also, those jars without $HgCl_2$ quickly became a home for a number of small crabs and zooplankters, while in those jars containing $HgCl_2$ the presence of macrofauna was never observed. This is interpreted as meaning that the jars with $HgCl_2$ were avoided by those organisms capable of doing so, or if the organisms did settle they died due to the presence of $HgCl_2$. However, bacterial titers enumerated as CFU by the dilution spread-plate method, revealed as many colonies from the detritus with $HgCl_2$ as from that without $HgCl_2$.

The dilution spread-plate technique for enumerating bacteria consisted of the following. The material in the jars was allowed to settle and the sea water was decanted. The slurry left in the jars was mixed manually and a 1.0 ml aliquot was taken and placed into 9.0 ml

FIGURE 7

Baffled sedimentation trap showing 89 mm screw-cap jar lids with center cut out (A), the 4 layers of 12.5 mm eggcrate louvered flourescent light diffusers (B) and the center hole (C) for the insertion of trap onto 2.5 cm O.D. iron pipe.


C
30.5 cm
B
30.5 cm
A

of sterile sea water. Successive ten-fold dilutions were made and duplicate 0.1-ml aliquots of all dilutions were spread with a glass rod on 80% sea water C-P media (composition given in section on Laboratory Methods). This was done for samples from the detritus with $HgCl_2$ and those without $HgCl_2$.

Although the numbers of bacteria indicated no difference between the detritus with $HgCl_2$ and that without $HgCl_2$, oxygen uptake studies revealed subtle differences. The method used to determine oxygen uptake rates was a modification of classical BOD (Biochemical Oxygen Demand) techniques. Into each of a number of glass-stoppered bottles of known volume, a known weight of fallout was added. The bottle was then filled with sterile sea water which had been equilibrated with oxygen at 17°C. Some of the samples were immediately "pickled" for analysis by the Winkler titration (Strickland and Parsons, 1968), whereas others were incubated at 17°C for nine days and then pickled. All values were corrected for the volume of the BOD bottle, the weight (as dry weight) of fallout added and the total time of incubation. Also, in the case of the nine-day samples the values were corrected for initial uptake rates.

The initial oxygen uptake rates were not the same (with $HgCl_2$ = 0.090 mM O_2/g and without $HgCl_2$ = 0.092 mM O_2/g). These rates were not significantly different but they indicated that the fallout in the jars without $HgCl_2$ had a slightly greater uptake rate indicating more reducing substances were present. This observation can be interpreted that there had been more biological activity occurring in the fallout without $HgCl_2$ prior to its collection. Also, over a nine day incubation

at 17°C, the fallout with $HgCl_2$ had a greater uptake rate than did the samples without $HgCl_2$ (with $HgCl_2$ = 1.9 x 10^{-3} mM O_2/g/hr and without $HgCl_2$ = 8.5 x 10^{-4} mM O_2/g/hr). This difference indicated that in the jars with $HgCl_2$ the fallout contained more oxidizable organic matter than did the fallout from the jars without $HgCl_2$. The conclusion of this study was that prior to collection, there had been more biological activity in the jars without $HgCl_2$ and, therefore, less oxidizable organic matter remained.

Overall, the presence of the $HgCl_2$ in the fallout reduced the amount of organic matter lost due to the metabolism of all organisms as compared to that lost from the fallout without $HgCl_2$. Therefore, all of the fallout rates given in this dissertation are conservative, with the ones before August 22, 1972, being more conservative than the subsequent rates since $HgCl_2$ was not in the collection jars. The rate of metabolism that occurred in the jars in the field is unknown, therefore, no estimate can be given as to how much organic matter was oxidized prior to collection. However, by employing the Nemenyi Adaptation to the Kruskal-Wallis Analysis of variance using ranks (analysis performed by Dr. A. Barnett, SIO), it was found that with 95% confidence it is certain that the amount of time the traps are in place does not change the percent organic carbon to such an extent that the time factor overshadowed other factors for determining the variability in percent organic carbon. The interpretation of this is one or a combination of the following: 1) the variability in percent organic carbon is due to the chemical nature of the fallout; 2) other factors determine the percent organic carbon; 3) organic carbon respiration and loss is accompanied by a loss of a relatively equal amount of inorganic matter; and 4) the amount of

organic carbon lost is so low that it cannot be detected.

The procedure used for sampling the traps was as follows. A new trap with bottles and vials in place was brought to the site and turned upside down to prevent sand from entering while it was not in place on the stake. Each jar on the trap already in place was slowly unscrewed until it was free of the screw cap and baffle. Quickly a complete cap was placed on the jar and tightly secured. When all jars had been removed from the old baffle, the baffle was removed from the stake and brought back to the laboratory for cleaning. The new trap was installed on the stake. Since the area of the screw cap which was open was known ($42\ cm^2 = 0.0042\ m^2$) and the amount of material which fell into the trap over a given time interval was known, the amount of material falling per square meter per unit of time was calculated:

$$g\ material/m^2/day = g/jar \times \frac{1}{number\ of\ days\ jar\ in\ place} \times \frac{1}{0.0042}\ m^2$$

per jar.

The analytical techniques used for analysis of the collected material are given in the section on Laboratory Methods.

Temperature

The temperature, measured in degrees Celsius (°C), was taken with a hand-held mercury thermometer and recorded to the nearest tenth of a degree. Bottom water temperature was taken by holding the thermometer one or two centimeters off the bottom, while sediment temperatures were taken by inserting the thermometer approximately one centimeter into the sediment and recording temperature after equilibration. In all cases the sediment temperature was the same as bottom water temperature inside

the box, therefore, only bottom water temperatures were recorded. During some of the period a Ryan model F-15® recording thermometer was used in conjunction with the mercury thermometer. Daily surface and five meter depth temperature measurements were obtained from data recorded by the SIO Aquarium Museum.

Sediment Incident Irradiation

This measurement was made using data gathered from two separate sources. The first source was a recording bimetallic actinograph (Kahl Scientific Corporation, San Diego, California) placed on the roof of Sverdrup Hall (SIO), and the second was a secchi depth taken at the experimental site. Since the bimetallic actinograph measures total solar radiation, and only the photosynthetically active spectrum of sunlight (3800 Å - 7200 Å) was of concern, all sunlight energy values obtained were corrected by multiplying by a factor of 0.5 (Strickland, 1958). At the sea surface a substantial portion of the total radiant energy is reflected and back-scattered from particles just below the surface and perhaps lost by a third unknown process (Strickland, 1958).

Upon entering the water the vertical extinction of sunlight is dependent on the sum of three separate coefficients: the coefficient for pure water, the coefficient due to absorption by suspended particulate material and dissolved substances, and the scattering coefficient due to suspended particles (Strickland, 1958). The scattering light coefficient, unlike the other two, has the effect of increasing the total available light to an organism (organisms are exposed to back-scattered as well as vertical illumination) by a factor of 1.2 to 1.3 (Jerlov, 1947). However, since the experimental substrate of these

studies was sediments which receive chiefly vertical illumination, the scattering coefficient was not used.

One must consider the depth of light penetration into the sediment. Taylor (1964), using sandy sediments similar to the ones found off SIO in 18.3 m of water, found that only 10% of the sediment surface irradiation reaches 1.5 mm below the sediment surface. According to Fenchel and Straarup (1971), less than 50% of the sediment surface illumination will penetrate one millimeter into a clean siliceous sand, and the greatest penetration is by quanta at the red end of the spectrum. They also found that the larger the sand grain diameter the deeper the penetration. Since the red light is essentially completely absorbed in 18.3 meters of water and because the sand is fine-grained with a great deal of detritus in it, the amount of light penetrating greater than one millimeter approached zero. For this reason it was assumed that all light effects are predominant only at the surface of the sediment.

To determine the percent of the surface irradiation reaching the sediment surface, an approximation of the vertical extinction coefficient (k) of the water was made by taking a secchi depth. The coefficient is derived from the equation $I = I_o e^{-kz}$ (Strickland, 1958), where z = depth in meters, I = percent light at z, I_o = percent light at the surface, and in this case, equalled 100. To approximate k, z was assumed to remain constant at 18.3 m and three times the secchi depth (S.D.) was taken as being the 1.0% light level. This has been shown to be fairly good estimate in the waters off of SIO (Strickland, 1958, 1970). Using this estimation the above equation reduced to $1 = 100\ e^{-k\ (3 \times S.D.)}$. Solving this equation yields k = 1.535/S.D., where S.D. is in units of meters.

The k for each secchi depth was calculated from this equation and that value was used in the equation $I = 100\ e^{-k(18.3)}$ to determine the percent of surface irradiation reaching the sediment surface. The final calculation consisted of multiplying the percent surface irradiation reaching the sediment surface on a particular day, by the amount of photosynthetically active light striking the sea surface on the same day as measured by the bimetallic actinograph. This data was then expressed as calories/cm^2/day or langleys/day.

IV LABORATORY METHODS

This section details the methods used in the laboratory to analyze the numerous field samples.

Oxygen

Oxygen was determined using the Winkler method (Strickland and Parsons, 1968) and was modified for use with 35 ml to 40 ml samples.

As soon as possible after the water samples were taken (described previously in the Field Methods section) they were brought to a laboratory at the SIO pier where several 35 ml to 40 ml glass-stoppered bottles were filled and the contents immediately "pickled" with the Winkler reagents. At the beginning of an experiment four bottles were usually filled while in subsequent samplings each experimental box or bottle had duplicate oxygen values determined. The time between taking the sample and pickling was, in almost all cases, less than one-half hour. To ascertain whether or not there was an effect on the oxygen concentration in the sample bottles over this period, a time series experiment was performed. On a number of samples taken at the same time the following series of oxygen determinations were made: 1) as soon as possible after the skiff was boarded after collecting the samples (10 minutes), 2) at the laboratory at the end of the pier (20 minutes), 3) immediately after storage of the diving gear (40 minutes) and 4) after returning to the shore-based laboratory (100 minutes). The results of this time series showed that there was no change in the oxygen concentration from the skiff (10 minutes) to the laboratory (100 minutes). Therefore, in the time it took to reach the pier and to "pickle" the

samples in an experiment, there was no measureable change in the oxygen concentrations.

The oxygen analysis yielded values in units of mM O_2/liter. Values were then corrected for the number of liters of sea water contained in the box or bottle, and also, in the case of the boxes the values were corrected for the number of square meters covered or enclosed (9.0×10^{-2} m^2). This gave values in terms of mM O_2/box (bottle)/m^2 (ℓ). To obtain the production or uptake rate of oxygen, the values derived at the second or later samplings were subtracted from the zero time values, and this was multiplied by 1/number of hours of incubation. The results were then in the form of mM O_2/m^2/hour either produced (+) or taken up (-).

Sea Water Filtration and Sample Storage

The sea water samples, in the plastic sample bottles, were brought back to the laboratory within two hours of collection. There, the samples from each box or bottle were prefiltered through a clean 35-µm mesh Nitex-phytoplankton net into a large acid-cleaned Erlenmyer flask. Visual examination of the material trapped on the net taken from the boxes showed it to sometimes contain a few zooplankton. This was rare, probably because the zooplankton could actively avoid being sucked up by the sampler since it took several minutes to fill a one liter sample bottle (Fleminger and Clutter, 1965). The prefilter also trapped some of the larger phytoplankton, but it was a rare occurrence since the numbers of large phytoplankton are low in the water off SIO (Strickland, 1970). The prefilters used for the samples from the bottles showed similar results.

The prefiltering of a sample was necessary, however, to remove all fine-grained sand particles from the samples of sea water. These particles, if allowed to remain, would interfere with some of the subsequent analyses. The particles, being denser than sea water, would settle quickly in the sample bottle even when the sample was mixed thoroughly. The first aliquots taken from these sample bottles would contain few, if any, particles, but aliquots taken closer to the bottom of the samples contained more and more of the particles. Therefore, those analyses that required filters of these later aliquots would give extraneous values. The filters which were analyzed, therefore, contained only bacteria and phytoplankton, and essentially no zooplankton.

The prefiltered samples were immediately refiltered for specific determinations and then stored until analyzed. For the second filtration the glassware was acid-washed (acid washing, unless otherwise stated, used a chromic acid solution of concentrated sulphuric acid and potassium dichromate) and heated to 550°C for 4 hours. The filters were Reeve Angle 984H 2.4 cm glass-fiber filters papers® which had been prewashed in deionized water to remove inorganic contaminants (NH_3-N was found to be prevalent on unwashed filters) and then combusted at 450°C for two hours to remove insoluble organic contaminants. These filters were suitable for removing bacteria from the filtrate. A vacuum of 170 mm of mercury (Millipore® pump) was used for each filtration.

Since particulate samples were also needed (chlorophyll *a* and phaeopigment analysis) specific volumes of the prefiltered sample were filtered. The filters for chlorophyll *a* and phaeopigment analysis were placed in conical 15-ml glass-stoppered centrifuge tubes. The filters

were covered with 90% acetone and stored in the dark at room temperature. During filtration for chlorophyll a and phaeopigments, several drops of a 1% suspension of $MgCO_3$ in water were added to ensure that the chlorophyll a solution did not become acidic.

After obtaining the desired number of filters for particulate analyses and after removing the final filter, the filtrate was stored in two glass-stoppered 250-ml acid-washed and baked (190°C for 4 hours) bottles. After filling each bottle approximately 4/5 full, a number of 5.0-ml samples were taken with an acid-washed 10cc syringe and injected into combusted 10-ml ampoules which were then covered with aluminum foil. These ampoules, for DOC analyses, were frozen at -20°C. The 250-ml bottles containing the filtrate were stored after replacing the stoppers and covering them with aluminum foil. The filtrates were placed in a freezer (-20°C) until analyzed. To prepare the filtering apparatus for the next sample, the remainder of the filtrate was emptied, and the flask rinsed with the next sample after filtering approximately 100 ml.

Ammonia

The method to determine ammonia was that of Solorzano (1969), modified for use with 10-ml samples. A 250-ml sample was thawed, shaken thoroughly and duplicate 10-ml aliquots were pipetted into acid-washed and aluminum foil-covered test tubes (18 mm). The ammonia analysis was always performed on the first thawing of a sample. The sea-water sample, in an alkaline citrate medium, was treated with sodium hypochlorite and phenol in the presence of sodium nitroprusside catalyst. The extinction of the color complex formed was measured in a spectrophotometer at 643 nm and the results are given in μM NH_3-N/l.

To obtain the production or uptake rates in μM NH_3-N/m^2/hour, the values obtained were treated as described under Oxygen at the beginning of this section.

Nitrite

The method for nitrite analysis used was based on the classical Griess reaction, in which nitrous acid is converted to an "azo" dye and the μM NO_2-N/l determined by obtaining the extinction of the sample solution at 543 nm. The method is outlined in Strickland and Parsons (1968) but was modified for use with 10-ml aliquots. Duplicate 10-ml aliquots were obtained from the 250-ml sample bottles as previously described in this section.

The production or uptake rate of nitrite in μM NO_2-N/m^2/hour was obtained as described under Oxygen in this section.

Nitrate

The procedure used for nitrate analysis was that described in Strickland and Parsons (1968). The method was further modified for use with 10-ml aliquots. As with ammonia a 250-ml sample was thawed, shaken thoroughly and duplicate aliquots were pipetted into acid-washed and alumimum foil covered test tubes (18 mm). The nitrate was determined by its reduction to nitrite in a cadmium-copper column. The nitrous acid was then converted to an "azo" dye. The extinction of the complex was measured in a spectrophometer at 543 nm and the results expressed in μM NO_3-N/l.

Production of uptake rates of nitrate were obtained as described under Oxygen at the beginning of this section. The final results were in units of μM NO_3-N/m^2/hour either taken up or produced.

Phosphorus

The procedure used for phosphorus determination was that given in Strickland and Parsons (1968). In this method the phosphorus in sea water reacts with a solution of molybdic acid, ascorbic acid and trivalent antimony. The resulting complex acid gives a blue color. The extinction of this solution was measured in a spectrophometer at 885 nm to yield μM PO_4-P/l. This method determined the total concentration of soluble "reactive" phosphorus (Strickland and Parsons, 1968). As with the other methods for determining inorganic plant nutrients, this one was also modified for use with 10-ml aliquots. The duplicate 10-ml aliquots were obtained from the 250-ml sample bottles as described earlier in this section.

The production or uptake of phosphorus in μM PO_4-P/m^2/hour was obtained as given in this section under Oxygen.

Dissolved Organic Carbon (DOC)

The method used to determine DOC was that described in Strickland and Parsons (1968). The 5-ml aliquots of filtered sea water in 10-ml ampoules were prepared as described previously. To analyze for DOC, the samples were thawed, treated with 3% phosphoric acid (v/v in organic free water) and approximately 200 mg of potassium persulphate, and then bubbled with nitrogen for five minutes to remove inorganic carbonate. Finally the ampoules were hermetically sealed and the organic carbon oxidized to carbon dioxide (CO_2) by heating the sealed ampoules to 130°C for 40 minutes in a high pressure autoclave (124 cm Hg for 40 min.). The amount of carbon dioxide in each ampoule was determined with an infrared absorption spectrophotometer coupled with an integrator.

The only modification to the described method was, in some analyses, gas standards of known carbon dioxide content were used instead of the liquid standards normally used. The gas standards were from a bottle of nitrogen gas of known carbon dioxide content. The equation for converting the CO_2 content of the bottled gas, given in parts per million (ppm), to mg C/l of sea water was:

$$\text{mg C/l sea water} = \frac{\text{ppm } CO_2 \times 10^{-6} \text{ ml/ppm } CO_2 \times 12 \text{ mg C/mM}}{22.4 \text{ ml/mM}} \times 200/1$$

A factor of 200 was used since 5 ml of sample was analyzed and not 1000 ml.

The standard data was used to compute a linear regression equation of $y = a + bx$ (where y = mg C/l; a = y intercept in mg C/l; b = slope and x = area under the curve). The integrated area of the CO_2 in a sample minus the blank value was then substituted for x and the equation solved for y. When using liquid standards the blank value was subtracted from both the standards and samples before solving the above equation. When using gas standards the blanks were subtracted only from the samples and the above equation was solved for the unaltered standard data.

Dissolved Organic Nitrogen (DON)

The method employed for DON analysis was that given in Strickland and Parsons (1968) and is based on the observation that when oxygenated sea water is exposed to high intensity radiation of a wavelength less than 250 nm (UV light) most of the organic nitrogen is oxidized to give a nitrate-nitrite mixture. The UV irradiation is effective on almost all organic nitrogen compounds. However, urea is extremely resistant to oxidation, therefore, one suspects that there may be other organic

nitrogen molecules which are not affected by UV irradiation. This probably introduces slight error, if any, and comparisons of results obtained by the classical Kjeldahl determination and UV irradiation show that there are no systematic differences (Strickland and Parsons, 1968).

The nitrate-nitrite mixture was then analyzed for nitrate with a cadmium-copper column as described under Nitrate in this section. The value obtained was compared with the same un-irradiated sample. The difference between the irradiated samples minus the concentration of NH_3-N, NO_3-N, plus NO_2-N in the un-irradiated sample equals the concentration of DON in μM N/l.

For UV irradiation, a 250-ml sample was thawed, shaken thoroughly, and then an aliquot (approximately 100 ml) was poured into a quartz-glass irradiation tube, capacity of approximately 125 ml. Five drops of 30% hydrogen peroxide were added and the entire contents of the tube mixed. The tube was then placed into the UV irradiator. There were two modifications made to the method as given in Strickland and Parsons (1968). The first was that, after irradiation, 10-ml aliquots were collected for total nitrate-nitrite analysis. The second modification was that the samples were irradiated overnight. As all of the irradiated water was not used for DON analysis the remainder was used for the analysis of DOP described below.

The production or uptake of DON in μM N/m^2/hour was calculated as outlined under Oxygen in this section.

Dissolved Organic Phosphorus (DOP)

The method for DOP determination was that given in Strickland and Parsons (1968). As with the DON analysis high intensity radiation of a

wave length of less than 250 nm catalyzes the oxidation of organic molecules containing phosphate-ester or phosphinic acid bonds. The phosphorus is liberated as orthophosphate. All organic phosphorus molecules are decomposed except polyphosphate where the linkages are not broken (Strickland and Parsons, 1968). This method, therefore, simply measures the difference in orthophosphate concentrations before and after irradiation to determine the organic phosphorus concentrations in sea water.

The method of preparation and treatment of the samples through the irradiation procedure was the same as that given for DON. The modifications to the method were also the same as was mentioned for DON analysis. The concentrations of DOP are in the form of μM P/l, and to convert these values to μM P/m^2/hour, the same calculations were used as in the Oxygen section.

Sea Water Chlorophyll a and Phaeopigment

The filters in conical test tubes, obtained as previously described in this section, were removed from the tubes, and ground in a tissue homogenizer. The filters and extracted pigment were transferred to their respective centrifuge tubes and the volume of extract made to 10 ml with 90% acetone (v/v in acetone). The tubes were centrifuged and the concentration of chlorophyll a, in units of μg chlorophyll a/l, was measured using a Turner Fluorometer® (Strickland and Parsons, 1968). The same extract was then acidified with two drops of a dilute hydrochloric acid solution and the concentration of phaeopigments (μg phaeopigments/l) determined, also using the fluorometer (Strickland and Parsons, 1968).

Number of Bacteria in Sea Water

The spread-plate technique for enumerating bacteria was used throughout this study. The freshly collected sample of sea water (before prefiltering) was thoroughly shaken. A 1-ml subsample was pipetted into 9.0 ml of sterile sea water and the resultant suspension shaken. This ten-fold serial dilution procedure was continued until the concentration of bacteria was reduced to approximately 10^2/ml in the highest dilution tube. Duplicate 0.1-ml aliquots were taken from each dilution and placed on the surface of an 80% sea water C-P agar medium (Carlucci and Pramer, 1957). C-P agar medium contained 5.0 g Difco peptone, 0.1 g Difco yeast extract, a trace of ferric phosphate, 15 g Difco agar and 1000 ml of 80% sea water in deionized water. The aliquot was spread evenly over the surface of the agar using a sterile glass rod. The plates were inverted and placed in a large plastic bag to prevent dehydration of the agar medium. The plates were incubated at 15°C in the dark. After two weeks the number of colonies growing on the plates were counted and expressed as colony forming units (CFU) per milliliter of sample.

Extrusion and Subcoring of Sediment Cores

The sediment cores (obtained as described in the Field Methods section) were treated in one of two manners. The long (deep) cores were taken solely for the purpose of enumerating the number of bacteria with sediment depth. These cores were, therefore, not disturbed until extruded and subcores obtained. The subcoring technique is described below and the bacteriological analysis follows later in this section.

The shorter cores were routinely taken in each experiment. These cores were used for; 1) bacterial enumeration at the sediment surface,

2) total sedimentary organic and inorganic carbon analysis, and 3) sediment chlorophyll a and phaeopigment analysis. To obtain sediment samples for these analyses it was necessary to extrude and subcore the core.

To extrude short cores, the rubber-tubing band holding the bottom plate in place (Fig. 5) was removed and the top rubber stopper pulled out. Most of the sea water overlying the sediment was aspirated with a large rubber bulb. The bottom plate was pulled off just as the core was placed over the core extruder (Fig. 5). The extruder consisted of a wooden base to which was attached the metal support of the plunger. The plunger was a disc of polyvinyl chloride (PVC) which was machined to a diameter of slightly smaller than the inside diameter of the corer. This small difference in diameter allowed the sea water overlying the sediments to slowly seep out. The rate of seepage was low enough so that no debris was removed from the surface of the sediment by being sucked down the sides of the corer. Once the core was in place on the extruder, with a little of its overlying water still remaining, it was ready for subcoring.

The subcorer consisted of a 10-ml pipette which had been cut at one of the gradation marks. In order to take a sample, the subcorer was gently pushed and rotated into the sediment. The subcorer was removed and the sediment sample was obtained by pipetting the desired amount.

Number of Bacteria in Sediment

The spread-plate technique using 80% sea water C-P agar medium (composition listed previously) was used throughout this study for enumerating heterotrophic bacteria in the sediment. A 0.5 cm^3 subcore

was transferred into 9.5 ml of sterile sea water. This initial dilution (1 to 20 dilution) was serially diluted in ten-fold steps until the concentration of bacteria was approximately 10^2/ml in the highest dilution. The dilutions were enumerated by spreading 0.1 ml on the agar surface with a sterile glass rod. The plates were inverted and placed in a large plastic bag to prevent dehydration of the media. The plates were incubated at 15°C in the dark. After two weeks the number of colonies growing on the plates were counted and the results expressed as CFU/cm^3 of sediment.

The method to enumerate the bacteria in the sediment of the long cores was the same as above. However, the core was extruded by gravity-flow onto a clean surface. The core was sectioned with a sterile spatula. A 0.5 cm^3 subcore was taken from an uncontaminated center section and placed into 9.5 ml of low-oxygen, sterile sea water. The low-oxygen sea water was prepared by autoclaving sea water in loosely secured screw-cap test tubes. The heat forced the gases out of the solution. While the tubes were hot, the screw caps were tightened. A noticeable rush of air into the tubes upon opening for inoculation of a sample was observed.

Aliquots of these low oxygen dilutions were plated aerobically as described above and anaerobically as follows. Duplicate 0.1-ml aliquots were spread onto C-P agar medium previously kept in anaerobic jars and equilibrated with nitrogen gas for three days. These plates were returned to the anaerobic jars after inoculation and flushed three times with nitrogen gas. Between each flushing nitrogen in the jars was evacuated by vacuum. The anerobic plates were incubated up-side down

and under one atmosphere of nitrogen at 15°C in the dark. These plates and the aerobic plates made from the same dilution tubes were counted after two weeks and reported as CFU/cm^3 of sediment.

