THE CONTRIBUTION BY PHYTOPLANKTON, BACTERIA AND DETRITUS TO A ROCKY SHORE ECOSYSTEM.

GEREMY CLIFF

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ABSTRACT

An investigation has been carried out on the particulate organic matter (POM) in suspension over the large inter- and subtidal reef at Dalebrook in False Bay. Standing stocks of phytoplankton, bacteria and detritus were monitored for 13 months, at three localities on the reef, on incoming and outgoing tides. A number of seasonal trends emerged, despite day-to-day variation in these stocks.

In spring and summer chlorophyll levels were low : 1 – 2 µg/l. Due to the extremely low nitrate concentrations (< 2 µg at/l) and to a lesser extent, silicates (< 6 µg at/l), little autochthonous phytoplankton production was recorded over this period. Concentrations of nitrates, silicates and chlorophyll a were highest at the offshore edge of the reef in incoming water. After a strong south-easterly wind, chlorophyll concentrations of 19 µg/l were recorded 0,5 km offshore. Chlorophyll concentrations were in the region of 5 µg/l in winter.

Detritus accounted for almost 80% of the POM and never dropped below 0,5 mg/l. There were no marked spatial and tidal influences on the mass of detritus in suspension. However, considerable import and export of material is believed to be associated with the strong water movements over the reef. Most of the detritus was in advanced stages of decomposition, making it extremely difficult to determine its origin.

A Coulter Counter provided particle size spectra over the range 5 - 112 μm. It was found that particles with apparent diameters of 10 - 30 μm contributed the highest volume.

Bacterial densities ranged from 4×10^5 to 16×10^5 cells/ml; numbers were highest in late summer and autumn. 95% of the cells were not attached to particles, but were free in suspension.

These results are compared with those from other inshore environments.

CONTENTS

CHAPTER 4
RESULTS

CHAPTER 1

INTRODUCTION

The emphasis behind much of the current marine ecological research in South Africa lies in the analysis of energy flow through inshore ecosystems. Three such programmes are operative in the Western Cape; namely studies of the communities of kelp beds and sandy and rocky shores. This work forms part of an investigation into the ecological energetics of rocky shores, with research being concentrated at Dalebrook in False Bay (34° 6'S, 18°28'E).

Dalebrook lies on the north-west coast of False Bay and is therefore directly exposed to the south-easterly wind which blows for much of the year. McQuaid (in prep.) has found that the most abundant benthic invertebrates on such exposed, rocky coastlines round the Cape Peninsula are the filter feeding species. At Dalebrook he found that the biomass of these animals was of an order of magnitude greater than that of browsing and grazing animals and three times greater than the biomass of seaweeds on the shore.

Upwelling is known to occur in False Bay (Cram, 1970). Such regions of coastal upwelling are recognised as being the most productive of the world ocean, followed by waters over the continental shelf (Ryther, 1969). One would therefore expect phytoplankton to provide a rich supply of organic matter to the filter feeders at Dalebrook.

In addition to this, there is overwhelming evidence (see Mann, 1972) that seaweeds are far more productive than phytoplankton in the immediate vicinity of the coast. The result is that in contrast to the open oceans, where phytoplankton provides the majority of organic matter, food chains in the intertidal zone and shallow coastal waters rely mainly on the production by communities of attached macrophytes.

McQuaid (in prep.) found a small herbivore biomass at Dalebrook, suggesting that very little of the seaweed production is consumed by grazing animals, but is liberated into solution or as detritus (particulate organic matter - POM). Bacteria play an important role in making the macrophyte energy stores available to the filter feeders. These micro-organisms are able to assimilate the dissolved organic matter (DOM) released by the macrophytes. Unlike most other heterotrophs, they are also capable of digesting complex, structural plant compounds. The bacteria living in the water column may then be filtered out by the suspension feeding animals. In this way, organic matter which is not utilised by the herbivores still passes through the food web of the rocky shore, creating a far more efficient transfer of energy from primary producers than is at first apparent.

The amount and distribution of detritus is dependent to a large extent on the hydrographical conditions prevailing in the area. On an exposed shoreline such as Dalebrook, wave action will exert an abrasive effect on the macrophytes, resulting in the almost continuous production of POM and DOM. The movement of water will also serve to retain particles in suspension where they are available to the filter feeders, whereas they might settle out in calm conditions. However, under the influence of the tide and currents, much of the macrophyte detritus may be swept out of the area before it is utilised by the animals. At the same time water movements may import phytoplankton and nutrients into the area.

Indications are that the animals on the Dalebrook shore have access to a large standing crop of PGM as their basic food source. This crop is not necessarily utilised uniformly, its availability depending largely on the size range of the particles. There is little evidence to suggest that filter feeders are capable of qualitative food selection, such as discriminating between a phytoplankton cell and a detrital particle of the same size. Particle size seems to be the principal criterion for selection; food intake is governed by the size of the animals and the construction of their filtering apparatus (Lenz, 1977). Therefore, when considering the availability of food to the animals, the size distribution of the particles in suspension is extremely important.

Suspended particulate organic matter and detritus have been investigated in a number of environments. These include estuaries (Odum and de la Cruz, 1967; Quasim and Sankaranarayanan, 1972), coastal waters (Zeitzschel, 1970, Lenz, 1974, 1977; Eppley et al, 1977), open ocean surface waters (Mullin, 1965; Menzel and Goering, 1966) and deep waters (Gordon, 1970). A symposium (Melchiorri-Santolini and Hopton, 1972) and several reviews (Riley, 1970; Parsons, 1975; Fenchel and Jorgensen, 1977) have been published on the subject. These environments differ in so many characteristics that results from one do not necessarily apply to another. Furthermore, even within a single environment, there is no reason to believe that the results will be identical spatially or temporally. Most of the work in coastal waters has been undertaken at least one kilometre from the shore. The only exceptions are the work by Schleyer (1979) in the rough, littoral waters of Natal and by Field et al.(in press) in a large west coast, subtidal kelp bed. No work of this nature appears to have been conducted in the turbulent waters of the intertidal zone.

Atkins (1970a, b) has presented a general overview of the wind, surface current, salinity and temperature patterns in False Bay. Tromp and Horstman (in press) monitored the upwelling of nutrient-rich water, but at stations off the mouth of False Bay, over 30 kilometres from Dalebrook. In describing the biology of False Bay, Day (1970) stated, 'practically nothing is known of the plankton or productivity of the water', and in the intervening nine years this situation appears to have remained unchanged.

An examination of the particulate organic matter in suspension over the Dalebrook reef is essential in understanding the functioning of this rocky shore ecosystem. Phytoplankton, bacteria and detritus all play important roles, particularly in the filter feeders' food web. This study is aimed at determining the relative contributions of these three components to the POM in suspension. It assesses the importance of phytoplankton in the autochthonous production of organic matter. In spite of a lack of information on currents in the area, it attempts to detect sources of organic input and loss by the reef system.

The seasonal and daily variations in phytoplankton, bacterial and detrital standing stocks were monitored for 13 months during 1977 and

1978. Samples were taken at three stations on the reef, on both incoming and outgoing tides, to detect any import or export of material. Particle size distribution was determined and phytoplankton production measured a short distance beyond the reef. The offshore water was also analysed for comparison with that over the reef.

These results have been discussed in relation to the complex hydrographic conditions that exist in the Bay and they have been compared with information from other South African nearshore environments.

CHAPTER 2

STUDY AREA

False Bay, Figure 1, covers over 1000 square kilometres; it is almost square in shape and is open to the ocean in the south. It is deepest at the southern entrance, shelving gradually towards the northern shores, where the coastline is a vast expanse of gently sloping, sandy beaches, interspersed with rocky outcrops. One such rocky stretch extends almost uninterrupted from Kalk Bay Harbour eastwards to St. James, a distance of close on one kilometre. The study area, Dalebrook, lies 300 metres to the east of the harbour. Here one finds a flat intertidal rocky platform, about 80 metres wide, with scattered pools and narrow gulleys. The only sand in the immediate vicinity is a narrow strip above the high water mark. The rocks occurring subtidally cover a similar area.

In summer the prevailing wind is from the south-east, and it often reaches gale force strength over the bay. Blowing directly onshore at Dalebrook, it results in extremely rough and choppy seas. In winter north-westerly winds are more common; this offshore wind flattens the sea and the water is often very calm during this period.

Dalebrook's intertidal filter feeding fauna is dominated by the barnacles, *Octomeris angulosa* and *Tetraclita serrata*. Large beds of *Pyura stolonifera* occur subtidally; the black mussel *Choromytilus meridionalis* and various sponges are also present. The macrophytes include *Bifurcaria sp.*, *Gelidium pristoides*, *Gigartina hystrix*, *Ulva sp.* and *Laurencia glomerata*, but none of the laminarian kelps which are so abundant on the south-west cost of False Bay.

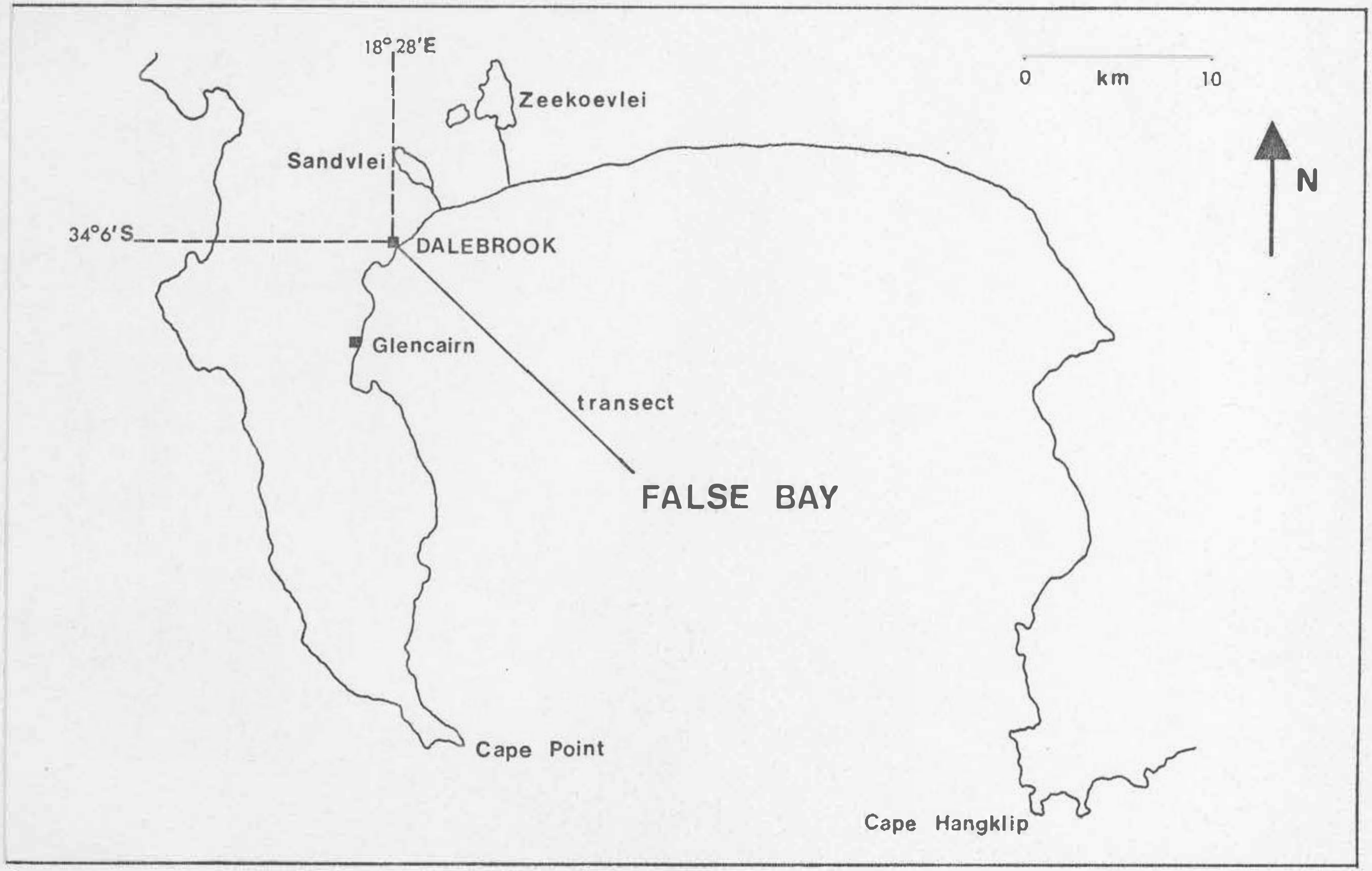

Figure 1. The study area, Dalebrook, in relation to the rest of False Bay. The position and length of the transect line is indicated.

CHAPTER 3

METHODS

3.1 : SAMPLING PROCEDURE

3.1.1 : Monthly Sampling

The seasonal variation in the amount and composition of the seston was determined by collecting 12 water samples on one particular day each month for 13 months. They were divided into six samples from an incoming tide and six from the following outgoing tide, taken from three different localities on the reef. The stations were situated over the reef on a line running normal to the shore. The first, termed the INSHORE STATION, was located in the intertidal zone and the third, the OFFSHORE STATION, at the end of the reef where the water depth was 5 m. The distance between the two stations was approximately 150 m with the MIDDLE STATION situated midway between them, where the depth varied between 2 and 3 m. All samples were taken 1 m above the bottom.

Initial observations showed that different conditions prevailed at each of the three stations. The water at the inshore station was generally turbulent and foamy as the waves moved in over the rocks. Waves and white water were never seen at the offshore station; however, it was not uncommon to find a ground swell moving water over the reef. The conditions at the middle station fell somewhere between the two; it was just behind the line of breakers and while white water was not common, the surging effect of the swells was marked.

Preliminary investigations in the winter of 1977, at a number of localities on the reef, revealed a distinct gradient in the amount of suspended matter. Chlorophyll concentrations and bacterial densities increased as one moved offshore, although the levels of total seston decreased. Sampling at the three stations would seem to provide a fairly representative picture of the amount and distribution of seston over the reef. At the same time it was hoped that this sampling pattern would give an indication of any net loss or gain of POM, i.e. if the levels were higher in outgoing water one might infer that the excess amount had been produced on the reef and was being exported from the system; higher levels in incoming water and at the offshore station would be indicative of import and gain by the system.

Samples were collected in 5 litre plastic cans by a snorkel diver operating from the shore. These containers were washed with a concentrated solution of sodium hypochlorite and carefully rinsed before use. Initial operations were conducted from a ski boat so that *in situ* primary production experiments could be performed simultaneously and a small 200 μm mesh net be towed to quantify the zooplankton population in the area. However, conditions did not always favour the operation of a boat so close inshore, and accurate hauls for zooplankton were not possible with the equipment available.

Each 5 l sample was split for the various analyses as follows:

1 l for chlorophyll a determination
2 l for gravimetric analysis
500 ml for microscopic examination

500 ml for particle size determination
150 ml for inorganic nutrient analyses
100 ml for estimation of bacterial densities.

3.1.2 : Daily Sampling

It was very difficult to distinguish seasonal trends from random fluctuations by sampling on only one particular day in the month. A second sampling programme was introduced to determine the day-to-day variation in the composition of the seston and to verify any summer-winter differences apparent in the monthly analysis. It is possible that any upsurges in numbers of phytoplankton or bacteria may be dependent on the availability of nutrients and detritus several days before. While the interval between monthly visits to the reef was too great to show this, any relationships of this nature may become apparent by analysing the water each day for a number of days. Simple cross correlations were calculated for all the parameters measured with lags of up to 4 days.

A single 5 litre sample was processed daily for two 15 day periods. The first was in summer, when onshore winds prevail and the sea is generally rough; the second in winter when offshore winds are more common and the water calmer. The collection was made as close to high tide as possible, at the inshore station, so as not to involve any diving.

The samples were processed in the same manner as the monthly ones. A careful note was made of general sea conditions, which were expressed on a scale 1-5, with the roughest conditions designated the highest values. Water temperature was also measured at the time of collection. Mean daily wind velocity and direction were calculated from hourly recordings at the Cape Point Lighthouse.

3.1.3 : False Bay Transects

In the monthly and daily programmes, sampling was confined to the water over the reef. An additional programme was introduced to investigate the seston in the open waters of the bay. The aim was to detect any changes in the composition of the seston as one moved away from the influence of the reef.

Tromp and Horstman (in press) have established that inshore and west of Cape Hangklip, where the coastline runs diagonally across the path of the south - easter, this wind induces the upwelling of cold, nutrient-rich water. This phenomenon results in large scale primary production, with phytoplankton present in high concentrations in the surface waters. Cram (1970) has followed the movement of this water into the centre of False Bay. The results of the present study indicate that during the summer months, when the south-easters are common, the chlorophyll content of the water at Dalebrook was extremely low. The results of samples taken at a number of points on a transect into the bay, two to three days after a strong south-easterly wind would indicate how close these phytoplankton-rich waters extend towards the Dalebrook shoreline. This would clarify the question of net gain or loss of organic matter by the reef ecosystem.

The transect was undertaken again in September after a week free of south-easter winds, when the thermal stratification of the water was unlikely to have been disturbed, and the surface waters low in phytoplankton and nutrients.

Table 1 illustrates the position of the eight sampling stations which fall on a line, passing through the three reef stations, linking Dalebrook to Cape Hangklip (Fig. 1). Where depth allowed, samples were taken at 2, 6 and 15 metres. The two most inshore stations were situated over the reef. Of the 18 samples collected, six were analysed only for chlorophyll and inorganic nutrient concentrations.

TABLE 1 : False Bay transect : Position of the stations along the transect line and the depths at which the samples were taken. Asterisks indicate complete analysis of the sample; crosses indicate chlorophyll and inorganic nutrient analysis only.

DISTANCE OFFSHORE Kilometres		0	0,1	0,5	1	1,5	3	6	18
WATER DEPTH Metres		2,5	7	9	13	17	22	30	46
SAMPLING DEPTH Metres	2	*	*	*	*	*	*	*	+
	6			*	+	*	+	*	+
	15					*	+	*	+

3.2 : SAMPLE ANALYSIS

3.2.2 : Inorganic Nutrients

Duplicate 5 litre water samples were collected every month at each of the three stations on an incoming tide and the procedure was repeated for the following outgoing tide. Subsamples for ammonia, nitrate, orthophosphate and silicate analysis were taken from only one of the duplicates. Three 50 ml aliquots were decanted into small, screw-top, plastic vials and stored at $- 10^{\circ}C$ until they could be processed in the laboratories of the Sea Fisheries Branch.

The methods for ammonia determination were based on those of Grasshoff and Johannsen (1972) and Slawyk and MacIsaac (1972). The seawater sample was treated in an alkaline citrate medium with phenol and a stable chlorine donor, in the presence of sodium nitroprusside, which acts as a catalyser. Indophenol was produced and the extinction of this solution was measured. Concentrations of ammonia were expressed in µg atoms $NH_3 - N/l$.

Concentrations of nitrates and phosphates in solution were determined according to the methods of Armstrong et al. (1967). A reduction column of cadmium filings and copper sulphate pentahydrate solution was prepared. The seawater was allowed to pass through the column and the nitrates in solution were reduced to nitrites. The nitrites produced were diazotised with sulphanilamide in hydrochloric acid to form a highly coloured azo dye. The extinction of this solution was measured in a colorimeter and the concentration of nitrate expressed in µg atoms NO_3 - N/l. The concentration of naturally occurring nitrite in the seawater was so low that it was not necessary to make any correction for it.

Phosphates are found in solution in a number of forms. In this study the concentration of the reactive, inorganic fraction or orthophosphate ion was determined and expressed in µg atoms PO_4 - P/l. The orthophosphate in solution was allowed to react with a composite reagent containing concentrated sulphuric acid, ammonium molybdate, ascorbic acid and potassium antimony tartrate. The resulting, complex heteropoly acid was reduced *in situ* to give a blue solution. The extinction of this solution was measured at 885 nm.

Silicates, expressed in µg atoms SiO_3 - Si/l, were analysed using the technique of Grasshoff (1965). The seawater was allowed to react with molybdate and silico-molybdate complexes were formed. A reducing reagent, comprising freshly prepared stannous chloride in hydrochloric acid,was added to give a blue reduction compound, the extinction of which was measured colorimetrically.

3.2.2 : Chlorophyll Analysis

Concentrations of the photosynthetic pigment, chlorophyll a, were measured as an estimate of phytoplankton standing stock. Although this method has been criticised on the grounds of the variability in chlorophyll content of phytoplankton cells, the speed and simplicity of analysis have made it a popular method of crop estimation (Strickland, 1960). The techniques adopted in this study were based on those proposed by UNESCO (1966) and Strickland and Parsons (1972).

One litre of seawater was filtered through a Sartorius cellulose nitrate filter of pore size 0,45 µm. As the samples were processed immediately on return to the laboratory, no powdered $MgCO_3$, which is believed to prevent acidification of the chlorophyll and hence pigment degradation (Vollenweider, 1974), was added. The filters were washed briefly under suction with distilled water to remove salts and extracted in 10,0 ml of 90% acetone (analytical grade) in centrifuge tubes. The tubes were stoppered, shaken vigorously to dissolve the filters and held in complete darkness at 5°C for 20 hours.

The extracts were centrifuged for 20 minutes at 5 000 r.p.m. A Beckman SP 25 spectrophotometer with 5 cm path length cells was used to measure the light absorbance of the clear supernatant. Absorbance at 750, 663, 645 and 630 nm was read against a 90% acetone blank. The extinction at 750 nm was subtracted from the extinctions at 663, 645 and 630 nm and the answers multiplied by 10 (the volume of acetone in ml), divided by 1 (the volume of seawater in litres), and divided by 5 (the light path of the cells in cm). These corrected extinctions were inserted in the following UNESCO (1966) equation to give the concentration of chlorophyll a in µg/l of seawater:

$$\text{chl a} = 11{,}64e_{663} - 2{,}16e_{645} + 0{,}10e_{630}$$

Phytoplankton standing stocks had to be converted to organic matter in order to estimate the amount of detritus in suspension. Carbon : chlorophyll ratios in phytoplankton are a function of temperature, nutrient concentration, illumination and species composition, with values ranging from 15 to 130 (Strickland, 1960). It is therefore extremely difficult to select a simple conversion factor. Following the recommendations of Strickland (1960) for mixed, natural populations subject to high light intensities or warm, nutrient-deficient waters, a ratio of 60:1 was used. Carbon constitutes a consistent 50% of phytoplankton organic matter (Strickland, 1960) and so chlorophyll concentrations, in µg/l, were converted to phytoplankton organic matter, in mg/l, by multiplying by 0,12.

3.2.3 : Primary Production

Methods for the determination of phytoplankton photosynthetic rates usually involve measuring either the amount of carbon dioxide taken up or the oxygen produced per unit time. The ^{14}C-technique for the measurement of carbon dioxide uptake, first proposed by Steemann Nielsen (1952), is most commonly used today since it is possible to detect very low photosynthetic rates with this method. The apparatus required for ^{14}C experiments was not available and production measurements in this study were based on oxygen evolution. This was done using the Winkler titration technique. Vollenweider (1974) states that the oxygen method should not be attempted in water whose chlorophyll a concentration is less than 1 µg/l. In spite of the low chlorophyll concentrations at Dalebrook, the oxygen method does provide a meaningful measure of phytoplankton production.

Essentially the technique consists of measuring the changes in oxygen concentration in subsamples of water exposed in clear and dark bottles. An incubation site was selected in water 8 metres deep and approximately 300 m beyond the reef. A water sample was collected in a 7 litre NIO bottle at 2 and 4 m. Each sample was used to fill five 250 ml bottles, three light and two dark; water was also retained for chlorophyll and inorganic nutrient analysis.

The initial oxygen content of the water was determined by immediately fixing a light bottle with the Winkler reagents, manganous sulphate and alkali iodide. The remaining oxygen bottles were suspended in perspex holders beneath an anchored float at their respective depths. After a 4 hour incubation the oxygen in these bottles was also fixed. In the laboratory the oxygen content of each bottle was measured according to the standard Winkler technique. Three aliquots were taken from each bottle and each titrated against a freshly prepared solution of 0,005 N sodium thiosulphate.

Assuming that the respiration in the dark bottle was equal to that in the light bottle, the difference in oxygen content between the 2 bottles was taken as a measure of gross production. The increase in the amount of oxygen in the light bottle was taken as a measure of net production. Respiration was taken as the difference between the initial oxygen level and that in the dark bottle. The volume of oxygen evolved was converted to carbon assimilated using the factor proposed by Svedrup et al (1942):

$$1 \text{ ml } O_2 \text{ evolved} = 0{,}536 \text{ g carbon assimilated}$$

Photosynthetic and respiratory quotients of 1,2 and 1,0 respectively (Strickland and Parsons, 1972) were used.

3.2.4 : Bacterial Counts

Epifluorescent microscopy was used to estimate bacterial densities. This is a direct count technique, with acridine orange as the fluorescent dye, which has been widely applied in routine ecological sampling (Ferguson and Rublee, 1976; Mazure and Branch, in press; Field et al., in press). The methods adopted in this study were those proposed by Hobbie, Daley and Jasper (1977) using Nuclepore polycarbonate filters, pore size 0,2 µm. From each water sample a 100 ml subsample was fixed with membrane filtered formalin (analytical grade) at a final concentration of 5% and stored in sterile glass jars at 5°C in the dark.

To eliminate autofluorescence the filters were first stained by soaking them for 1 - 2 hours in a solution of 2 g of irgalan black in 1 litre of 2% acetic acid. The filters were rinsed in distilled water and placed on top of media pads on the filtration apparatus; these backing pads were found to give a better distribution of the vacuum. The filters were often partially hydrophobic. This was overcome by briefly wetting the filtering surface with several drops of a 1% solution of surfactant (Photoflo 200, Eastman Kodak Company).

A 0,1% solution of acridine orange was prepared, fixed with membrane-filtered formalin and stored at 5°C in the dark. This solution was filtered through a 0,2 µm Nuclepore filter prior to use. 5 ml was added to a 5 ml aliquot of seawater. After a 3 minute incubation the seawater-acridine orange solution was drawn through the filter under a suction of 0,5 atmospheres.

Immediately after filtration a portion of the filter was cut out and placed on a microscope slide. A few drops of immersion oil were placed on the filter, a cover slip added, followed by another drop of immersion oil. Nikon immersion oil (N_D = 1,515 at 25°C) was used as it showed no fluorescent or destaining properties. The preparation was viewed with a Zeiss standard microscope and epifluorescent illumination system comprising a 50 W high pressure mercury lamp, 455 - 500 band pass filter, FT 510 beam splitter and LP 520 barrier filter.

The numbers of bacteria were estimated from a count of 10 randomly chosen fields (magnification x1000, field diameter 112 μm). The bacteria tended to fluoresce bright green and only those with a distinct bacterial morphology were counted. Cells were noted as being free living or attached to particles. Brief notes were made on the nature of the particulate matter present. A graduated eye piece was used to measure cell dimensions. This gave an estimate of average cell volumes, necessary for biomass calculations. The bacterial density, in cells per ml, was calculated using the formula (Mazure, 1978):

$$D = \frac{S \times 10^6 \times n}{s \times v} \text{ in cells/ml}$$

S = filtering area of apparatus in mm^2

s = surface area of the field of observation in μm^2

n = average number of cells per field

v = volume of sample filtered in ml

Bacterial biomass, expressed in mg/l of organic matter, was calculated using the average cell volume in each sample. Mazure (1978) quotes Luria (1960) who gives the density of the bacterial cell as 1,1. Factors of 0,2 for conversion from wet mass to dry mass and 0,875 from dry mass to organic matter were used.

3.2.5 : Particulate Matter

The dry weight of seston, i.e. total particulate matter (T.P.M.) was determined in a manner very similar to that proposed by Strickland

and Parsons (1972). From each 5 l sample a 2 l subsample was filtered through a pretreated GF/C filter. This treatment involved incinerating the filters at 450°C for 30 minutes to drive off any organic matter; soaking the filters in distilled water for 5 minutes to remove soluble matter and drying in an oven at 60°C overnight. The filters were allowed to cool in a desiccator with dry silica gel for a few minutes. Each filter was weighed to the nearest 0,01 mg and stored individually in the desiccator. Glass filters do absorb dissolved organic matter during filtration but have negligible hydroscopic and electrostatic properties.

After filtration the filters were washed twice under suction with an isotonic solution of ammonium formate to remove salts. Ammonium formate has the advantage of being volatile and unlike distilled water prevents lysis of any living cells (Banse, Falls and Hobson, 1963). At this stage any large zooplankters, such as amphipods, were removed (this was necessary on only one occasion). The filters were dried overnight at 60°C and allowed to cool in the desiccator prior to reweighing. The amount of particulate organic matter (POM) was determined by difference after the filters had been incinerated at 450°C for 2 hours.

Midway through this study it was decided to split the particulate matter into two size fractions by pouring the sample through a screen of nylon netting with 100 μm mesh prior to filtering. The screen was then backwashed with particle-free seawater.

Having determined the levels of organic matter one also needs some indication of the nutritive value of this material. This may be achieved by determining the carbon : nitrogen ratio of the seston. An additional 10 l sample of seawater was filtered through a pre-treated GF/C filter. The filter was washed, dried, weighed and ground into a fine powder. Approximately 15 mg of this powder was carefully weighed out and processed in a Heraeus C:H:N analyser. A pre-treated GF/C filter was run as a blank. Due to the high ratio of filter material to seston, the instrument was unable to detect any differences between the C and N levels of the sample and those of the blank.

3.2.6 : Particle Size Spectra

Particle size distributions were determined using a 16 channel Coulter Counter, model TA-11, equipped with a tube of aperture 280 µm. This instrument enables the rapid processing of a number of samples, but it does not distinguish between plankton and detritus, or between particles of organic and inorganic matter. An electric current is established through the orifice between an electrode inside the tube and an outside electrode in the sample. Particles drawn through the aperture interrupt the electrical current in proportion to the volume of the particle. The instrument expresses the size of a particle as the diameter of a sphere whose volume is equal to that of the particle. The amount of current change is linearly related to particle diameter for diameters of between 2 and 40% of the aperture diameter. For a tube with a 280 µm orifice, this represents a range of 5 to 112 µm.