Bacterial Respiration Component

To determine the bacterial respiration component of the sediments the following method was used. To the water contained above the sediment in a short core, 200 mg/l of streptomycin and 40 mg/l of chloramphenicol were added. These cores were incubated at 15°C submerged in sea water. Several cores at the beginning of an experiment were opened and used for zero-time oxygen analysis. This method will give only an estimate of the respiratory activity by the organisms affected by antibiotics. The assumptions are that the antibiotics will only cease the metabolic activity of the bacteria, and will do it immediately and will affect all bacteria. All of these assumptions may not be valid. Chloramphenicol is known to affect some algae (Berland and Maestrini 1969). Both of these antibiotics, at the concentrations used, do not affect all bacteria or affect them immediately. However, if the effect of chloramphenicol on the benthic flora and other organisms is slight, and if most bacteria are affected by the antibiotics then the decrease in sediment respiration will be a reflection of the bacterial respiration component of that sediment system.

Sediment Chlorophyll *a* and Phaeopigment

Triplicate 0.5 cm^3 subcores were placed into a mortar and treated as outlined below. Five drops of a 1% $MgCO_3$ (w/v in water) suspension were added. Enough 90% acetone (v/v in water) to cover the sediment was then added. The extraction of the chlorophyll *a* was done by grinding the

suspension with a pestle for about one minute. The acetone containing the pigment was decanted into a glass-stoppered 25-ml graduated cylinder. Acetone was again added to the sediment and the process was repeated until an extract was obtained that was visibly free of pigments; usually three to four grindings were sufficient. The volume of extract in the graduated cylinder was made to 25 ml with 90% acetone. To determine the amount of chlorophyll a in the extract, 11 ml were transferred, after thoroughly mixing, into a 15-ml glass-stoppered conical, centrifuge tube. The extracts were then stored overnight in the dark at room temperature. The following day the extracts were centrifuged and the concentration of chlorophyll a (in µg chlorophyll a/cm^3 of sediment) was determined in the supernatant with a Turner Fluorometer® as described by Strickland and Parsons (1968). To analyze for the concentration of phaeopigments (in µg phaeopigment/cm^3 of sediment), the above extracts were acidified with two drops of a dilute hydrochloric acid solution and measured fluorometrically as described by Strickland and Parsons (1968).

Sediment Organic and Inorganic Carbon Content

The method used to determine the organic and inorganic carbon content was combustion of sediments in an induction furnace and the concomitant determination of the amount of liberated carbon dioxide. Six 0.5 cm^3 subcores were put into preweighed combustion crucibles. The sediments were dried at 60°C and reweighed to determine the dry weight of sediment. Three subcores were acidified with 0.1 N HCL to drive off inorganic carbon while being heated on a hot plate. The acidified samples were washed four times with 10 ml of distilled water. These samples were again dried at 60°C and then all samples were combusted

and the quantity of carbon dioxide liberated determined volumetrically by the method outlined for the use of the Leco Induction Furnace®.

The amount of carbon in a sediment sample was expressed as percent of dry weight. The unacidified samples gave total carbon present in the sample while the acidified samples gave the quantity of organic carbon. Therefore, the percent inorganic carbon equals the percent total carbon minus the percent organic carbon.

Detrital Fallout

The jars, containing fallout that had been collected as described in the Field Methods section, were brought to the laboratory with their screw caps tightly in place. After all the material had settled (about one hour) the caps were removed, and the small mercuric chloride plastic vials (if any) were removed. The sea water was decanted by suction, and if the material was not analyzed immediately, the jar, with its screw cap in place, was put at -20°C.

For analysis, the detritus was transferred to a number of 50-ml centrifuge tubes. After centrifugation at 5000 x g for 5 minutes and decanting the supernatant water, the fallout was placed into preweighed combustion crucibles. The fallout was dried at 60°C and weighed to obtain the dry weight of the material. The fallout was placed into a muffle furnace and the organic material burned at 550°C. The crucibles were cooled and the ashed weights determined. The difference between the dry weight minus the ashed weight equalled the weight of organic matter in a sample. The factor, 0.5 times the weight of organic matter, was used to calculate the weight of organic carbon contained in the sample. The results were corrected for the open surface area of the

jars (4.2×10^{-3} m^2) and the number of days the jars had collected detritus. The final results were expressed as grams of organic carbon input to the sediment surface/m^2/day.

Macro-Detritus

The material collected in the mesh bags (described previously in the Field Methods section) was brought to the laboratory. There, while still in the mesh bags, it was rinsed with deionized water to remove loose sand grains. After rinsing, the detritus in the bags was either put into plastic bags or first separated into the three categories listed below. When separated into three categories the material in each category was placed into a separate plastic bag. The three categories were: 1) Phyllospadix blades plus attached epifauna and epiflora, 2) worm tubes and attached assemblages and 3) other debris. These three groups were easy to distinguish and separate from one another. In practice, the Phyllospadix and worm tubes were separated from the remaining material, which was mostly algal debris.

To analyze the macro-detritus for its organic matter content, the plastic bags were placed into an oven at 60°C and the detritus dried. The dried detritus in each bag was manually broken into fine pieces and placed into a number of preweighed combustion crucibles. These were weighed to determine the dry weight of detritus. The crucibles were placed into a muffle furnace at 550°C combusting the organic matter in the detritus. The crucible was cooled and the ashed weight of the detritus determined. The difference between the dried weight and the ashed weight equalled the weight of organic matter in the sample. To calculate the weight of organic carbon in the sample, the weight of

organic matter was multiplied by 0.5. This weight was then corrected for the four square meter quadrat size and the number of days since the last collection and the results expressed as grams of organic carbon input to the area/m^2/day.

Areal Variability in Sediment Respiration

These studies were undertaken to estimate the extent to which community respiration varies areally. The method described below allows for the analysis of a large number of samples.

The analyses for the variation of respiration in space was performed using three distinct sampling schemes. These were coupled with similar incubations and laboratory analyses. The first sampling scheme was to take a number of short cores (described in the Field Methods section). The location of these cores were determined non-randomly by the experimentor. The second sampling scheme was a 10-meter transect line laid out in a randomly preselected direction. Then at preselected spacings short cores were collected. This method gave random selection of all coring sites. In the third sampling scheme the diver swam out in a preselected random direction from an underwater buoy, about three meters off the bottom. After a randomly picked number of kicks, the diver would release a 25 cm x 25 cm quadrat. Within this quadrat a number of short cores were taken, the sites of these within the quadrat was determined by the diver. This procedure gave random quadrat locations and non-randomly selected coring sites. All random directions and numbers were obtained using a random numbers table.

After taking the cores they were brought upright to the pier laboratory in a large plastic container submerged in sea water. Several of

the cores were opened and used for zero-time oxygen analysis. The remaining cores in the container were transported to the shore-based laboratory and incubated at 15°C. At the end of the experiment, the oxygen concentrations in the remaining cores were determined. A time series experiment of the type described previously (Oxygen section) showed no significant oxygen change between the time the samples were taken and the time required to reach the pier laboratory. The oxygen uptake rate per core was corrected for the surface area of sediment in the corer, the volume of sea water above the sediment contained in the corer, and the number of hours the cores were incubated. The final results of these experiments were then expressed as mM O_2/m^2/hour.

V RESULTS AND DISCUSSION

Temperature

a. Time scale (hours). Temperature variations at the experimental site of up to 8°C in a single day were recorded. A reproduction of data from the recording thermistor for a portion of the month of August, 1972 (Fig. 8B) shows this magnitude of variation. However, this was an extreme range of temperature variation and the usual variation was of the order of 0°C to 2°C, as represented typically by the month of February, 1973 (Fig. 8A).

Temperature changes during the course of an experiment sometimes varied as much as 4°C. However, this was unusual and the normal variation during the course of an experiment was less than 1°C. The average temperature, taken before and after an experiment, is given in Figure 9.

b. Time scale (seasonal). There was no obvious trend in seasonal temperature values at the 18.3 meter station (Fig. 9). The expected cooling of water in the winter months and its warming in the summer was masked by the movement of the thermocline towards the surface in summer and towards deeper depths in winter. Figure 10 shows that, although there appeared to be no definite seasonal trend in the 18.3 meter water temperature, the water did, in general, follow the warming and cooling cycles of the surface waters.

Mixing of Nutrients into the water Column

The rate at which nutrients, arising from or taken up by the benthos, are mixed into the overlying water is a function of: 1) water movement;

FIGURE 8

Reproduction of thermograph recordings (3 cm off bottom) at the experimental site in February, 1973 (A) and August, 1972 (B).

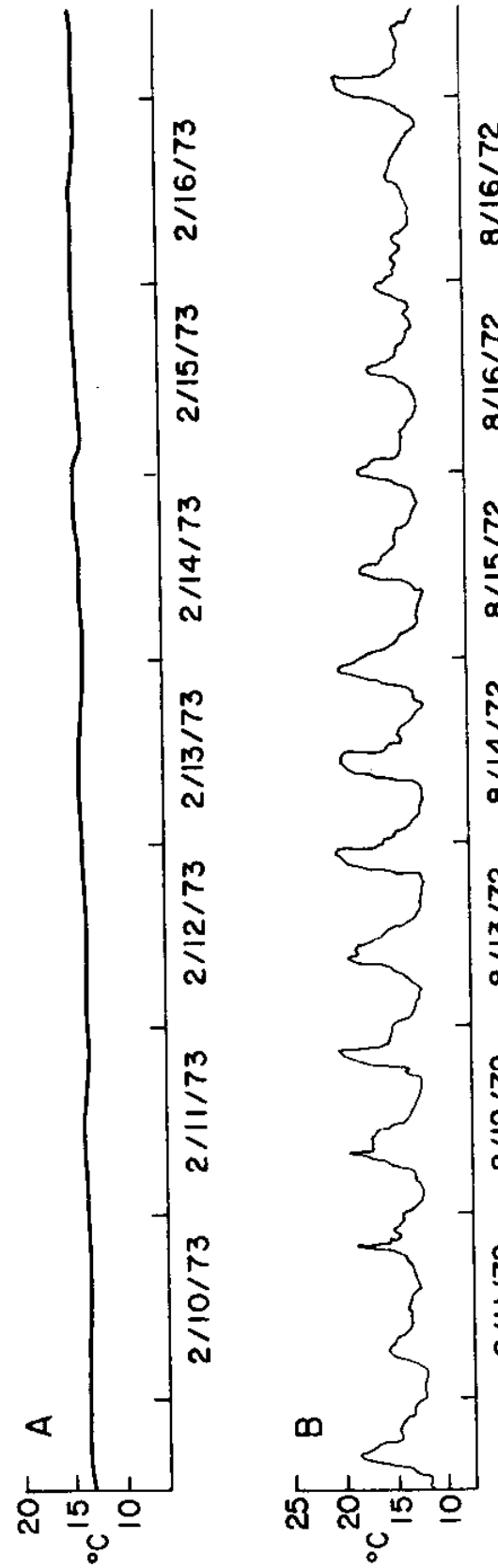

A
20
15
10
°C
2/10/73
2/11/73
2/12/73
2/13/73
2/14/73
2/15/73
2/16/73
B
25
20
15
10
°C
8/11/72
8/12/72
8/13/72
8/14/72
8/15/72
8/16/72
8/16/72

FIGURE 9

Temperature at experimental site (o) and seasonal means (•).

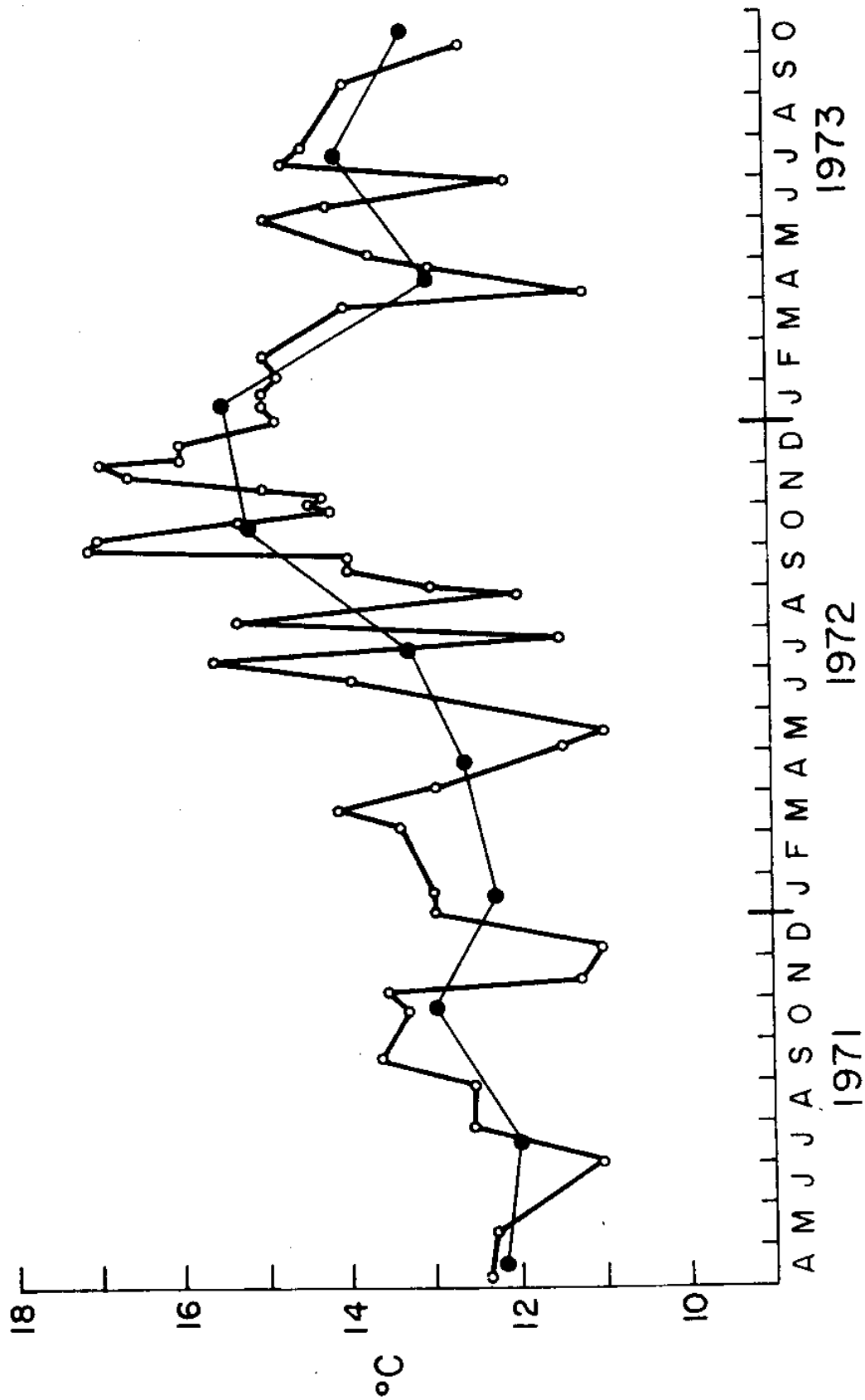
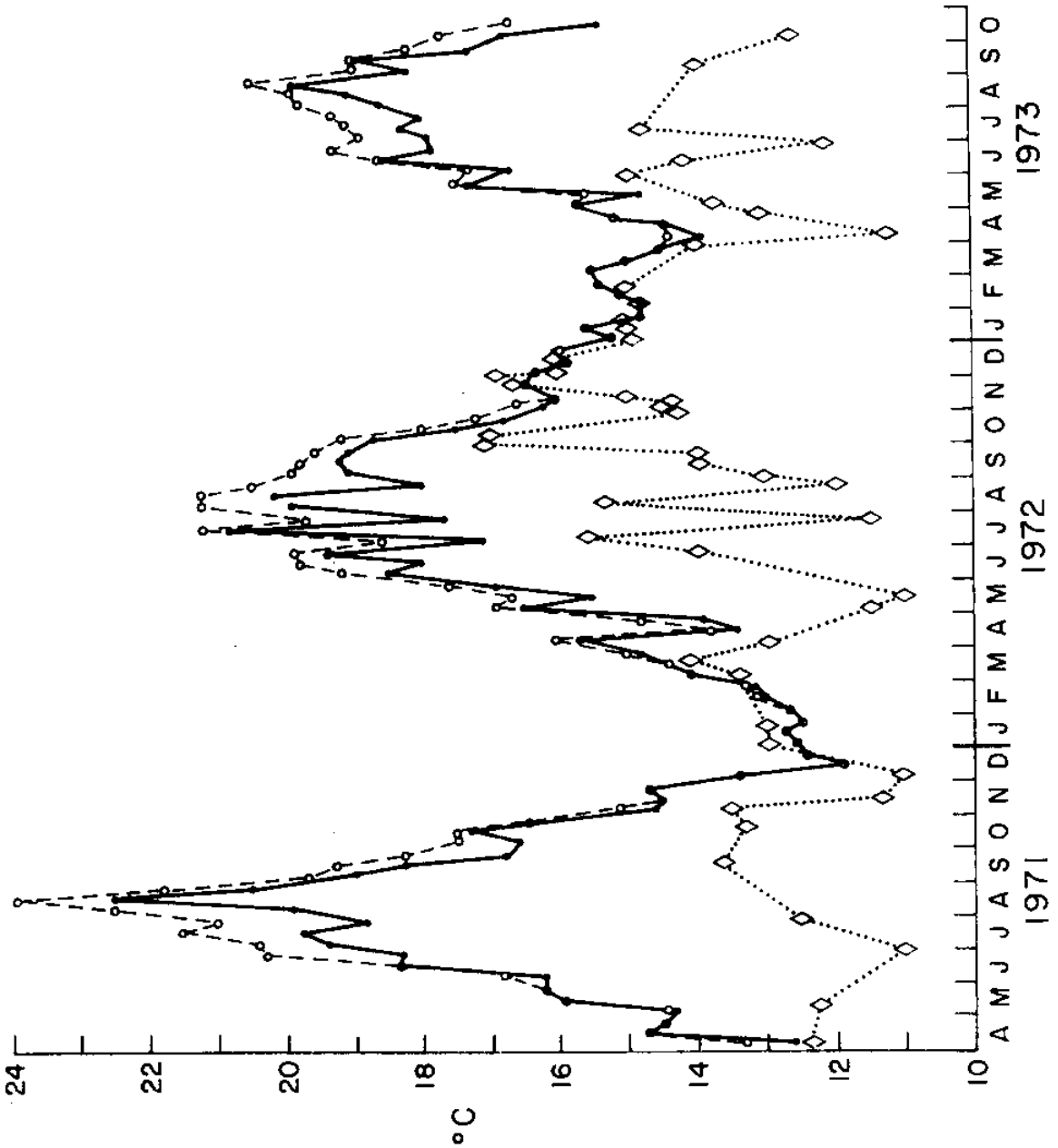

18
16
14
12
10
°C
A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1971
1972
1973

FIGURE 10

Temperature at experimental site (◆) and at the SIO pier at the surface (o) and 5 meter depth (●).


24
22
20
18
16
14
12
10
°C
A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1971
1972
1973

2) sediment nutrient flux; 3) distance or depths through which the nutrients are considered to be diluted or mixed; and 4) the concentration gradient (R. Davis, SIO, personal communication).

Given enough time the nutrients arising from or taken up by the sediments at the experimental site will become completely mixed with or diluted from the 18.3 meters of water above it. From Figure 10 one sees periods when the surface waters and the bottom waters have the same temperatures. At these times the water is mixed from top to bottom and mixing occurs rapidly. At other times there is stratification of the water column and the time needed for complete mixing is longer. However, mixing does occur, and nutrient exchanges due to benthic activity will, therefore, eventually affect the entire 18.3 meter water column.

Light

Figures 11A and 11B show the quantity of photosynthetically active irradiation reaching the sea surface and the sediments at the experimental station. The wide fluctuations within 10 day averages are the result of both differences in the quantity of light striking the surface and differences in the vertical extinction coefficient of the water. By averaging the irradiation data over 10 day periods the large fluctuations which would be present due to the intermittent secchi depth readings are mostly eliminated. The dates for which an individually recorded secchi depth are valid for the purposes of this study are all dates midway between successive secchi depth readings. Therefore, even if the water transparency would slowly, but substantially change over a several day period, the daily light values would note

FIGURE 11

Ten day averages of photosynthetically active incident irradiation at 18.3 m depth (A) and at the surface (B). Vertical lines through each point represent total range of values for each point.

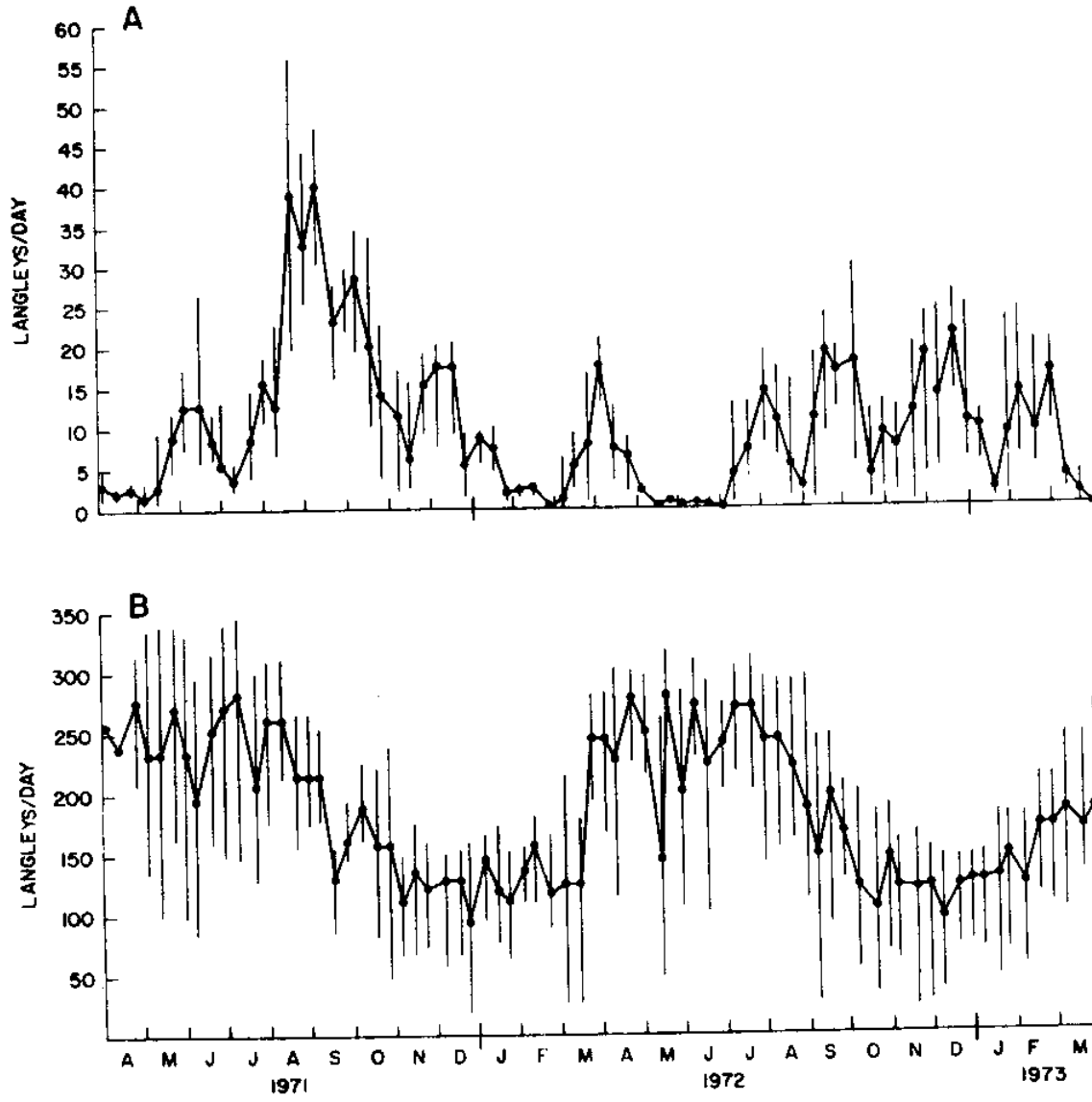

A
B
LANGLEYS/DAY
LANGLEYS/DAY
60
55
50
45
40
35
30
25
20
15
10
5
0
350
300
250
200
150
100
50
A M J J A S O N D J F M A M J J A S O N D J F M
1971
1972
1973

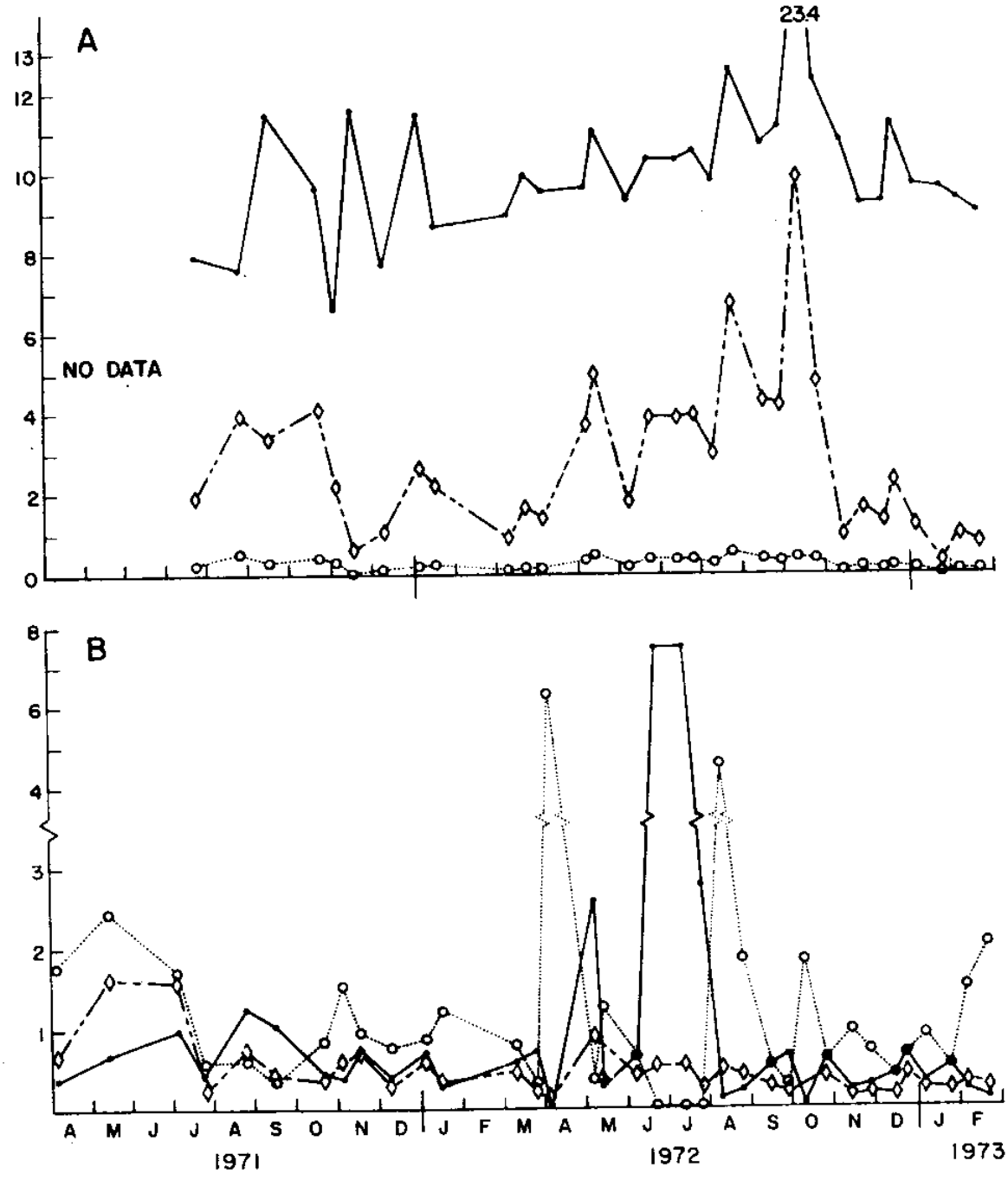
FIGURE 12

Plant pigment concentration in the sediment at experimental site (A) and water immediately above sediment (B).

(●—●) represents µg chlorophyll *a* per cm^3 sediment (A) or per liter (B),

(◇—◇) represents µg phaeopigment per cm^3 sediment (A) or per liter (B),

(o--o) represents phaeopigment/chlorophyll *a* ratio in sediment (A) and water (B). Change of scale in 12B due to large increases in µg chlorophyll *a*/l and phaeopigment/chlorophyll *a* ratio.


A
234
13
12
10
8
6
NO DATA
4
2
0
B
8
6
4
3
2
1
A M J J A S O N D J F M A M J J A S O N D J F
1971
1972
1973

only one drastic change in the vertical extinction coefficient midway between the two secchi readings. Table 1 lists the inclusive dates and number of days for each secchi depth reading. If the secchi depths were the same on consecutive measurements, they were grouped together into one larger time block.

The cyclic nature of the irradiation reaching the earth's surface at this latitude is evident in the surface irradiation measures. Energy values of between 200-300 langleys/day were common in the spring and summer, while in the fall and winter the values were commonly between 100-200 langleys/day. This cyclic irradiation period does not hold for the amount of light energy penetrating to the sediment surface. The average irradiation reaching the sediment surface was 10.2 langleys/day and varied from 0.012 to 55.7 langleys/day. If one compares surface irradiation with sediment irradiation the importance of water turbidity in determining the quantity of light available for the benthos becomes apparent.

The late spring and early summer of 1971 and 1972, markedly reflect the effect of water clarity on light penetration to the benthos. Whereas surface irradiation is at a high, the benthic irradiation is at a low. The low vertical extinction coefficient of the water is attributable to the upwelling conditions which exist during the spring and early summer (Smith, 1969). The incursion of nutrient-rich waters into the euphotic zone in this region produces large increases in the phytoplankton biomass and on occasion a red tide develops (Holmes et al, 1967). In the late fall and early winter the appearance at the surface of a counter-current, the Davidson Current, influences the source and

Table 1. Secchi depth (S.D.) at site with dates and number of days the secchi depth was used.

Dates	# Days	S.D. (m)
1971		
3/29 - 4/3	6	7
4/4 - 4/9	6	5
4/10 - 5/2	23	6
5/3 - 5/7	5	5
5/8 - 5/12	5	6
5/13 - 5/16	4	5
5/17 - 5/25	9	8
5/26 - 6/2	8	9
6/3 - 6/7	5	10
6/8 - 6/12	5	13
6/13 - 6/23	11	8
6/24 - 6/28	5	9
6/29 - 7/3	5	7
7/4 - 7/12	9	6
7/13 - 7/20	8	7
7/21 - 8/7	18	10
8/8 - 8/13	6	8
8/14 - 8/18	5	12
8/19 - 8/25	7	18
8/26 - 8/31	6	14
9/1 - 9/11	7	16
9/12 - 9/20	9	17
9/21 - 9/26	6	15
9/27 - 10/2	6	14
10/3 - 10/19	17	15
10/20 - 10/27	8	11
10/28 - 11/3	7	12
11/4 - 11/10	7	13
11/11 - 11/14	4	8
11/15 - 11/17	3	7
11/18 - 11/23	6	12
11/24 - 12/2	9	14
12/3 - 12/21	19	14*
1972		
12/22 - 1/20	29	10*
1/21 - 2/19	30	7*
2/20 - 2/28	9	5*
3/1 - 3/5	5	5

Dates	# Days	S.D. (m)
1972		
3/6 - 3/8	3	7
3/9 - 3/15	7	8
3/16 - 3/21	6	10
3/22 - 3/26	5	5
3/27 - 4/2	6	10
4/3 - 4/10	8	11
4/11 - 4/26	16	8
4/27 - 5/9	13	6
5/10 - 6/27	47	5
6/28 - 7/7	10	4
7/8 - 7/15	8	5
7/16 - 7/22	7	9
7/23 - 7/28	6	7
7/29 - 8/4	7	10
8/5 - 8/6	2	11
8/7 - 8/12	6	8
8/13 - 8/19	7	10
8/20 - 8/26	7	7
8/27 - 8/30	4	6
8/31 - 9/7	8	7
9/8 - 9/17	10	11
9/18 - 9/24	7	12
9/25 - 10/1	7	13
10/2 - 10/8	7	12
10/9 - 10/17	9	15
10/18 - 10/27	10	8
10/28 - 11/1	5	10
11/2 - 11/12	11	11
11/13 - 11/17	5	8
11/18 - 11/24	7	12
11/25 - 12/5	11	15
12/6 - 12/14	9	14
12/15 - 12/17	3	17
12/18 - 12/28	11	16
1973		
12/29 - 1/14	17	11
1/15 - 1/28	14	7
1/29 - 2/13	16	14
2/14 - 2/22	9	9

* Estimate of secchi depth

exchange of water over the La Jolla Bight. At this time the combination of lower temperatures and light levels decreases the standing crop of phytoplankton.

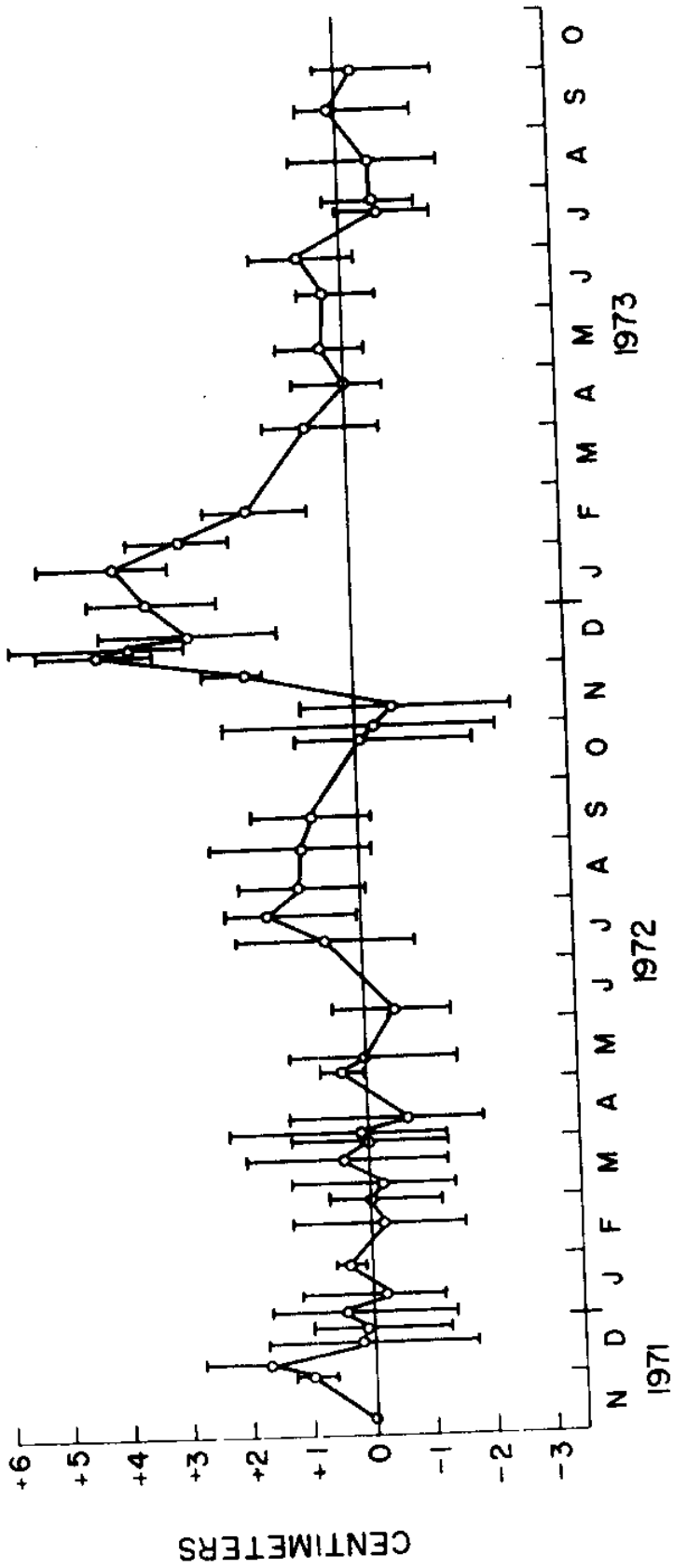
In Figures 12A and 12B one can follow the changes in chlorophyll a and phaeopigments in the sediments and in the water overlying the sediments at the experimental site. In part of July, August and September, 1971, and April, May, June, July, September and October, 1972, there is an increase in the quantity of chlorophyll a in the water indicating an increase in phytoplankton biomass (12B). In the fall and winter months there is a decrease in the total amount of plant pigment in the water. However, even though plant biomass does affect the vertical extinction coefficient, the turbidity of sea water is more a function of inorganic and organic debris than of living organisms since most particulate matter is non-living (Mullin, 1965). During phytoplankton blooms there is a concomitant increase in the number of zooplankton, whose bodies and feces contribute to the particulate matter in the water. After periods of large surf, the material put into suspension from the sediments, increases water turbidity. Also, rainfall increases the turbidity of these nearshore waters by adding particulate material from terrestrial runoff.

Relative Sediment Height

Figure 13 shows the relative height flux of sediment at the experimental site, using the sediment height of November 9, 1971, as zero level. This survey indicated a total range of height movement of between -2.6 cm to +5.7 cm or a maximum variation of only 8.3 cm. Shepard and Inman (1951) measured sand movement in this region in terms

FIGURE 13

Relative sediment height at experimental site. Zero level determined by height of first measurement on November 9, 1971. Vertical bars through each average point represent the range of values for that point. (+) indicate increase in sediment height or sediment movement into area, (-) indicate decrease in sediment height or sediment movement out of the area.


CENTIMETERS
+6
+5
+4
+3
+2
+1
0
-1
-2
-3
N D J F M A M J J A S O N D J F M A M J J A S O
1971
1972
1973

of feet. They found a total range of four feet of sand movement. This is in sharp contrast to the total of 8.3 cm or 0.27 feet of sediment level changes observed in this study. This contrast may be attributed to the differences in the techniques of measurement. Whereas, they used large-scale echo sounding devices coupled with shore position control, the present study, and that of Inman and Rusnak (1956), directly measured sediment level at fixed locations. Inman and Rusnak (1956) found total sand level fluctuations of the same magnitude as reported here. The total range of movement decreases as one goes seaward from the beach. The total vertical change was about 60 cm at their 6-m station, about 9.0 cm at their 10-m station, about 5.0 cm at their 17-m station and about 5.0 cm at their 23-m station. They found seasonal trends in the sand level movement at depths of 10 m or shallower but these fluctuations were masked by shorter period events at the deeper stations. The amount of sediment in shallow water increased in the summer and decreased in the winter.

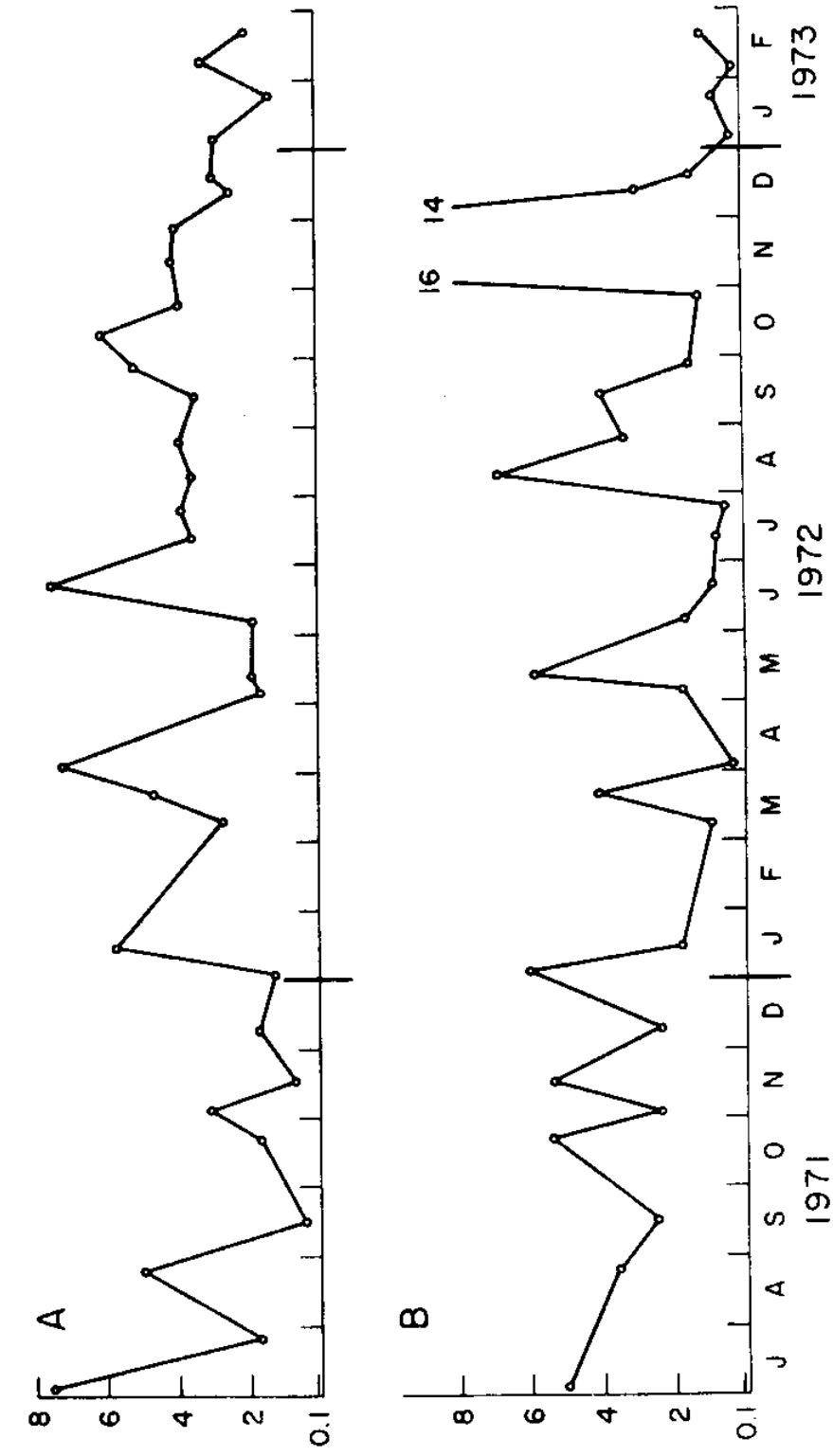
The data from this study, especially in the winter through summer of 1972-73, showed the same trends that were indicated in the studies of Shepard and Inman (1951), Inman (1953) and Inman and Rusnak (1956). These trends were the winter erosion of sand from the beach and its deposition in deeper waters. This sand is then either lost to the submarine canyons or in the periods of small waves in the spring and summer, transported back up onto the beach.

Bacterial Numbers: Sea Water and Sediment

There are marked fluctuations in the aerobic colony forming units (CFU) for both sea water and sediment (Figs. 14A and B). The CFU for

FIGURE 14

Bacterial CFU for sediment (A) and sea water immediately above sediment (B).


A
B
8
6
4
2
0.1
16
14
J A S O N D J F M A M J J A S O N D J F
1971
1972
1973
SEDIMENT BACTERIA
X 10⁻⁶
SEA WATER BACTERIA
X 10⁻³

the sea water goes from a low of 1.0 x 10^2/ml to a high of 1.6 x 10^4/ml of sea water while for the sediments the total variation in CFU is only from 4.0 x $10^5/cm^3$ to 7.5 x $10^6/cm^3$ of sediment. Due to problems inherent in the plate count method of enumeration; e.g. clumps of bacteria are counted as only one bacterium and the medium is selective for those bacteria which can utilize the nutrients it contains, it is impossible to conclude that variations of the magnitude given in Figure 14 represent the actual numerical fluctuations in the bacterial population. Nonetheless, the general conclusion can be made that the bacterial density in the sediments undergoes less dramatic fluctuations than that which occurs in the water column. This is especially evident in the period of November, 1972, through December, 1972, when large fluctuations in the CFU for the sea water occurred (low of 1.4 x 10^3/ml to a high of 1.6 x 10^4/ml) with only minor fluctuations in the CFU of the sediment (low of 2.4 x $10^6/cm^3$ to a high of 4.0 x $10^6/cm^3$).

The benthos, although subjected to the same extremes of temperature and light, plus the added stress of abrasion, is static while the planktonic populations are not. The changes in the CFU of the sea water at the experimental site thus reflects the myriad of processes that have occurred within the sea water both before and at the time the sea water was sampled. The continual movement of water will transport differing planktonic populations past the experimental site and a plate count of a water sample will be representative of that water mass. This is in contrast to the benthic bacterial population which, being mostly attached to sediment particles (Anderson and Meadows, 1969; Batoosingh and Anthony, 1971; Meadows and Anderson, 1968), is transported only when water movement is great enough to bring the sediment

into suspension. Therefore, the benthic bacterial population is a more confined population than the planktonic population. As such, the benthic population will be more affected by the environmental stresses at the experimental site than the planktonic population.

The benthic bacterial population, although it is relatively constant, is affected by major events occurring within the sediment. During the benthic floral bloom, which began in mid-September and ended in mid-November, 1972 (see Fig. 12A), there was a rise and then a fall of CFU in the sediment. Simultaneously, there was an increase in the organic carbon content of the sediment (see Fig. 25). During other periods of a relatively high organic carbon content of the sediment there was a concomitant increase of the CFU in the sediment. Specifically, the higher organic carbon content in January, March and June, 1972, were also marked by a higher CFU in the sediment.

Two other periods are also of interest. During the first period, from June until September, 1972, there was a continual decrease in the organic carbon content of the sediment (see Fig. 25). The CFU in the sediment during this period declined rapidly and remained stable until the initiation of the benthic bloom in September. During this time there was a continual input of organic matter from fallout (see Fig. 22) and macro-detritus (see Fig. 19), coupled with little or no surge (see Fig. 15). This combination of factors provided for a continual input of organic matter that was not washed out. (The problem of "washing out" of organic matter is discussed later under the heading of Sediment Carbon.) The benthic bacteria, therefore, had a continuous organic matter supply, even though organic matter content was declining.

The second period was from the end of October, 1972, through February, 1973. At the beginning of this period the CFU declined to approximately the stable level mentioned above and then decreased to a lower, more variable level. This period also showed a distinctly different pattern in the surge and organic matter input parameters. Surge activity during this period was almost constant (see Fig. 15). The fallout of organic matter was a little higher than during the previous period (see Fig. 22) but macro-detritus went from its highest input rate to its lowest (see Fig. 19). However, until the rate of macro-detritus input decreased to its lowest level the CFU was at a stable level. With the large decrease in macro-detritus input there was a general decrease in the organic carbon content and the CFU decreased to its lower, more variable level. With the increase in macro-detritus input in February, 1973, and with the surge and fallout remaining approximately constant, there was a concomitant increase in the organic carbon content of the sediment and in the CFU.

Therefore, the benthic bacterial population (CFU) is influenced by the following: 1) the organic carbon content of the sediment; 2) blooms of the benthic flora; and 3) events which affects changes in the rate of organic matter input to the benthos, this involves surge activity, fallout input and macro-detritus input.

The aerobic bacterial CFU in the sediment was highest near the surface and decreased with increasing depth. The same was true for the anaerobic CFU except for a short segment of the core beginning 2 cm above the anaerobic zone and extending 3 cm into the anaerobic zone. In this segment the anaerobic CFU stabilized instead of continuing to

decrease. Below 3 cm into the anaerobic zone the CFU decreased and then remained relatively constant throughout the rest of the core to a depth of 14 cm below the beginning of the anaerobic zone. The anaerobic zone was detected visually by a black color and by an H_2S odor which is indicative of anaerobiosis. It usually began about 5 cm below the surface but was detected as shallow as 2 cm below the surface or as deep as 8 cm below the surface.

The anaerobic CFU was high near the surface because the bacteria in this zone may have been facultative anaerobes capable of growth under oxidizing as well as reducing conditions. The CFU declined before reaching a transition zone. In the transition zone (2 cm above anaerobic zone to 3 cm into anaerobic zone) the numbers stabilized with the emergence of the anaerobic bacterial population and the dying of the facultative bacteria. At 3 cm below the anaerobic zone the CFU decreased rapidly and stabilized, marking the zone below which only anaerobes were present.

A highest number of CFU occurred below the surface under both the aerobic and anaerobic growth conditions. This peak occurred approximately 2 cm below the sediment surface. Since the surface layer has a greater supply of both oxygen and nutrients, the limiting factor at the surface was probably sediment movement. Surge activity at the surface creates abrasive conditions in addition to suspending the lighter material and translocates it either to another location in the sediments or into the water column.

Chlorophyll a and Phaeopigments: Sea Water and Sediment

Figures 12A and 12B show the chlorophyll a and phaeopigment

concentrations, and also the phaeopigment/chlorophyll a ratios, in the sediments and the overlying water. As discussed in the section on Light, the chlorophyll a concentration in the water is greater in the late spring, summer and early fall than in the other months (Fig. 12B). This is attributable to the increase in both temperature and light during this part of the year. Blooms in this region, such as occurred in May, June, and July of 1972, are most probably due to the upwelling of nutrient-rich, deeper waters, but the sequence of events from upwelling to the initiation of the bloom is not known (Strickland, 1970).

The chlorophyll a concentrations in the sediments at the experimental site (Fig. 12A) show no trend towards summer peaks, but do tend to decline in the winter. As is true in the water column, the quantity of photosynthetically active light reaching plant cells is important in influencing the chlorophyll a concentration. Chlorophyll a/cm^3 was statistically not significantly correlated with light reaching the benthos but in numerous personal observations when light intensity increased and there was no surge, there was the development of an algal scum on the sediment surface. Taylor (1964) found that benthic intertidal diatoms require 12 langleys/hr for maximum photosynthesis. At my experimental site the average irradiation was 10.2 langleys/day. If one assumes that there are 12 hrs of light and 12 hrs of dark per day at the site, then only about 0.95 langleys/hr are reaching the benthic algae at the surface. Dividing Taylor's (1964) number by 2, to correct for non-photosynthetically active light, yields a value of 6 langleys/hr, which is still about 6 times more than the average irradiation at my experimental site. Even at the highest irradiation value received

at my experimental site of 55.7 langleys/day (4.6 langleys/hr), the benthic algae were light limited if they required 6 langleys/hr.