A 500 ml subsample was poured through a 125 µm mesh nylon screen. Although the act of screening is known to trap irregular shaped particles far smaller than the mesh size (Sheldon, 1967), it was necessary to eliminate any large particles which might block the orifice of the tube.

At least 3 counts were performed on each sample, and the water stirred between counts to ensure random distribution of the particles in suspension. Successful operation of this instrument was often hampered by unpredictable electrical interference. This resulted in highly elevated counts, particularly in channel 2 (the smallest particles). The model TA-11 does allow the operator to eliminate channel 2, but this was then found to have adverse effects on the numbers of particles in channel 3. For this reason channel 2 was included but the counts in this channel subtracted from the total count. This appeared to be the most effective means of reducing the problem of interference.

The mean number of particles in each channel was divided by the volume of seawater drawn through the orifice to determine the number of particles per ml in each channel. These values were in turn divided by the mean particle volume of each channel to give particle concentration by volume in parts per million (p.p.m.). The size spectrum of particulate matter was expressed graphically as total particle volume (concentration in p.p.m.) against the logarithm of particle diameter. Sheldon and Parsons (1967) have found this to be the most informative way to present the data.

3.2.7 : Microscopic Examination

For the microscopic examination of the seston, 500 ml was taken from each of the duplicate samples collected at a particular station and combined. This 1 litre aliquot was fixed with 10 ml of Lugol's Iodine (10 g iodine and 20 g potassium iodide dissolved in 250 ml of seawater). This solution acts as both a fixative and general carbohydrate stain.

The seawater-iodine solution was allowed to stand for 48 hours and filtered through a Sartorius cellulose nitrate filter, pore size 0,45 µm. The filter was washed under suction with an isotonic solution of ammonium formate and dried overnight at 40°C. The acts of preserving and drying the samples undoubtedly caused structural deformation of certain particles and lysis of the naked flagellates, however it was not possible to examine the fresh material.

Each filter was placed on a microslide, cleared with anisole (methyl phenyl ether)(Holmes, 1962) and mounted with Kleermount. Slides prepared in this manner lasted indefinitely.

CHAPTER 4

RESULTS

4.1 : MONTHLY SAMPLING

4.1.1 : Inorganic Nutrients

The seasonal variation in the concentration of the four inorganic nutrients, ammonia, nitrates, phosphates and silicates are shown in Figures 2, 3, 4 and 5 respectively. Analysis was performed on only one of the duplicate samples taken at each station. A striking feature was the appearance of a body of water, rich in all four nutrients, over the reef in May. In order to illustrate spatial and tidal differences in nutrient concentrations, mean and standard deviation values for each station and tide are listed in Table 2.

There was no obvious seasonal pattern in the levels of ammonia (Fig. 2), values generally lying between 2 and 4 μg at/l. A maximum value of 6 μg at/l was recorded in May. Concentrations were marginally higher in the outgoing water, but there were no spatial differences evident (Table 2).

Nitrates (Fig. 3) did not exceed 2 μg at/l over the six-month period, November to April, the December offshore samples being the only exception. After soaring as high as 15 μg at/l in May, concentrations remained between 3 and 4 μg at/l throughout the winter. The spatial and tidal differences apparent in Table 2 were the result of high concentrations in December and May at the offshore station and in the incoming water.

Phosphates (Fig. 4) showed little variation, fluctuating between 1 and 2 µg at/l, with no evidence of any seasonal pattern. Concentrations approached 4 µg at/l in January and May. Table 2 indicates that concentrations were slightly higher in outgoing water.

Silicates closely followed the trend shown by nitrates; a high correlation coefficient (r = 0,80) indicated a strong relationship between these two nutrients. From January through to March silicate concentrations did not exceed 4 µg at/l (Fig. 5). Winter values were generally 2 to 3 µg at/l higher than those in summer. Silicate-rich water was encountered in October, November, May and July, with values in May exceeding 25 µg at/l on the incoming tide. It is interesting to note the extremely high silicate and nitrate concentrations, 20 and 9 µg at/l respectively, in December at the offshore station, for these nutrients occurred only at very low levels during the rest of summer and early autumn. Concentrations of silicates were higher in incoming water and highest at the offshore station (Table 2).

It was not possible to use a 3-way analysis of variance (ANOVA) to investigate the combined effects of months, stations and tides on each of the four nutrients, as has been applied to the other parameters measured. Because only one of the duplicate samples was analysed, there was no measure of both interaction and error variability. In this case it appears that the interactive effect might be significant and so it was not possible to use this value as the error term.

Figure 2. Concentrations of ammonia (μg atoms NH_3 - N/l) at the inshore station (triangles), middle station (circles) and offshore station (squares) on incoming and outgoing tides.

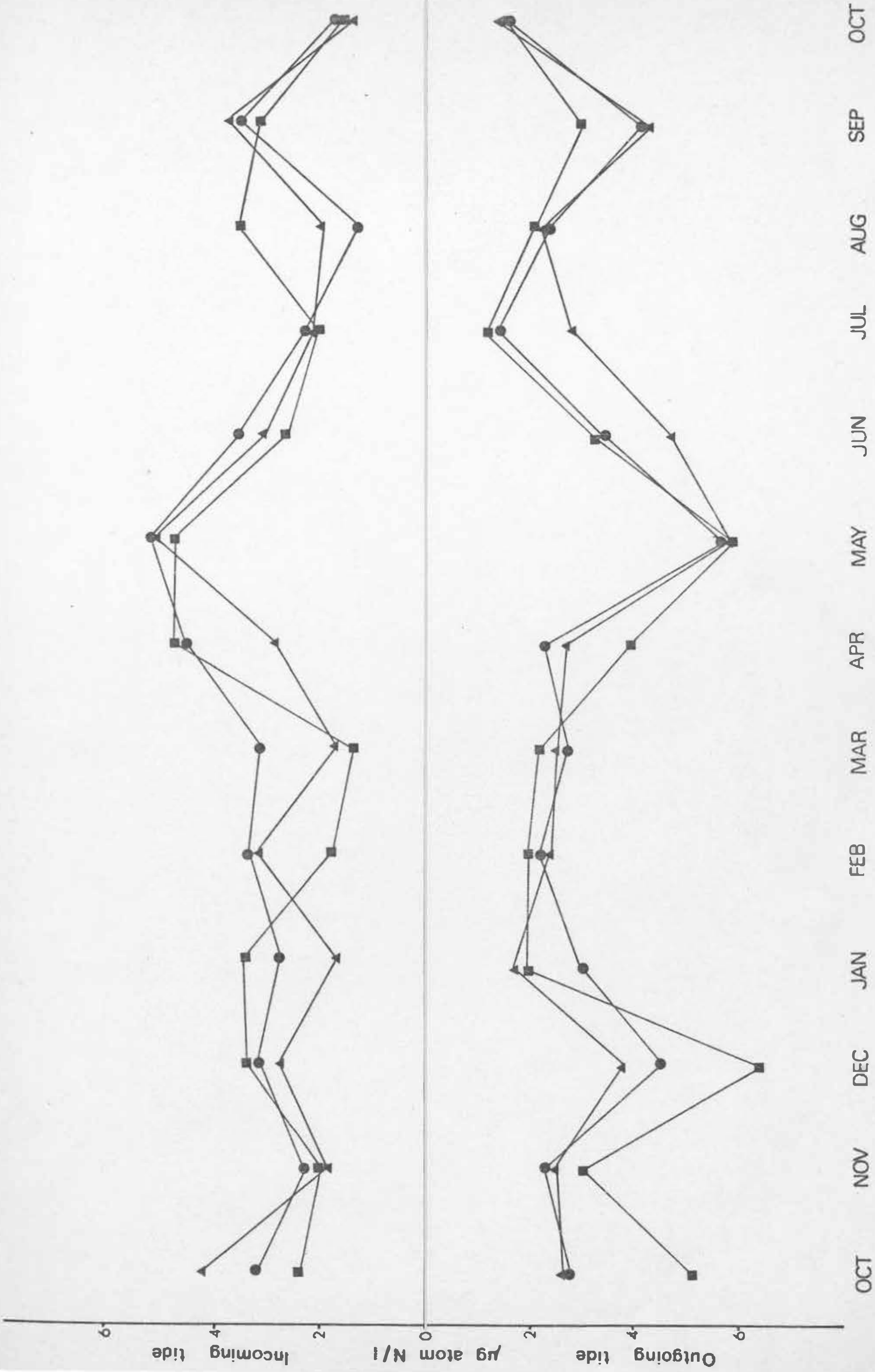
Incoming tide
µg atom N/l
Outgoing tide
6
4
2
0
2
4
6
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT

Figure 3. Concentrations of nitrate (μg atoms NO_3 - N/l) at the inshore station (triangles), middle station (circles) and offshore station (squares) on incoming and outgoing tides.

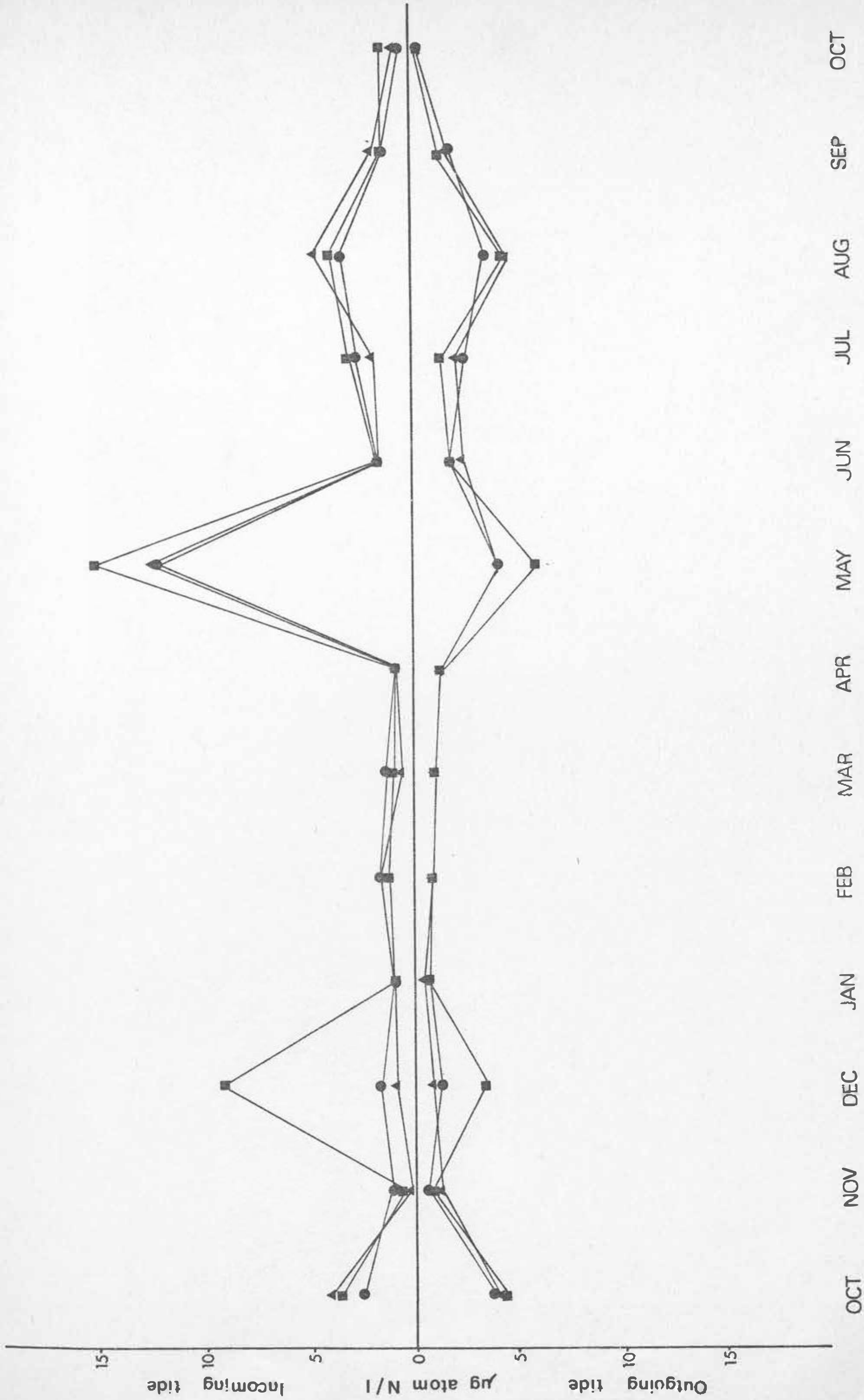
Incoming tide
µg atom N/l
Outgoing tide
15
10
5
0
5
10
15
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT

Figure 4. Concentrations of phosphate (μg atoms PO_4 - P/l) at the inshore station (triangles), middle station (circles) and offshore station (squares) on incoming and outgoing tides.

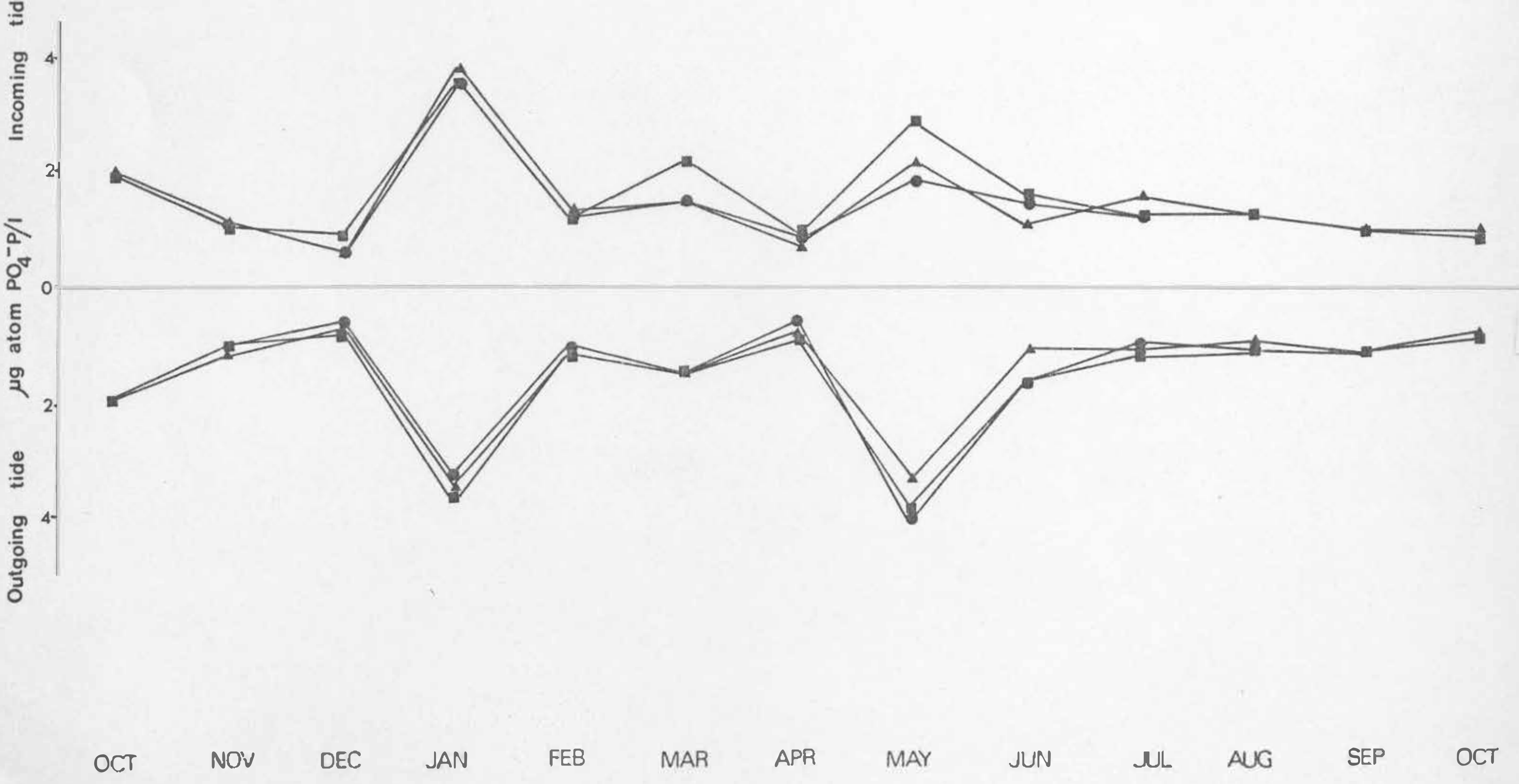
Incoming tide
μg atom PO_4-P/l
Outgoing tide
4
2
0
2
4
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT

Figure 5. Concentrations of silicate (μg atoms SiO_3 - Si/l) at the inshore station (triangles), middle station (circles) and offshore station (squares) on incoming and outgoing tides.

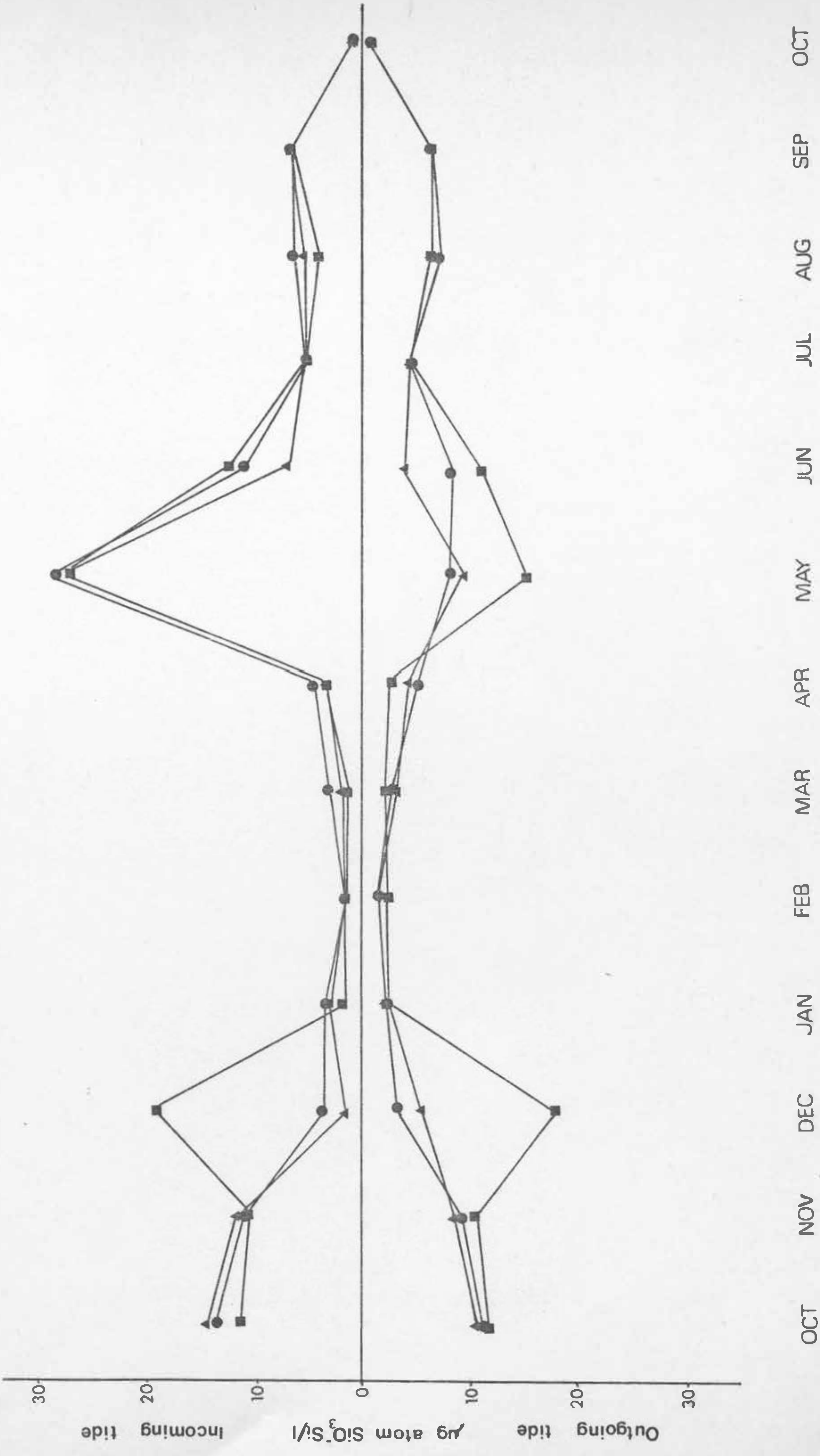
Incoming tide
μg atom SiO$_3$-Si/l
Outgoing tide
30
20
10
0
10
20
30
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT

TABLE 2 : Inorganic Nutrients : Mean monthly levels and standard deviations of ammonia, nitrates, phosphates and silicates at each station on incoming and outgoing tides for the 13 months of sampling.

TIDE	STATION	n	AMMONIA Mean	µg at N/l S. D.	NITRATES Mean	µg at N/l S. D.	PHOSPHATES Mean	µg at P/l S. D.	SILICATES Mean	µg at Si/l S. D.
INCOMING	Inshore	13	2,85	1,09	2,50	3,32	1,42	0,84	6,81	7,29
	Middle	13	3,08	1,14	2,43	3,02	1,42	0,77	7,61	7,41
	Offshore	13	2,82	1,20	3,32	4,20	1,58	0,85	8,62	8,23
OUTGOING	Inshore	13	3,04	1,27	2,08	1,40	1,55	0,94	5,15	3,10
	Middle	13	2,95	1,23	1,88	1,19	1,58	1,03	5,48	3,20
	Offshore	13	3,22	1,67	2,34	2,02	1,64	1,02	7,28	5,57

A 1-way ANOVA to investigate the effects of locality on nutrient concentrations revealed that only silicates were significantly influenced by the station sampled. Using the student t-test for matched pairs, the levels at the offshore station were found to be significantly higher at the 5% level than either the middle or inshore stations. Concentrations were also found to be significantly higher on the incoming tide, additional evidence that silicates are imported from richer offshore waters. Although concentrations of ammonia and phosphates were slightly lower and nitrates slightly higher in incoming than in outgoing water, these differences were not significant.

4.1.2 : Chlorophyll Concentrations

Figure 6 shows the seasonal variation in the concentrations of chlorophyll a (ignoring spatial and tidal differences for the present, each value is the mean of the 12 samples taken in that month). Throughout spring and summer, levels were very low : below 2 µg/l. There was a steady increase in autumn and into winter, with the highest levels recorded in May and July. They fell to 2 µg/l in August. The large 95% confidence limits in May and July were due to the large differences in chlorophyll levels between incoming and outgoing water.

Figure 7 shows a breakdown of the seasonal variation for each station. From this it is evident that the incoming water contains more chlorophyll than the outgoing water. Levels were highest at the offshore station, especially in October, December and May.

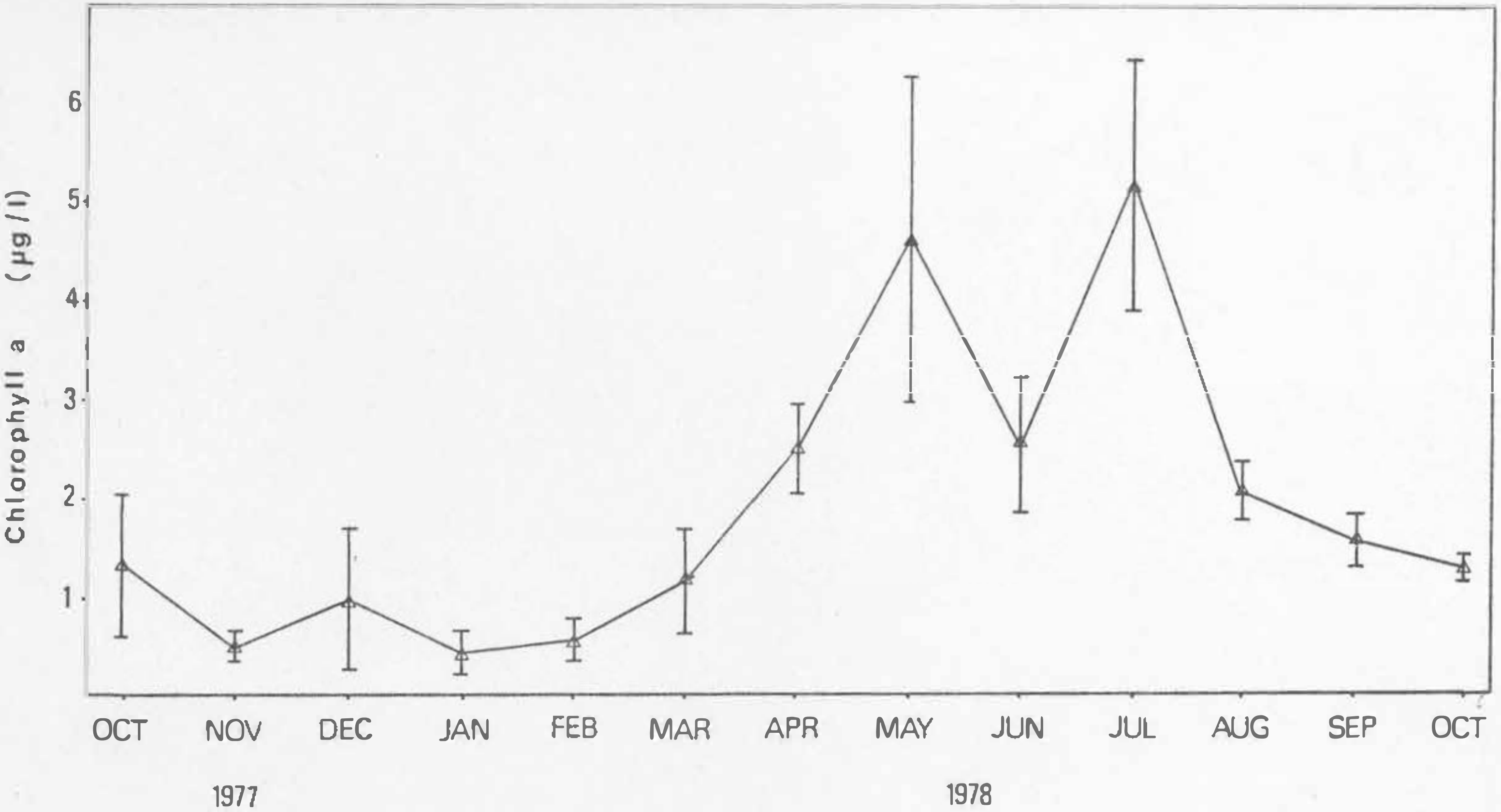

Figure 6. Seasonal variation in the concentration of chlorophyll a (µg/l). Vertical lines indicate 95% confidence limits. For each month n = 12.

Figure 7. Concentrations of chlorophyll a (μg/l) at each station for incoming and outgoing tides. Two samples were taken at each station.

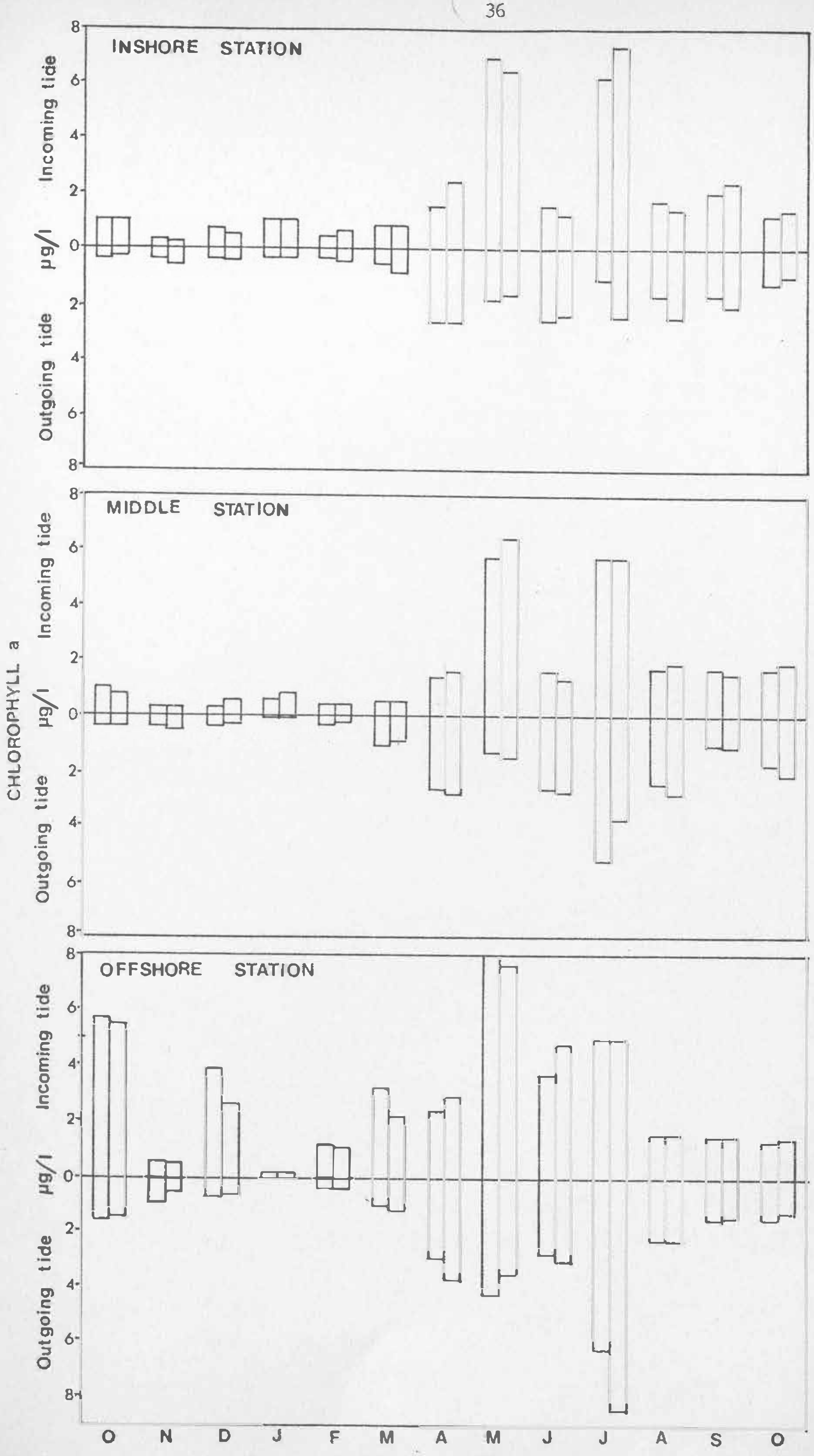
INSHORE STATION
MIDDLE STATION
OFFSHORE STATION
CHLOROPHYLL a
Incoming tide
Outgoing tide
µg/l
8
6
4
2
0
2
4
6
8
O
N
D
J
F
M
A
M
J
J
A
S
O

TABLE 3 : Results of a three-way analysis of variance (Model 1) with replication (2 replicates)

Dependent variable : Chlorophyll a.