Nutrients, however, are of less importance in the sediments than in the water column due to the breakdown of organic matter within the sediments and release of nutrients into both the interstitial water and the water above the benthos. Therefore, the beneficial effects of upwelling (increase in nutrient concentrations) to phytoplankton would not necessarily be represented, by a bloom of benthic flora. Blooms in the water column would be beneficial to the benthos when the organic debris of the phytoplankton sank to the bottom and was regenerated. Although the benthic flora does not appear to be subjected to nutritional stress, it is subjected to surge. Whereas wave motion and mixing in the water column are beneficial to the phytoplankton, wave motion along the benthos produces several undesirable conditions for the benthic flora. The movement of sand particles is abrasive and could rupture the cells. Suspension of attached benthic flora into the water column can be followed by their transport into deeper, colder, less-lighted locations. Wave surge can result in the movement of sediment into an area burying the flora or can cause the production of a highly turbid, bottom-boundary zone which reduces the amount of light reaching the sediments.

Surge, therefore, represents an extremely important environmental stress on the benthos. Figure 15 represents a qualitative assessment of surge strength measured on different SCUBA dives over the course of two years. As stated above, the chlorophyll _a_ content of the sediment depends on other factors besides surge, but the importance of surge can

FIGURE 15

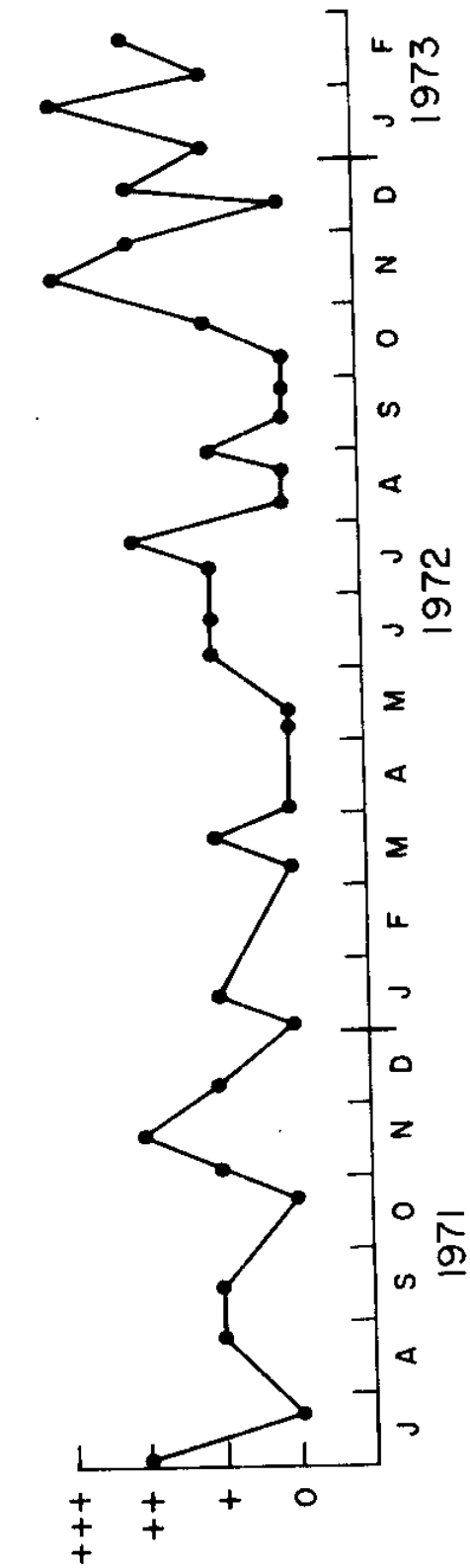
Relative surge at experimental site.

o: no surge;

+: surge - no sand movement but possible disturbance of surface scum;

++: surge - sand movement intermittant, but ripples forming;

+++: surge - sand movement constant and ripple formation which are constantly changing obliterated due to sand movement.


RELATIVE SURGE
+++
++
+
0
J A S O N D J F M A M J J A S O N D J F
1971
1972
1973

be seen if one compares Figures 12A and 15. In April through mid-May, 1972, the lack of surge action on the sediments was accompanied by an increase in both the chlorophyll a and phaeopigment content of the sediment. At the onset of surge activity in May the pigment content of the sediment was substantially reduced. In part of June and July, 1972, when surge was low the pigment content was constant although less than when no surge was observed. A period of greater surge activity in July was followed by a reduction in the pigment content of the sediment. With no surge activity for most of August, 1972, the pigment content increased until at the onset of surge and there was a decrease in sediment pigment concentration. The last few weeks of September, 1972, and the first week of October, 1972, had little or no surge activity, and at the end of that period, the pigment concentration of the sediment greatly increased. In October and November, 1972, the surge activity increased greatly and the pigment concentration in the sediment declined sharply. With the decrease in surge activity in November and December, 1972, there was a concomitant increase in pigment concentration, until in December, 1972, there was an increase in surge activity and the pigment concentration again decreased. In January and February, 1973, the period of constant surge activity was also represented as a time of constantly low pigment concentrations in the sediment. However, even though this was a period of much sediment turbulence, the surface layer of sediment maintained a relatively high floral population. This indicates that the benthic population can maintain itself in the surface layers without migrating into deeper layers.

There is an apparent anomaly in the above scheme. One would expect

a lower phaeopigment/chlorophyll a ratio in the times of surge activity, as the detrital plant material would be put into suspension and transported away and the living benthic diatoms, being attached to sand grains, would settle back to the bottom. In November, 1971, June, 1972, October through November, 1972, and January, 1973, when there was an increase in surge activity there was a decrease in the phaeopigment/chlorophyll a ratio. However, in January, 1972, March, 1972, and in the middle of December, 1972, an increase in surge was also represented by an increase in the phaeopigment/chlorophyll a ratio. This increase may have been caused by a combination of factors. Abrasion during periods of surge activity may kill many attached benthic diatoms which would then settle to the bottom. During periods of high waves and surge there is a seaward transport of nearshore and beach sand (Inman, 1953). This material may contain quantities of phaeopigment that were suspended in the nearshore region and which would settle out in the relatively calm waters at the experimental site. However, since the ratio changes were very slight, perhaps they are not sufficiently precise enough to compare.

Respiration and Photosynthesis by the Benthos

Changes in the oxygen concentration in the sea water contained in the light (L) and dark (D) boxes were used to calculate respiration and primary productivity by the benthic flora and fauna. Data from the bimetallic actinograph was used to determine the total number of hours of daylight and darkness on the day of an experiment (Table 2). For conversion of oxygen data into units of organic carbon for Net Photosynthesis (N.P.; eq. 1) and Gross Respiration (G.R.; eq. 2) analyses,

Table 2. Hours of daylight (daylight period) and darkness (dark period) at experimental site and the factor(F*)for each experiment.

Date	Hours daylight	Hours darkness	F
4/2/71	12.5	11.5	14.3
5/12/71	13.5	10.5	16.9
7/3/71	13.5	10.5	13.1
7/22/71	13.5	10.5	15.4
8/24/71	12.5	11.5	16.7
9/15/71	12.5	11.5	16.0
10/20/71	10.5	13.5	17.15
11/3/71	10.5	13.5	14.3
11/16/71	10.5	13.5	14.3
12/8/71	10	14	14.3
1/3/72	10	14	15.0
1/14/72	9.5	14.5	16.67
3/8/72	11.5	12.5	20.7
3/20/72	11	13	21.4
4/4/72	12.5	11.5	16.67
5/5/72	13	11	19.34
5/12/72	13.5	10.5	19.05
6/6/72	13.5	10.5	19.05
6.21/72	13.5	10.5	18.45
7/11/72	14	10	18.45
7/25/72	13.5	10.5	19.34
8/8/72	13	11	18.18
8/22/72	13.5	10.5	8.31
8/29/72	13	11	18.76
8/31/72	13	11	15.38
9/14/72	12	12	19.05
9/27/72	11.5	12.5	20.0
10/10/72	11.5	12.5	20.7
10/23/72	10.5	13.5	18.76
11/13/72	10.5	13.5	19.69
11/27/72	10	14	21.82
12/13/72	9.5	14.5	21.05
12/19/72	10	14	20.0
1/5/73	9.5	14.5	19.34
1/23/73	11	13	20.0
2/6/73	10.5	13.5	19.34
2/20/73	11	13	18.76

* F: factor used to convert units of measurement to per m^2/per hour. This factor took into account the volume of water in the box, the sediment area covered by the box and the number of hours the experiment was run.

a photosynthetic quotient (PQ) of 1.2 (or 10 mg C/mM O_2) and a respiratory quotient (RQ) of 1.0 (or 12 mg C/mM O_2) were used. In addition, for the determination of Gross Photosynthesis (G.P.; eq. 3) a factor (F), which was specific for each individual experiment, was used to convert the oxygen exchange values (mM O_2/l) to mM O_2/m^2/hr (Table 2). This factor took into account the volume of water in the box, the sediment area covered by the box and the number of hours the experiment was run. The experiments of August 29, 1972, and August 31, 1972, were treated differently than the others since the former used only dark boxes and the latter used only light boxes. The rates of respiration, gross photosynthesis, net photosynthesis and respiratory carbon loss were calculated by combining the light and dark oxygen data and treating them as if they occurred on the same day.

N.P. = mM O_2/m^2/hr in L x 10 mg C/mM O_2 x hrs daylight
= mg C/m^2 for hrs of daylight on day of experiment (daylight period) (eq.1)

G.R. = mM O_2/m^2/hr in D x 12 mg C/mM O_2 x hrs darkness
= mg C/m^2 for hrs of darkness on day of experiment (dark period) (eq.2)

G.P. = (mM O_2/l in L - mM O_2/l in D) x F x 10 mg C/mM O_2 x hrs daylight
= mg C/m^2 for hrs of daylight on day of experiment (daylight period) (eq.3)

To calculate the daily loss or gain of organic carbon to the sediments due to respiration and photosynthesis (R.C.) the gross respiration in the dark was subtracted from the net photosynthesis occurring during

the light.

$$\text{R.C. (mg C/m}^2\text{/day)} = \text{N.P.} - \text{G.R.} \qquad \text{(eq.4)}$$

In all experiments the respiratory gain or loss of organic carbon was negative showing that there was a daily organic carbon loss from the sediment (Fig. 16). This loss varied from a low of -72 mg C/m^2/day in July, 1971, to a high of -634 mg C/m^2/day in March, 1972, with an average loss of -337 mg C/m^2/day. Figure 16 shows that although gross respiration in the dark accounts for most of the respired carbon loss from the sediments, the photosynthetic activity of the benthic flora may substantially affect this value. Gross respiration averaged -278 mg C/m^2/dark period with a range of from -74 to -458 mg C/m^2/dark period. In all experiments, except that of May 5, 1972 (Fig. 17), gross photosynthesis did occur. Gross photosynthesis averaged +158 mg C/m^2/daylight period with a range of from 0 to 513 mg C/m^2/daylight period. However, in the light, only on nine of the experimental dates was there a net gain of organic carbon in the sediments due to photosynthesis (Fig. 17). In the remainder of the experiments, except that of January 3, 1972, when the net photosynthesis equaled zero, there was a net loss of organic carbon from the sediment in the light. Net photosynthesis averaged -56 mg C/m^2/daylight period with a range of -294 to +175 mg C/m^2/daylight period. On the nine days of positive net photosynthesis the average value was +77 mg C/m^2/daylight period with a range of from +2 to 175 mg C/m^2/daylight period. The average value and range for those experiments which had negative net photosynthesis are -109 mg C/m^2/daylight period and -8 to -294 mg C/m^2/daylight period.

FIGURE 16

Total calculated respiratory organic carbon loss rates (solid bars,——, in mg C/m^2/day) by the sediment biota and gross respiration rates (dashed lines, ---, in mg C/m^2/dark period) by the sediment biota. Dark period is defined as the number of hours of darkness on the day of an experiment.

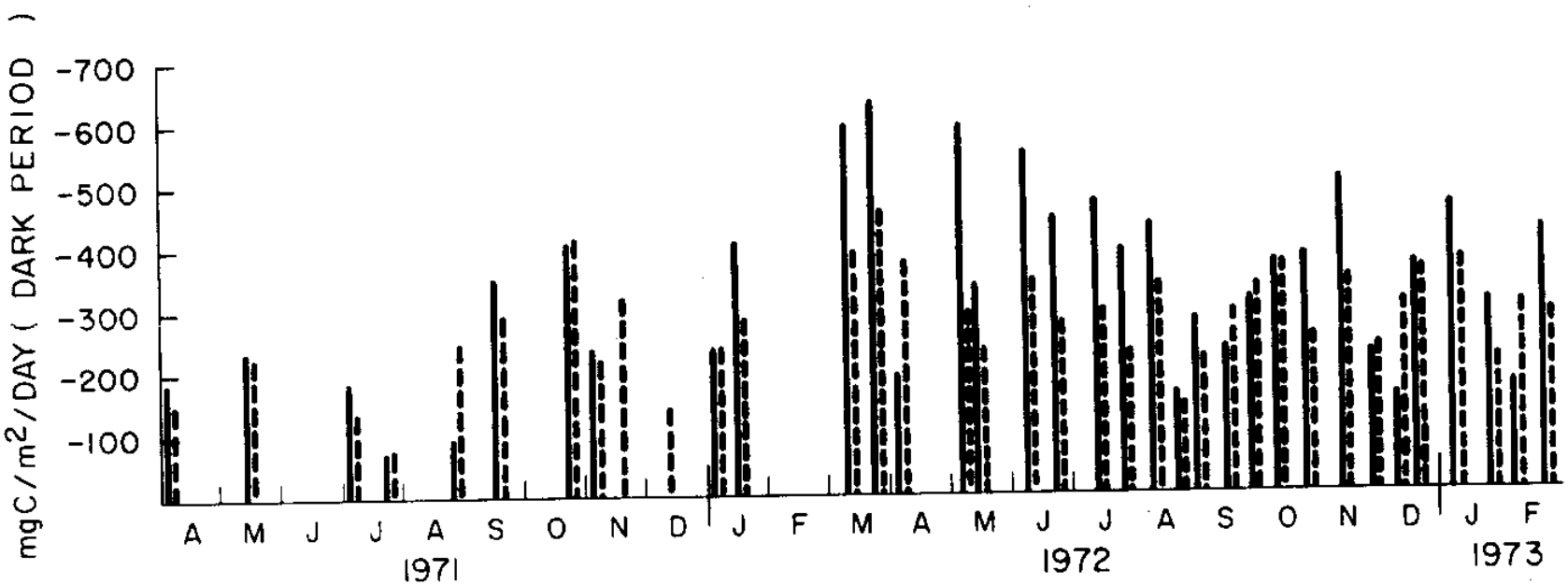
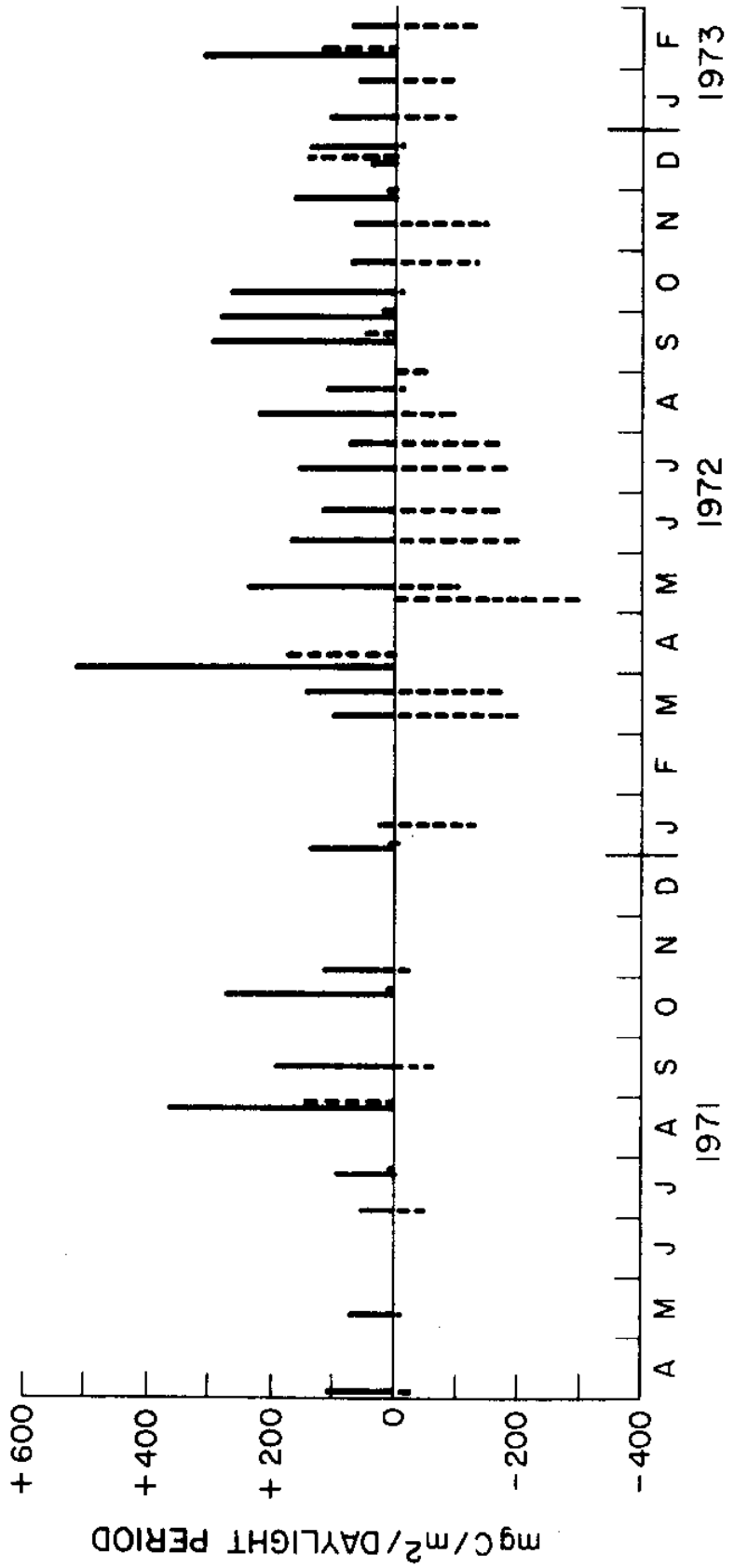

mgC/m²/DAY (DARK PERIOD)
-700
-600
-500
-400
-300
-200
-100
A M J J A S O N D J F M A M J J A S O N D J F
1971
1972
1973

FIGURE 17

Gross photosynthesis rates (solid bars, ——, in mg C/m^2/daylight period) by the sediment flora and the net photosynthesis rates (dashed lines,---, in mg C/m^2/daylight period) by the sediment flora (+ indicates C production and - indicates C loss). Daylight period is defined as the number of hours of daylight on the day of the experiment.


mgC/m²/DAYLIGHT PERIOD
+600
+400
+200
0
-200
-400
A M J J A S O N D J F M A M J J A S O N D J F
1971
1972
1973

Therefore, even though there was a photosynthetically active benthic flora, it was never capable of a net production rate that was greater than the amount of carbon respired during the night. This means that the benthos must be supplied with another source of oxidizable organic matter.

Bacterial Respiration Component

The results of two experiments are given in Table 3. In the first experiment the addition of antibiotics inhibited 71% of the oxygen consumption while in the second experiment 95% of the oxygen consumption was inhibited. If only bacteria were inhibited by the added antiobiotics, the values in Table 3 would be a good measure of the bacterial respiration component. However, since this assumption is not valid (see Field Methods section on Bacterial Respiration Component), the measurements serve only as an indication of the bacterial respiration component. These results are, in general, in agreement with the estimated 70 to 80% values given as the component of subtidal benthic respiration due to bacteria (Kanwisher, 1962).

Areal Variability in Sediment Respiration

Table 4a gives the results of a number of experiments where experimental coring sites were selected in a completely non-random fashion (see Field Methods section on Areal Variability in Sediment Respiration). Table 4b gives the results of randomly selected quadrat sites coupled with non-randomly selected coring sites within the quadrat. Table 4c gives the results of the experimental coring sites selected in a completely random fashion. The results are inconclusive as to the best method of selecting an experimental site. The best method desired in

Table 3. Oxygen uptake in sediment cores after the addition of 200 mg/l streptomycin and 40 mg/l chloramphenicol.

Experiment 1:	
Sediment:	0.620 mM $O_2/m^2/hr$
Sediment with antibiotics:	0.177 mM $O_2/m^2/hr$
Experiment 2:	
Sediment:	0.902 mM $O_2/m^2/hr$
Sediment with antibiotics:	0.048 mM $O_2/m^2/hr$

Table 4. Uptake of oxygen using completely non-random coring site selection (a); random quadrat selection with non-random coring sites (b); and completely random coring site selection (c).

	Uptake ($mM\ O_2/m^2/hr$)			Ranges of percent variability
a.	Expt 1	Expt 2	Expt 3	
	0.656	1.03	0.673	8% to 24%
	0.690	1.16	0.949	
	0.513	1.01	———	
	x = 0.620	1.07	0.811	
	± = 5%	8%	24%	
b.	Expt 1	Expt 2		
	0.897	0.931		2% to 35%
	1.31	0.912		
	0.648	0.946		
	x = 0.952	0.930		
	± = 35%	2%		
c.	Expt 1	Expt 2	Expt 3	
	0.666	0.566	0.931	11% to 21%
	0.674	0.747	0.912	
	0.532	0.562	0.946	
	0.555	0.670	0.811	
	0.572	0.748	0.482	
		0.572	0.999	
	———	0.692	0.813	
	x = 0.600	0.651	0.842	
	± = 11%	13%	21%	

this investigation is the one yielding minimum variability. This is because in an experiment only one light and one dark box were inserted.

In selecting sites for nutrient exchange experiments, the non-random method was used. Sites were chosen that visually appeared to contain all segments of the benthic community. Usually, worm holes, brown scum indicating benthic diatoms, and clean areas were all contained within the enclosed area of the box. This, hopefully, made each measurement more representative of benthic activity.

Macro-Detritus

Macro-detritus collections were made from October, 1971, through February, 1973. The results of these collections are shown in Figures 18, 19 and 20. The major problems with the collections are that they do not accurately represent the dynamic nature of the macro-detritus flow in the experimental site. The collection represent the materials that came to rest upon the sediment at the experimental site, regardless of time of deposition, and were in some manner stopped or trapped at the experimental site (by burial in the sediment or attachment to a worm tube) and were not ingested or decomposed by the benthic biota. A large amount of material moves across the sediment at different times. Most of this material does not come to rest on or in the sediment but is moved to depositional sites next to the mouths of the canyons, or directly into the canyons or onto the beach (Chamberlain, 1960; Zobell, 1971).

During the 17 months' observations at the experimental site, the input of macro-detritus to the sediments ranged from 0.011 to 0.33 g (dry wt)/m^2/day, the mean rate being 0.13 g (dry wt)/m^2/day. The input of macro-detrital organic carbon ranged from 0.001 to 0.076 g C/m^2/day,

FIGURE 18

Total macro-detrital input rate (as dry weight) to the sediment at the experimental site. Solid horizontal lines are the time periods between collections and the rates are averaged over the whole period.

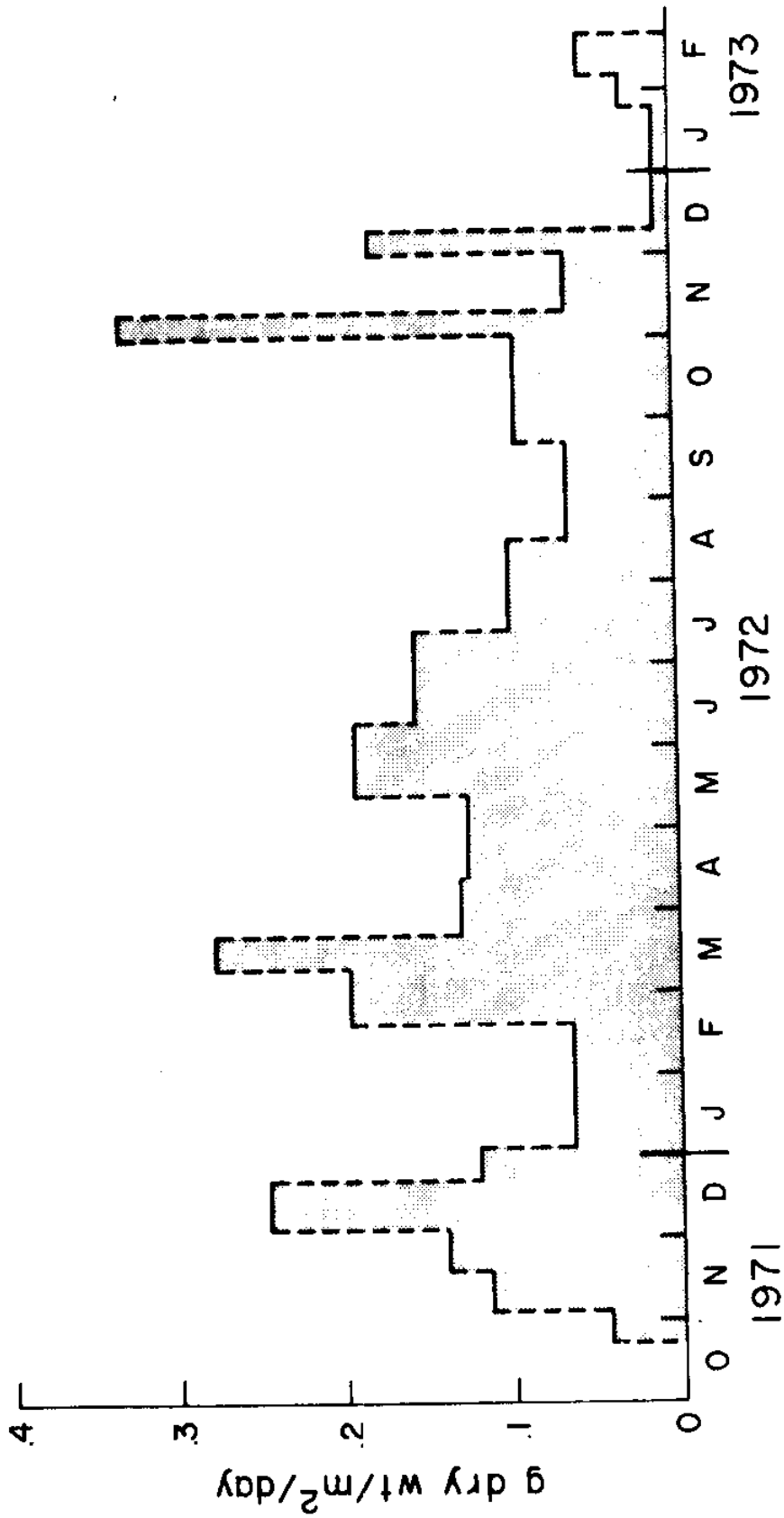

g dry wt/m²/day
0
1
2
3
4
O N D J F M A M J J A S O N D J F
1971
1972
1973

FIGURE 19

Percent organic carbon of dry weight of macro-detritus (A) and the macro-detrital input rate of organic carbon (B). The solid horizontal lines in B are the time periods between collections and the rates are averaged over the whole period.