SOURCE OF VARIATION	DEGREES OF FREEDOM	MEAN SQUARE	PROBABILITY
Month A	12	26,89	P < 0,001
Tide B	1	13,35	P < 0,001
Station C	2	10,66	P < 0,001
A x B	12	5,39	P < 0,001
A x C	24	1,03	P < 0,001
B x C	2	0,66	P = 0,005
A x B x C	24	1,61	P < 0,001
Within cells	78	0,11	

The results of a 3-way ANOVA to investigate the effects of months, tides and stations on chlorophyll concentrations are summarised in Table 3. From this we can conclude that there were significant monthly, tidal and spatial differences. There was also a significant interactive effect of all three factors, which means that chlorophyll concentrations were dependent on the locality sampled, the state of the tide and the time of the year.

Having established that chlorophyll concentrations were significantly higher in incoming water, the paired t-test was used to determine which spatial differences were significant at the 5% level. Concentrations at the offshore station were significantly higher than those at both the middle and inshore stations. There was no significant difference between levels at the middle and inshore stations. No correlation was found between chlorophyll concentrations and those of the four inorganic nutrients although the high chlorophyll levels in December and May were associated with high nitrate (Fig. 3) and high silicate (Fig. 5) values.

4.1.3 : Primary Production

The results of the primary production experiments are presented in Table 4. Net production values were extremely low, but were often higher than those for gross production. Negative net production and respiration values were also recorded.

Chlorophyll and nitrate concentrations rarely exceeded 1 µg/l and 1 µg at/l respectively. In view of the extremely low phytoplankton

TABLE 4 : Results of four primary production experiments.

Date	Incubation Time (hours)	Depth (metres)	Gross Production µg C/l/hr	Net Production µg C/l/hr	Respiration µg C/l/hr	Chlorophyll µg/l	Nitrates µg at N/l
30.8.77	4	1	0	6,3	-5,0	1,01	0,7
		1	0	13,7	-17,7	1,07	0,8
		4	199,7	37,8	207,8	2,46	0,7
		4	42,0	31,5	12,6	2,40	0,3
4.10.77	4	1,5	6,7	-3,3	12,1	0,75	2,9
		1,5	4,5	7,8	9,4	0,79	3,1
		4	4,5	1,1	4,0	1,56	3,4
		4	0	-6,7	8,0	1,40	3,0
7.12.77	4	1,5	9,0	12,8	-4,6	0,67	0,4
		1,5	3,6	-4,2	8,7	0,63	0,3
		4	2,1	1,2	1,1	0,41	0,4
		4	9,3	-10,8	24,1	0,84	0,5
21.2.78	3	1,5	*	-23,8	*	0,95	1,2
		1,5	10,4	13,0	16,1	1,10	1,1
		4	7,4	-19,4	32,2	0,89	0,9
		4	7,4	11,9	-4,5	0,80	1,2

* No dark bottle

stocks and nitrate concentrations in the water it is not surprising that it was difficult to detect any net production. From these experiments we may conclude that there is negligible production by phytoplankton in the immediate vicinity of Dalebrook reef.

4.1.4 : Bacterial Densities

Figure 8 shows the seasonal variation in numbers of bacteria : both cells freely suspended in the water column and those attached to particles in suspension. Each monthly value is the mean of the 12 samples taken over the reef. Densities of free bacteria, fluctuating between 4 and 16 x 10^5 cells/ml, appeared to show some seasonal trends. The low values during the winter months increased through spring and summer, despite the inexplicably low values in January, to a maximum in March and April. Densities of attached bacteria, in the region of 0,3 x 10^5 cells/ml, were low in comparison to those of unattached bacteria and showed no seasonal pattern. Only in July did they exceed the number of free bacteria.

Figure 9 shows the seasonal variation at each of the three stations, with mean and standard deviation values summarised in Table 5. Densities of free bacteria were highest offshore, particularly in October, December and March. The reverse is true for the attached bacteria; these cells were present in greater numbers in the incoming water. Tides did not appear to influence numbers of free bacteria.

The results of a 3-way ANOVA to investigate the effects of months,

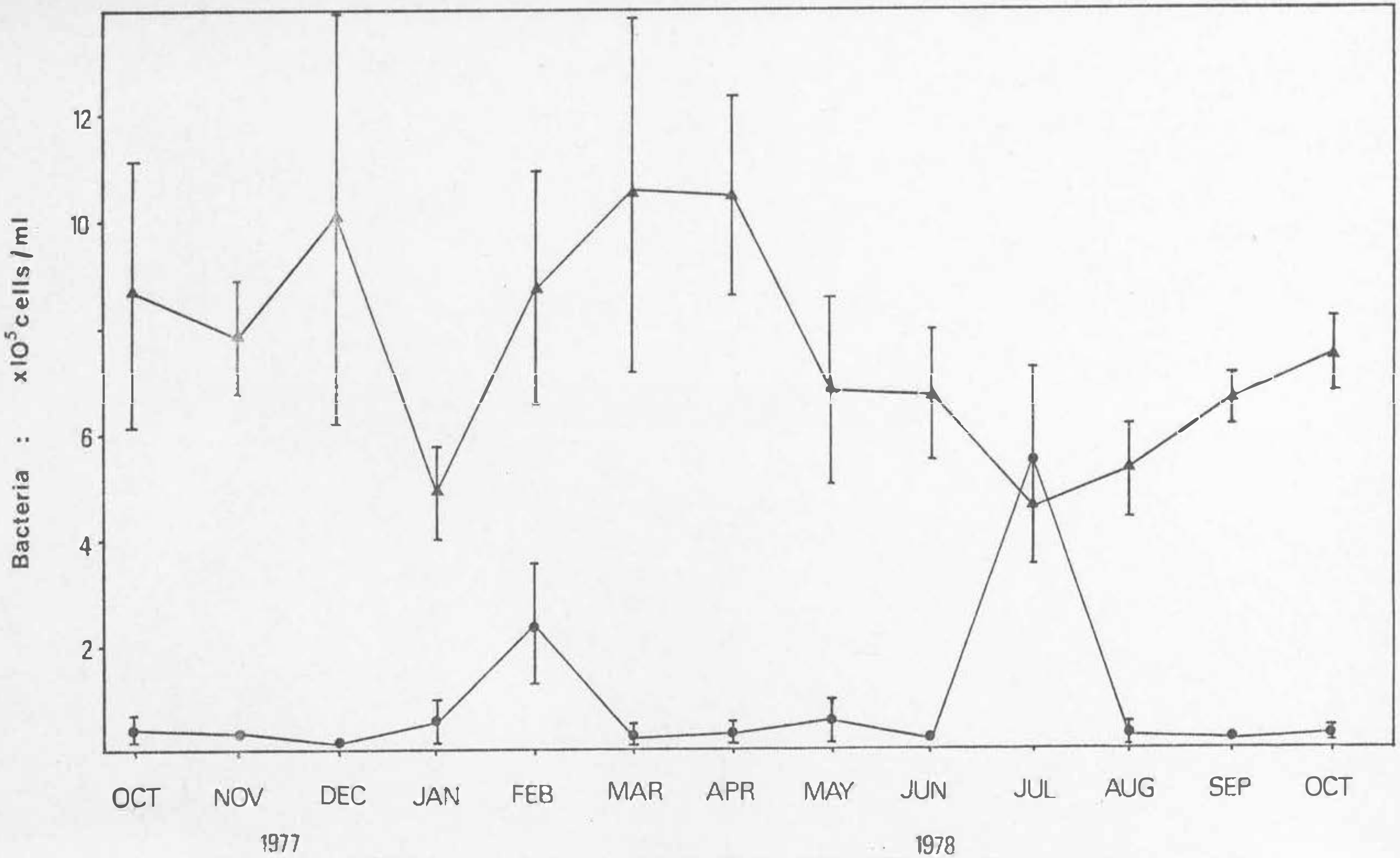

Figure 8. Seasonal variation in the numbers (x 10^5/ml) of free bacteria (triangles) and attached bacteria (circles) in suspension. Vertical lines indicate 95% confidence limits. For each month n = 12.

Figure 9. Numbers of bacteria (x 10^5/ml) at each station on incoming and outgoing tides. Two samples were taken at each station. Shaded regions represent unattached bacteria.

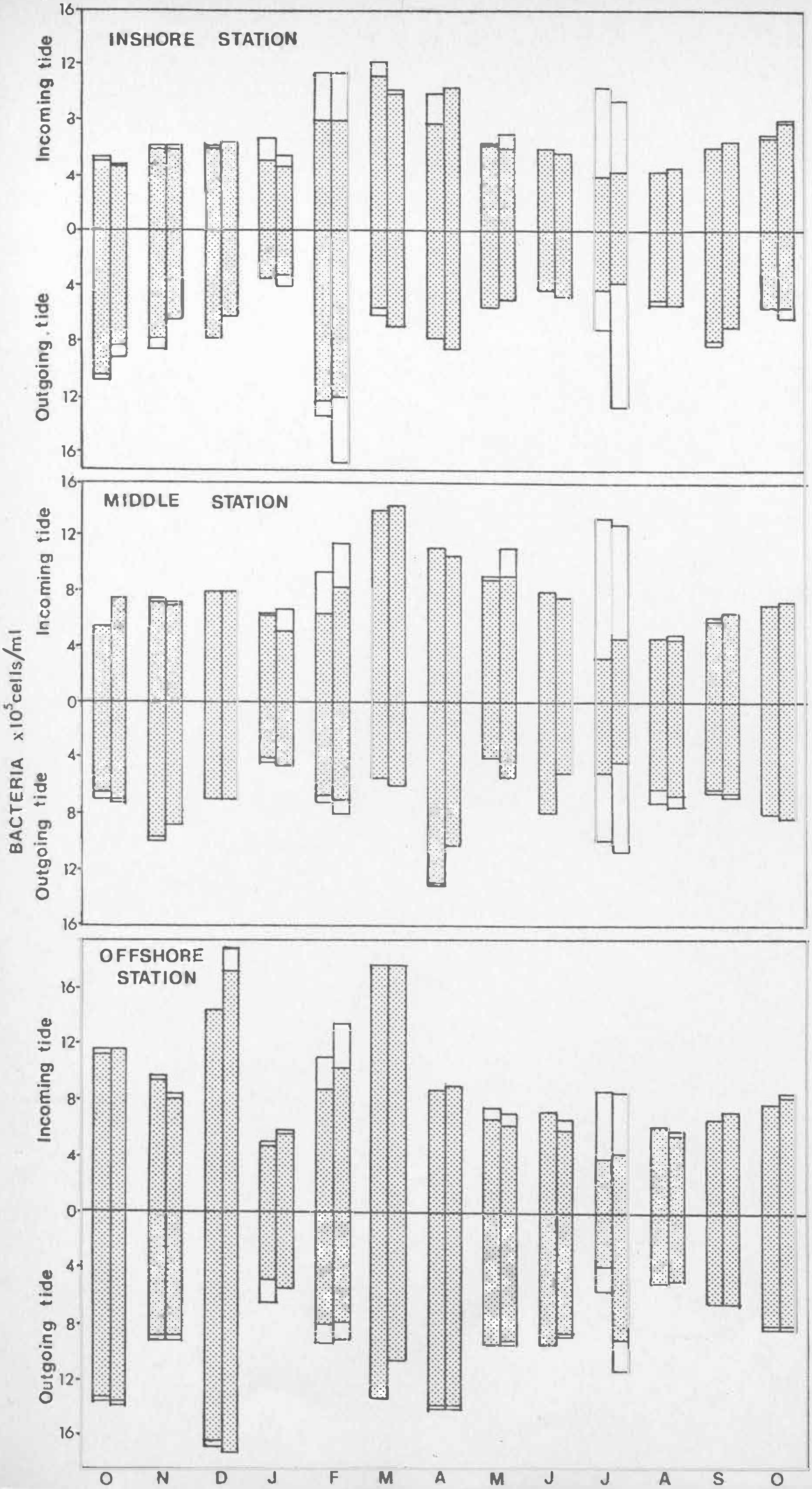
INSHORE STATION
Incoming tide
Outgoing tide
16
12
8
4
0
4
8
12
16
MIDDLE STATION
Incoming tide
Outgoing tide
BACTERIA x10^5 cells/ml
16
12
8
4
0
4
8
12
16
OFFSHORE STATION
Incoming tide
Outgoing tide
16
12
8
4
0
4
8
12
16
O
N
D
J
F
M
A
M
J
J
A
S
O

TABLE 5 : Mean numbers of bacteria and standard deviations (no. cells x 10^5/ml) for each station on incoming and outgoing tides for the 13 months of sampling.

TIDE	STATION	n	FREE BACTERIA		ATTACHED BACTERIA	
			Mean	S.D.	Mean	S.D.
INCOMING	Inshore	26	6,39	1,90	1,07	1,72
	Middle	26	7,59	2,66	1,26	2,69
	Offshore	26	8,97	5,81	0,67	1,31
OUTGOING	Inshore	26	6,60	2,40	0,91	2,04
	Middle	26	6,81	2,13	0,66	1,47
	Offshore	26	9,38	3,65	0,42	0,60

TABLE 6 : Results of a three way analysis of variance (Model 1) with replication (2 replicates)
Dependent variables : (a) Free bacteria (b) Attached bacteria.

SOURCE OF VARIATION	DEGREES OF FREEDOM	FREE BACTERIA		ATTACHED BACTERIA	
		MEAN SQUARE	PROBABILITY	MEAN SQUARE	PROBABILITY
Month A	12	55,94	P < 0,001	28,44	P < 0,001
Tide B	1	0,05	P > 0,5	3,09	P < 0,05
Station C	2	100,53	P < 0,001	2,84	P < 0,001
A x B	12	13,97	P < 0,001	1,34	P < 0,005
A x C	24	12,80	P < 0,001	1,58	P < 0,001
B x C	2	4,79	P < 0,005	0,26	P > 0,5
A x B x C	24	3,99	P < 0,001	0,50	P > 0,25
Within cells	78	0,68		0,50	

tides and stations on bacterial densities are summarised in Table 6. Numbers of both free and attached bacteria were significantly different from month to month and station to station. There was no significant tidal influence on the numbers of free bacteria; in the case of the attached bacteria tidal differences were significant at the 1% level. There was a strong interaction between the effects of months, stations and tides on the numbers of free bacteria. Although there was no significant interactive effect on attached bacteria, numbers of these cells in suspension on a given month were dependent on both station and tide, but tidal differences were independent of differences between stations.

The ANOVA has indicated that there were significant spatial differences in bacterial densities. Paired t-tests showed that there were significantly more free bacteria at the offshore station that at either the middle or the inshore stations; the numbers at the middle station were significantly higher than those at the inshore station only on the incoming tide. Numbers of attached bacteria were significantly higher inshore than offshore and significantly higher at the middle station than at the offshore station during the incoming tide;differences between the inshore and middle stations were not significant.

4.1.5 : Total particulate matter and particulate organic matter

The seasonal variation in levels of total particulate matter (TPM) and particulate organic matter (POM) in suspension is illustrated in Figure 10. Each value represented the mean of the 12 samples taken that month. Although there was considerable monthly variation, no seasonal pattern seems to be evident. The mean monthly levels of TPM were in the region of 3 mg/l, rising to 8 mg/l and higher in May and August. Levels of POM tended to closely follow those of TPM, with peaks in May and August, only dropping below 1 mg/l in November. The TPM was dominated by inorganic matter, the organic fraction representing between 33% and 57% of the TPM with a mean of 39%. Owing to the scattering of values (Fig. 10) no pronounced seasonal difference in the ratio of inorganic to organic fractions was evident. This ratio was also independent of the amount of TPM in suspension.

Figure 11 shows the amounts of particulate matter encountered at each station for incoming and outgoing tides. Table 7, with mean values and their standard deviations, illustrates the absence of any marked tidal and spatial differences.

In the final 7 months the particulate matter was split into two fractions using a 100 μm mesh screen. These results are illustrated in Figure 12 (TPM) and Figure 13 (POM). In both cases it is clear that a very large portion of the particulate matter was found in the < 100 μm fraction : 76% of the TPM and 73% of the POM. In May, when the highest levels of seston were encountered, the < 100 μm fraction was at its largest; however, the relative proportions of the two fractions were little different from the previous month when the seston load was low. This suggests that the ratio between the two fractions was independent of the absolute amount of TPM in suspension. Inorganic particles are denser than organic ones and therefore will

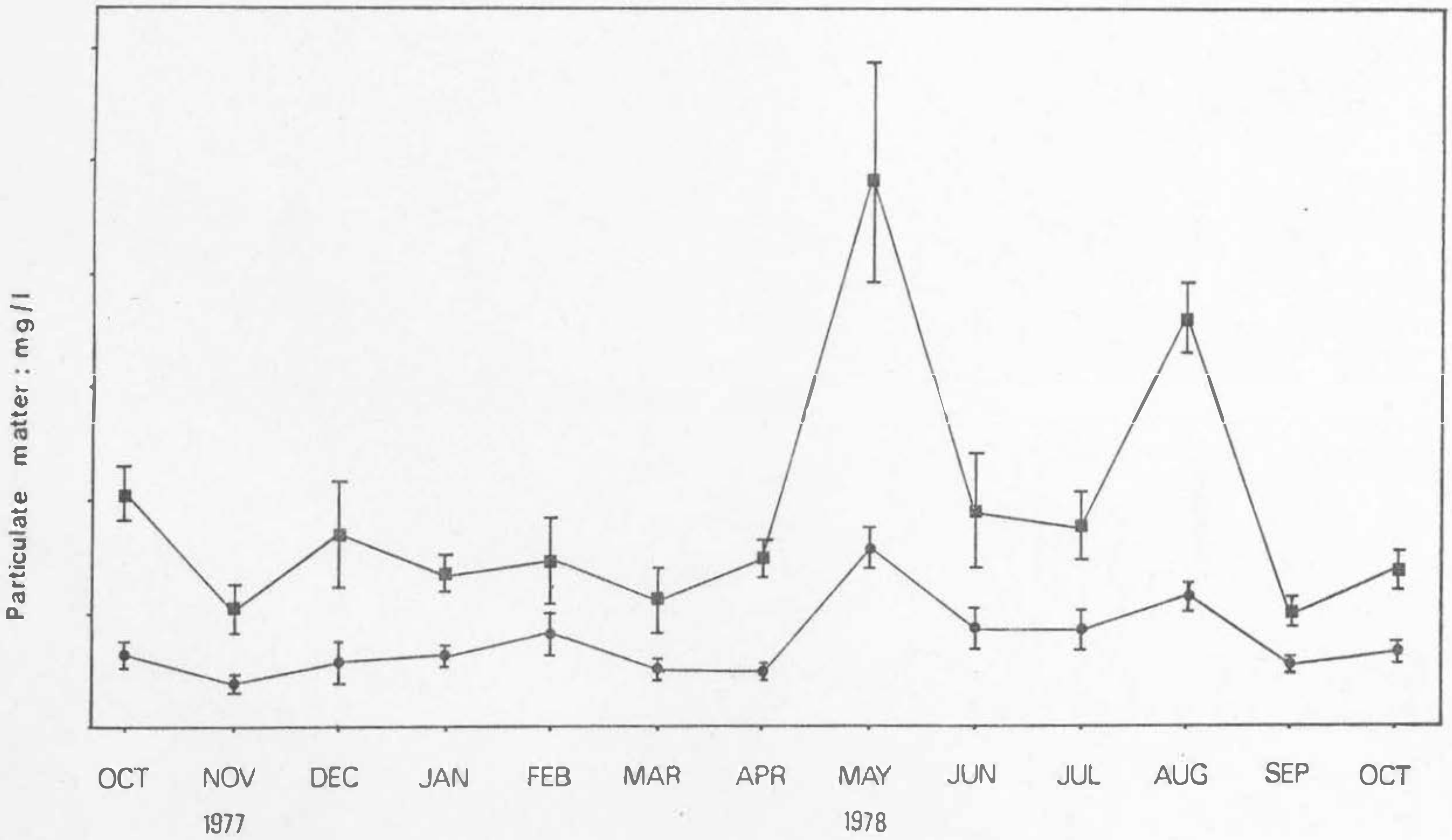

Figure 10. Seasonal variation in the dry mass (mg/l) of total particulate matter (squares) and particulate organic matter (circles) in suspension. Vertical lines indicate 95% confidence limits. For each month n = 12.

Figure 11. Dry mass (mg/l) of total particulate matter and particulate organic matter (shaded regions) in suspension at each station on incoming and outgoing tides. Two samples were taken at each station.

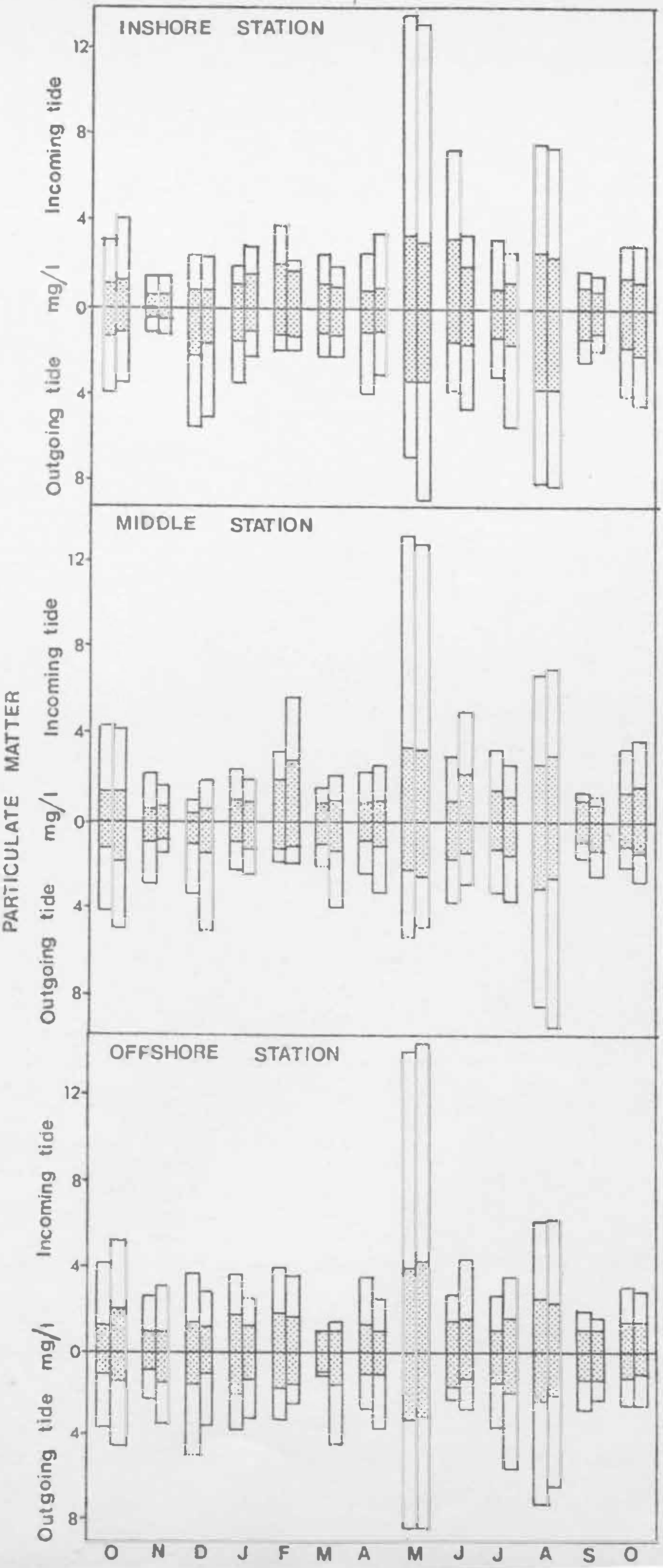
INSHORE STATION
MIDDLE STATION
OFFSHORE STATION
PARTICULATE MATTER mg/l
Incoming tide
Outgoing tide
mg/l
12
8
4
0
4
8
O
N
D
J
F
M
A
M
J
J
A
S
O

TABLE 7 : Mean levels and standard deviations of Total Particulate Matter (TPM) and Particulate Organic Matter (POM) for each station and tide over the 13 months of sampling. Units : mg/l.

TIDE	STATION	n	TPM		POM	
			Mean	S.D.	Mean	S.D.
INCOMING	Inshore	26	3,86	2,97	1,48	0,84
	Middle	26	3,69	2,91	1,44	0,87
	Offshore	26	4,00	3,15	1,57	0,80
OUTGOING	Inshore	26	3,86	2,21	1,51	0,76
	Middle	26	3,49	1,89	1,40	0,56
	Offshore	26	3,74	1,84	1,46	0,60

Figure 12. Size distribution of the total particulate matter (mg/l) in suspension at each station on incoming and outgoing tides. Shaded regions represent the <100 μm fraction. Two samples were taken at each station.

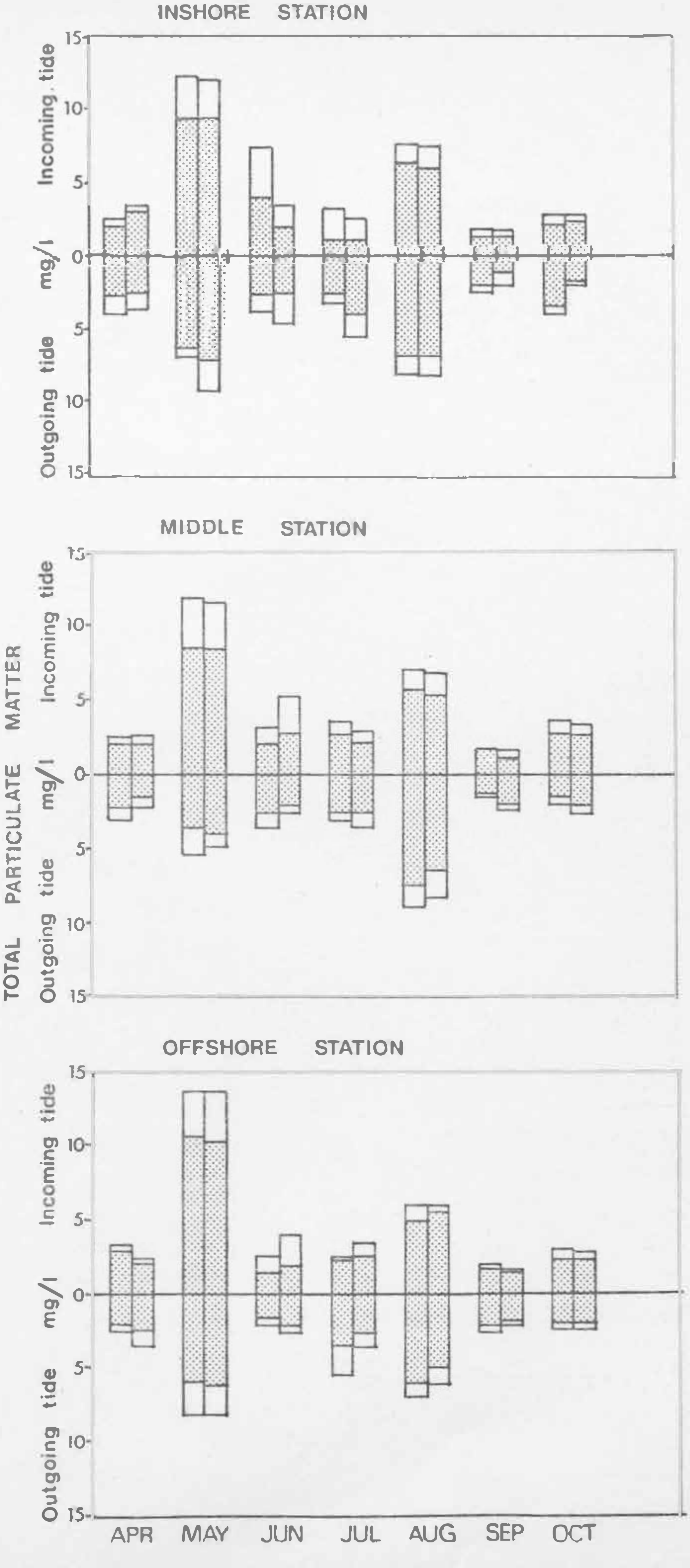
INSHORE STATION
MIDDLE STATION
OFFSHORE STATION
TOTAL PARTICULATE MATTER
Incoming tide
Outgoing tide
mg/l
15
10
5
0
5
10
15
APR
MAY
JUN
JUL
AUG
SEP
OCT

Figure 13. Size distribution of the particulate organic matter (mg/l) in suspension at each station on incoming and outgoing tides. Shaded regions represent the <100 μm fraction. Two samples were taken at each station.