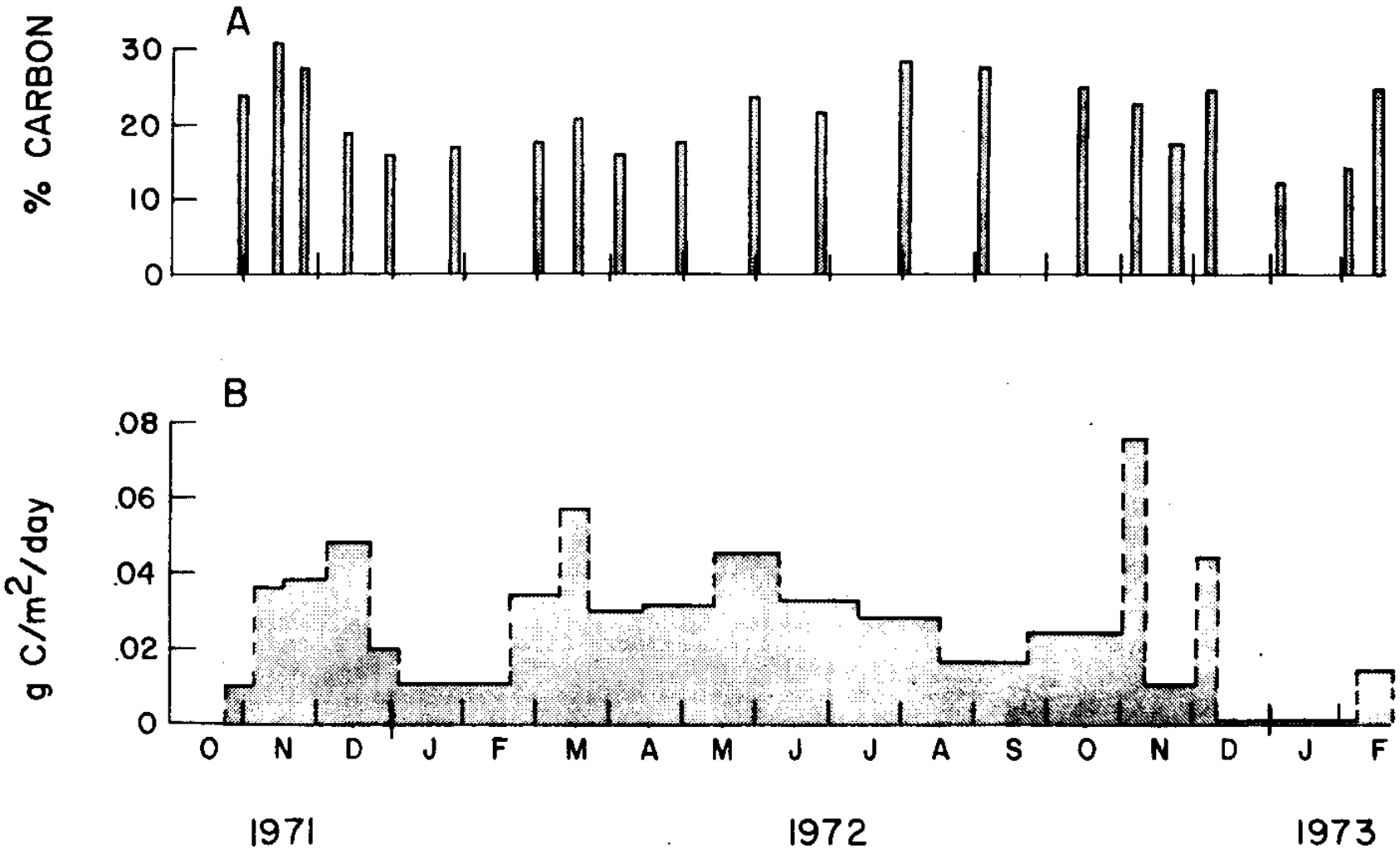
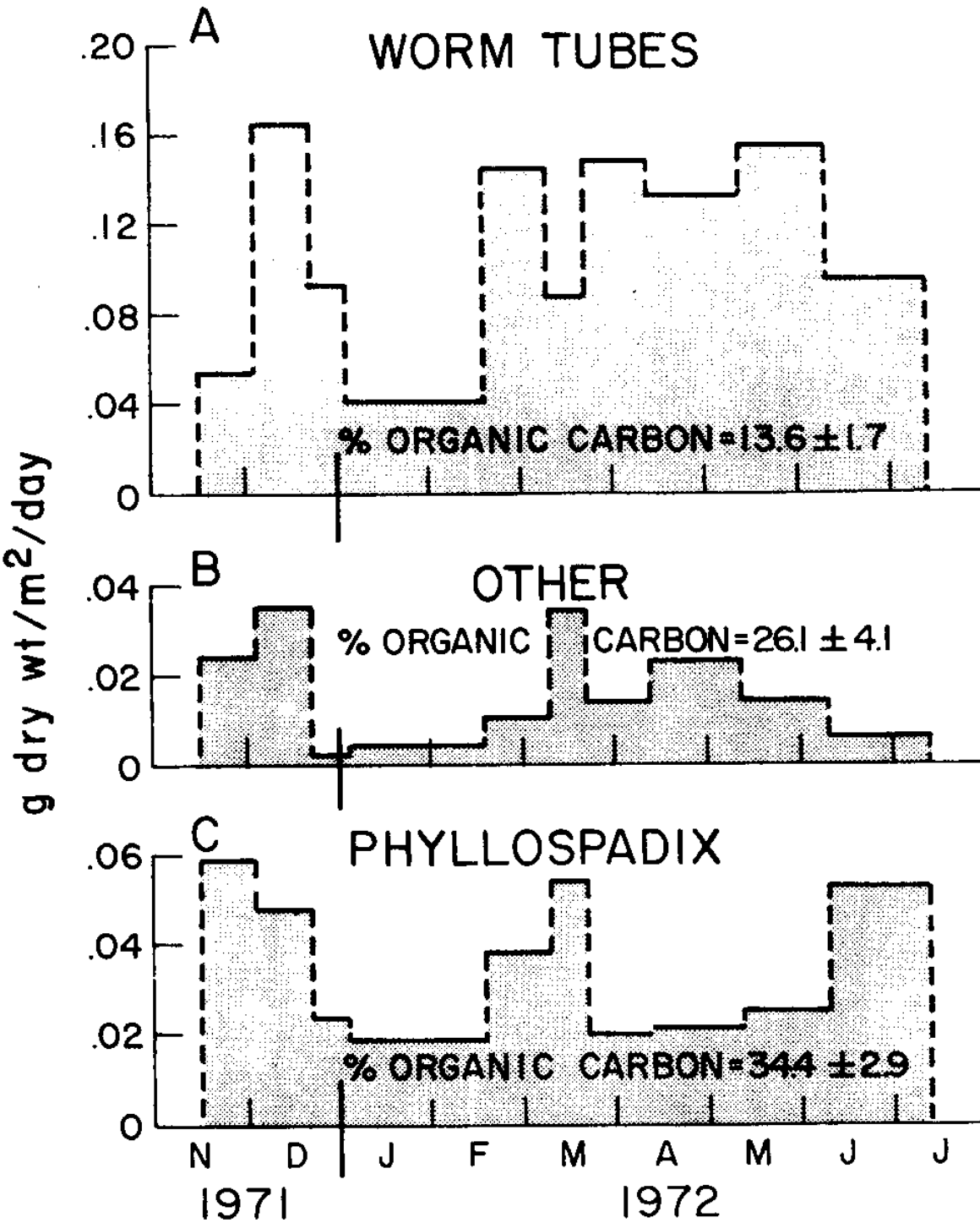

A
% CARBON
30
20
10
0
B
g C/m2/day
.08
.06
.04
.02
0
O N D J F M A M J J A S O N D J F
1971
1972
1973

FIGURE 20

Categories of macro-detritus: dry weight of input due to worm tubes (A, mean equals 0.11 $g/m^2/day$), other input (B, mean equals 0.02 $g/m^2/day$). and Phyllospadix (C, mean equals 0.04 $g/m^2/day$). The solid horizontal lines represent the time periods between collections and the rates are averaged over the whole period.


A
WORM TUBES
.20
.16
.12
.08
.04
0
% ORGANIC CARBON = 13.6 ± 1.7
B
OTHER
.04
.02
0
% ORGANIC CARBON = 26.1 ± 4.1
C
PHYLLOSPADIX
.06
.04
.02
0
% ORGANIC CARBON = 34.4 ± 2.9
g dry wt/m²/day
N
D
J
F
M
A
M
J
J
1971
1972

the mean rate being 0.028 g C/m^2/day. The macro-detritus (dry wt) had an organic carbon content of 12.3% to 32.2%, with a mean organic carbon content of 21.4%.

Data on the categories which comprise the macro-detritus were obtained on November 16, 1971, through July 11, 1972, in a series of ten collections. These data are presented in Figure 20. The input rate of organic carbon and the percent organic carbon of dry weight along with its standard deviation for the three categories was; 0.017 g C/m^2/day for worm tubes and attached assemblages (13.6% $\pm$ 1.7%); 0.013 g C/m^2/day for Phyllospadix blades (34.4% $\pm$ 2.9%) and 0.0045 g C/m^2/day for the "other" component (26.1% $\pm$ 4.1%). The greater variability of percent organic carbon in the "other" component is attributable to the heterogenous nature of this material, whereas the Phyllospadix and worm tube components were homogenous. The worm tube component, being comprised of a great deal of sand grains, contained a surprisingly high percentage of organic carbon. This was due to: 1) the organic nature of the cementing substance secreted by the worm to attach the sand grains (Fager, 1964); 2) the large amounts of Phyllospadix that were firmly attached to the tubes; and 3) to the worms which were in the tubes. Fager (1964) found that, although the organic matter of the tube is present while the worm is alive, the organic matter rapidly decomposes after its death, and the tube disintegrates. Therefore, the worm tubes analyzed in these experiments probably had worms inside. In some cases, after collection, worms were observed, but all tubes were not analyzed for the presence or absence of worms.

A number of species of tube-building polychaetes exist in the

sediments at the experimental site (J. Oliver, SIO, personal communication). Owenia fusiformis, a common, shallow living species, has been shown to be selective in the material it uses to form its tube (Fager, 1964) and the same might be expected for other species. Although other algal fragments were seen attached to worm tubes, visual examination showed that Phyllospadix fragments comprised almost all of the attached plant material. This attached material could be utilized by the worms in two manners. One is, that as the blades decomposed, they could be ingested by the worm and used as food. Another use is that the long Phyllospadix blades, spreading out from an attached point and becoming buried by the sediment, would tend to stabilize the sediment and anchor the worm tube. Fager (1964) states that Owenia fusiformis and a small anemone, Zaolutus actius, act to stabilize the sand surface against movement by wave surge.

The importance of macro-detrital input to the benthos is difficult to analyze. This is due to both the method of collection of macro-detritus and the complex inter-relationships among the various environmental parameters. However, it was found that macro-detritus organic carbon input was always more closely positively correlated with the nutrient exchange parameters tested than was organic carbon input due to fallout. Whereas, both macro-detritus and fallout were not significantly correlated with any of the nutrient exchange parameters in the analyses, the interpretation of these analyses are very tenuous. But, it would appear that macro-detritus input is of more importance than fallout with regards to nutrient regeneration rates by the benthos at this station. This may be due to the "washing out" phenomenon

discussed under Sediment Carbon in the results section. The effect of "wash out" would be different for macro-detritus than for fallout. This is because the macro-detritus is already lying on the sediment and even in the process of moving across the sediment surface could provide some organic matter to the benthos. This is in contrast to the fallout, which is measured before it reaches the sediment surface. Therefore, "wash out" of fallout would occur before it adds significant organic matter to the benthos.

Fallout

There appears to be a seasonal trend in the total dry weight of fallout (Fig. 21). In general, the quantity of fallout is at a maximum in early spring and then declines throughout the late spring and summer. In fall and winter the quantity of fallout again begins to increase. Few studies of detrital fallout input to the benthos have been made. Stephens et al (1967) found a bimodal maxima of fallout in Departure Bay, British Columbia, in October to December and May to June there was a maxima in total fallout. However, their study area and the study area of this investigation are not comparable in that the average rate of fallout in Departure Bay was 8.3 g dry wt/m^2/day with an average carbon content of 7.5% while the mean fallout rate in the La Jolla Bight was 110 g dry wt/m^2/day with an average organic carbon content of only 3.7%.

The percent organic carbon in the fallout at the experimental site varied inversely with the total dry weight of fallout (Figs. 21 and 22A). The peak in percent organic carbon occurred in the summer and fall with the lowest values in winter and spring. The net result of this inverse

FIGURE 21

Total fallout rate at the experimental site. Solid horizontal lines represent time periods between collections and the rates are given as an average (•) over the whole period. The vertical bars represent the total range of rates obtained for the collection period.

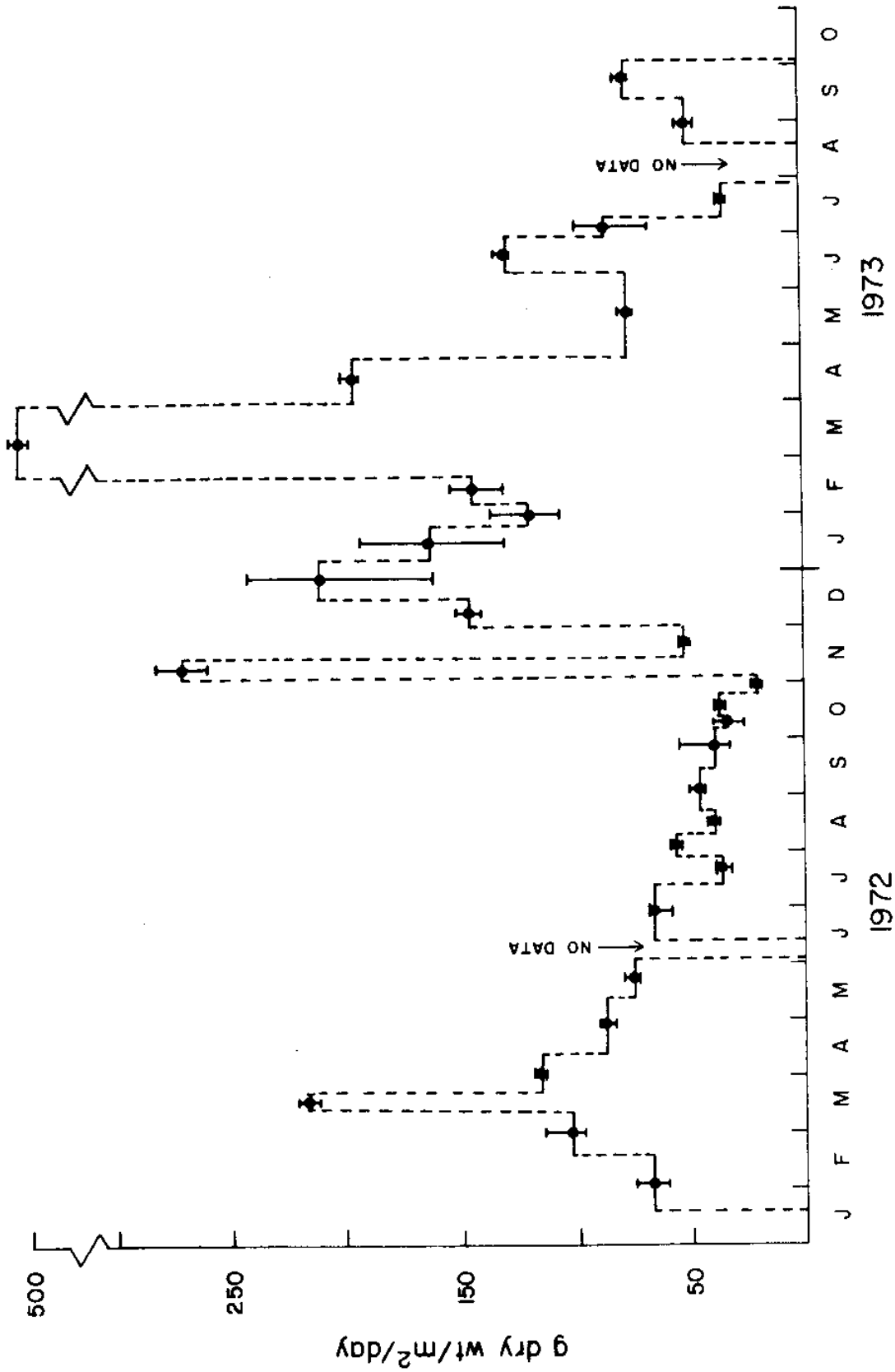
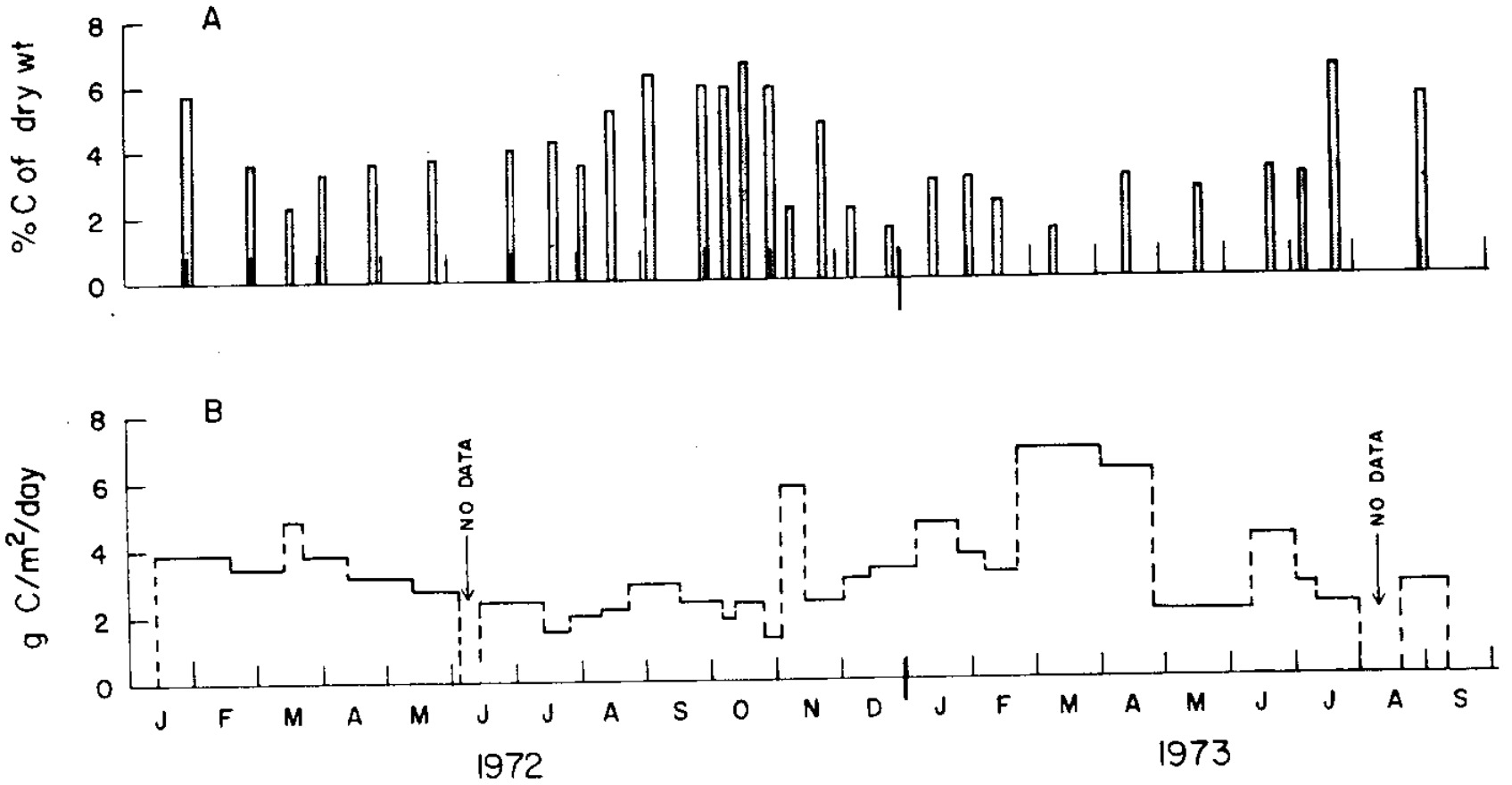

g dry wt/m²/day
500
250
150
50
J F M A M J J A S O N D J F M A M J J A S O
1972
1973
NO DATA
NO DATA

FIGURE 22

Percent organic carbon of dry weight of the fallout (A) and the fallout rate of organic carbon (B). Solid horizontal lines represent the time periods between collections and the rates are averaged over the whole period.


A
% C of dry wt
8
6
4
2
0
B
g C/m²/day
NO DATA
NO DATA
J F M A M J J A S O N D J F M A M J J A S
1972
1973

relationship was that the amount of organic carbon in the fallout remained relatively constant (Fig. 22B). The mean rate of organic carbon fallout was 3.3 g C/m^2/day with a range of from 1.2 g C/m^2/day in late October, 1972, to a high of 6.9 g C/m^2/day in February and March, 1973. These rates suggest a possible sampling error with the baffled fallout trap. Since the average productivity of these waters is of the order of 1.2 g C/m^2/day, what could account for an average fallout rate of 3.3 g C/m^2/day? One possibility is that there is a sampling error and that particulate material, due to some unexplained reason, is concentrated in the traps. Surge may suspend particulate material lying on the sediment and this material, which is not from the water column, would enter the trap. Another explanation is that particulate material in the Bight, due to physical transport processes, tends to remain within the region and, therefore, becomes concentrated.

There is no obvious relationship in comparing the rate of dry weight of fallout, organic carbon fallout rate, and the percent organic carbon of the fallout (Figs. 21 and 22) with the pigment concentration of both the sediment (see Fig. 12A) and the water above the sediment (see Fig. 12B). Therefore, the fallout parameters are not related either to the phytoplankton or sediment floral biomass. No relationship between the standing crop in surface waters and the concentration of particulate organic carbon in deeper waters is to be expected (Menzel, 1967). This is due to nutrient recyling in the upper waters (Redfield et al, 1963; Riley, 1951). Even in the upper waters there is no relationship between particulate organic matter and phytoplankton (Parsons and Strickland, 1962). The results of this investigation also show no relationship

between particulate organic matter and phytoplankton. These observations indicate that the flora of these sediments is indigenous and not one that is dependent upon the water column for continual floral inoculation. This was also indicated, as previously discussed in the Chlorophyll a and Phaeopigments: Sea Water and Sediments of the Results section. It was shown that the benthic flora was a permanent component of the sediment ecosystem.

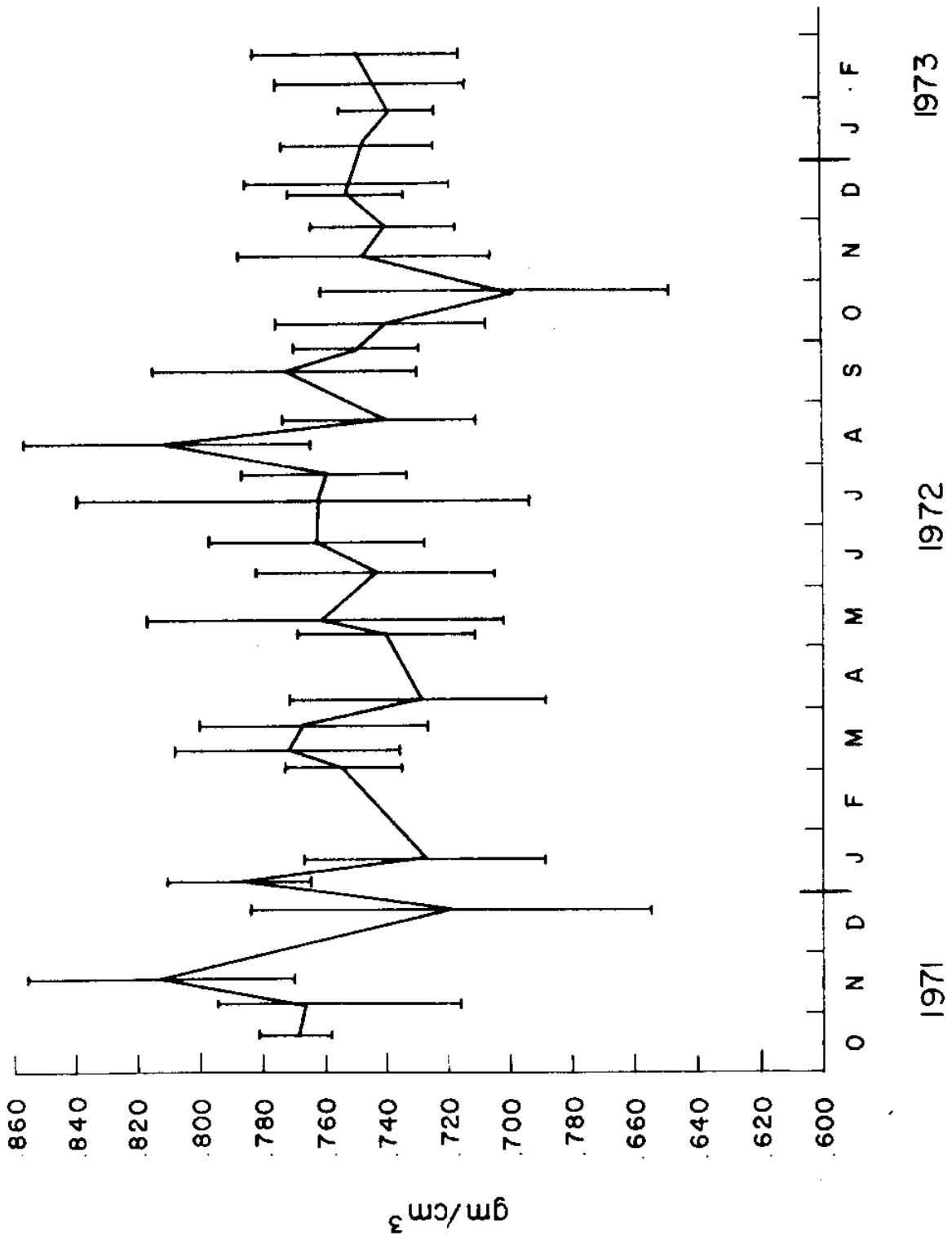
Sediment Unit Dry Weight and Porosity

Analysis of sediment unit dry weight (γ_{dry}) is given in Figure 23. The mean value was 0.756 g/cm^3 with a range from 0.649 g/cm^3 to 0.856 g/cm^3 (Fig. 23). Not only was the total range of values great but each mean point shown in Figure 23 was calculated from highly variable data. This variability was both real and due to sampling technique. Since the coring and subcoring method used was the same as for pigment analysis, and since this parameter did not show great variability, indicates that the variability in unit dry weight is mostly a real phenomenon. However, benthic algae are mostly at the surface and, therefore, the concentration of pigment will be more a function of surface area sampled, not the volume sampled or technique used to sample the area; whereas sediment unit dry weight and porosity measures are critically affected by volume sampled and the technique used to obtain the sample.

Porosity (n) is defined as the ratio of pore space volume to total volume and is given as percent. To obtain porosity from the unit dry weight the specific gravity of the particulate matter of the sediments must be known. The sediments in the La Jolla Bight were found by Inman (1953) to consist of about 90% quartz (specific gravity 2.65) and 10%

FIGURE 23

Unit dry weight of sediment at experimental site. The solid line (——) connects the mean values for each measurement. Vertical bars are the total range of values obtained for each measurement.


gm/cm³
860
840
820
800
780
760
740
720
700
780
660
640
620
600
O N D J F M A M J J A S O N D J F
1971
1972
1973

green hornblende (specific gravity = 3.20) and, therefore, the particle specific gravity (G) is approximately 2.705. The void ratio (e) is determined from the equation:

$$e = G \frac{\gamma w}{\gamma dry} - 1 \text{ (Hough, 1957).}$$

Where γw is the unit weight of sea water and equals 1.025. The void ratio is related to the porosity by the expression

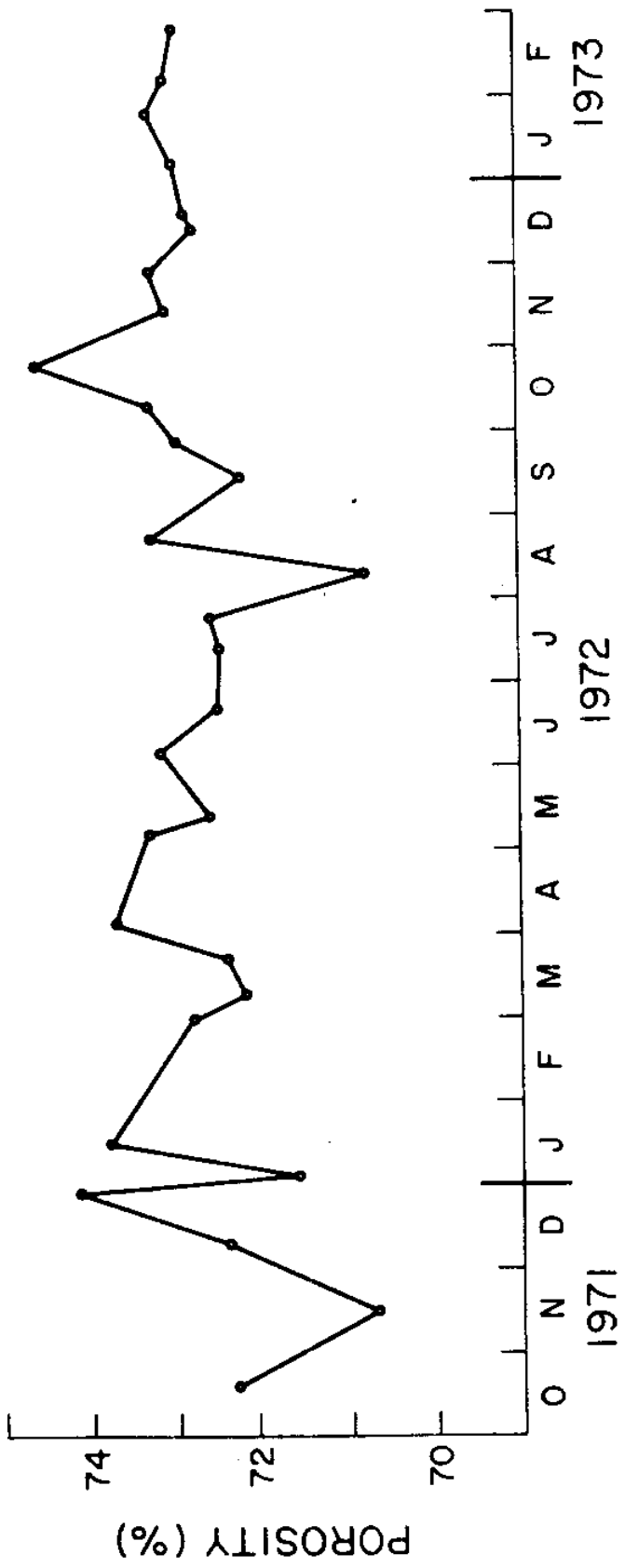
$$n = \frac{e}{1+e} \qquad \text{(Hough, 1957).}$$

The porosity at the experimental site was not found to vary substantially (Fig. 24). The mean porosity values ranged from 70.7% to 74.6% and the overall mean was 72.8%. The porosity varies with particle size and shape, sorting, compaction, etc. (Fraser, 1935). The porosity of the surface sediment layer at the experimental site is, therefore, highly dependent upon the degree of surge and its concomitant effects, e.g. particle sorting, removing light particles, etc.

The significance of porosity is that it is a measure of the amount of water contained within the sediment. The micro-and meio-flora and fauna are dependent upon this water for their supply of nutrients and oxygen and also for removal of their waste products. Therefore, water flow through the sediments, or its permeability, is an important parameter of the sediments for the benthic fauna and flora. Permeability is affected by the same factors that determine sediment porosity plus temperature and hydraulic gradient. Permeability of a sediment, although vitally dependent on void space is governed quantitatively by their size, shape and continuity. In a sediment, changes in its porosity indicate changes in its permeability if all other physical properties are

FIGURE 24

Sediment porosity at the experimental site, expressed as the percent of total sediment volume which is void space.


POROSITY (%)
74
72
70
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
1971
1972
1973

identical (Fraser, 1935). However, no conclusions as to fluctuations of the permeability of the sediments at the experimental site can be made, since the porosity deviations are the result of changes due to sediment physical properties.

Sediment Carbon

Analysis for sediment carbon included percent total carbon, percent organic carbon, and percent inorganic carbon. The three were interrelated by the equation:

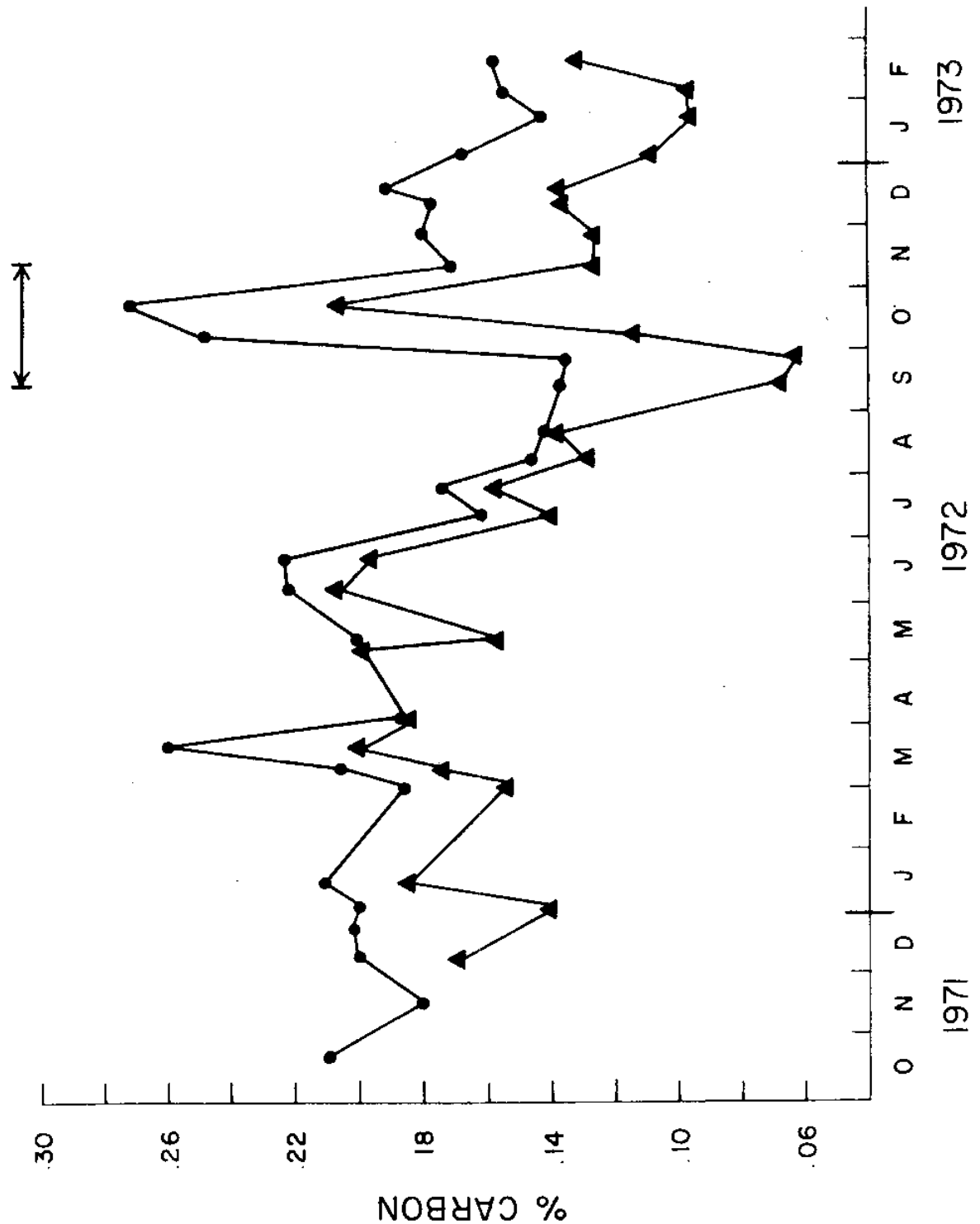
% total carbon = % organic carbon + % inorganic carbon.

Percent total carbon and percent organic carbon were measured directly and percent inorganic carbon was calculated from the above equation. Figure 25 gives the results of these analyses. The percent inorganic carbon (not shown in Fig. 25) is the difference between the two values shown by the lines and had a mean value of 0.041% with a range of from 0% to 0.13%. The percent inorganic carbon was usually a small fraction of the percent organic carbon but in three successive measurements it exceeded the percent organic carbon. These dates were September 14 and 27, 1972, and October 10, 1972. These dates coincide with the initiation and the peak dates of the bloom which occurred in the sediments (see Fig. 12A). The decline of the bloom marked the decline of the percent inorganic carbon.

During sediment blooms there is an increase in both organic and inorganic carbon. However, there is no statistical correlation between pigment concentration and either percent organic or inorganic carbon content of the sediment. This is to be expected if the organic matter of the sediments is composed chiefly of detrital organic material and not organic biomass. However, since the organic carbon content of the

FIGURE 25

Percent total carbon (●) and percent organic carbon (▲) of the sediments at the experimental site. Percent inorganic carbon (not shown in figure) is the difference between the two lines. The bloom of the benthic flora in indicated at the top (⟼).


% CARBON
.30
.26
.22
.18
.14
.10
.06
O N D J F M A M J J A S O N D J F
1971
1972
1973

sediments is low, blooms of the benthic flora may cause changes in the carbon balance of the sediments at this site.

The organic carbon content of the sediments had a mean value of 0.15% with a range of from 0.06% in September, 1972, to a high of 0.215% in June, 1972, and October, 1972. The average value for the percent total carbon was 0.19% with a range of from 0.13% in September, 1972, to a high of 0.27% in October, 1972.

Comparisons of the fallout rate (see Fig. 22) and the macro-detrital input rate (see Fig. 19) with the organic carbon content of the sediment show no relationship. There is also no apparent relationship between the total respiratory organic carbon loss by the sediments (see Fig. 16) and the percent organic carbon content of the sediments. The organic carbon content is probably controlled by two factors. The first is the effect of benthic floral blooms as discussed above. The second factor is a complex one, and involves the input of organic matter to the sediments, and the factors affecting this.

A "washing out" phenomenon occurs with organic matter sinking to the sediments at the experimental site. "Washing out" is the translocation, of organic matter sinking towards the sediments or the translocation of organic matter already on or in the sediments by water currents. It is essentially a cleansing activity caused by both the movement of the surface sediment layers due to surge activity and the transport of particulate material in the water by currents. Several results support the occurrence of this phenomenon. The organic carbon content is not related to the amount of organic matter in the fallout (see Fig. 22) or in the macro-detritus (see Fig. 19). Macro-detritus

is known to accumulate at the heads of the underwater canyons and on the beaches (Chamberlain, 1960; ZoBell, 1971). If all of the fallout reached the sediments it would either be metabolized or buried. Since the average respiratory carbon loss of the sediments is -.034 g C/m^2/day, the average input of fallout and macro-detritus is 3.43 g C/m^2/day and the average sediment organic carbon content is stable at about 0.15%, approximately 3.09 g C/m^2/day or 90% of the organic matter falling to the bottom is transported away from the experimental site. It is this process which appears to control the percent organic carbon content of the sediments.

Nutrient Exchange

The results of the nutrient exchange experiments are given in Figures 26, 27, 28, 29, 30, 31 and 32. The mean value for the exchange of each nutrient and the total range of nutrient exchange values are given in Table 5. The exchange of ammonia (NH_3-N) (Fig. 26) was positive, except in one case, and resulted in a net input of NH_3-N into the water column. The mean rate of NH_3-N input was +872 μM/m^2/day with a range of values from an uptake of -47 μM/m^2/day to an input of +3290 μM/m^2/day. Likewise nitrite (NO_2-N) exchange was positive (Fig. 27), except for two instances which occurred in the experiments where NH_3-N was taken up and when NH_3-N was produced at its lowest rate (16 μM/m^2/day). The mean rate of NO_2-N input was +34 μM/m^2/day with a range of values from an uptake of -5 μM/m^2/day to a high production value of +97 μM/m^2/day. Phosphate (PO_4-P) was also generally produced, but not as consistently as NH_3-N and NO_2-N. The mean rate of PO_4-P input (Fig. 29) was +77 μM/m^2/day with a range of values from an uptake of -438 μM/m^2/day to a high input rate

FIGURE 26

Ammonia production (+) or uptake (-) by the benthos (μM NH_3-N/m^2/day), (*) values used data from only dark boxes, all other values used data from light and dark boxes.

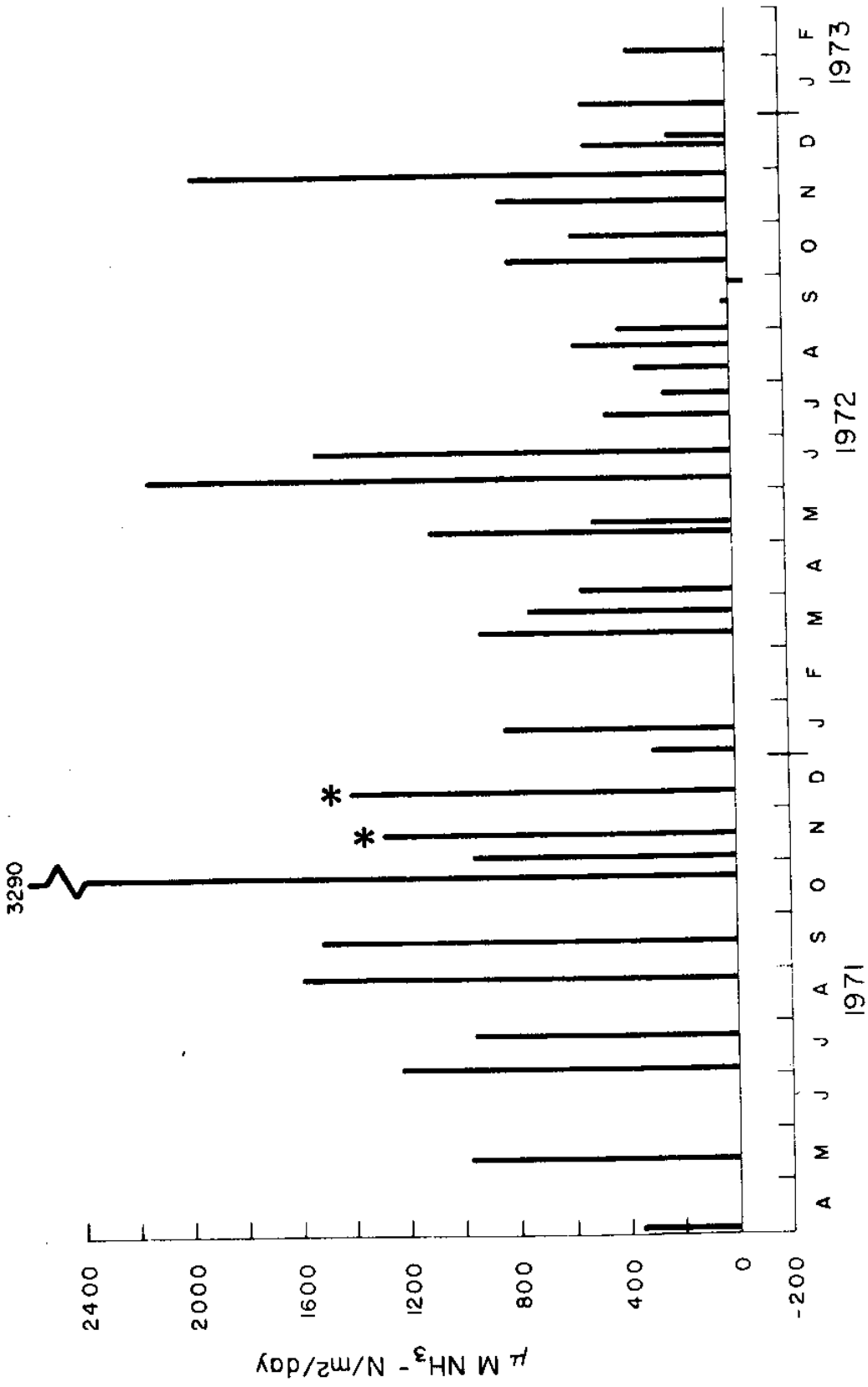

3290
*
*
2400
2000
1600
1200
800
400
0
-200
μ M NH3- N/m2/day
A M J J A S O N D J F M A M J J A S O N D J F
1971
1972
1973

FIGURE 27

Nitrite production (+) or uptake (-) by the benthos ($\mu M\ NO_2\text{-}N/m^2/day$), (*) values used data from only dark boxes, all other used data from light and dark boxes.

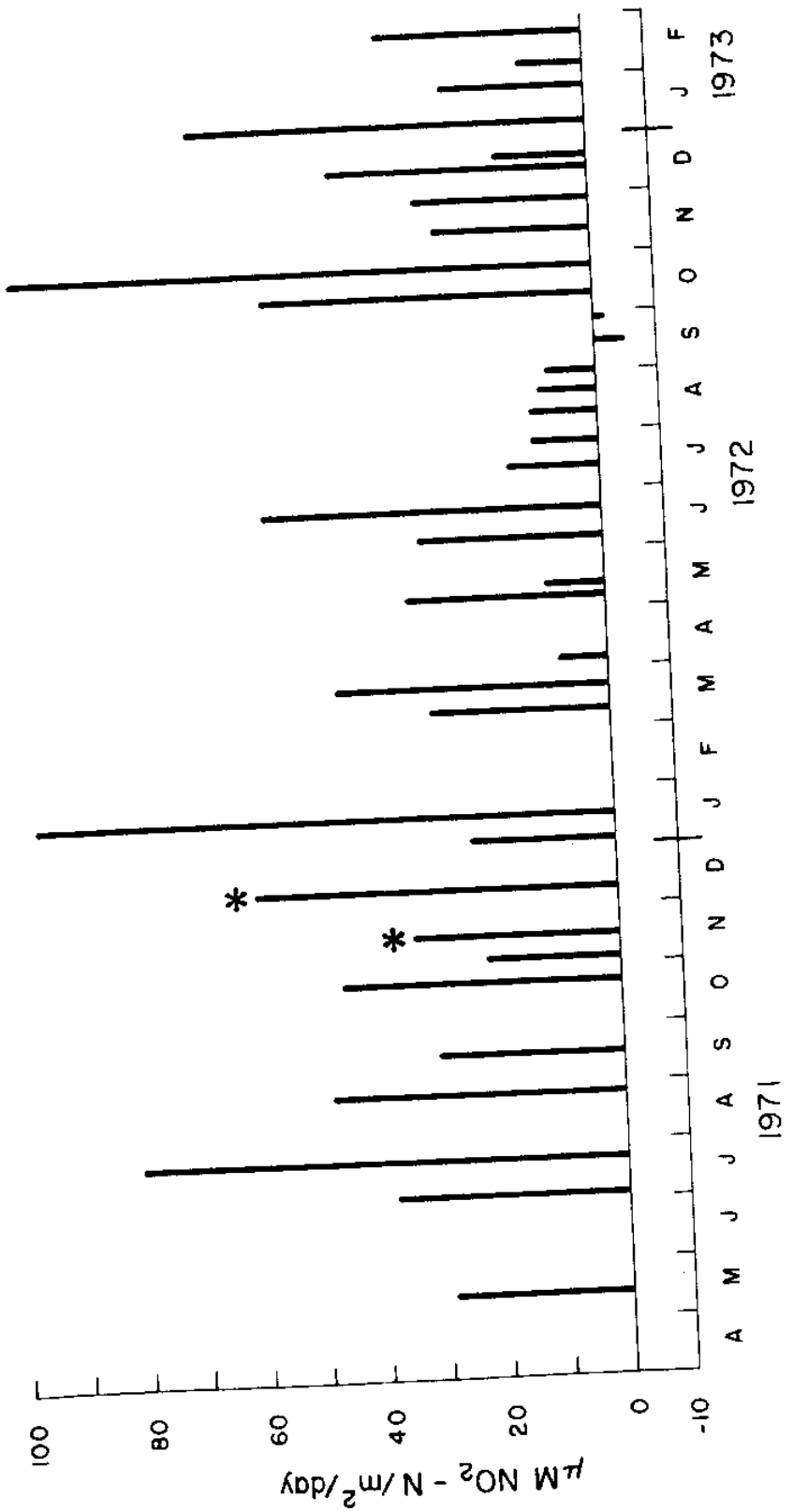

μM NO2 - N /m2/day
100
80
60
40
20
0
-10
A M J J A S O N D J F M A M J J A S O N D J F
1971
1972
1973
*
*

FIGURE 28

Nitrate production (+) or uptake (-) by the benthos ($\mu M\ NO_3$-N/m^2/day), (*) values used data from only dark boxes, all other values used data from light and dark boxes.