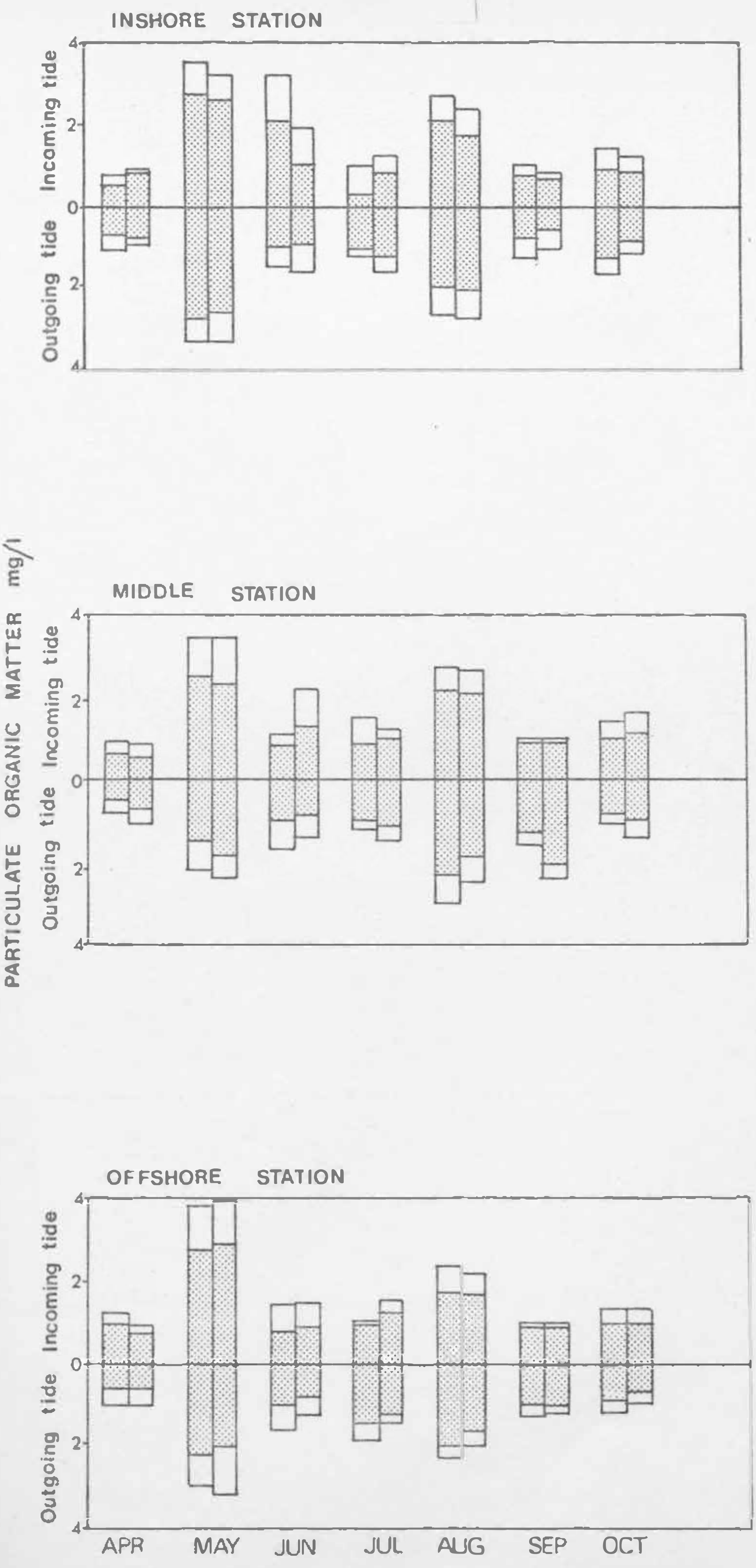
INSHORE STATION
MIDDLE STATION
OFFSHORE STATION
PARTICULATE ORGANIC MATTER mg/l
Incoming tide
Outgoing tide
4
2
0
2
4
APR
MAY
JUN
JUL
AUG
SEP
OCT

TABLE 8 : Results of a three way analysis of variance (Model 1) with replication (2 replicates)
Dependent variables : (a) Total Particulate Matter (TPM) (b) Particulate Organic Matter (POM).

SOURCE OF VARIATION	DEGREES OF FREEDOM	TPM		POM	
		MEAN SQUARE	PROBABILITY	MEAN SQUARE	PROBABILITY
Month A	12	61,73	P < 0,001	5,58	P < 0,001
Tide B	1	1,04	0,1 < P < 0,5	0,09	0,1 < P < 0,5
Station C	2	1,04	0,1 < P < 0,5	0,10	0,1 < P < 0,5
A x B	12	10,21	P < 0,001	0,35	P < 0,001
A x C	24	1,64	P < 0,001	0,17	P < 0,005
B x C	2	0,28	P > 0,5	0,06	0,1 < P < 0,5
A x B x C	24	0,49	P > 0,5	0,11	0,05 < P < 0,1
Within cells	78	0,61		0,72	

settle out faster when conditions are calm. In September TPM levels were at their lowest and the > 100 µm fraction was almost entirely organic.

The results of the 3-way ANOVA to investigate the effects of months, tides and stations on the amounts of TPM and POM in suspension are summarised in Table 8. This test confirms the observation that there were significant monthly differences but no spatial or tidal ones. There was a significant interaction between the effects of months and tides, and months and stations but not between tides and stations on both TPM and POM. This means that monthly levels of TPM and POM were dependent on the state of the tide and the locality sampled. However, for any one particular month the state of the tide and the locality sampled had no significant effect on the amounts of particulate matter in suspension.

4.1.6 : Particle Size Spectra

The Coulter Counter provided the size distribution of particles over the range 5 to 112 µm, for samples collected between December and October. Instrument malfunction prevented the processing of samples collected in October and November 1977, and the following January and April. Intermittent electrical interference upset analysis in June and although apparently acceptable results were obtained for some of the samples, these should be viewed with caution.

The curves tended to be unimodal with broad plateaus covering the diameters 11 to 30 µm. Some curves displayed distinct peaks which appeared to coincide with elevated chlorophyll concentrations. A prominent feature was the sharp decline in particulate volume in the region of 60 µm; this will be discussed in detail in section 5.8.

In December (Fig. 14) the curves had broad plateaus and chlorophyll concentrations were below 1 µg/l. However, at the offshore station, incoming tide, the curves peaked sharply at 14 µm (curve a) and 11 µm (curve b) and the chlorophyll concentrations were much higher, being 3,9 and 2,6 µg/l respectively. A similar situation was encountered at the offshore station, incoming tide, in March (Fig. 15).

In May (Fig. 16) the levels of seston were extremely high and the vertical scale has been greatly reduced to accommodate all 12 curves on the same figure. These curves all have broad peaks in spite of the high chlorophyll concentrations in the incoming water. In the outgoing water there was an unusually large concentration of particles of diameter 5 µm. These may have been naked, ultraplanktonic forms which would not have been detected in the visual examination.

In June (Fig. 17) the curves indicated a high concentration of particles of diameter 45 µm, expecially at the offshore station, incoming tide. Microscopic examination of the samples confirmed the presence of large dinoflagellate cells which would have accounted for the shift in peak height from 14 µm.

In July (Fig. 18) all the samples showed very sharp peaks in the

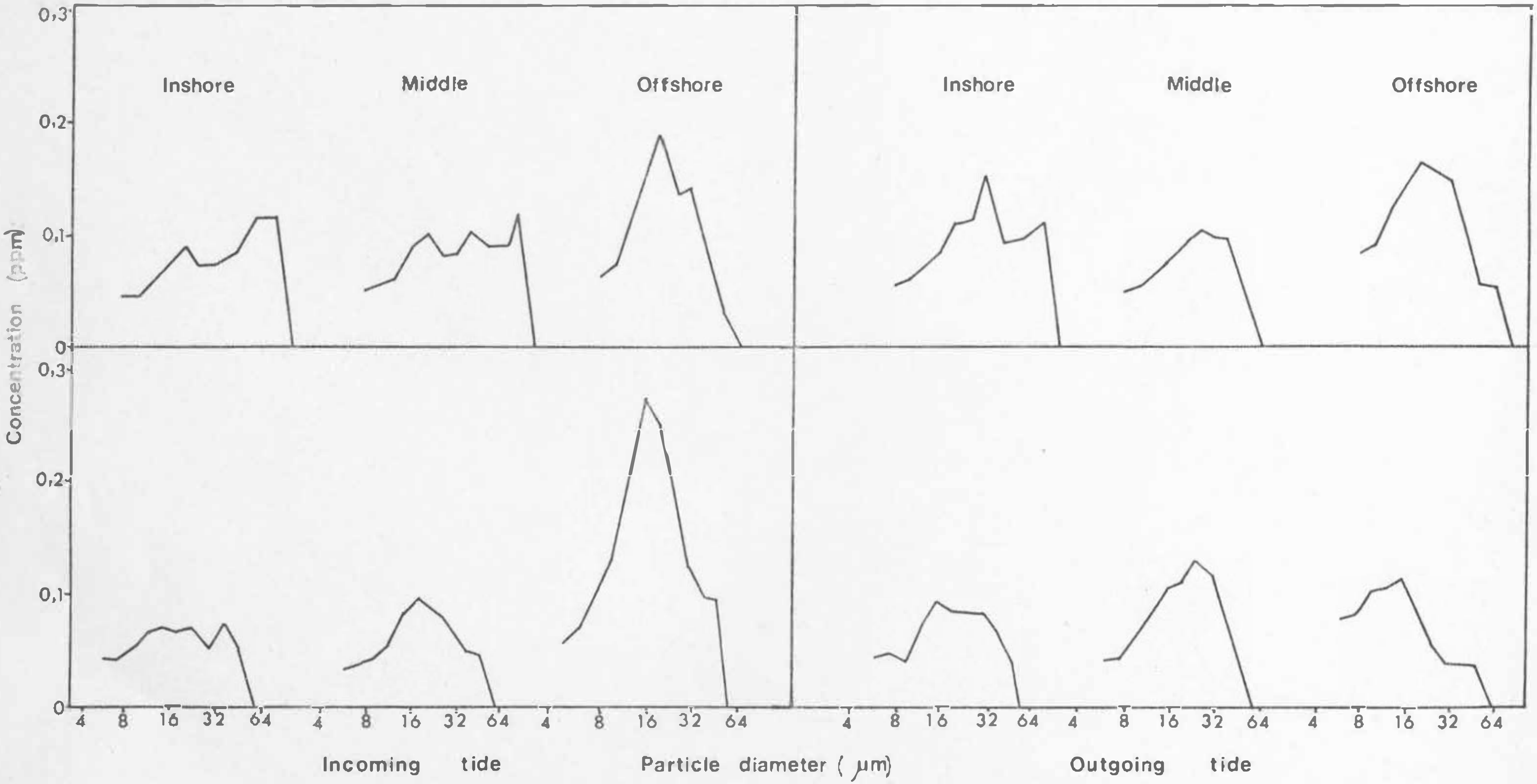

Figure 14. Particle size spectra of replicate samples collected in December at the three stations on the reef.

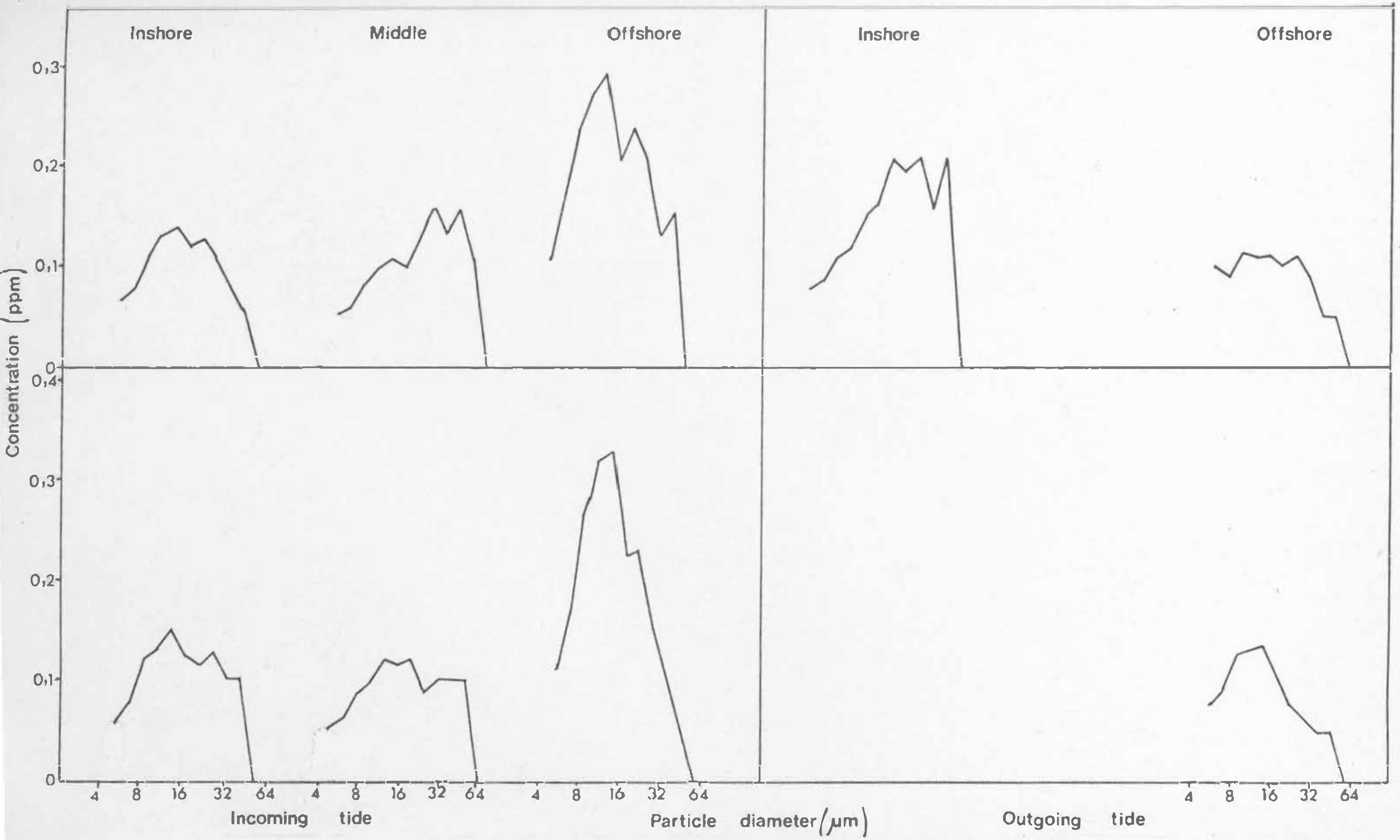

Figure 15. Particle size spectra of replicate samples collected in March at the three stations on the reef.

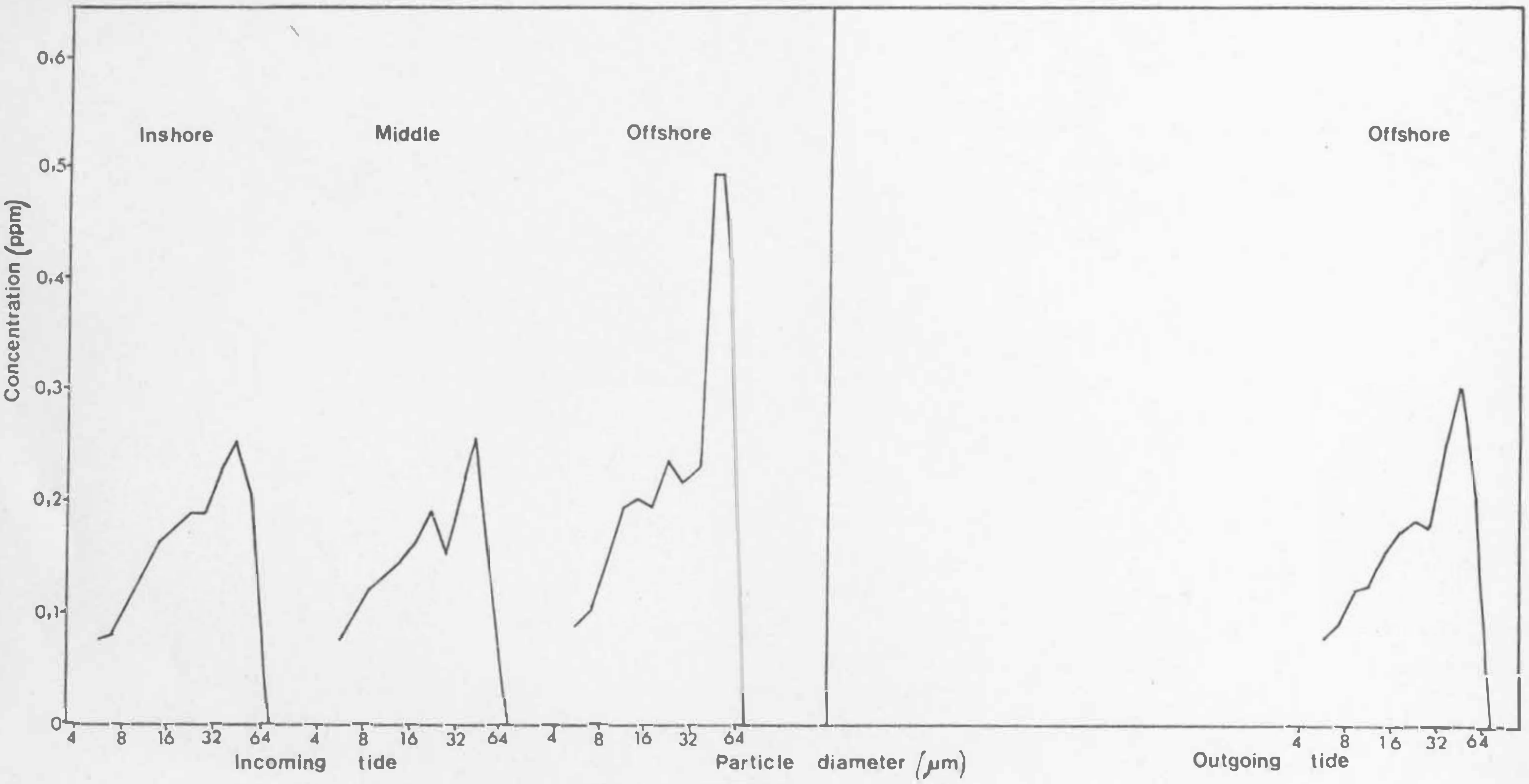

Figure 17. Particle size spectra of replicate samples collected in June at the three stations on the reef.

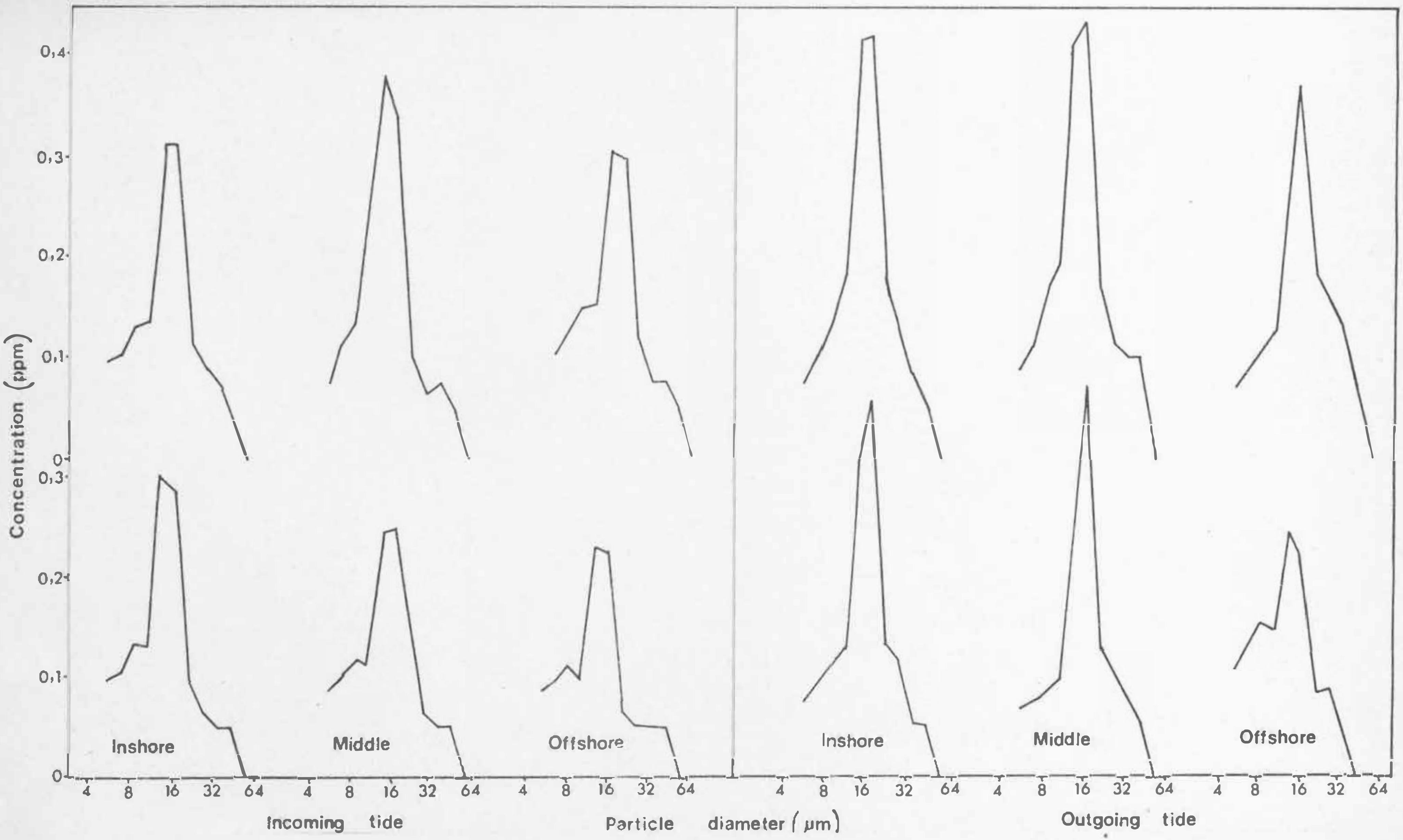

Figure 18. Particle size spectra of replicate samples collected in July at the three stations on the reef.

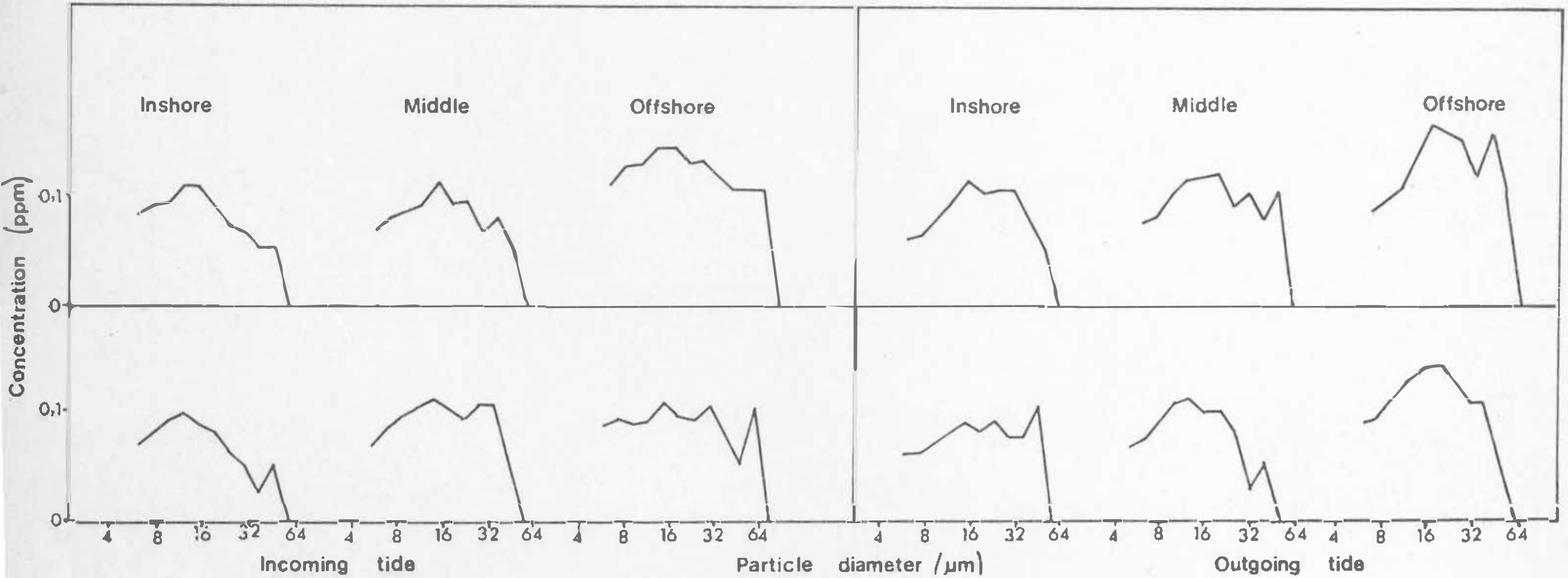

Figure 19. Particle size spectra of replicate samples collected in September at the three stations on the reef.

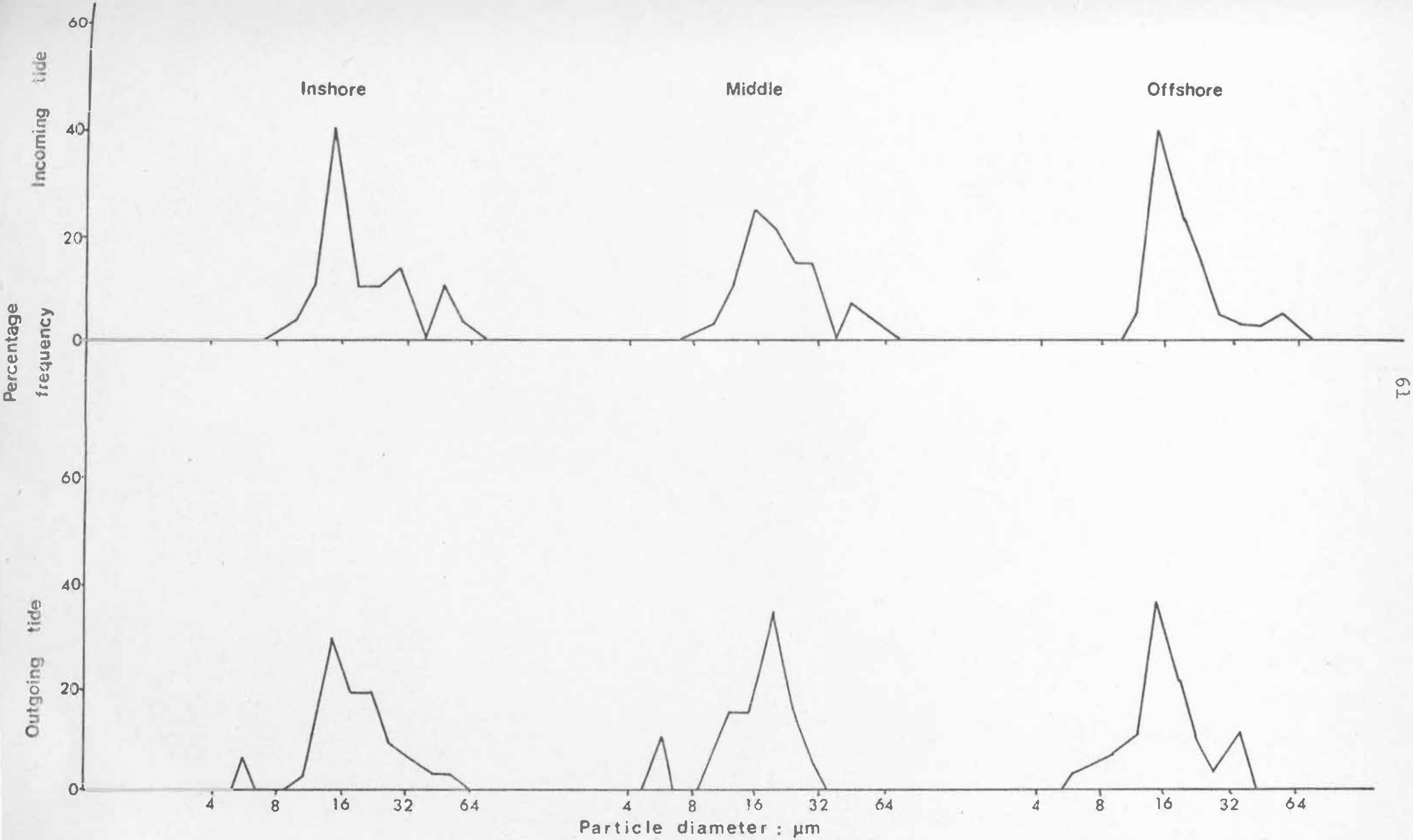

Figure 20. Relative frequency distribution of modal particle diameter at each station, using the results from Fig. 14 to 19.

region of 14 µm while concentrations of both smaller and larger particles were very low. Seston levels were low in these samples but chlorophyll concentrations high.

In September (Fig. 19) one encounters curves with a broad plateau, indicating a more-or-less equal distribution of particle volume over the range 6 – 60 µm. This appeared to be typical of water with low seston loads and low chlorophyll concentrations. The latter reflected the scarcity of phytoplankton cells which might boost the concentrations of particles of any one particular diameter.

Although many of the curves did possess broad plateaus, it was possible to determine modal peak height for a majority of the samples and thereby derive a frequency distribution for each station. This is shown in Figure 20. It is clear that particles of apparent diameter 14 µm contributed the largest volume of particulate matter over the reef.

4.1.7 : Composition of Organic Matter

Chlorophyll concentrations and bacterial densities were converted to phytoplankton and bacterial organic matter respectively. These values were summed for each sample and subtracted from the total amount of POM to determine the mass of detrital organic matter in suspension. From this, the mean monthly detrital load was calculated and plotted in Figure 21, along with the mean monthly masses of phytoplankton, bacteria and detritus. In the first five months the

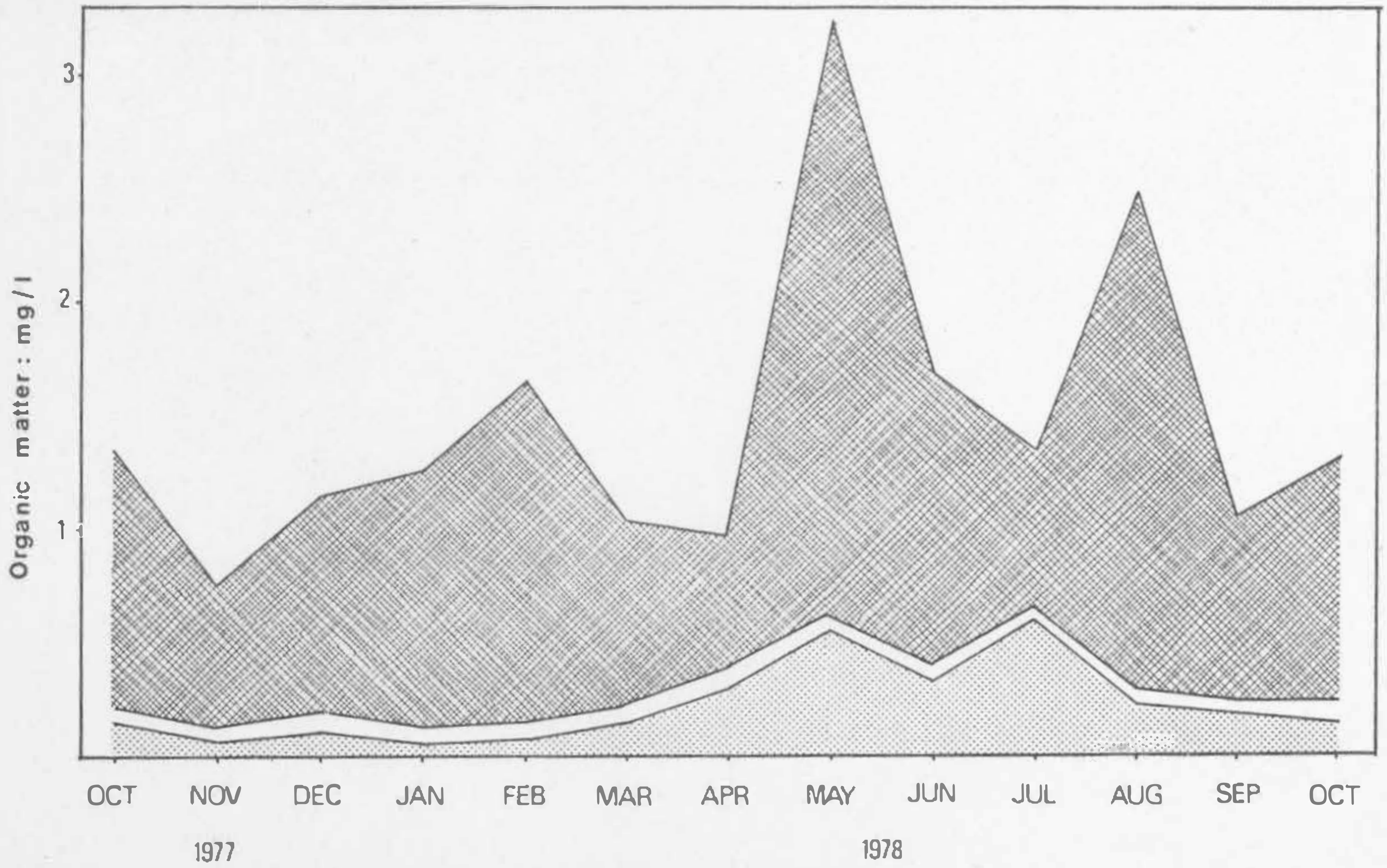

Figure 21. Seasonal variation in the composition of particulate organic matter (mg/l):

□ bacterial organic matter
░ phytoplankton organic matter
▩ detrital organic matter

biomass of bacteria exceeded that of the phytoplankton but fell in the autumn and winter months while the biomass of phytoplankton rose during this period. The contribution by detritus was enormous, with a mean of 1,2 mg/l. Levels never fell below 0,5 mg/l and always constituted 50% or more of the total POM in suspension. It must be remembered that in these calculations no allowance has been made for the contribution by microzooplankton. However, it is unlikely that this would alter the picture of an environment dominated by detritus throughout the year.

4.1.8 : Microscopic Examination of Particulate Matter

Microscopic examination of the seston was performed on specially prepared filters after filtering 1 litre of sample water. The results are presented in section 4.1.8.1. However, it was impossible to operate at magnification greater than x320, and any small particles (±25 µm) were obscured by large numbers of bigger particles. In the bacterial counts only 5 ml of sample was drawn through the filter and operating at a magnification of x 1000 the small seston particles were easily observed (see 4.1.8.2).

4.1.8.1 : Larger Particles

Gravimetric analysis has shown that 60% of the seston was inorganic matter (Table 1). This may be accounted for by the large numbers of inorganic grains or flakes in suspension, generally 50 µm and smaller. No large sand grains were encountered. Some of the inorganic matter was biogenic, with the main contributors being spicules ranging in diameter from approximately 10 to 65 µm. The larger ones often had a narrow central bore running the entire length of the spicule, and some were arranged as a 3-pointed star. A second source was microzooplankton tests, calcareous in the case of the Forminifera, and siliceous in the case of the Radiolaria. The diatoms also contributed to the inorganic pool.

Three types of detrital particles were distinguished:

1. Fragments: Angular fragments of macrophyte material with some cellular structure still visible. These were present in very small numbers in most samples; however, they were common in the inshore waters in November, December, May and June. Occasionally very large pieces of macrophyte material, greater than 200 µm, were encountered, usually as a flat sheet of cells.

2. Aggregates: Heterogeneous, amorphous mass of flocculent material, often with small but distinctive particles, which appeared loosely bound together in a gelatinous matrix. Occasionally the particles formed a tightly packed complex. The embedded particles were too small to be identified and might have been minerogenic. The aggregates or flocs had no distinct shape and often were not sharply defined. They ranged in diameter from a few microns to approximately 150 µm and were by far the most common form of detritus.

3. Faecal pellets and packages: Like the flocs, these were compact or diffuse but there was always some evidence of a delimiting boundary and distinct shape, usually long and cylindrical. These particles never exceeded 150 µm in diameter and were up to 500 µm long. It was impossible to identify the contents, although they did include the occasional diatom test and most commonly a cluster of small spicules. These particles tended to be larger than the flocs and much darker in colour. They were common at the inshore station and in outgoing water, suggesting that they originated from animals on the reef. A particularly striking example of this was encountered in December, when the surface area of faecal matter on the filter represented approximately 50% of the particulate matter inshore, but only 10% at the offshore station. In July there were four times as much faecal matter inshore as that present offshore.

When swimming over the reef, it was not unusual to find long mucoid-like strands in the undisturbed offshore water. However, these were never found in the samples, having disintegrated due to their fragile nature.

The phytoplankton was dominated by diatoms, though many samples contained very few cells. Dominant forms were: October, offshore station, incoming tide - both *Chaetoceros* and *Nitschia*; December, offshore, incoming - *Chaetoceros* and *Nitschia*; April - chains of *Rhizosolenia*; May - very few phytoplankton cells in spite of the high chlorophyll concentrations; June - dinoflagellates, possibly

Gymnodinium; July - *Nitschia*; September and October - the dinoflagellates *Ceratium* and *Peridium*. *Asterionella*, *Coscinodiscus* and *Thalassionema* cells were also encountered, but in small numbers. *Chaetoceros* was always found as chains of 3 - 4 cells, *Nitschia* is also known to occur linked in chains but over the reef was found almost entirely as single cells. Cells were invariably most numerous at the offshore station.

Microzooplankton was frequently encountered, but generally only 1 - 2 cells per sample. Foraminifera were the main contributors, followed by Radiolaria. In those samples where the chlorophyll concentrations were extremely low, the biomass of microzooplankton often appeared to exceed that of the phytoplankton. Larvae were rarely encountered - brachyuran zoeae in April, barnacle nauplii and lamellibranch larvae in November.

Copopods were also rare, but this is not surprising as they are capable of escaping the sampling bottle. The sample from December, offshore station, incoming tide, contained 10 calanoid copepods. Portions of crustacean exoskeletons were sometimes found.

4.1.8.2 : Bacteria and Small Particles

The bacteria were dominated by short rods, 1 - 2 µm x 0,5 µm, which constituted approximately 65% of the total number. The cocci, 0,2 - 0,4 µm in diameter, averaged 20% of the total numbers, long rods, 3 - 4 x 1 µm, 10% and curved and helical forms the remaining 5%.

The diameter of these blobs was less than 5 µm. Approximately 95% of the attached bacteria found in the July samples were present in these transparent films.

4.2 : DAILY SAMPLING

4.2.1 : Summer

The results of the daily sampling programme conducted during the last 2 weeks in February are shown in Figures 22 to 28. Figure 22 shows water temperature and sea conditions, rated on an arbitrary scale of 1 - 5 according to roughness, at the time of collection and the mean daily strength of onshore winds as measured at Cape Point lighthouse. The wind generally blew onshore (from the south-east), the offshore component was only dominant on 2 of the 15 days sampled. Over the 72-hour period, days 8 - 11, the average wind speed recorded was 40 knots. It was therefore not surprising that extremely choppy and rough seas were encountered at Dalebrook. There was a significant correlation (r = 0,81) between onshore wind velocity and sea conditions. Water temperatures fluctuated between 19 and 21^{O}C, dropping to 17,5^{O}C on day 13 when the wind was offshore.

Figure 23 shows the concentrations of the four inorganic nutrients - ammonia, nitrates, reactive phosphate and silicates. Ammonia levels ranged between 2 and 5 µg atoms/l, with one reading reaching as high as 8 µg at/l. Nitrates were extremely low in the first 11 days, rising to 4 µg at/l on day 13. Phosphates were steady around 1,5 µg at/l. Silicates showed the greatest fluctuations, 2 µg at/l on days 6 and 7, rising to 8 µg at/l on day 10.

Figure 24 shows concentrations of chlorophyll a. These were very low, 0,5 - 1,0 μg/l, as one would expect from the monthly summer samples (Fig. 6). It is interesting to note that the highest levels, recorded on day 13, coincided with the peak in nitrate concentrations. Densities of both free and attached bacterial cells are shown in Fig. 25; fluctuations were large, the former ranging from 7 to 14 x 10^5 cells/ml, which represented a mean of 9,7 ± 2,1 (S.D.) x 10^5 cells/ml, a figure very close to the mean value from the February monthly samples (Fig. 8). Approximately 15% of the bacteria were attached to particles, however this varied from 0 on the first day to 6,2 x 10^5 cells/ml on the final day.

Figure 26 illustrates the day-to-day variation in the amounts of TPM and POM in suspension. TPM values were low, considering the rough sea conditions, the only exception being day 9. There was a slight drop in the levels over the final five days, when the seas were more settled. Particles smaller than 100 μm contributed an almost consistent 75% - 80% by mass of the seston; variations in these proportions were independent of sea conditions and the total amount of seston encountered. The amount of POM in suspension mirrored the trends shown by the TPM, also peaking on day 9. Generally more than 50% of the TPM was organic, however the rough seas on the 9th day resulted in a larger proportion of inorganic matter in suspension and the POM dropped to less than 40%. The particles > 100 μm were almost entirely organic.

Figure 27 shows the composition of the POM over the 15 days. The contributions by the phytoplankton and bacteria were consistently small. It is interesting to note that the mean mass of bacterial organic matter, 0,11 mg/l, exceeded that of the phytoplankton, which was only 0,10 mg/l. Detritus accounted for all the day-to-day variation in the amount of POM in suspension.

Figure 28 shows the particle size distributions of each sample. Excessive electrical interference on the Coulter Counter prevented the processing of the last three samples. The curves tended to be flattened, especially over the period days 4 - 8 inclusive, indicating an even distribution of particle volume over the broad range of particle sizes 6 - 50 µm. This phenomenon appears to be characteristic of water with low seston and chlorophyll levels. The sample from the 9th day, with its high seston load but low chlorophyll content, had a curve with a broad peak and modal frequency of 14 µm.

It was not possible to follow any distinct trends in the composition of the seston when examining the samples microscopically. The inorganic fraction comprised mainly small grains and spicules of various sizes. The detritus was dominated by small flocculent aggregates. Faecal pellets up to 140 µm wide were present, some of the aggregates might possibly have been broken up faecal matter. Macrophyte material was only present in small quantities in the samples from days 3, 5 and 8 - 11 inclusive. There was nothing to suggest why such particles should be present on certain days and then disappear for several days. The high seston level on day 9 was due to a general increase in all types of particles. Only a few phytoplankton cells were present in the samples; there was a sharp

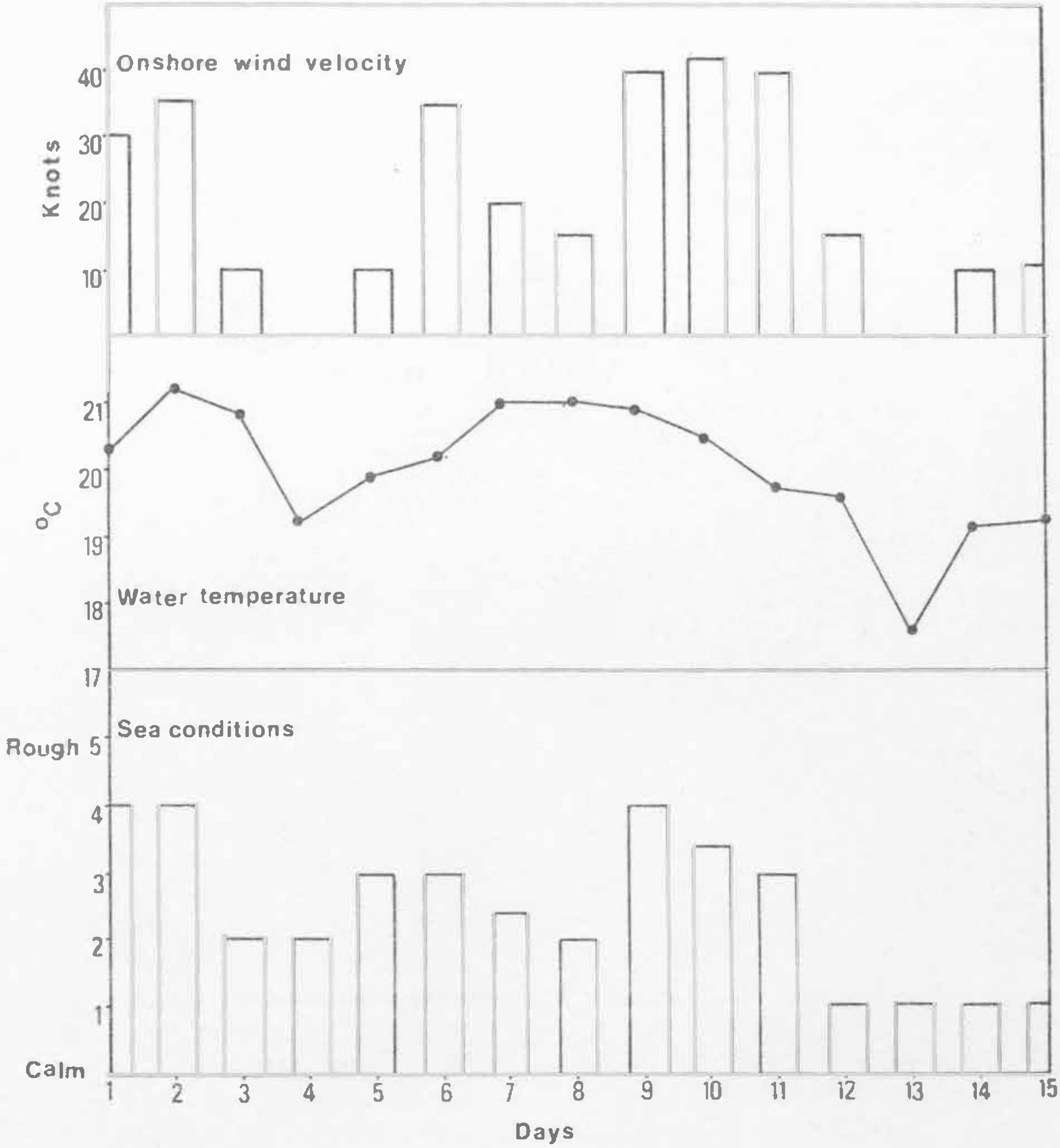

Figure 22. Summer daily sampling : Mean daily onshore wind velocity, and water temperature and sea conditions at the time of sampling.

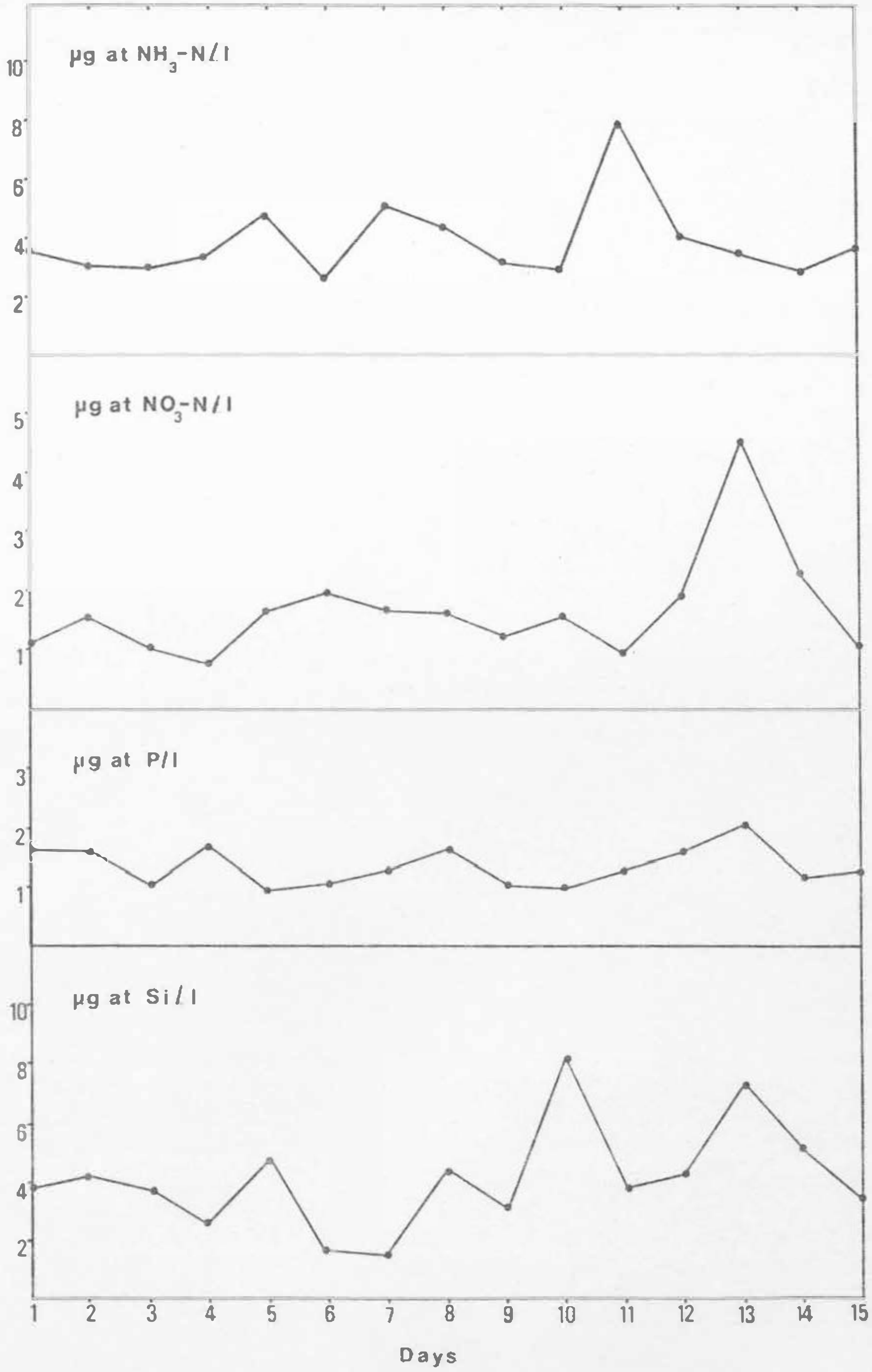

Figure 23. Summer daily sampling : Concentrations of ammonia, nitrates, phosphates and silicates at the inshore station.

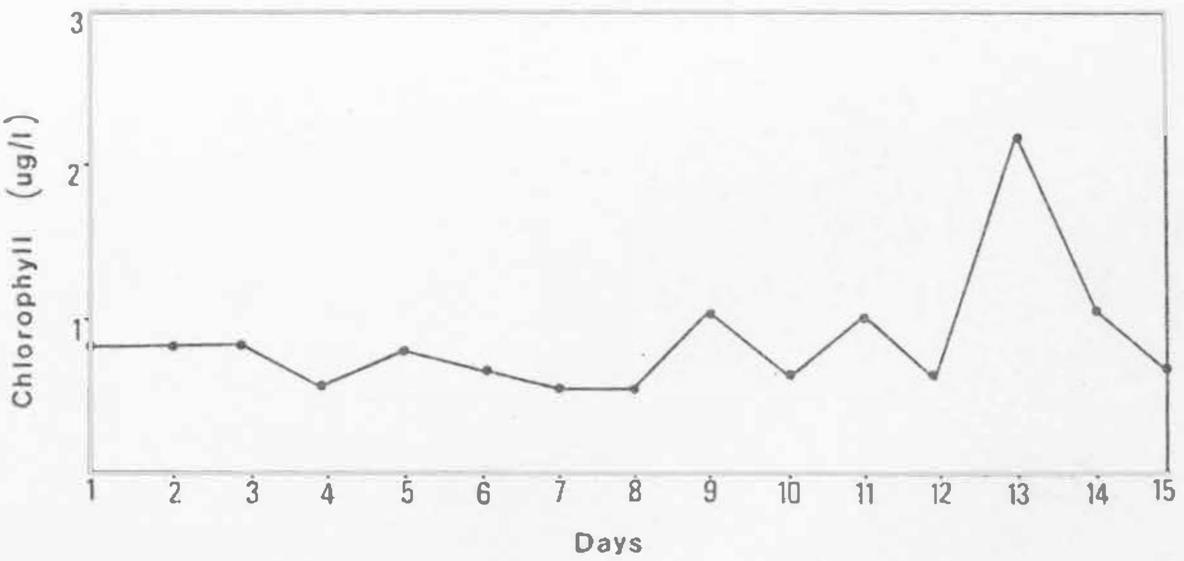

Figure 24. Summer daily sampling : Concentrations of chlorophyll a (μg/l) at the inshore station.

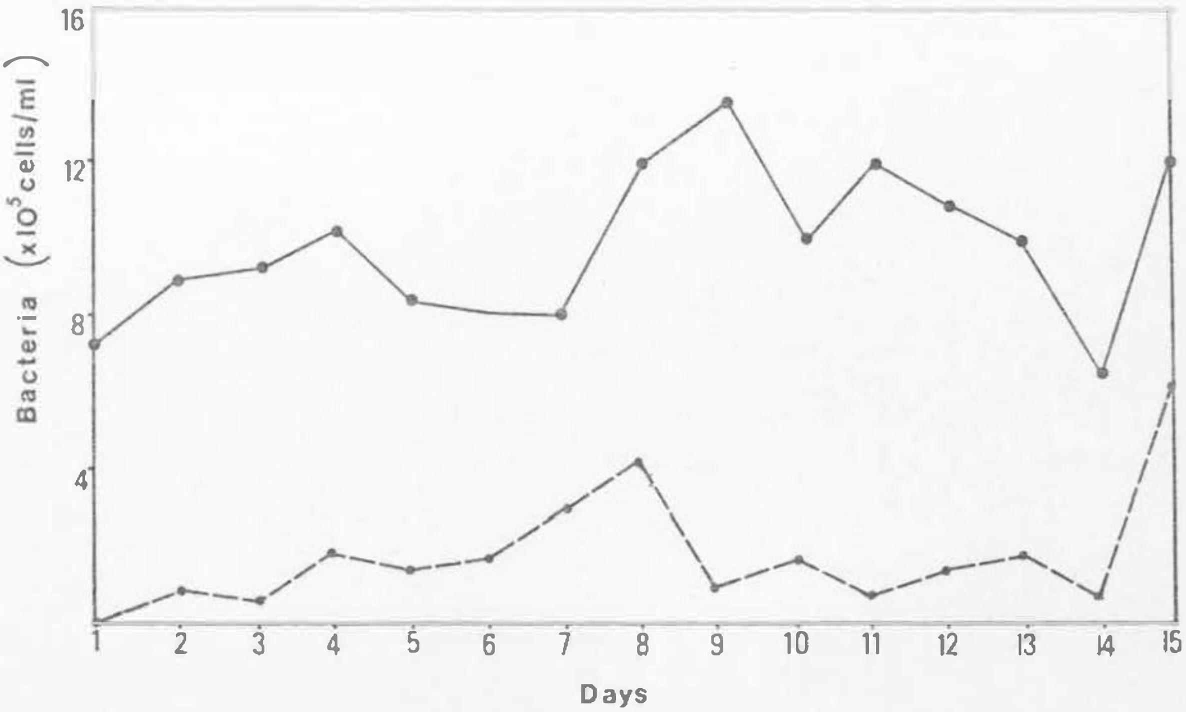

Figure 25. Summer daily sampling : Numbers (x 10^5/ml) of free bacteria —•— and attached bacteria –•– at the inshore station.

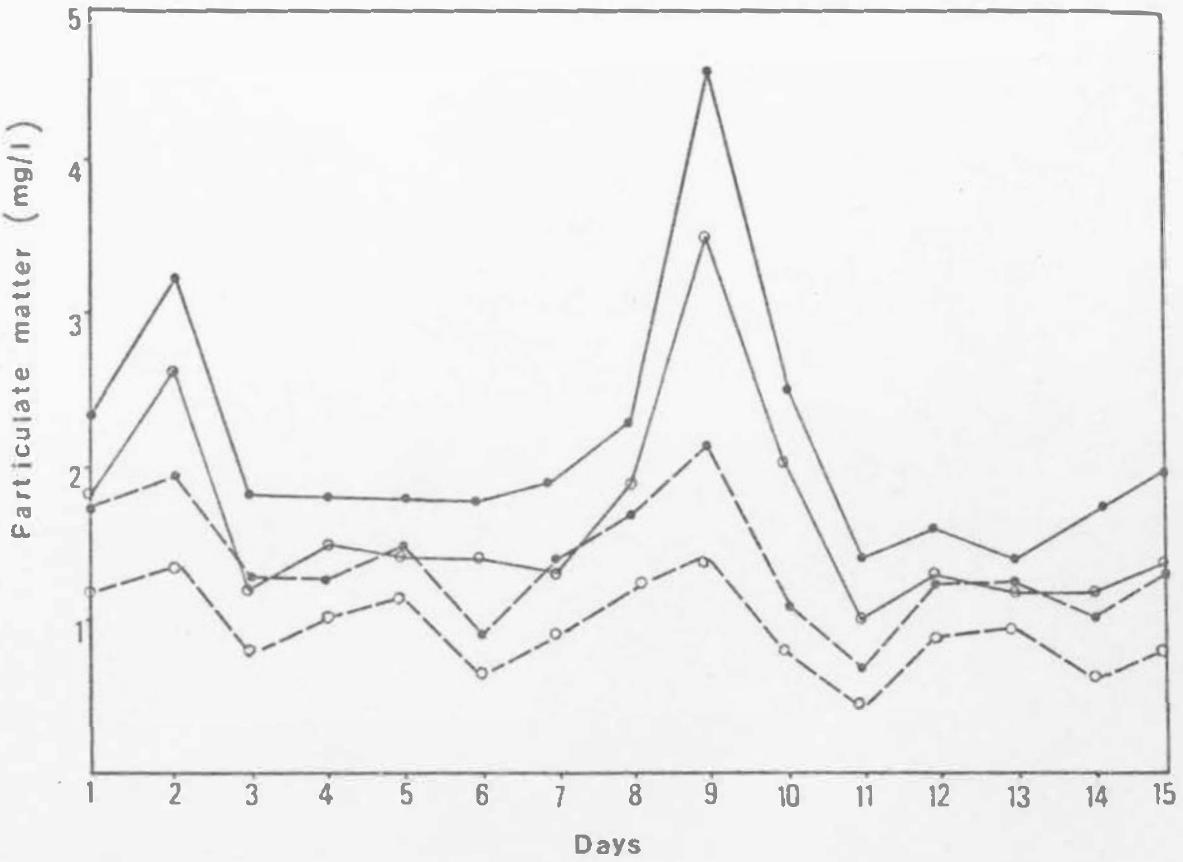

Figure 26. Summer daily sampling : Dry mass (mg/l) of total particulate matter (——•——) and particulate organic matter (— — —•— — —). Open symbols represent the <100 μm fractions.