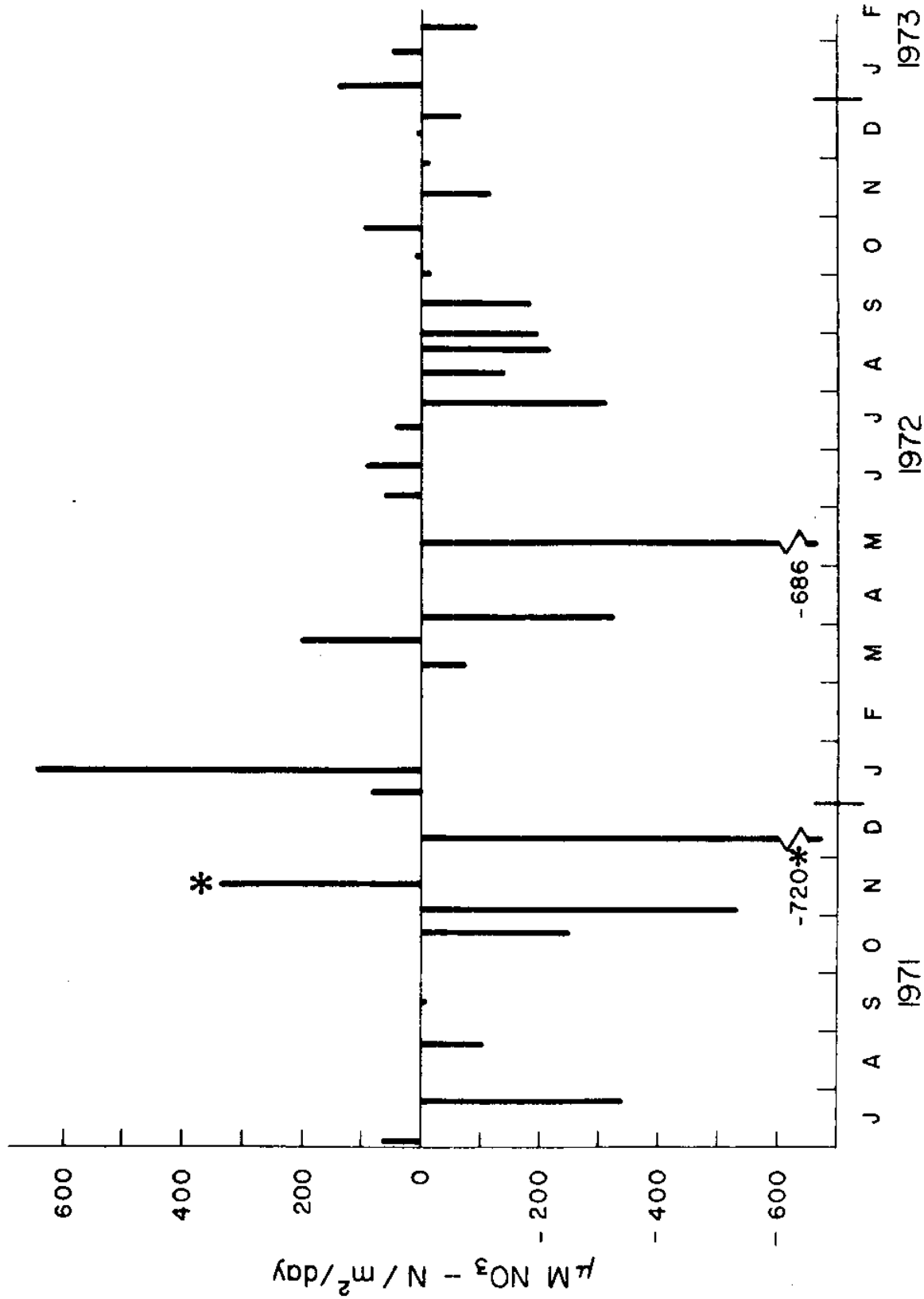

600
400
200
0
- 200
- 400
- 600
μM NO3 - N / m2/day
J A S O N D J F M A M J J A S O N D J F
1971
1972
1973
-686
-720*
*

FIGURE 29

Phosphate production (+) or uptake (-) by the benthos ($\mu M\ PO_4\text{-}P/m^2/day$), (*) values used data from only dark boxes, all other values used data from light and dark boxes.

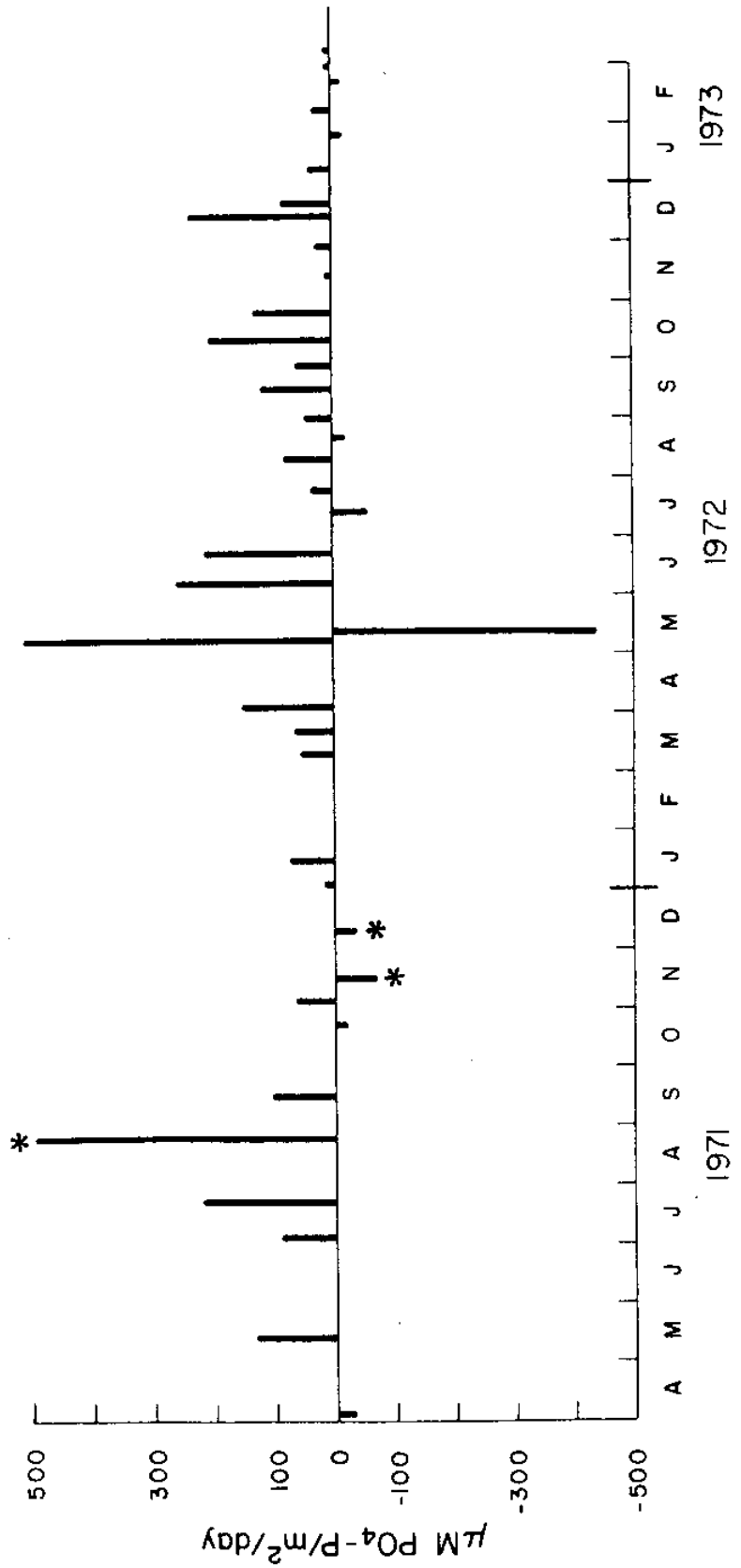

500
300
100
0
-100
-300
-500
μM PO4-P/m2/day
A M J J A S O N D J F M A M J J A S O N D J F
1971
1972
1973
*
*
*

FIGURE 30

Dissolved organic carbon production (+) or uptake (-) by the benthos (mg DOC-C/m^2/day), (*) values used data from only dark boxes, all other values used data from light and dark boxes.

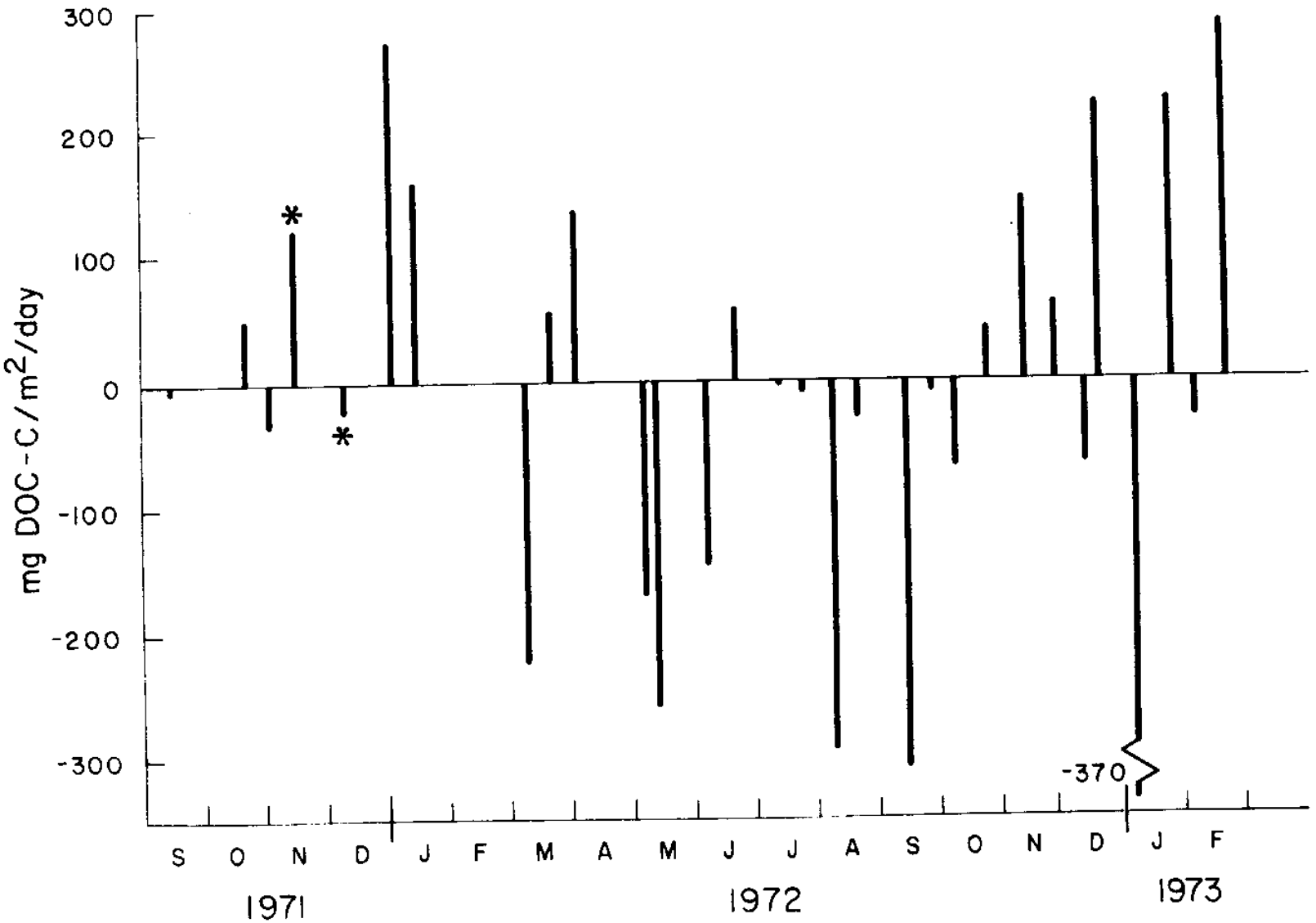

300
200
100
0
-100
-200
-300
mg DOC-C/m2/day
*
*
-370
S O N D J F M A M J J A S O N D J F
1971
1972
1973

FIGURE 31

Dissolved organic nitrogen production (+) or uptake (-) by the benthos (μM DON-N/m^2/day), (*) values used data from only dark boxes, all other values used data from light and dark boxes.

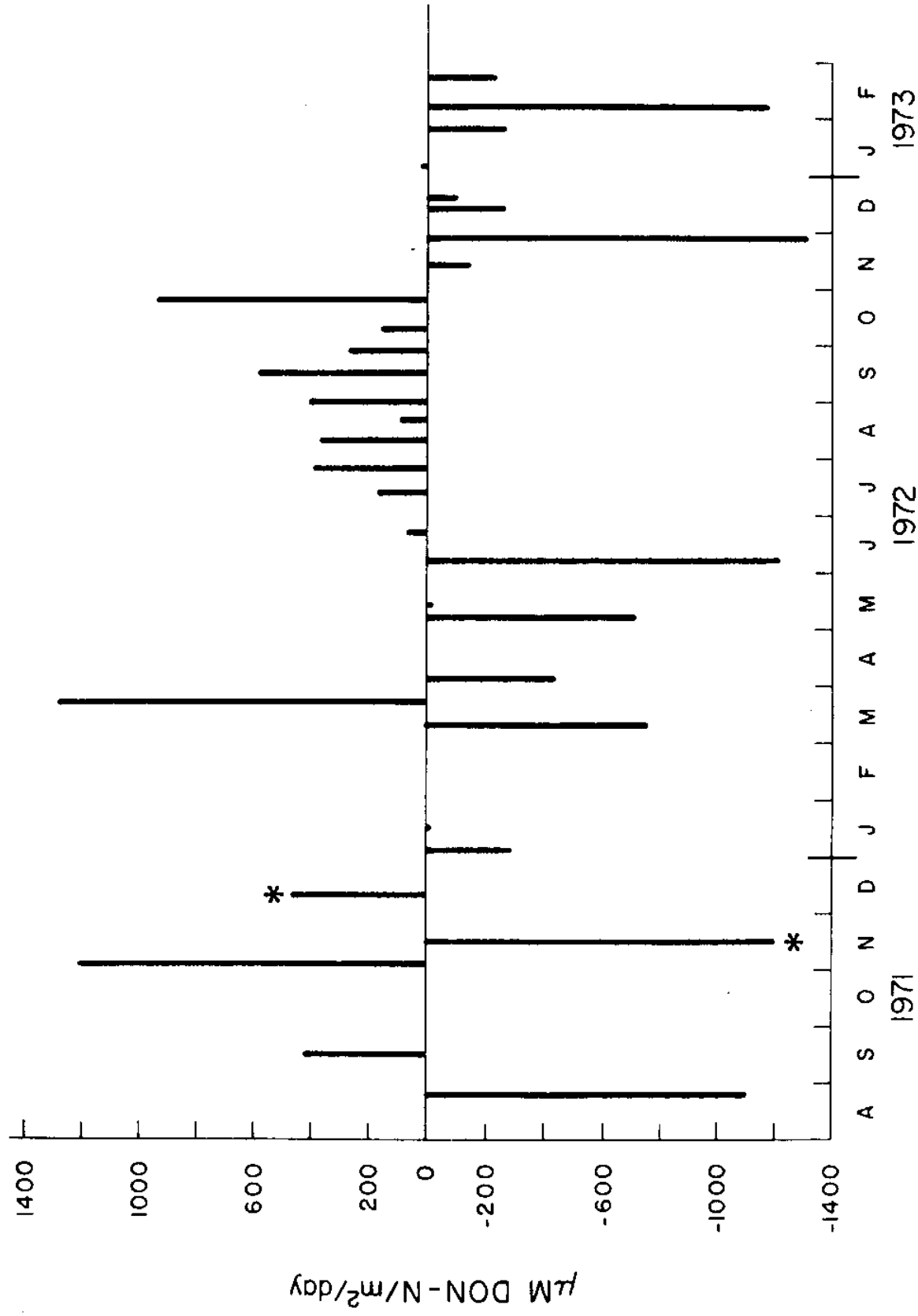

μM DON-N/m²/day
1400
1000
600
200
0
-200
-600
-1000
-1400
A S O N D J F M A M J J A S O N D J F
1971
1972
1973
*
*

FIGURE 32

Dissolved organic phosphorus production (+) or uptake (-) by the benthos (μM DOP-P/m^2/day), (*) values used data from only dark boxes, (**) values used data from only light boxes, all other values used data from light and dark boxes.

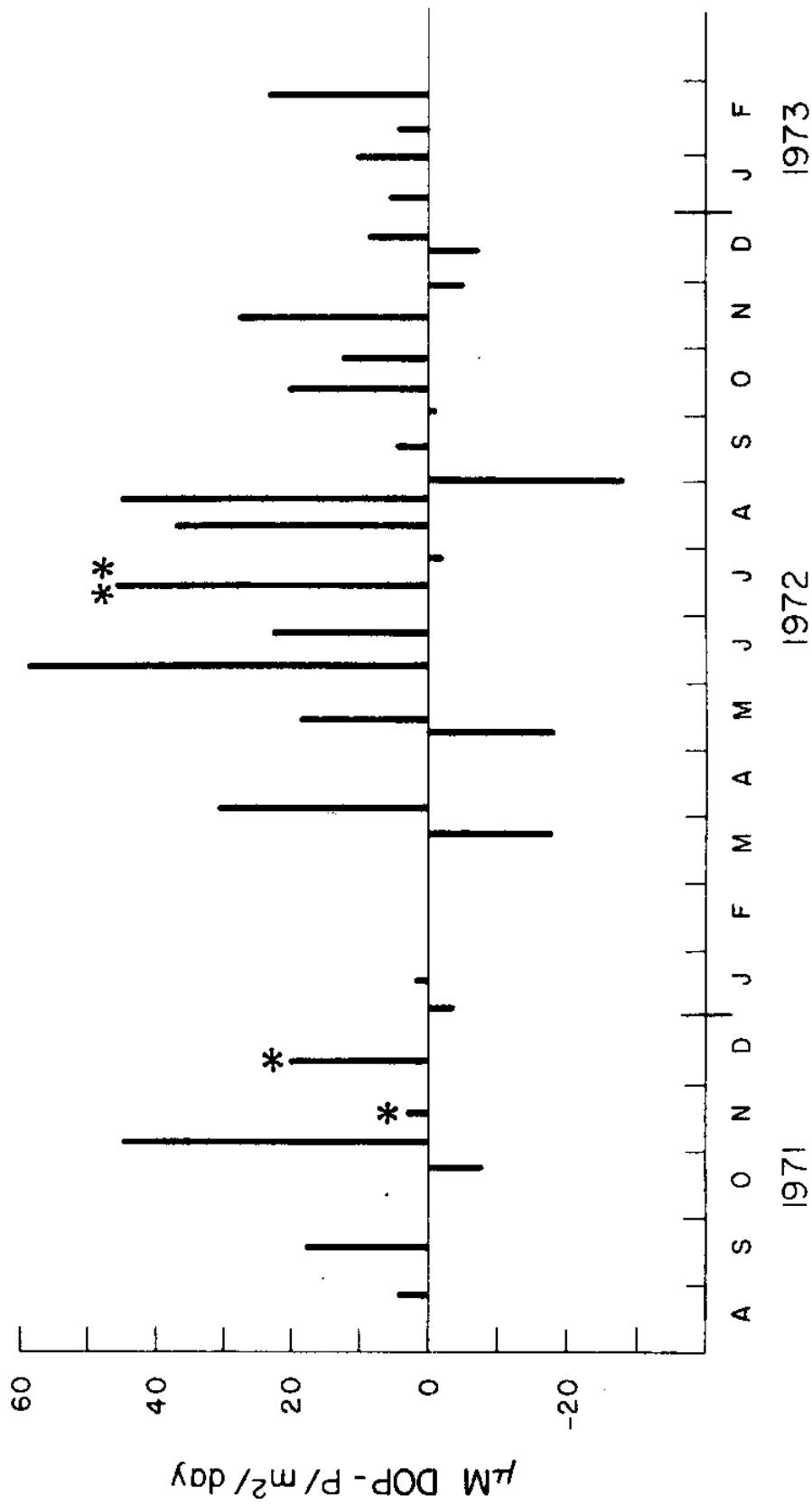

μM DOP- P/ m²/ day
60
40
20
0
-20
A S O N D J F M A M J J A S O N D J F
1971
1972
1973
*
*
**

Table 5. Nutrient exchange between the marine benthos and the overlying water.
Values given as production (+) or uptake (-) of the nutrient by the benthos.

Nutrient	Mean (x)	Range*
NH_3-N	+872μM/m^2/day	-47 to +3290μM/m^2/day
NO_2-N	+34μM/m^2/day	-5 to +97μM/m^2/day
NO_3-N	-77μM/m^2/day	-720 to +647μM/m^2/day
PO_4-P	+77μM/m^2/day	-438 to +502μM/m^2/day
DOP-P	+12μM/m^2/day	-28 to +59μM/m^2/day
DON-N	-75μM/m^2/day	-1326 to +1280μM/m^2/day
DOC-C	-7mg/m^2/day	-370 to +285mg/m^2/day

* Range - these values represent the highest uptake value obtained and the highest production value obtained.

of +502 $\mu M/m^2$/day. Dissolved organic phosphorus (DOP) (Fig. 32) as in the case of inorganic phosphate, was produced in approximately three-fourths of the experiments. DOP had a mean rate of input of +12 $\mu M/m^2$/day with a range of values from an uptake of -28 $\mu M/m^2$/day to a high input rate of +59 $\mu M/m^2$/day.

Nitrate (NO_3-N) dissolved organic carbon (DOC) and nitrogen (DON) all showed more complex patterns. NO_3-N (Fig. 28) had a mean rate of uptake of -77 $\mu M/m^2$/day. The values ranged from an uptake rate of -720 $\mu M/m^2$/day to an input rate of +647 $\mu M/m^2$/day. DOC (Fig. 30) had a mean rate of uptake of -7 mg/m^2/day. The values ranged from an uptake rate of -370 mg/m^2/day to an input rate of +285 mg/m^2/day. Likewise, DON (Fig. 31) was highly variable having a mean uptake rate of -75 $\mu M/m^2$/day with a range of from an uptake rate of -1326 $\mu M/m^2$/day to an input of +1280 $\mu M/m^2$/day.

In an aphotic benthic environment where at least the surface layer of sediment is aerobic and where there is a sufficient supply of organic matter, the production of all the nutrients discussed above is expected. However, since the sediment environment at the experimental site was neither aphotic nor could it be assumed to have a sufficient organic matter supply, there was not a continual production of these nutrients. The effect of both light and organic matter supply on nutrient exchange are discussed below.

The presence of a photosynthetically-active flora results in the uptake of some nutrients and, in some cases, the production of other nutrients. NH_3-N, NO_3-N and PO_4-P are nutrients required by algae and

therefore their exchange rates will be affected by the benthic flora. Some of the marine flora are known to be at least partially heterotrophic and capable of taking up dissolved organic matter (Hobbie and Wright, 1965; Sloan and Strickland, 1966; Wright and Hobbie, 1966). Also, phytoplankton release up to 49% (average is approximately 10%) of their photosynthetically produced organic matter (Anderson and Zeutschel, 1970; Samuel et al, 1971). Therefore, the exchange of nutrients across the sediment-sea water interface will be modified by the activities of the benthic algae.

NO_3-N exchange (Fig. 28) was dominated by uptake. Selecting only those experiments in which uptake occurred, the uptake kinetics for NO_3-N in this in situ mixed algal population were determined. The half-saturation constant (K_s) is a measure of the affinity of enzymes for a substrate, while the maximum velocity of uptake (V_m) is a measure of the maximum rate of reaction when the enzyme is saturated with substrate. The K_s and V_m for both the light and dark boxes were determined. In the light and dark the K_s for NO_3-N was approximately 27 μM. This K_s value for NO_3-N is higher than that for the neretic phytoplankton of this region (Eppley et al, 1969b). The V_m of NO_3-N in the light and dark differed significantly: V_m light = 139 $\mu M/m^2/hr$ while V_m dark = 86 $\mu M/m^2/hr$. Interpretation of these results are tenuous since NO_3-N concentrations never approached 27 μM and, therefore, the kinetic curve is very fragmentary. In general, it appears that the benthic algal population has a low affinity for NO_3-N (high K_s) and that there is a light requirement for NO_3-N uptake. The low affinity is expected in an environment where there is abundant NH_3-N. Eppley et al (1969a) found

that low concentrations of NH_3-N effectively inhibited the formation of nitrate reductase and the concomitant uptake of NO_3-N. Eppley and Coatsworth (1968) suggested that there is a photosynthetic nitrate reduction mechanism operating in Ditylum brightwelli, but that NO_3-N was also taken up in the dark. However, in the dark, most of the NO_3-N taken up was not reduced and was recovered as NO_3-N. Dugdale (1967) wrote an excellent summary of the significance of nutrient limitation in the sea, and in Strickland (1970), Eppley uses the kinetic parameters to examine phytoplankton species assemblages.

NO_3-N uptake is an anomaly if NH_3-N is the preferred form of nitrogen. Results of this study indicate that NH_3-N is the preferred form even though NO_3-N is taken up. Nitrification (NH_3-N and NO_2-N oxidation) occurs in the aerobic marine environment at a very slow rate (Carlucci and Strickland, 1968; Watson, 1965). The uptake of NO_3-N by an active, large, benthic algal population would, therefore, lead to a reduction of the NO_3-N concentration in the sea water. The kinetic analysis, discussed above, showed that the in situ benthic algal population had a high K_s (27 μM), indicating it had an extremely low affinity for NO_3-N. Finally, a multiple regression analysis, significant at greater than the 99.9% confidence limit, showed that the benthic exchange of NO_3-N could be determined using the following equation:

$$\mu M\ NO_3\text{-}N/m^2/day = 0.78 - 66.8\ [NO_3\text{-}N \text{ concentration } (\mu M) \text{ in bottom water}] - 82.2\ [\text{oxygen exchange in light in } \pm mM\ O_2/m^2/hr] + 72.4\ [NH_3\text{-}N \text{ concentration } (\mu M) \text{ in bottom water.}]$$

A negative value would indicate NO_3-N uptake while a positive value

would indicate NO_3-N production by the benthos. This analysis found that NO_3-N uptake was positively correlated with NO_3-N concentration (indicating NO_3-N uptake by a mass action effect), positively correlated with benthic algal activity (showing stimulation of NO_3-N uptake in the light, as discussed above) and negatively correlated with the NH_3-N concentration (indicating an increasing repression of NO_3-N uptake as the concentration of NH_3-N increases).