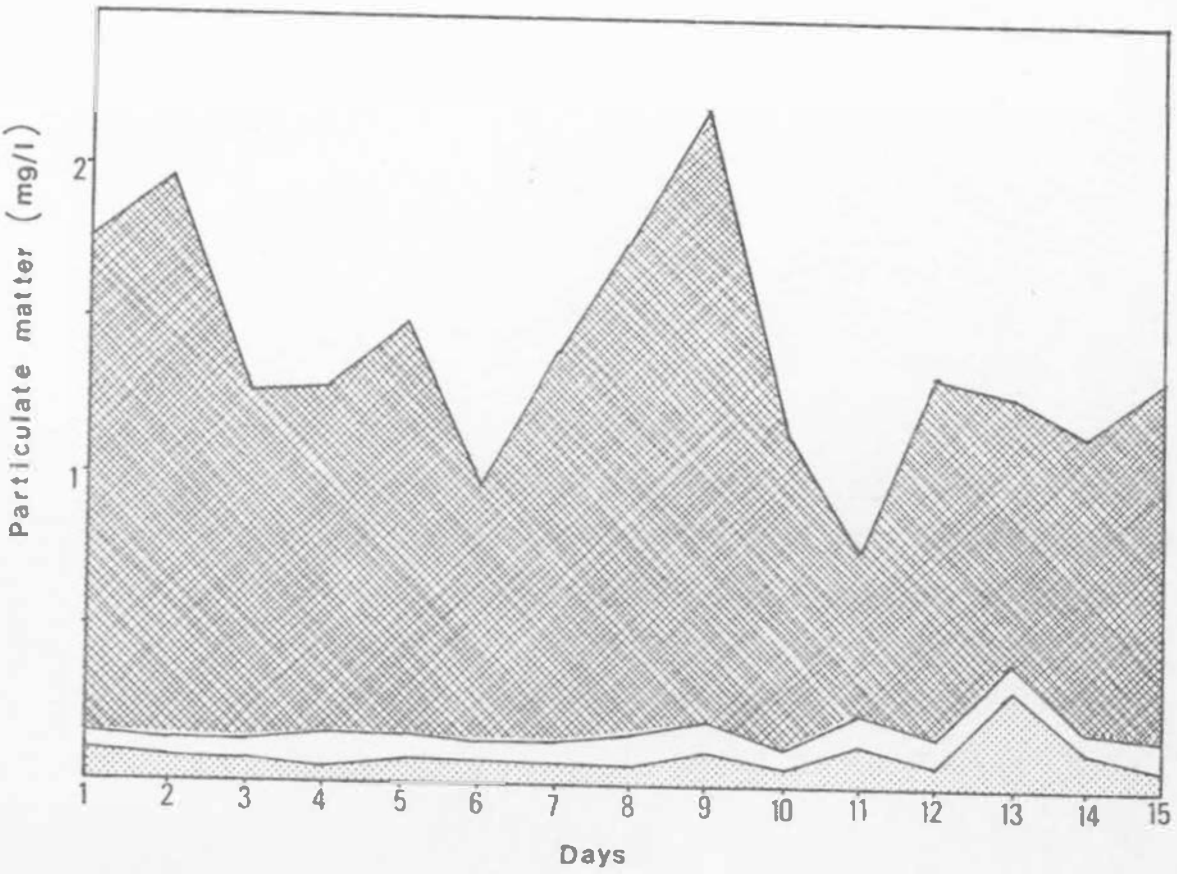

Figure 27. Summer daily sampling : Variation in the composition of particulate organic matter (mg/l) in suspension at the inshore station.

□ bacterial organic matter
░ phytoplankton organic matter
▨ detrital organic matter

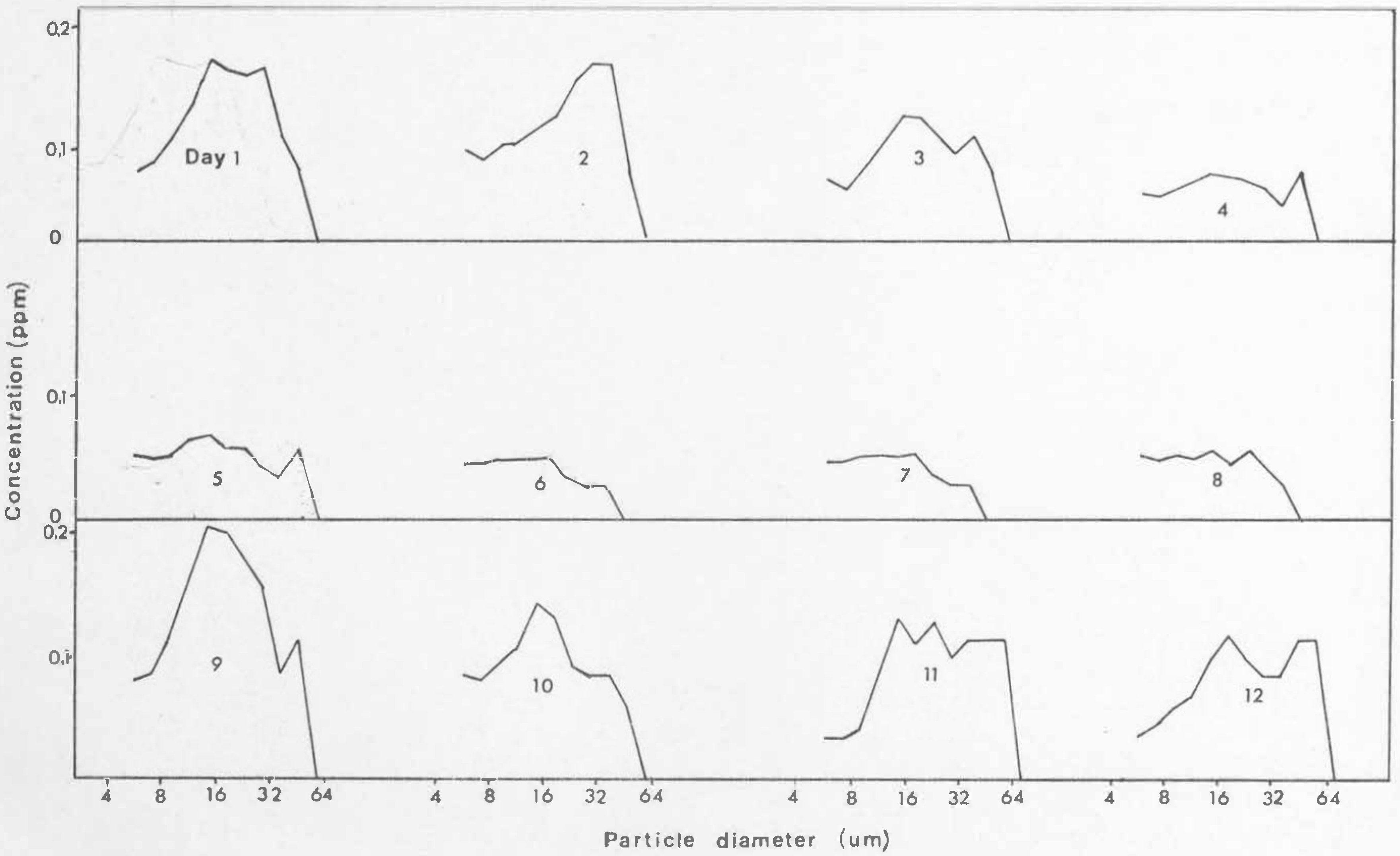

Figure 28. Summer daily sampling : Particle size spectra of samples collected at the inshore station.

increase in the number of *Nitschia* cells on day 13, some of these were present as chains of 2 - 3 cells. Zooplankton was scarce; the occasional Foraminiferan and Radiolarian test was encountered. Two copepods were found in the final day's sample.

Simple 2-way correlations were tested for all the factors measured, including correlations with a lag of up to four days. The only strong correlation was that mentioned earlier between wind speed and sea conditions on the same day. The ratio of organic to inorganic matter was fairly constant from day to day. One would therefore expect that total particle volume would be a good indication of the mass of particulate matter <100 μm. However the correlation was only 0,61, but this was significant at the 5% level. As was to be expected, the correlation between TPM and POM was high, r = 0,82.

4.2.2 : Winter

The second 15 day sampling programme was carried out in the first two weeks in August; the results are illustrated in Figures 29 to 35. Figure 29 shows the environmental conditions. As expected, there were two striking differences between the summer and winter conditions: the almost total absence of onshore winds in winter and the drop in temperature to 13 - 14°C. With the high incidence of offshore winds, the seas were much calmer than in February.

Daily variation in the concentrations of the four inorganic nutrients are shown in Figure 30. Ammonia levels, between 3 and 5 μg/l, were slightly higher than those recorded in summer (Fig. 23). The extremely high value of 11,8 µg at/l on day 4 might have been due to contamination, as levels much above 6 µg at/l have been rare. Nitrates were far higher than the summer values. Phosphates showed little deviation from 1 µg at/l, while silicates ranged from as low as 2 µg at/l to 16 µg at/l on day 11. This peak coincided with that of nitrates.

Chlorophyll concentrations (Fig. 31) were also much higher than the summer values (Fig. 26), exceeding 1 µg/l on most days. On the other hand, bacterial densities (Fig. 32) were lower, with a mean of only 5 x 10^5 cells/ml. In comparison with the summer values (Fig. 27), there was an increase in the number of attached cells and on several occasions these exceeded the number of unattached cells. There were large fluctuations in the numbers of both attached and unattached cells.

Although the sea conditions were not nearly as rough as during February, the amounts of TPM and POM were generally greater (Fig. 33). Approximately 90% of the seston was made up of particles smaller than 100 µm. This figure was higher than that for February by at least 10% and may be a reflection of the calmer conditions allowing the larger particles to settle out, retaining only the smaller ones in suspension. The POM showed less variation than the TPM with the result that the percentage contribution of the POM varied widely between 30% and 50% of the TPM. Levels of POM were initially low, increasing after 3 days to approximately 2 mg/l and then falling over the final 3 days. The > 100 μm fraction of the TPM was almost entirely organic.

Figure 34 shows the composition of the POM. The large fluctuations in bacterial densities were insufficient to influence the small amount of bacterial organic matter in suspension. Although chlorophyll levels were higher than in summer, the contribution by phytoplankton never exceeded 15%. The bulk of the POM was detritus and this accounted for the variation in the amount of POM in suspension.

Particle size spectra are illustrated in Figure 35. All the curves were unimodal with a modal frequency of 14 μm in all but 2 samples. Samples from days 1, 2 and 3 had low broad peaks which appear to be associated with low levels of TPM and chlorophyll a. The peaks became sharper as the chlorophyll concentrations increased (days 8, 11 and 12) and taller as the amount of seston increased (day 11).

Again it was not possible to follow any trends in the composition of the seston when examining the samples microscopically. The inorganic fraction comprised mainly grains, 75 μm and smaller; spicules of different lengths and thicknesses were common. The detritus was dominated by small flocculent aggregates, many with tiny particulate inclusions. Faecal pellets, varying in width from 30 - 150 μm, were abundant on days when the levels of POM were highest. Some blobs of macrophytic material were present on days 4 - 9 but disappeared thereafter in spite of the large amounts of TPM in suspension on days 10 and 11. It is interesting to note that generally there were two to three Foraminifera in each sample, with five tests on the 12th and 14th days. Phytoplankton encountered was mainly *Chaetoceros*, *Thalassionema* and *Coscinodiscus*; *Nitschia* cells dominated the phytoplankton on day 8.

There was a strong correlation, similar to that in the monthly samples, between nitrates and silicates (r = 0,88, lag 0). In spite of the fact that the phytoplankton constituted such a small amount of the organic matter, there was a correlation between chlorophyll and the < 100 µm fraction of the POM (r = 0,78, lag 0). Particle volume was correlated with the < 100 µm fraction of POM (r = 0,84, lag 0), the < 100 µm fraction of TPM (r : 0,82, lag 0) and chlorophyll a (r = 0,74, lag 0), which is evidence of the usefulness of the Coulter Counter in this study.

The results of the daily sampling programme generally support the summer - winter differences evident in the monthly samples. Chlorophyll, nitrates and silicates were higher in winter, while free bacteria, although showing considerable day-to-day variation, were present in higher numbers in summer. In spite of the calmer seas in winter the seston load was greater.

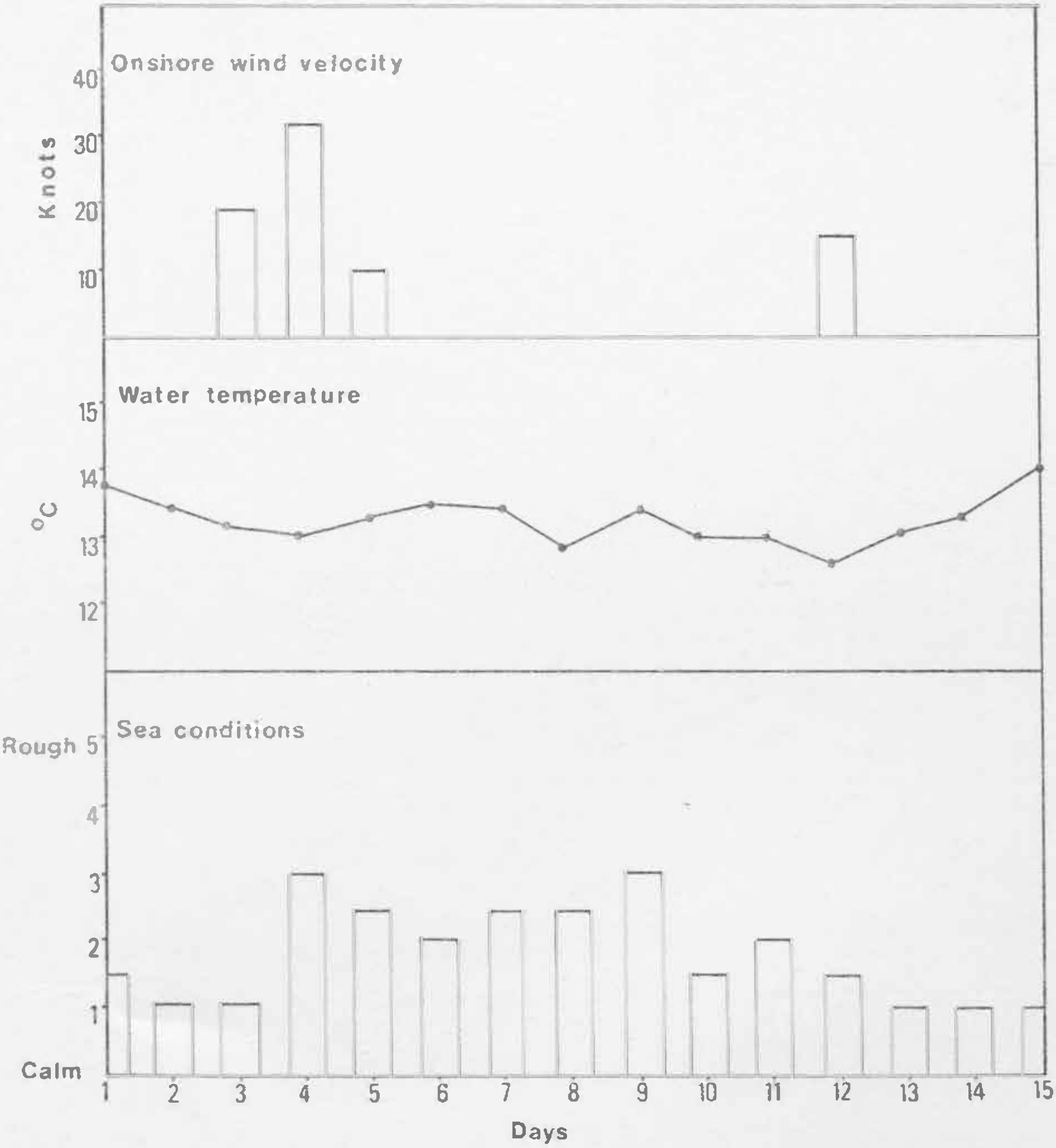

Figure 29. Winter daily sampling : Mean daily onshore wind velocity, and water temperature and sea conditions at the time of sampling.

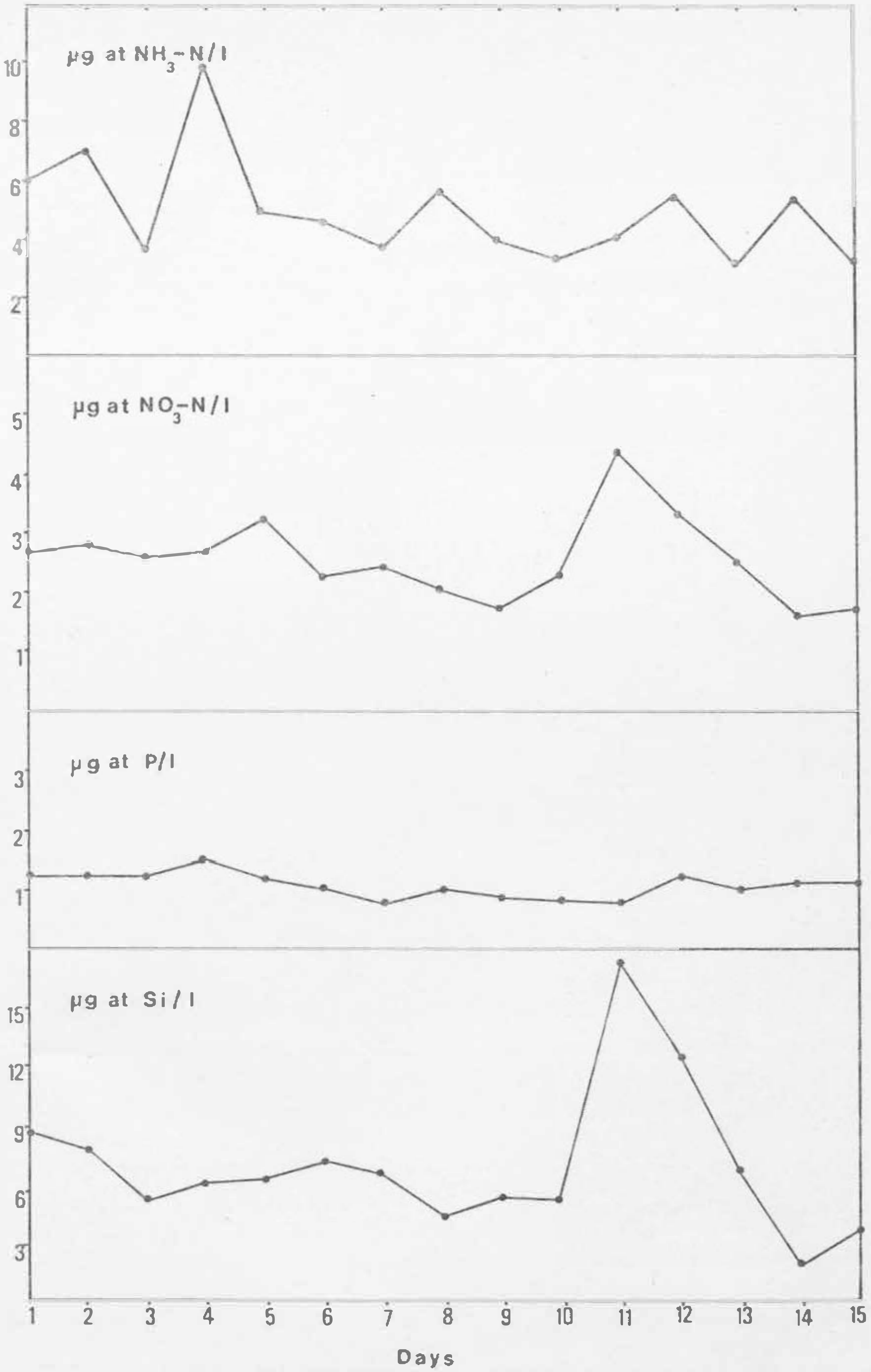

Figure 30. Winter daily sampling : Concentrations (μg at/l) of ammonia, nitrates, phosphates and silicates at the inshore station.

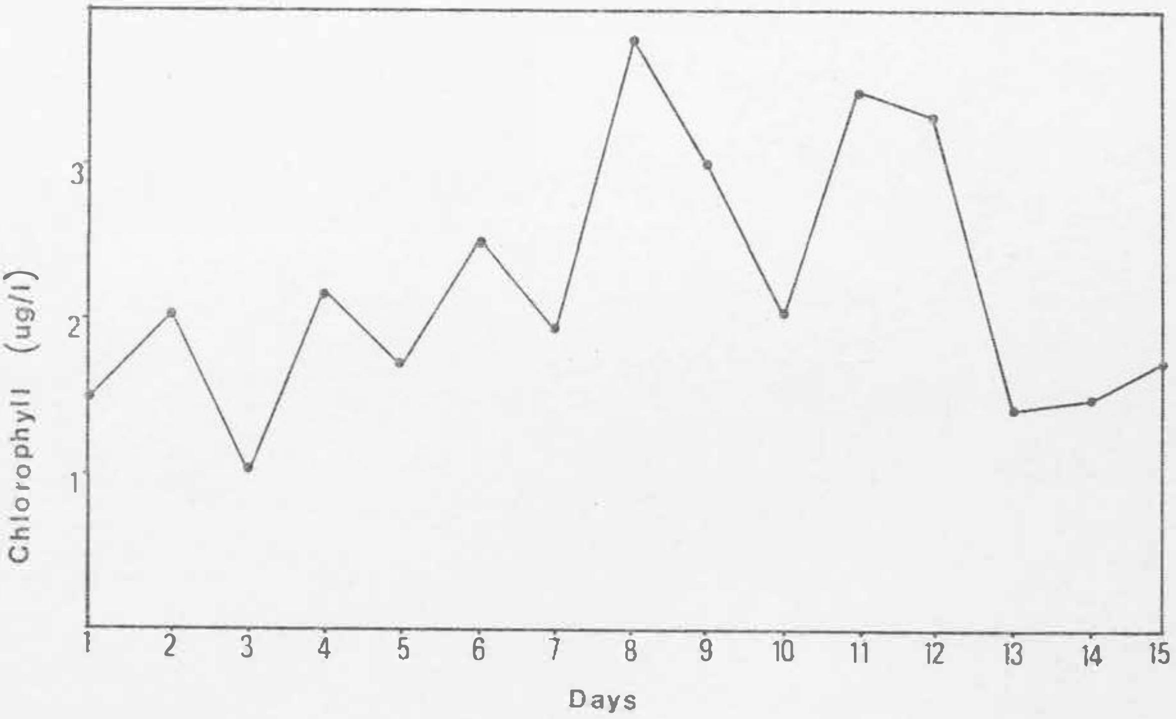

Figure 31. Winter daily sampling : Concentrations of chlorophyll a (μg/l) at the inshore station.

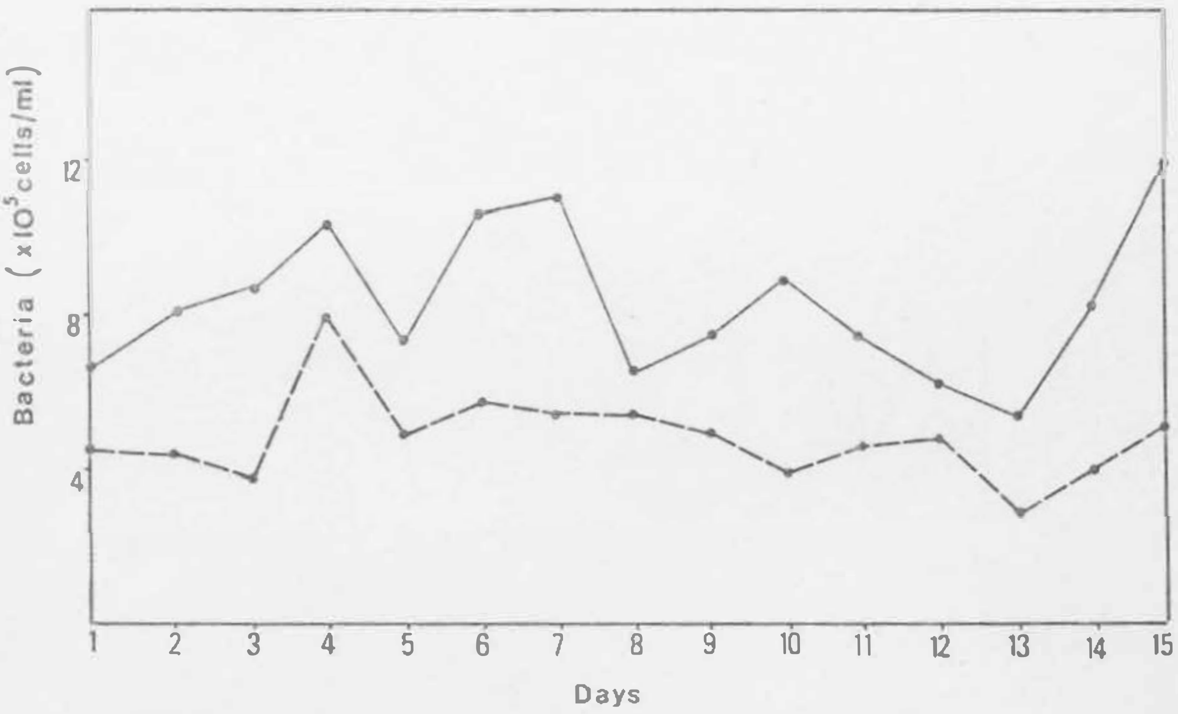

Figure 32. Winter daily sampling : Numbers (x 10^5/ml) of free bacteria (——•——) and attached bacteria (– –•– –) at the inshore station.

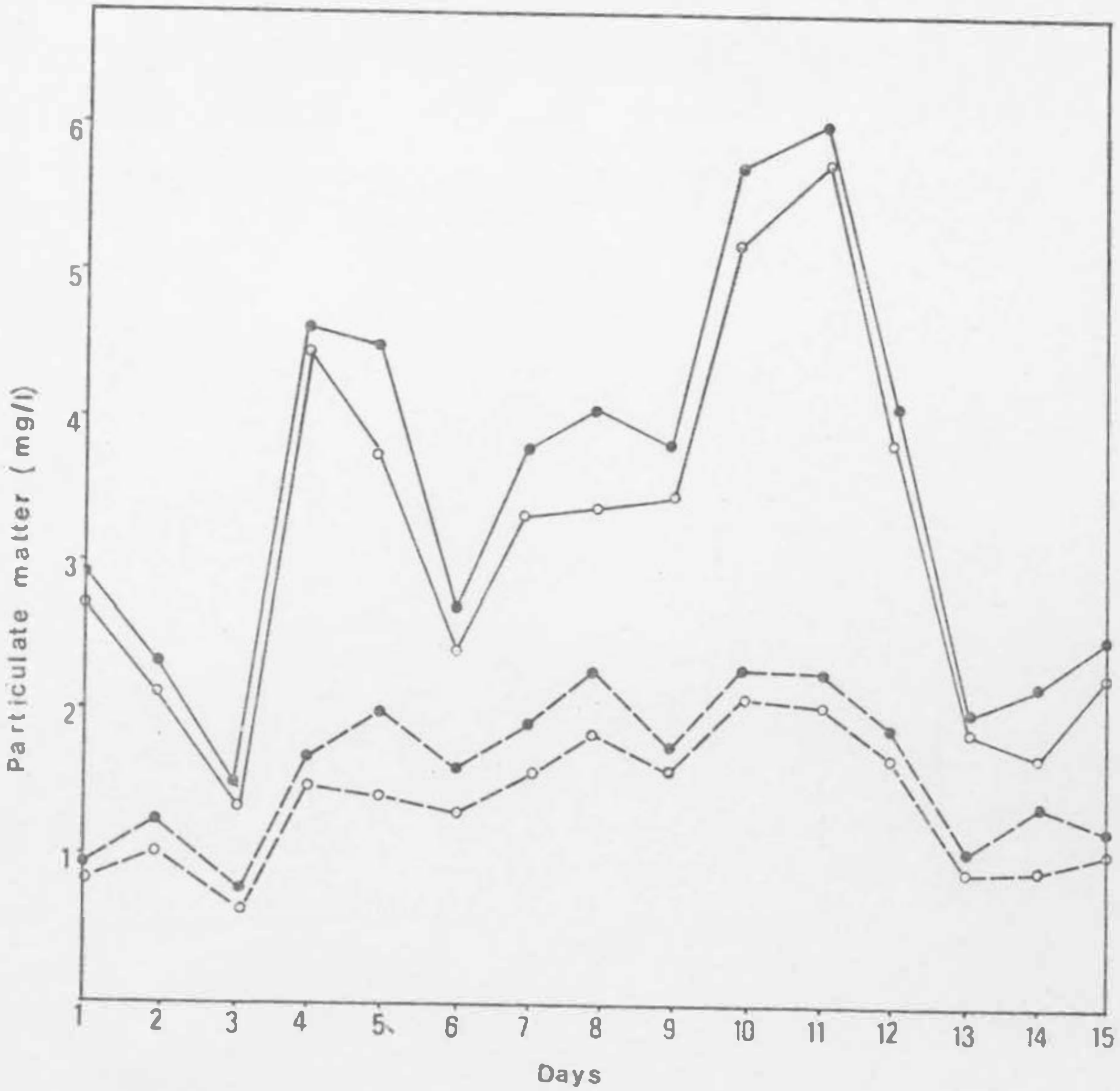

Figure 33. Winter daily sampling : Dry mass (mg/l) of total particulate matter (——●——) and particulate organic matter (– – –●– – –). Open symbols represent the < 100 μm fraction.

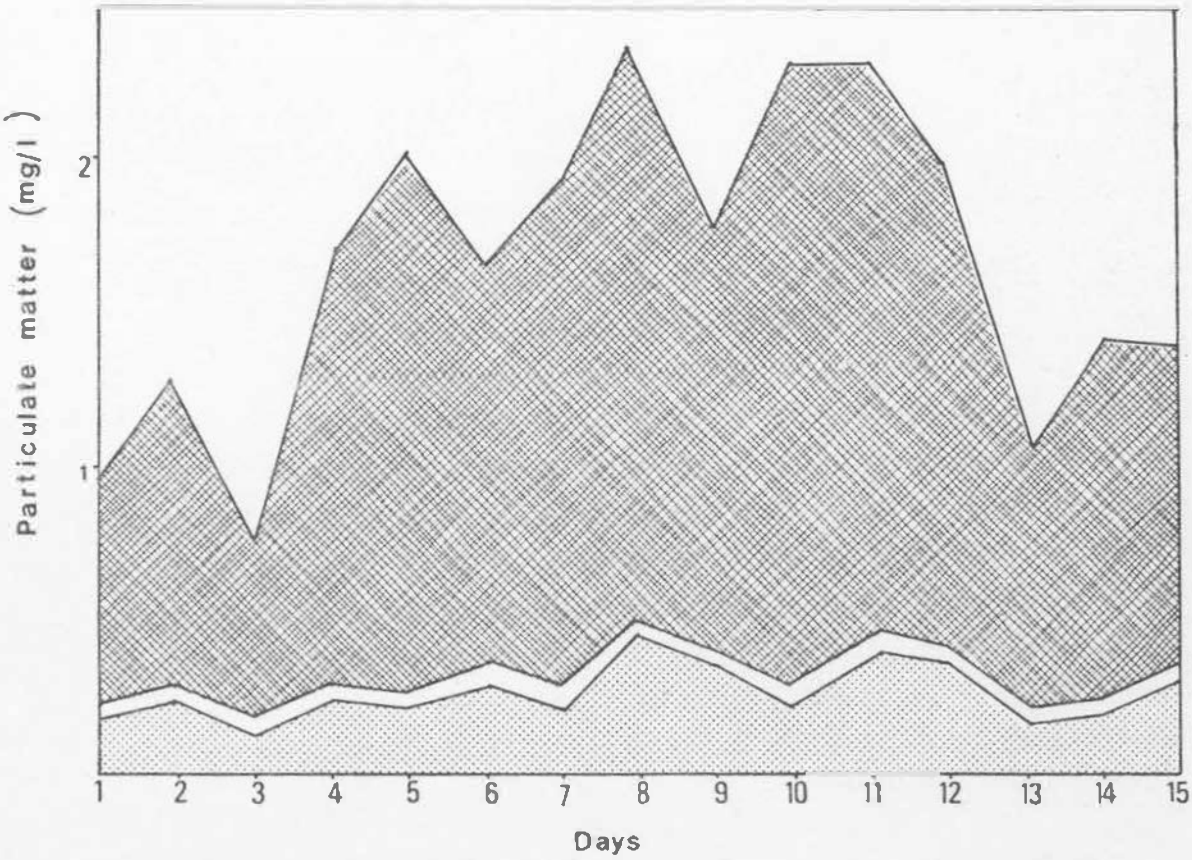

Figure 34. Winter daily sampling : Variation in the composition of particulate organic matter (mg/l) in suspension at the inshore station.

□ bacterial organic matter
░ phytoplankton organic matter
▩ detrital organic matter

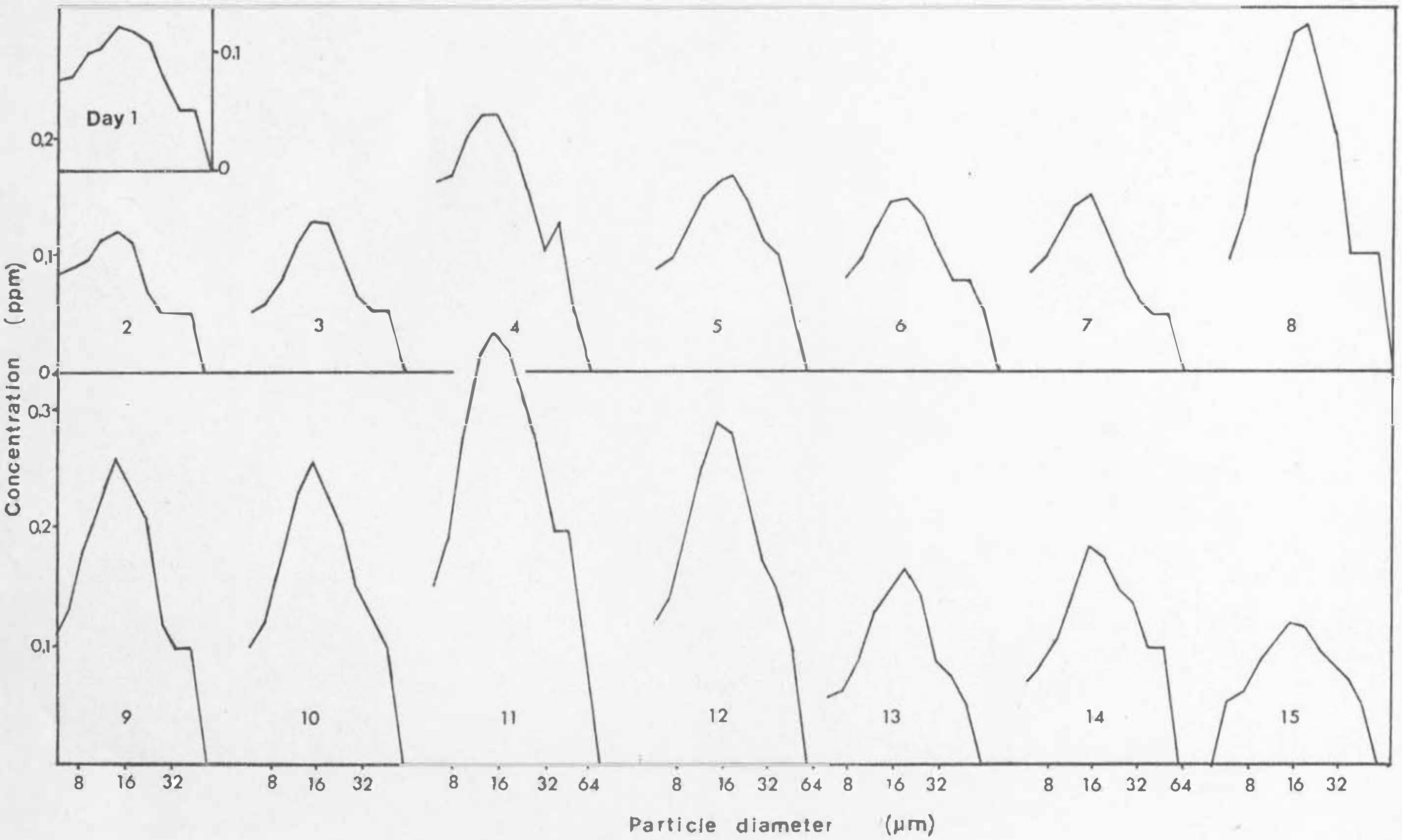

Figure 35. Winter daily sampling : Particle size spectra of samples collected at the inshore station.

4.3 : FALSE BAY TRANSECTS

4.3.1 : April Transect

The first of the two False Bay transects was undertaken on 30 April, 48 hours after a long period of south-easterly winds which often reached velocities of 40 knots.

The water temperatures (Fig. 36) showed a seaward decline; they were highest over the reef, dropping to 14°C offshore. This was probably due to solar heating of the shallow water over the reef but may be indicative of the existence of two distinct water masses, a warmer body of water over the reef and a colder body offshore. In the open water there was a decrease in temperature with depth; the water at 2 m was generally 2° warmer than that at 15 m, again evidence of surface warming.

Figure 37 shows the concentrations of the four inorganic nutrients. Beyond the reef the 2 m water was severely depleted of all four nutrients, with values in the region of 1 - 2 µg at/l. Levels of ammonia were highest over the reef, nitrates and silicates increased in the deeper, offshore waters, while phosphates remained more-or-less constant over the entire transect. Nitrates rose as high as 4 µg at/l and silicates as high as 7 µg at/l in the deep, offshore waters. There was a significant correlation ($r = 0{,}70$) between the concentrations of these two nutrients.

There were large increases in chlorophyll concentrations (Fig. 38) as one moved offshore. Levels over the reef were less than 4 µg/l but rose to 19 µg/l only 0,5 km offshore. With one exception, levels at 6 m were higher than those at 2 m, with those at 15 m the lowest. This may be a reflection of the conditions at the three depths - light intensities at 6 m approaching the optimal for production and photo-inhibition occurring at 2 m. There was no relationship between chlorophyll concentrations and any of the four inorganic nutrients.

Tromp and Horstman (in press) recorded surface temperatures of 10,5°C and nitrate and silicate concentrations as high as 29 and 39 µg at/l respectively in freshly upwelled water off the mouth of False Bay. From the results of the present study it is obvious that upwelling followed by considerable primary production had occurred, resulting in the enormous standing stock of phytoplankton only 0,5 km from the Dalebrook shoreline. If the site of upwelling was Cape Hangklip, this water mass would have been driven a vast distance, during which time it was warmed by the sun and thoroughly mixed with adjacent, warmer, nutrient-poor waters. This mixing, along with the rapid uptake by phytoplankton cells, appears to have drastically reduced the concentrations of inorganic nutrients in solution.

Figure 39 shows the extremely high bacterial densities encountered along the transect; values ranged from 15 x 10^5 cells/ml at the 1 and 1,5 km stations to 8 x 10^5 cells/ml. There was a marked decrease with depth; the water at 2 m contained twice the number of cells found at 15 m, with the densities at 6 m falling in between. Attached bacteria have not been included as they were only found at the 6 km station, where they amounted to less than 2% of the total numbers of cells. The large phytoplankton stocks were presumably releasing dissolved organic matter in large quantities to stimulate bacterial production. There was, however, no significant correlation between phytoplankton and bacterial stocks. There was no noticeable change in bacterial morphology along the transect line; rods were dominant throughout, with cocci comprising less than 15% of the number of cells.

The dry weight of particulate matter in suspension is shown in Figure 40. This fell from 5 mg/l over the reef to around 3,5 mg/l offshore. The exceptionally high value of 6,8 mg/l 0,5 km offshore was due largely to the contribution by the phytoplankton of 2,2 mg/l organic matter. The < 100 µm fraction represented about 75% of the seston over the reef with no noticeable change seaward.

The levels of POM (Fig. 41) remained constant with depth along the transect line, being 2 - 2,5 mg/l at 2 m and 6 m and 1,5 mg/l at 15 m. The seaward decrease in the amount of TPM was, therefore, due to a decrease in the inorganic fraction. This is not surprising, as in the shallow waters round the reef, inorganic particles are easily stirred up off the bottom and held in suspension by the strong water movements. Offshore, where the water is deeper and the turbulence reduced, those particles with high densities will settle out. The < 100 µm fraction of the POM represented 68% of the total POM as against 75% for the TPM. This means that the larger particles had a slightly higher percentage organic content than the smaller particles.

The particle size spectra were determined for some of the offshore samples and these are shown in Figure 42. The curves tended to have tall, sharp peaks which appear to be characteristic of waters with low detrital loads and high phytoplankton stocks. The 1,5 km sample from 15 m is an inexplicable exception to this trend. It is interesting to note that the modal frequency lay between 29 and 36 µm, as opposed to 14 µm over the reef (Fig. 20). This is possibly because the phytoplankton cells are linked in chains, which become broken up by the water turbulence over the reef. Correlations between particle volume and TPM, POM and chlorophyll a were low but significant at the 1% level: r= 0,53, r = 0,56 and r = 0,64 respectively.

A thick layer of low visibility, extending 12 to 15 m below the surface, was present at all the offshore stations. This water may be best described as a thin soup with delicate, mucoid strands, often several centimetres long. However, under the microscope there was no evidence of these long strands; obviously they had been broken up by the action of sampling and filtering, as only tiny, loosely-packed aggregates of unidentifiable detritus were present. In preparing the samples for examination, cellulose acetate filters were used. They did not clear as well as those made of cellulose nitrate, making it difficult to see the particles clearly.

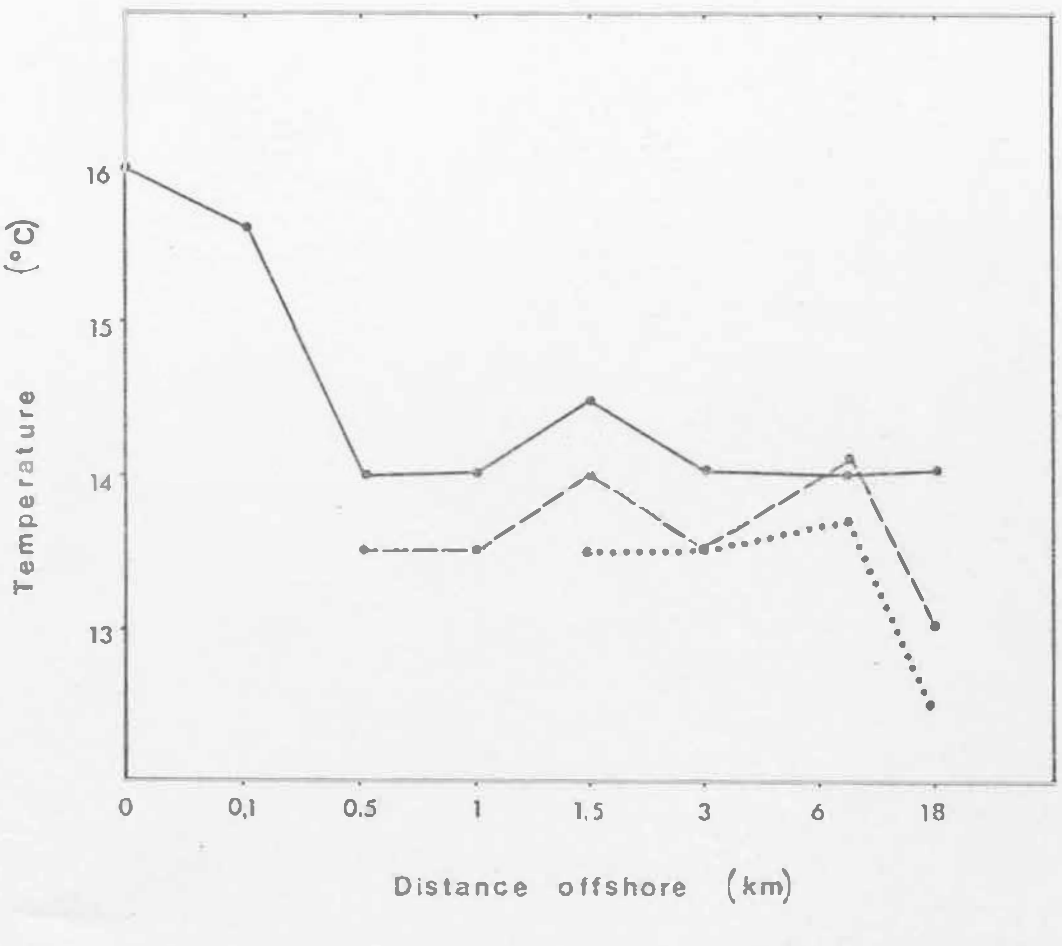

Figure 36. April False Bay transect : Water temperature at 2 metres (———), 6 metres (– – – –) and 15 metres (........).

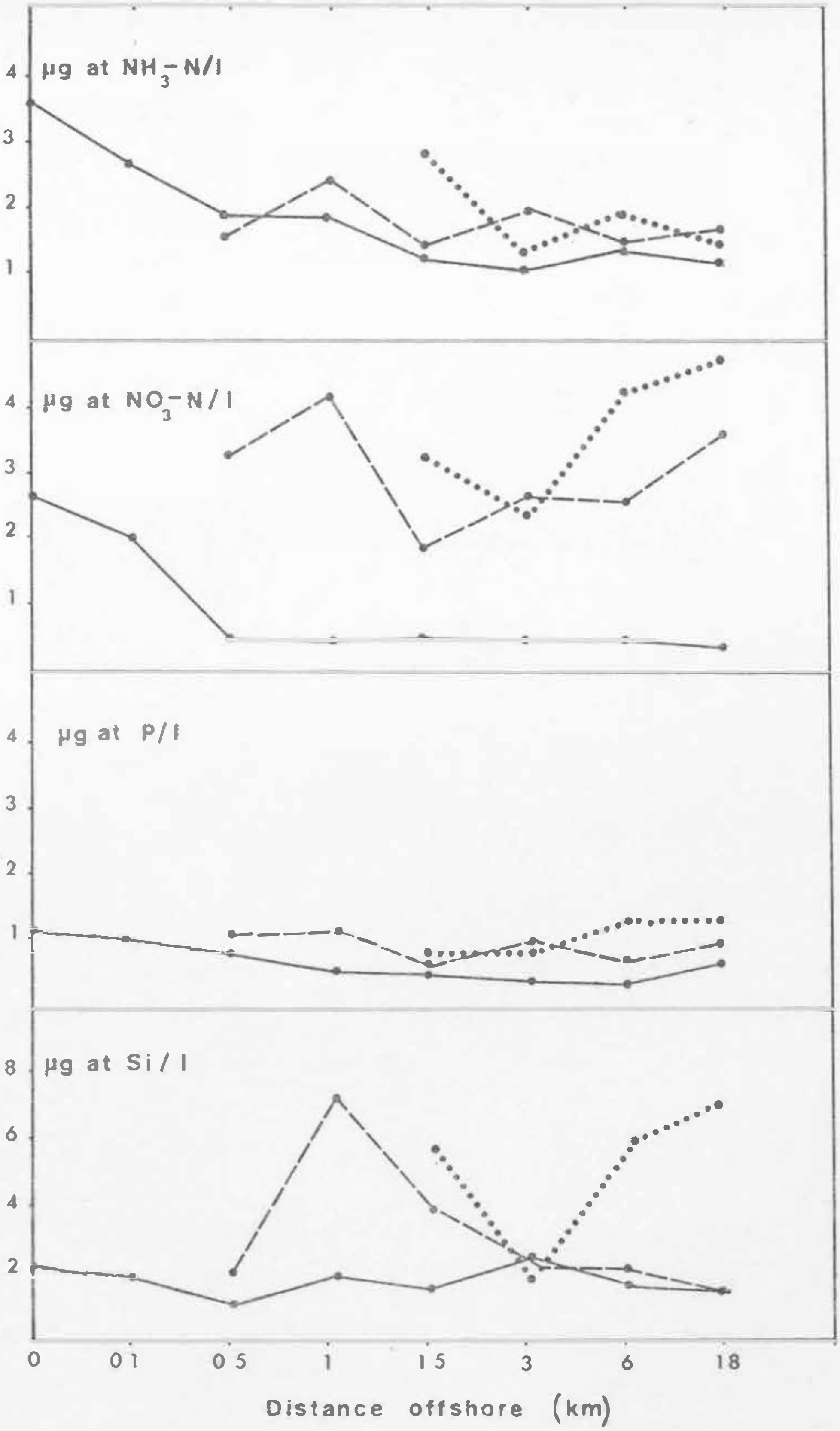

Figure 37. April False Bay transect : Concentrations (µg at/l) of ammonia, nitrates, phosphates and silicates at 2 metres (————), 6 metres (— — — —) and 15 metres (••••••••••).

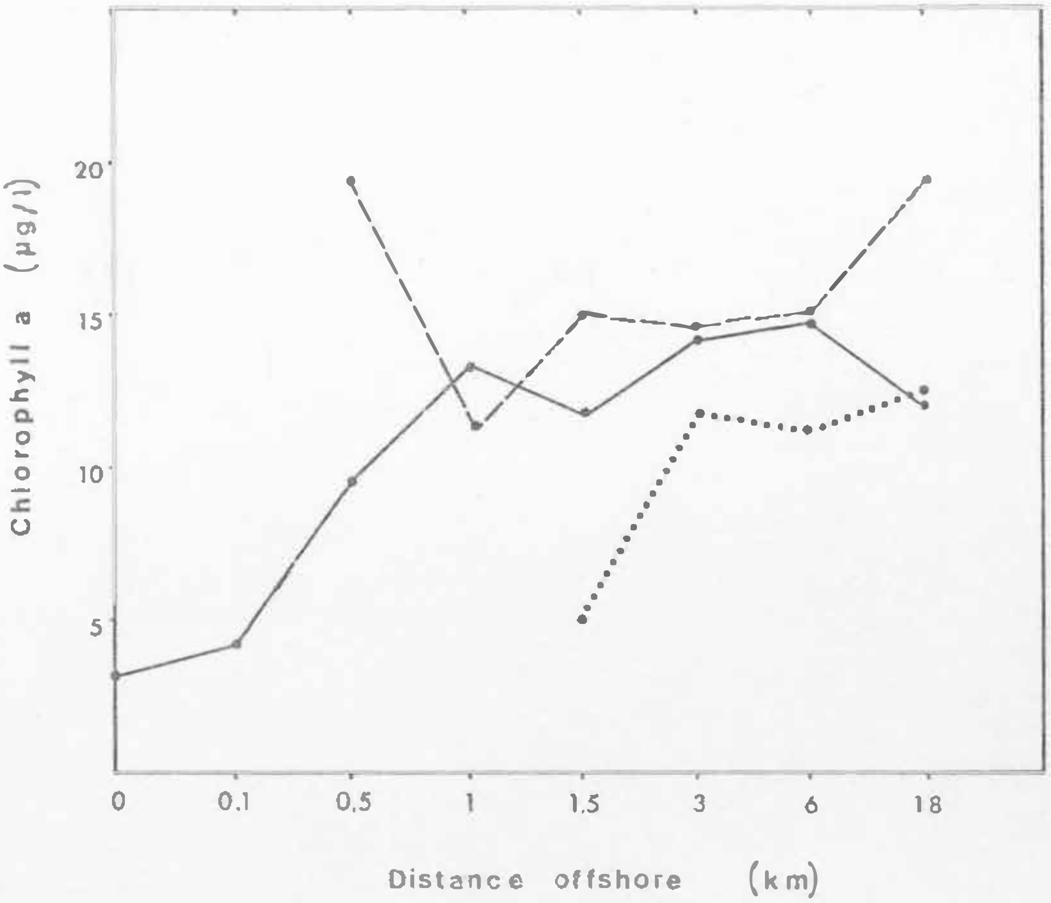

Figure 38. April False Bay transect : Concentrations of chlorophyll a (µg/l) at 2 metres (————), 6 metres (– – – –) and 15 metres (...........).

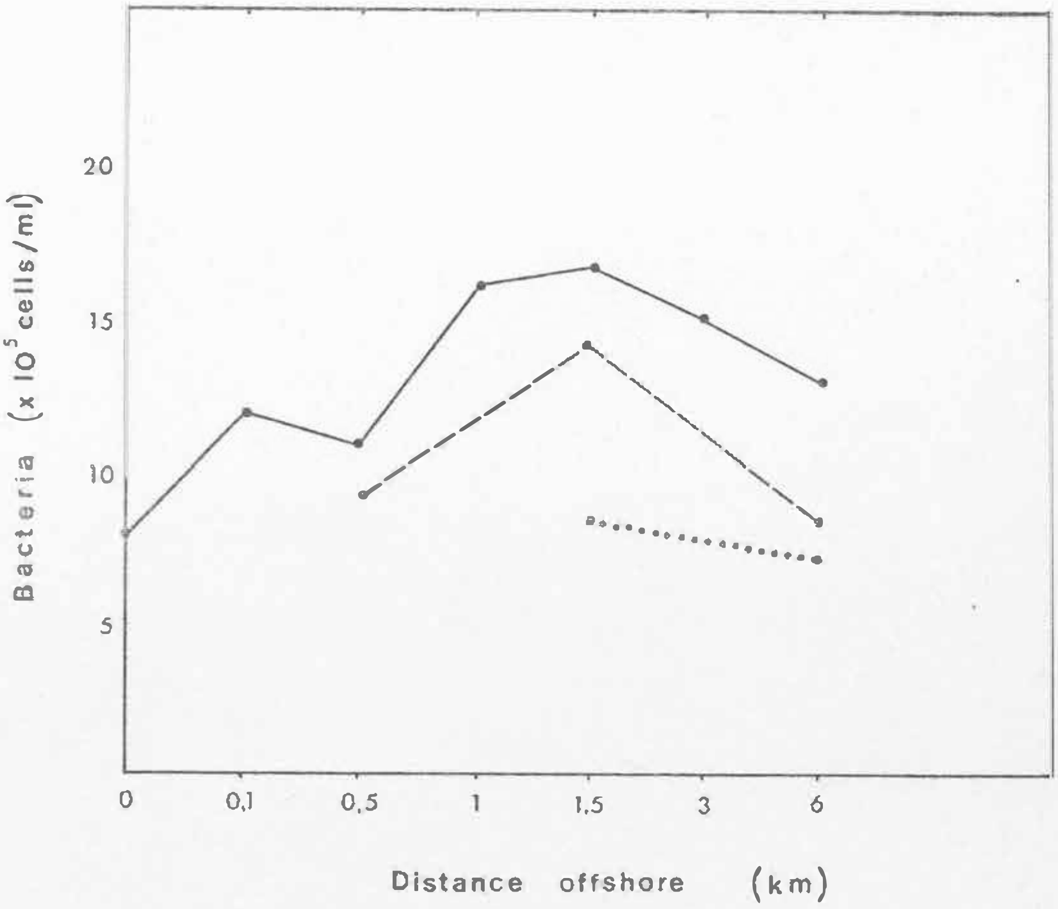

Figure 39. April False Bay transect : Numbers of free bacteria (x 10^5/ml) at 2 metres (———), 6 metres (– – – –) and 15 metres (··········).

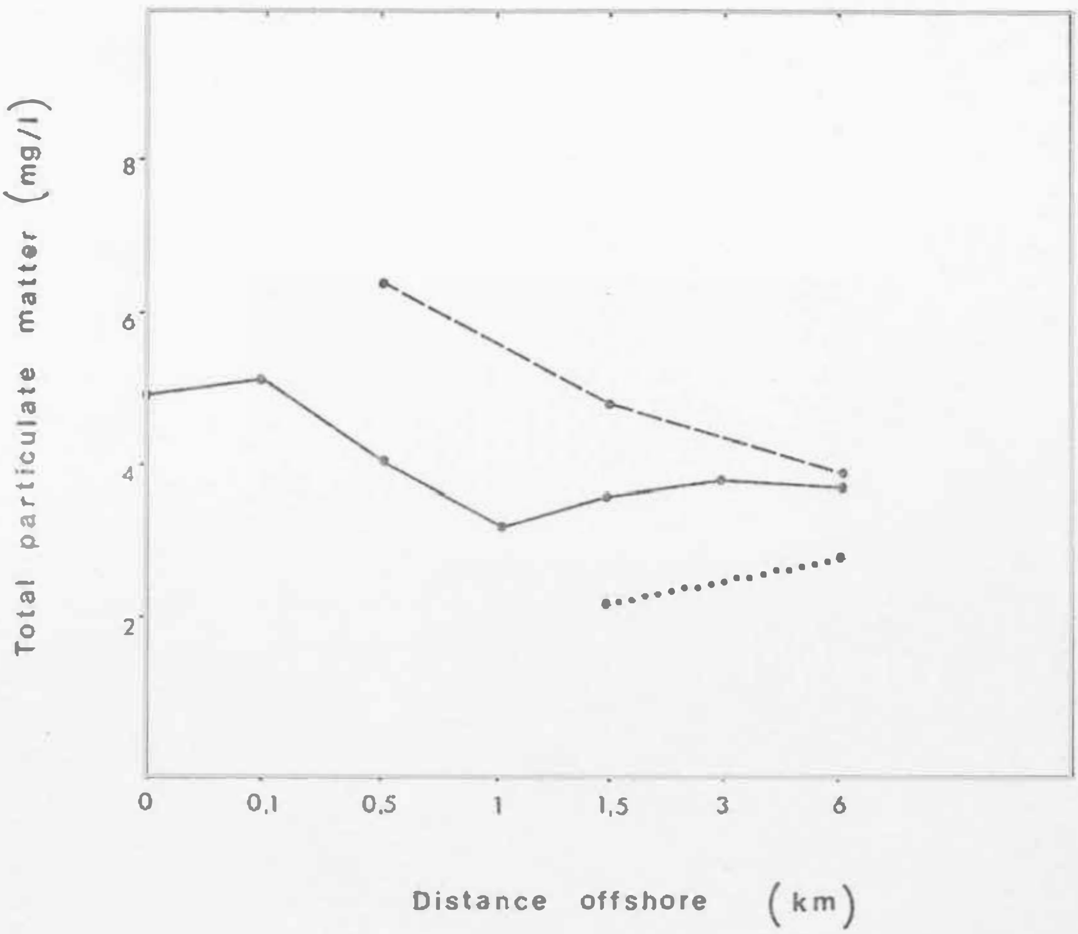

Figure 40. April False Bay transect : Dry mass (mg/l) of total particulate matter at 2 metres (————), 6 metres (— — — —) and 15 metres (••••••••••).

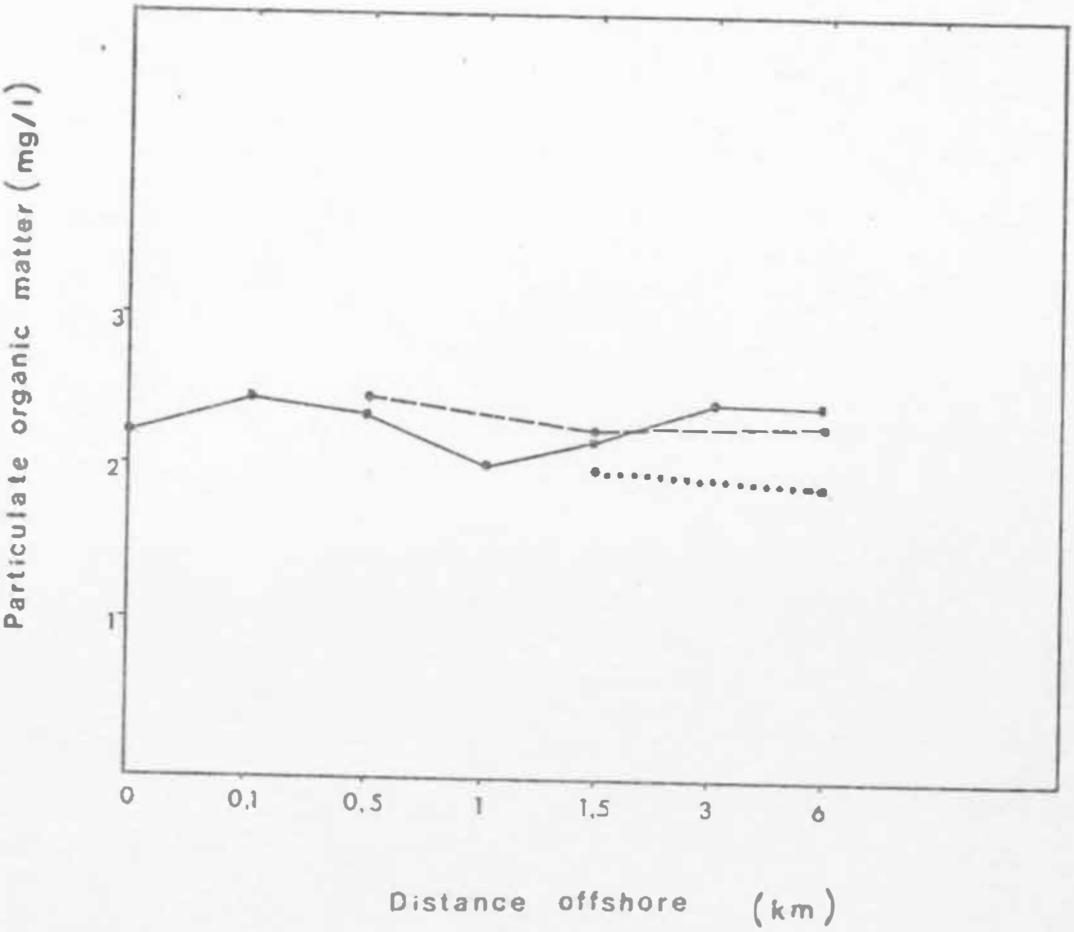

Figure 41. April False Bay transect : Dry mass (mg/l) of particulate organic matter at 2 metres (———), 6 metres (– – – –) and 15 metres (••••••••••).