The end of August and part of September, 1972, represented an unusual period in the benthic exchange of NH_3-N and NO_2-N. In this period the production of NH_3-N and NO_2-N decreased to their lowest rates and were, in fact, taken up (see Figs. 26 and 27). However, during this time there were no large fluctuations either in the rate of NO_3-N uptake or in gross photosynthesis by the benthic algae (see Figs. 17 and 28). It appeared that during this period NH_3-N and NO_2-N "actual total" (see below for definition) production decreased to a level that almost sustained benthic algal productivity, while in other periods there were large surpluses of NH_3-N and NO_2-N produced.

NO_2-N production is a function of both bacteria and algae and while it is not the preferred form of nitrogen by algae, NO_2-N is utilized (Carlucci et al, 1970; Eppley and Coatsworth, 1968; Vaccaro and Ryther, 1960; Watson, 1965). Of all the nutrients, NO_2-N production probably most closely represents the "actual total" production value by the benthos. "Actual total" production of a nutrient is defined as, "the gross in situ production rate of the nutrient, before it is corrected for any biochemical changes of the nutrient." NO_2-N represents this value to the closest extent because it is not a form preferred of

nitrogen by organisms and the oxidation of NO_2-N to NO_3-N in this environment occurs at a very low rate. NO_2-N production was most closely correlated with oxygen uptake in the dark. However, this positive correlation was not statistically significant at the 95% level. Correlation coefficients between NO_2-N exchange and other surface static and dynamic parameters were extremely low. Multiple regression analysis between NO_2-N exchange and these parameters yielded non-significant results. This indicates that NO_2-N exchange is a function of processes occurring within the sediment, and/or that parameters, other than those measured, determined its exchange rate. However, as discussed above, the exchange of NO_2-N may be affected by organisms, especially in periods when there is low NH_3-N production coupled with continued benthic algal activity.

These processes occurring within the sediment, are the aerobic and anaerobic processes governing the production of NO_2-N from NH_3-N or NO_3-N and the movement of NO_2-N into the water by diffusive and turbulent mixing. To have a constant production rate of NO_2-N there must be a constant supply of organic matter to the sediment and a constant regeneration rate within the sediment. Since the benthic bacterial population is relatively constant (see Fig. 14A), the main variable is the supply of organic matter. If it is not sufficient there will be a varying rate of regeneration. It appears from the rate of organic carbon input from fallout and macro-detritus (see Figs. 19 and 22) that there is a sufficient supply. However, these rates were shown to add little organic carbon to the benthos (see Results section on Sediment Carbon for discussion of this).

The exchange of NH_3-N, as with the exchange of NO_2-N appears to be a function of internal sediment processes or processes not measured. NH_3-N is correlated with NO_2-N exchange to a greater extent than it is to any other parameter, but the correlation is not statistically significant at the 95% confidence limit. Therefore, NH_3-N exchange, while being closely related to NO_2-N exchange, is affected by other parameters. The activities of benthic algae during periods of low NH_3-N production has been discussed. However, since the experiments in which this effect was of importance are unknown, no statistical analysis can be made.

NH_3-N production is reported to be a continuous process within sediments and the diffusion of NH_3-N into the water column from the sediments has been used to study its exchange rate (Rittenberg et al, 1955). Therefore, processes which would alter this diffusive rate would cause variations in the exchange rate of NH_3-N. Worm holes in the sediment would alter this rate since they would facilitate water movement into and out of the sediment. Surge activity which disturbs the top layers of sediment would likewise alter the rate of exchange, and moreover, the effects of surge would be operative until the sediments re-established their pre-disturbed equilibrium. These two unmeasured parameters (worm holes and surge) would also affect the exchange rate of NO_2-N.

The exchange of PO_4-P showed an average net production of 77 $\mu M/m^2$/day, indicating that the benthos is not PO_4-P limited. Statistical analysis of PO_4-P exchange by multiple regression analysis yielded the following equation significant at the 99.9% confidence limits:

$$\mu M\ PO_4\text{-}P/m^2/day = 235 - 199\ [PO_4\text{-}P \text{ concentration } (\mu M) \text{ in bottom water}].$$

Interpretation of this isolated equation is difficult. PO_4-P exchange is controlled by two factors. The main factor is the concentration gradient across the sediment-sea water interface. This PO_4-P gradient is maintained by the decomposition of phosphorus containing organic molecules within the sediment and by the low concentration of PO_4-P in the sea water above the sediment. The second factor controlling PO_4-P exchange is the effect of both the sediment surface algae and bacteria and the rate of supply of PO_4-P to them.

PO_4-P uptake is positively correlated with oxygen exchange in the dark and yet is negatively correlated with the number of bacteria in the sediment (CFU/cm^3). PO_4-P uptake is negatively correlated with oxygen exchange in the light and yet is positively correlated with chlorophyll $\underline{a}/cm^3$ of sediment. (All of the above correlations are statistically insignificant.) Also, PO_4-P uptake is negatively correlated with the photosynthetically active irradiation reaching the benthos (significant regression at the 98% confidence limit). However, a multiple regression analysis with PO_4-P concentration in the bottom water and photosynthetically active irradiation as independent variables regressed against PO_4-P exchange showed that the latter independent variable did not significantly improve the fit.

PO_4-P uptake is not a function of light intensity as is NO_3-N uptake. M.J. Perry (SIO, unpublished results) has found no significant light effect on PO_4-P uptake in the laboratory by a marine phytoplankter. PO_4-P uptake or production shows inconsistent results when correlated with the activities of benthic algae and bacteria. These "nonsense" results plus knowing that PO_4-P is produced on the average (but is taken

up on some occasions) suggests that PO_4-P exchange is a highly variable process where production is only marginal and the uptake and production activities of the benthic bacteria and algae may greatly affect the exchange rate.

Replicate Nutrient Exchange

Tables 6 and 7 give the results of the replicate dark box and light box experiments, respectively. The variability about the mean for the replicate experiments was greater for all nutrients in the light except for DOP and DOC. This probably results from the patchy distribution of benthic algae since the oxygen and NO_3-N exchanges were markedly more variable in the light, and these are influenced greatly by the activities of the benthic algae.

In the dark the inorganic nutrients vary by an average of ± 24% of the mean, while the organic nutrients vary by an average of ± 95% of the mean. In the light the values are ± 71% for the inorganic nutrients and ± 148% for the organic nutrients. Therefore, on the average the experimental dark values are expected to be valid within a factor of 2, and the experimental light values are expected to be valid within an average factor of 3.

Table 6. Results of replicate dark box experiments (RD)

Δ O_2 units are mM $O_2/m^2/hr$

Δ DOC-C units are $mg/m^2/hr$

Δ NH_3-N, NO_2-N, NO_3-N, PO_4-P, DON-N, and DOP-P units are $\mu M/m^2/hr$

The means ($\bar{x}$), the standard deviation are ± percent of the mean, and the average standard deviation from both experiments ($\bar{\bar{x}}$) are given.

	ΔO_2	ΔNH_3-N	ΔNO_2-N	ΔNO_3-N	ΔPO_4-P	ΔDON-N	ΔDOP-P	ΔDOC-C
RD-I	-1.90	+2.78	+0.260	0	+3.00		-0.880	-3.20
	-2.28	+1.76	+0.140	0	+5.04	+17.6	+0.660	+1.00
	-2.56	+3.90	+0.040	0	+3.06	+17.2	-1.10	+0.600
$\bar{x}$	-2.25	+2.81	+0.147	0	+3.70	+17.4	-0.440	-0.533
±	12%	31%	61%	0	26%	0.1%	178%	230%
RD-II	-1.99	+49.5	+1.46	+3.00	+11.1	+52.3	+1.48	-7.69
	-1.93	+22.2	+0.994	+2.21	+ 3.70	+40.5	0	-6.75
	-2.12	+47.8	+1.24	+3.60	+10.2	+27.4	+0.356	-3.94
$\bar{x}$	-2.01	+39.8	+1.23	+2.94	+8.33	+40.1	+0.612	-6.13
±	4%	31%	15%	19%	40%	25%	103%	32%
$\bar{\bar{x}}$	8%	31%	38%	10%	33%	13%	141%	131%

Table 7. Results of replicate light box experiments (RL).

Δ O_2 units are mM $O_2/m^2/hr$

Δ DOC-C units are $mg/m^2/hr$

Δ NH_3-N, NO_2-N, NO_3-N, PO_4-P, DON-N and DOP-P units are $\mu M/m^2/hr$

The means ($\bar{x}$), the standard deviation as ± percent of the mean, and the average standard deviation from both experiment ($\bar{\bar{x}}$) are given.

	ΔO_2	ΔNH_3-N	ΔNO_2-N	ΔNO_3-N	ΔPO_4-P	ΔDON-N	ΔDOP-P	ΔDOC-C
RL-1	+0.262	+15.0	+2.05	-1.09	+2.07	+8.51	-0.63	-1.75
	+0.131	+11.4	+1.24	-4.87	+3.84	+4.80	+0.17	-1.53
	+0.087	+4.34	+1.16	-1.53	+1.85	-26.6	-0.59	-5.67
$\bar{x}$	+0.160	+10.2	+1.48	-2.50	+2.59	-4.43	-0.35	-2.98
±	47%	43%	27%	68%	34%	355%	105%	78%
RL-11	-1.29	no	+0.638	-1.30	-0.732	-26.3	+0.788	-0.938
	-1.10	data	+0.019	-0.56	-1.29	+17.1	+0.788	+6.38
	-1.16		+0.638	+4.5	-0.338	-32.1	+0.300	+5.07
$\bar{x}$	-1.18		+0.432	+0.88	-0.787	-13.8	+0.625	+3.50
±	7%		68%	293%	50%	195%	45%	111%
$\bar{\bar{x}}$	27%	43%	48%	180%	42%	275%	75%	95%

VI SUMMARY

1. In situ benthic nutrient exchange and the environmental parameters which might affect this exchange were measured at a station located in about 18 m of water on a slightly sloping sand bottom of the La Jolla Bight off the Scripps Institution of Oceanography (SIO). Nutrient exchange was studied in situ using acrylic plastic boxes. Both transparent and darkened boxes were employed. When inserted 5 cm into the sediment, the boxes isolated 900 cm^2 of sediment and 9 liters of overlying water. Water samples taken from inside the box, after the initial or zero time (Ot) samples, introduced no outside water to the inside of the box. The method proved itself to be a reliable one, which, with certain limitations, could be used at all seasons. The main limitation to the method were the occasions when the surge activity at the experimental site was so great that the sand securing the boxes into the sediment was scoured away from the corners of the boxes.

2. The nutrients studied in detail were nitrate (NO_3-N), nitrite (NO_2-N), ammonia (NH_3-N) and phosphate (PO_4-P). The exchange of dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP) were not analyzed in detail.

3. The environmental parameters studied were: benthic respiration and photosynthesis, numbers of bacteria, chlorophyll a and phaeopigment concentrations, sediment inorganic and organic carbon content, organic macro-detritus input to the benthos, fallout of fine organic debris from the water column, temperature, relative surge strength, sediment porosity, relative sediment height, and sediment incident irradiation.

4. NO_3-N was taken up by the benthos at an average net rate of 77 $\mu M/m^2/day$ (range: 720 $\mu M/m^2/day$ taken up to 647 $\mu M/m^2/day$ produced). The criteria used was as follows: a nutrient is taken up when the concentration of the nutrient in the water inside of the box decreased in an experiment, and production means the concentration of the nutrient inside of the box increased. Kinetic analysis of only the experiments where NO_3-N uptake occurred showed that the in situ benthic algal population in both the light and dark had a K_s of 27 μM, while the V_m in the light of 139 $\mu M/m^2/hr$ was significantly higher than the V_m in the dark of 86 $\mu M/m^2/hr$. This and other data implied that the algal population preferred another form of inorganic nitrogen. Studies with phytoplankton have shown them to prefer NH_3-N. The fact that the V_m in the light was greater than the V_m in the dark also concurs with studies showing a light requirement for NO_3-N uptake. The following multiple regression expression for NO_3-N exchange was significant at greater than the 99.9% confidence limit:

$$\mu M\ NO_3\text{-}N/m^2/day = 0.78 - 66.8\ [NO_3\text{-}N \text{ concentration } (\mu M) \text{ in bottom water}] - 82.2\ [\text{oxygen exchange rate in light as } \pm\ mM\ O_2/m^2/hr] + 72.4\ [NH_3\text{-}N \text{ concentration } (\mu M) \text{ in bottom water}].$$

NO_3-N exchange was dominated by the activities of the surface benthic algal population.

5. NH_3-N and NO_2-N exchange appeared to be controlled by internal sediment processes plus some unmeasured processes that altered the rate of their diffusion through the sediments. NH_3-N exchange, being the

preferred form of inorganic nitrogen by the benthic algae, was altered by algal activities during periods of low NH_3-N production. The same may also have been true for NO_2-N exchange, but to a lesser extent, as NO_2-N is not a preferred form of inorganic nitrogen. The fact that NH_3-N and NO_2-N are produced in excess of the needs of the benthic algal flora indicated that the algae are not nitrogen limited. NO_3-N uptake appears to be an anomaly, but in fact it is not. NO_3-N uptake, being positively correlated with NO_3-N concentration, occurred as a mass action effect. Since NO_3-N production from the oxidation of ammonia is a slow process, uptake of NO_3-N, even of a small amount, by the benthic algal population will result in a decrease in the NO_3-N concentration in the water inside of the box. The production of NH_3-N and NO_2-N was continual but not at a constant rate. Alterations in the rate were due to a varying rate of organic matter input to the benthos. The average net rate of NH_3-N production was 872 $\mu M/m^2$/day (range: 47 $\mu M/m^2$/day taken up to 3290 $\mu M/m^2$/day produced). The average net rate of NO_2-N production was 34 $\mu M/m^2$/day (range: 5 $\mu M/m^2$/day taken up to 97 $\mu M/m^2$/day produced).

6. PO_4-P net production averaged 77 $\mu M/m^2$/day (range: 438 $\mu M/m^2$/day taken up to 502 $\mu M/m^2$/day produced). PO_4-P production implies, as with inorganic nitrogen, that the benthic algae are not phosphorus limited. However, the results indicate that PO_4-P is only marginally produced and PO_4-P exchange is highly dependent upon the diffusive gradient across the sediment-sea water interface, the activities of the sediment surface algae and bacteria and the production rate of PO_4-P by the benthos. The following regression equation was significant at the 99.9% confidence limit:

$\mu M\ PO_4\text{-}P/m^2/day = 235 - 199\ [PO_4\text{-}P$ concentration (μM) in bottom water].

7. The average net uptake rate of DOC was 7 mg $C/m^2/day$ (range: 370 mg $C/m^2/day$ taken up to 285 mg $C/m^2/day$ produced). The average net uptake rate of DON by the benthos was 75 $\mu M/m^2/day$ (range: 1326 $\mu M/m^2/day$ taken up to 1280 $\mu M/m^2/day$ produced). The average net production rate of DOP by the benthos was 12 $\mu M/m^2/day$ (range: 28 $\mu M/m^2/day$ taken up to 59 $\mu M/m^2/day$ produced).

8. The temperature at the experimental site ranged from a low of 11.0°C to a high of 17.1°C. Due to the movement of the thermocline (shallower in the winter and deeper in the summer) there was no obvious seasonal trend. The normal temperature variation over the course of an experiment (4-6 hr) was less than 1.0°C.

9. Photosynthetically active irradiation striking the sea surface was seasonal with values between 200-300 langleys/day common in the spring and summer and 100-200 langleys/day common in the fall and winter. Sediment surface irradiation was highly dependent upon the turbidity of the water and, therefore, did not show a seasonal trend.

10. Studies of relative sediment height showed a total movement range of 8.3 cm. The cycles of movement concur with other studies showing shoreward transport of sand from deeper waters in the summer and seaward transport of sediment in the winter.

11. The bacterial numbers in the water showed marked fluctuations (1.0×10^2 to 1.6×10^4 CFU/ml sea water). The fluctuations were almost an order of magnitude less for sediment bacteria (4.0×10^5 to 7.5 x

x 10^6 CFU/cm^3 of sediment). Benthic bacteria, being attached to sediment particles, would tend to remain in the same location while planktonic bacteria would not. The bacterial population density of the benthos appears to be influenced by factors that affect; 1) organic carbon content of sediment, 2) large scale changes in the benthic algae, and 3) changes in the rate of organic matter input to the benthos.

12. The benthic algal population is generally not nutrient limited. However, low light levels and surge activity appear to limit their population size. It is also an indigenous population and one that is not dependent upon continual inoculation from the water column. The benthic algal population is firmly attached to the sand grains and is able to maintain itself at the sediment surface even after much surge activity.

13. The average respiratory loss of carbon from the sediments was 337 mg C/m^2/day (range: loss of 72 mg C/m^2/day to a loss of 634 mg C/m^2/day). These values are from the equation:

Carbon loss = net photosynthesis in light - gross respiration in dark.

Bacterial respiration accounted for 71% to 95% of the total respiration. On all but one occasion, when gross photosynthesis equalled zero, gross photosynthesis occurred, indicating that there was sufficient light and nutrients and that the algae present were photosynthetically active. However, only on nine occasions was there a net gain of organic carbon in the light. Net photosynthesis averaged - 56 mg C/m^2/daylight period (daylight period is the number of hrs of daylight on the day of an experiment) with a range of -294 to +175 mg C/m^2/daylight period. Also,

net photosynthesis in the daylight was always less than the gross respiration in the dark. Therefore, even though there was a photosynthetically active benthic flora, it was not capable of supplying all the organic matter needed by the benthic biota. As a result the benthos must have another source of oxidizable organic matter.

14. The mean rate of macro-detritus input was 0.13 g dry wt/m^2/day with an average organic carbon input of 0.029 g organic C/m^2/day. This material contained two major components (worm tubes and Phyllospadix blades) and a third or "other" component. The input rates of organic carbon for these three categories, along with the percent organic carbon of dry weight with its standard deviation, were, on the ten occasions they were measured; 0.017 g C/m^2/day for worm tubes and attached assemblages (13.6% $\pm$ 1.7%), 0.013 g C/m^2/day for Phyllospadix blades and attached assemblages (34.4% $\pm$ 2.9%), and 0.0045 g C/m^2/day for the other component (26.1% $\pm$ 4.1%). Since a large amount of material moves across the sediment surface and these measurements were made periodically, they were not an actual rate of input. The detritus collected may have been transitory and not adding any organic matter to the sediment at the experimental site. Also, detritus, that had moved into the area and had been buried or broken into smaller fragments was not accounted for in these measurements.

15. The mean rate of fine detrital fallout was 110 g dry wt/m^2/day or 3.4 g organic C/m^2/day (average percent organic carbon of dry weight was 3.7%). Due to water motion this material added little organic matter to the sediments. Although neither macro-detritus nor fallout was significantly correlated with nutrient exchange measurements,

macro-detritus was more closely positively correlated with nutrient exchange than was fallout.

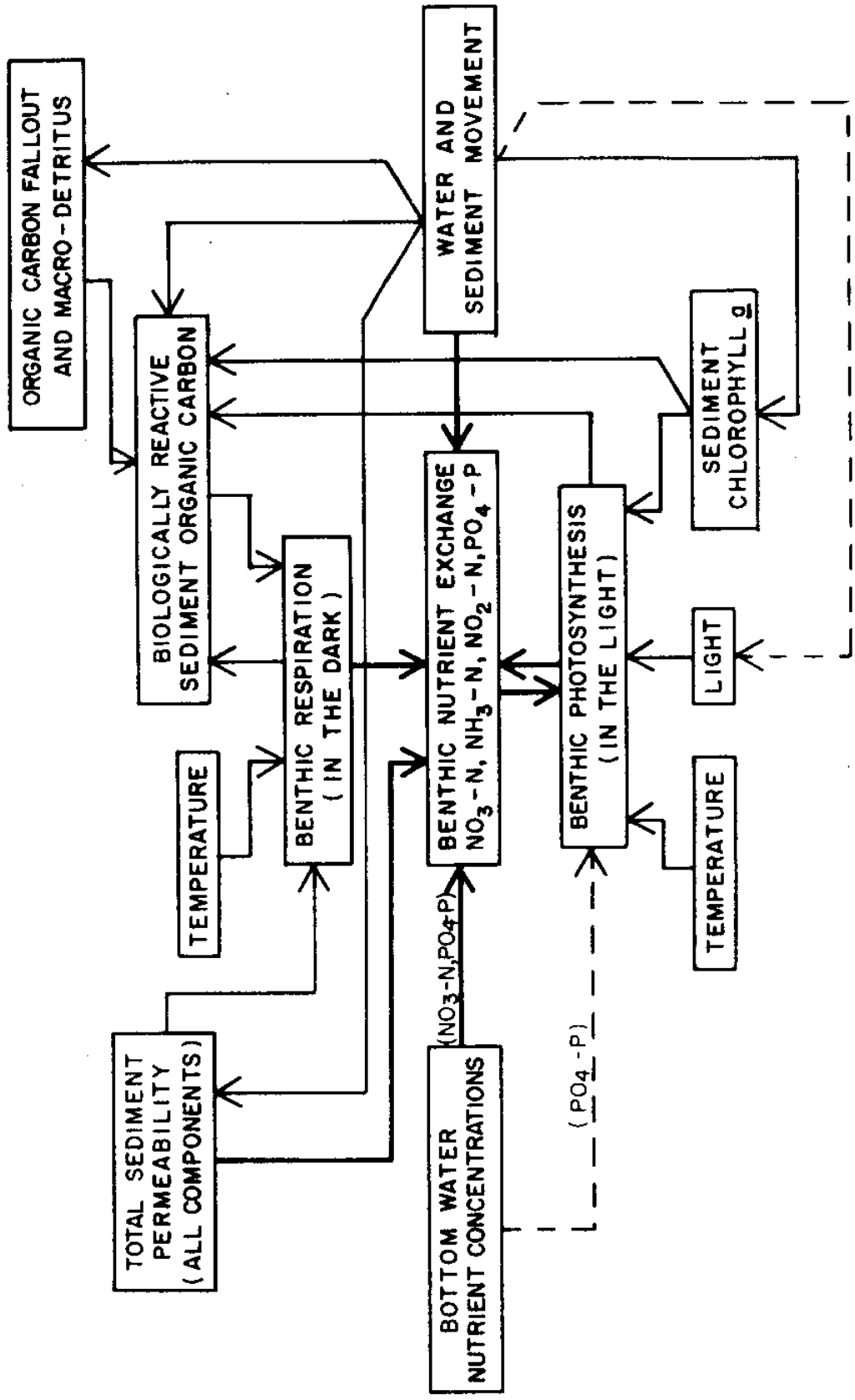
16. Average percent organic carbon of sediment dry weight was 0.15% and for inorganic carbon equalled 0.041%. Sediment organic carbon was not affected by macro-detritus or fallout organic carbon input rate, by respiration and, in all cases except when there was benthic algal blooms, was not affected by the benthic algal population. Sediment carbon content is probably controlled by a "washing out" phenomenon. "Washing out" is the translocation of organic matter already on or in the sediments by water currents. It is essentially a cleansing activity caused by both the movement of the surface sediment layers by surge activity and the transport of particulate material in the water by currents.

17. Sediment unit dry weight averaged 0.756 g/cm^3. The porosity for these sediments averaged 72.8% and ranged from 70.7% to 74.6%.

18. From the results of this in situ study the following conclusions are made: 1) that the average net rate of nutrient exchange is too low to have a substantial effect on the individual nutrient concentrations in the 18 m water column above the experimental site (example: total inorganic nitrogen production was at an average rate of 829 $\mu M/m^2/day$, the average total inorganic nitrogen content of the water column was 3.0 μM N/l x 1.8 x 10^4 l = 5.4 x 10^4 μM, therefore, the exchange due to the sediment was insignificant); and 2) the interactions which govern the exchange of each nutrient are complex. Figure 33 is a summary diagram of the interactions found to govern nutrient exchange between the marine benthos and the overlying water.

FIGURE 33

Summary diagram of the interactions found to govern nutrient exchange between the marine benthos and the overlying water. Thicker lines represent factors which most directly interact with nutrient exchange. Dotted lines represent interactions which exist only during special conditions.


ORGANIC CARBON FALLOUT AND MACRO-DETRITUS
WATER AND SEDIMENT MOVEMENT
BIOLOGICALLY REACTIVE SEDIMENT ORGANIC CARBON
SEDIMENT CHLOROPHYLL a
BENTHIC RESPIRATION (IN THE DARK)
BENTHIC NUTRIENT EXCHANGE NO_3-N, NH_3-N, NO_2-N, PO_4-P
BENTHIC PHOTOSYNTHESIS (IN THE LIGHT)
LIGHT
TEMPERATURE
TEMPERATURE
TOTAL SEDIMENT PERMEABILITY (ALL COMPONENTS)
BOTTOM WATER NUTRIENT CONCENTRATIONS
(NO_3-N, PO_4-P)
(PO_4-P)

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