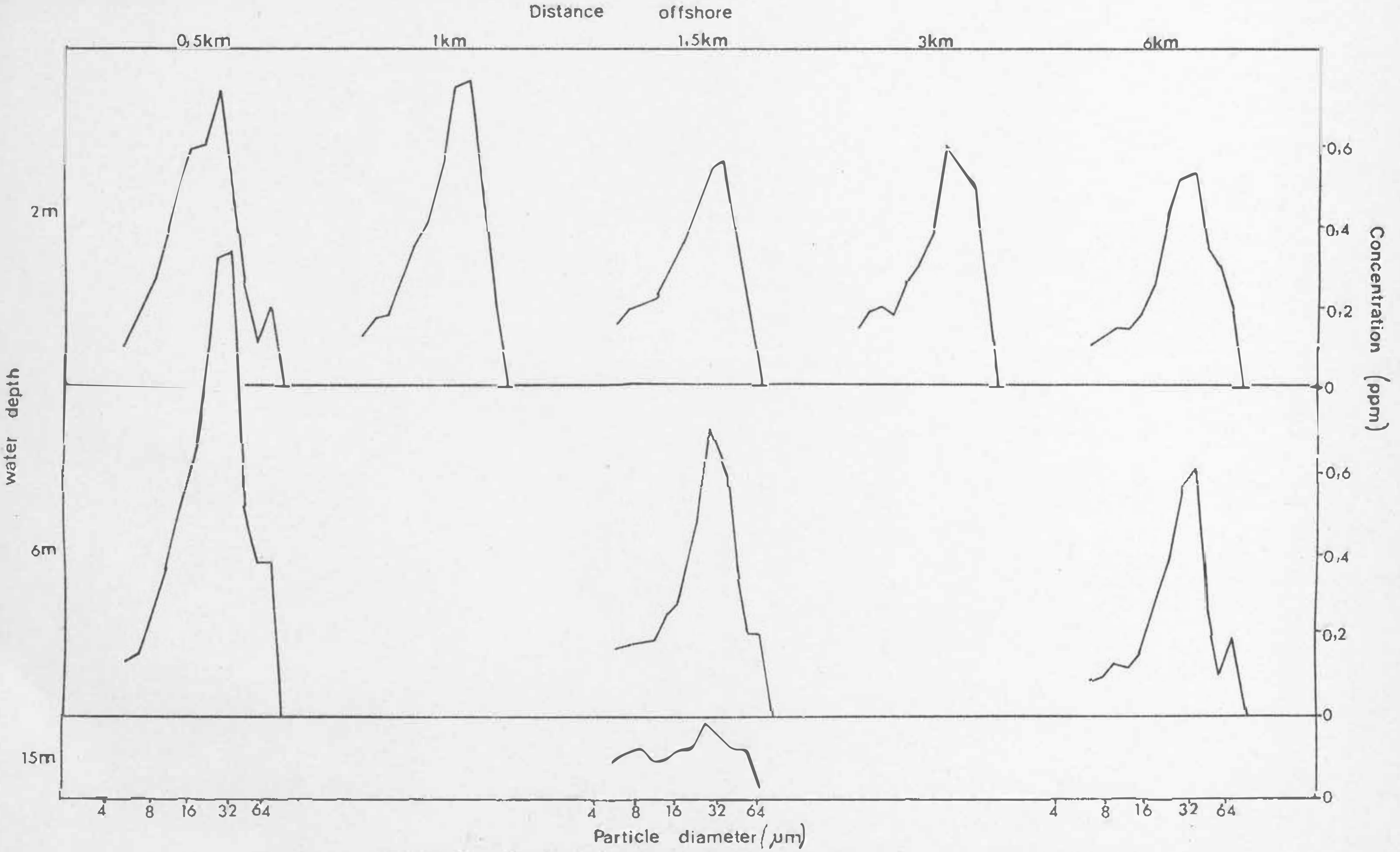

Figure 42. April False Bay transect : Particle size spectra of samples collected at different depths and distances offshore.

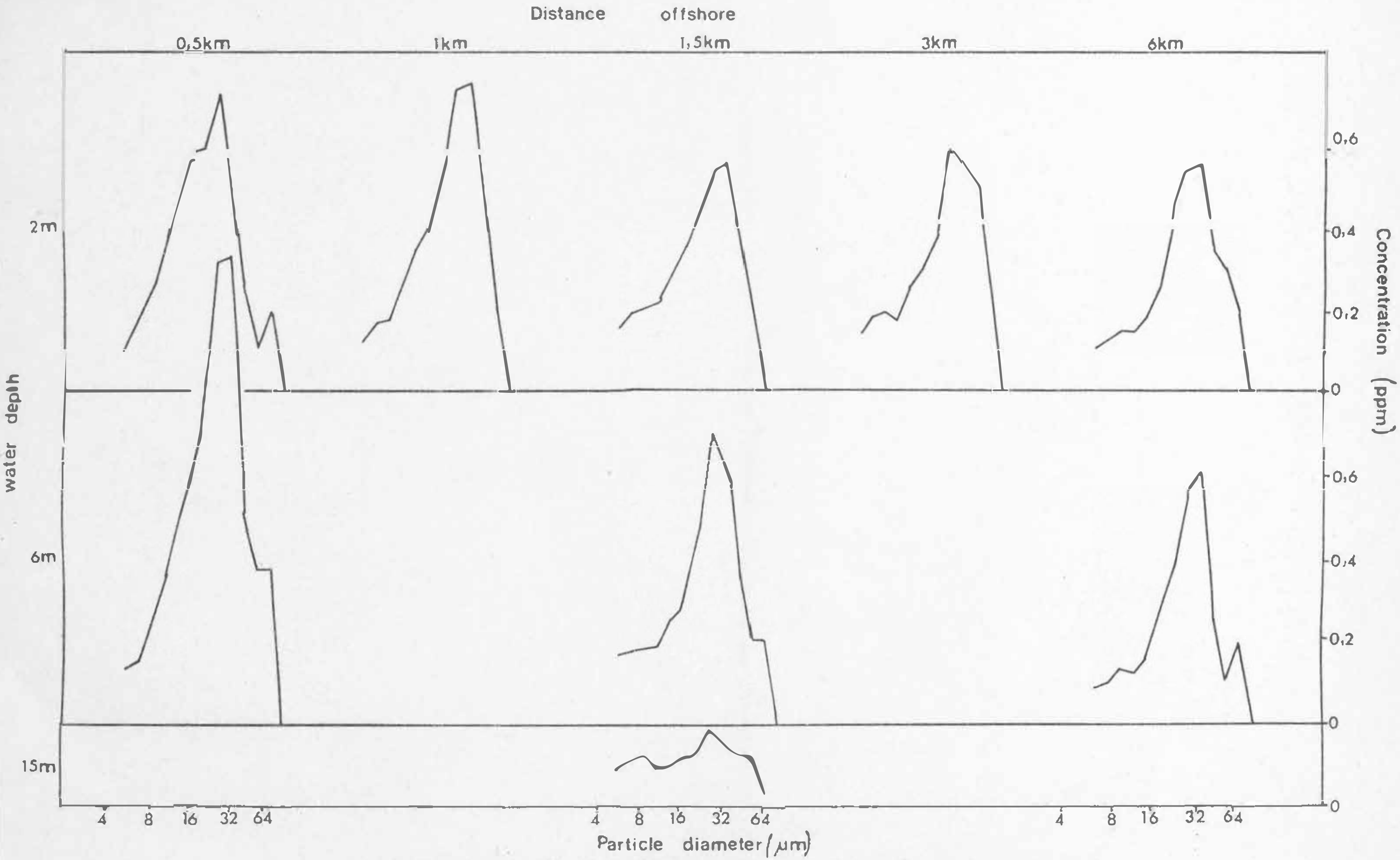

Figure 42. April False Bay transect : Particle size spectra of samples collected at different depths and distances offshore.

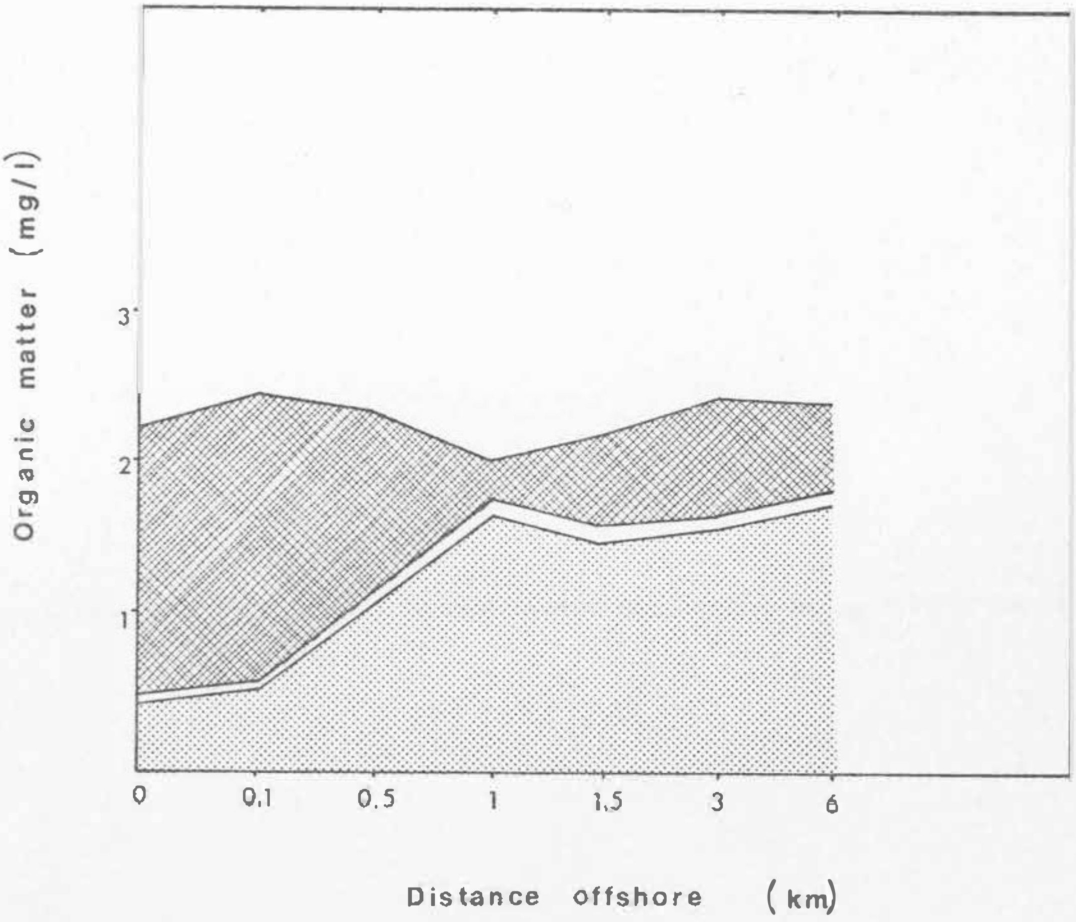

Figure 43. April False Bay transect : Spatial variation in the composition of particulate organic matter (mg/l) at 2 metres.

□ bacterial organic matter
░ phytoplankton organic matter
▩ detrital organic matter

The phytoplankton was dominated by chains of *Nitschia*. The offshore waters contained little, other than phytoplankton cells and aggregates smaller than 60 μm. In the water over the reef were minerogenic particles, some *Nitschia* cells, small detrital aggregates, faecal pellets, spicules of different sizes and a few pieces of macrophyte material.

Figure 43 shows the composition of the POM at the 2 m stations along the transect. As has already been pointed out, the total amount of POM remains constant with increasing distance offshore. The contribution by bacteria was very small, and although there was considerable variation in their numbers, this had little effect on the amount of POM in suspension. The phytoplankton contributed 20% of the POM over the reef but this increased to more than 50% at some of the offshore stations. There was a marked, seaward decline in the amount of detritus, suggesting that the detritus-dominated environment is restricted to the waters in the immediate vicinity of the reef. It also suggests that much of the detritus in suspension over the reef is autochthonous or is produced in adjacent inshore waters.

4.3.2 : September Transect

The results of the second transect, which was completed in September, are shown in Figures 44 to 50. The wind during the preceding five days was from the western quarter and did not exceed 10 knots. Water temperature (Fig. 44) remained between 15 and 16°C over the entire transect. There was a slight decrease with depth and distance offshore.

Figure 45 shows the concentrations of the four inorganic nutrients - ammonia, nitrates, phosphates and silicates. With the exception of silicates, levels were low, nitrates in particular, with little change along the transect line. Ammonia concentrations were between 2 and 3 µg at/l; the high levels 1,5 km offshore were probably the result of excretion by a large bed of mussels directly below. Nitrates only exceeded 1 µg at/l at the 18 km station. Phosphates remained at about 1 µg at/l in all samples. Silicate levels all exceeded 5 µg at/l, with a single value of 10 µg at/l; these values were noticeably higher than those encountered in April (Fig. 37) and it is not surprising that there was no correlation between nitrate and silicate concentrations ($r = 0,20$). Unlike the April transect there was no increase in the concentration of these two nutrients with depth.

Chlorophyll concentrations did not exceed 2 µg/l. Figure 46 shows that levels increased marginally with depth. Bacterial densities were also low (Fig. 47) in comparison with the April results (Fig. 39), rising to a maximum of 10×10^5 cells/ml at the 6 km station. Less than 10% of the cells were attached to particles in suspension. There was a marked change in bacterial morphology along the transect. 1,5 km and further offshore the population was dominated by small cocci, smaller than 0,1 μm^3, while inshore a majority of the cells were rods whose volume varied between 0,2 - 0,4 μm^3. The numbers of cocci increased from 1,4 x 10^5 cells/ml over the reef to 6,4 x 10^5 cells/ml 6 km offshore. Consequently, although bacterial numbers were relatively constant along the transect, biomass was higher nearer the reef.

Figure 48 shows that the amount of TPM in suspension was highest over the reef. At the 1,5 km station the sample from 15 m was taken 2 m above a large bed of mussels and a large amount of particulate matter was visible in suspension. The POM (Fig. 49) showed no seaward decline. As in April (Fig. 40 and 41) this meant there was a decrease offshore in the inorganic fraction; over the reef the POM represented 35% of the seston, rising to almost 100% 6 km offshore. Beyond the reef the > 100 µm fraction was entirely organic. Instrument malfunction prevented the processing of any of the samples through the Coulter Counter.

Figure 50 illustrates the breakdown in composition of the POM. There was a seaward decline in the amount of detritus but, unlike the April transect (Fig. 43), detritus was the dominant component throughout. The phytoplankton was comparatively unimportant and exceeded 15% of the POM only at the 6 km station.

Microscopic examination revealed differences between the seston over the reef and that from further offshore. The reef samples contained the typical, inorganic grains, 60 µm and smaller, and spicules of various sizes. The detritus was dominated by small, loosely-packed aggregates of unidentifiable origin, followed by larger faecal pellets, almost all 80 μm wide. There was very little identifiable macrophyte material, no microzooplankton and only a few *Chaetoceros* and *Coscinodiscus*-like diatoms. The offshore samples contained little minerogenic material and no spicules. The only detritus was in the form of small, flocculent aggregates. A few Foraminiferan tests and the dinoflagellates, *Ceratium* and *Peridium*, were present. The bulk of the seston from the 15 m sample, 1,5 km offshore, comprised large faecal pellets, presumably originating from the mussel beds below.

The transects have highlighted two contrasting situations. In September the only striking difference between the water over the reef and that from further offshore was the seaward decrease in the amount of inorganic matter in suspension. Nutrient and chlorophyll concentrations were extremely low along the entire transect. Bacterial numbers and levels of POM also showed little variation along the transect. In April there were higher nitrate and silicate concentrations in the offshore waters together with an increase in phytoplankton and bacterial biomass. Over the reef there was more inorganic matter and detritus in suspension than offshore.

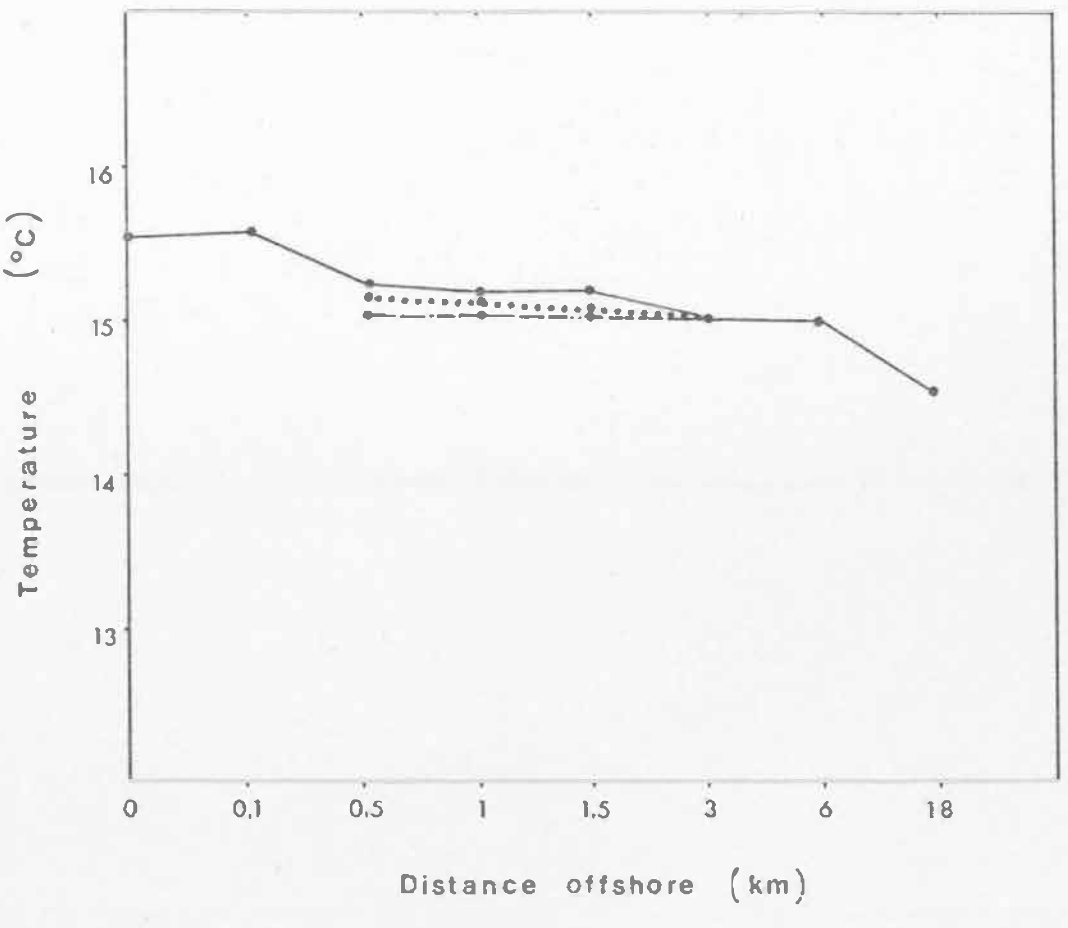

Figure 44. September False Bay transect : Water temperature at 2 metres (————), 6 metres (– – – –) and 15 metres (••••••••••••).

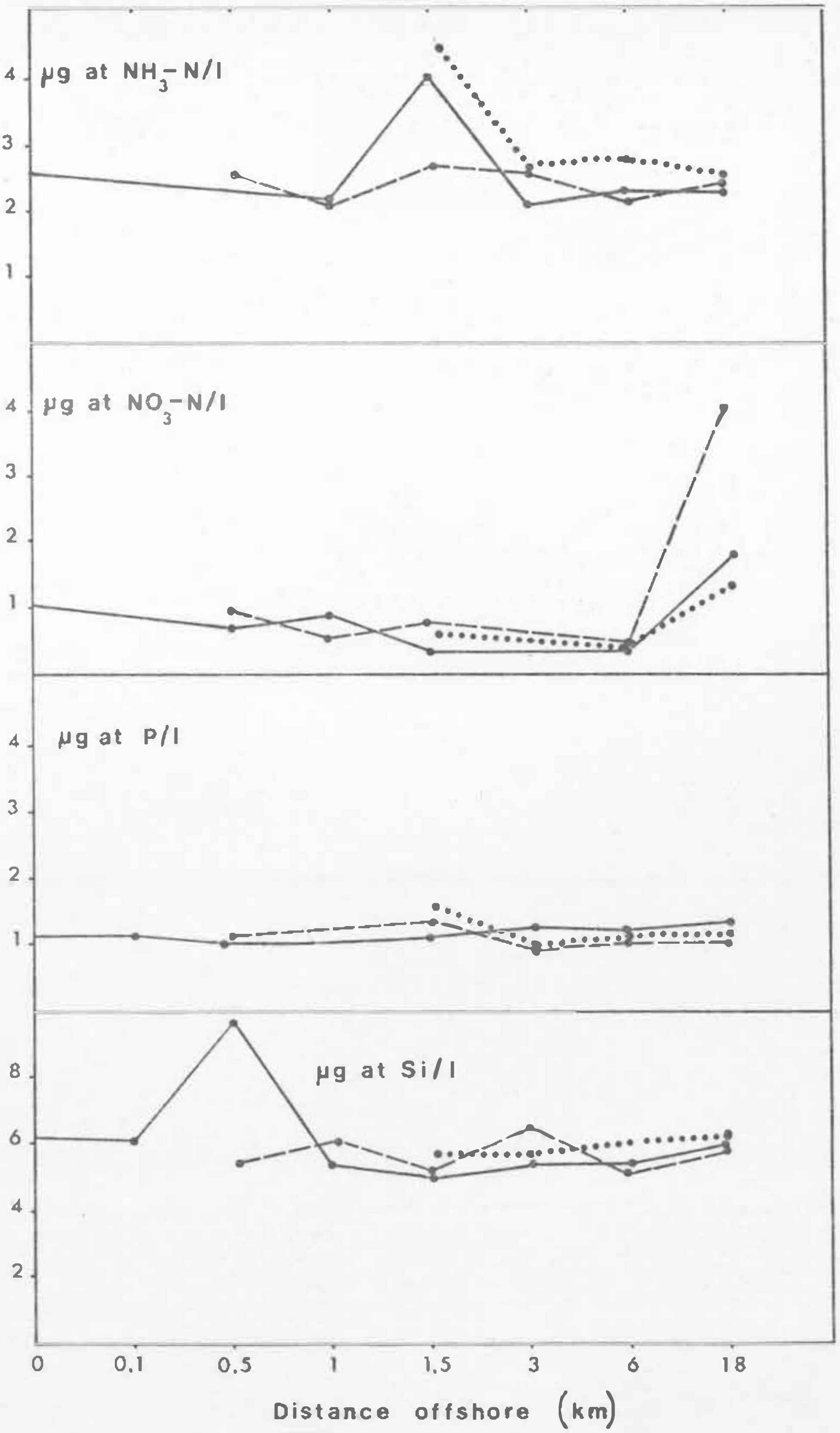

Figure 45. September False Bay transect : Concentrations of ammonia, nitrates, phosphates and silicates at 2 metres (————), 6 metres (– – – –) and 15 metres (••••••••••).

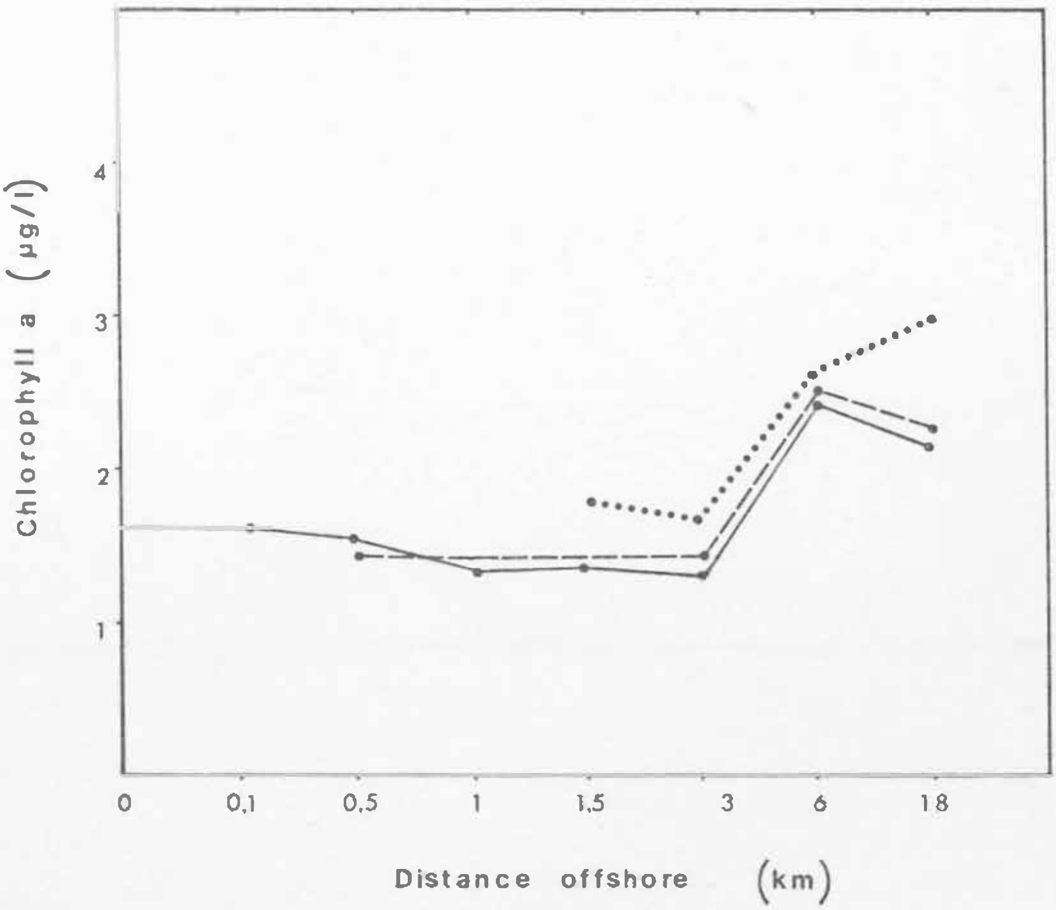

Figure 46. September False Bay transect : Concentrations of chlorophyll a (µg/l) at 2 metres (————), 6 metres (— — —) and 15 metres (•••••••••••).

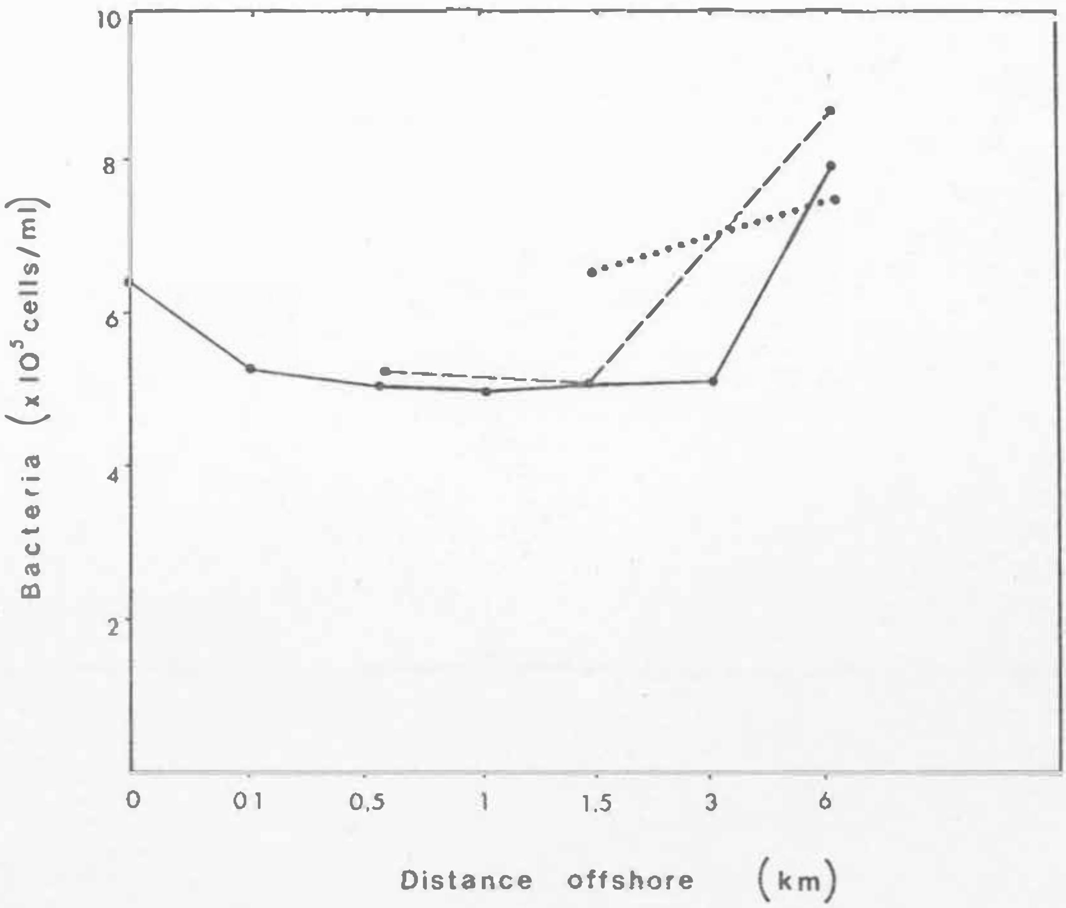

Figure 47. September False Bay transect : Numbers of free bacteria (x 10^5/ml) at 2 metres (———), 6 metres (– – – –) and 15 metres (..........).

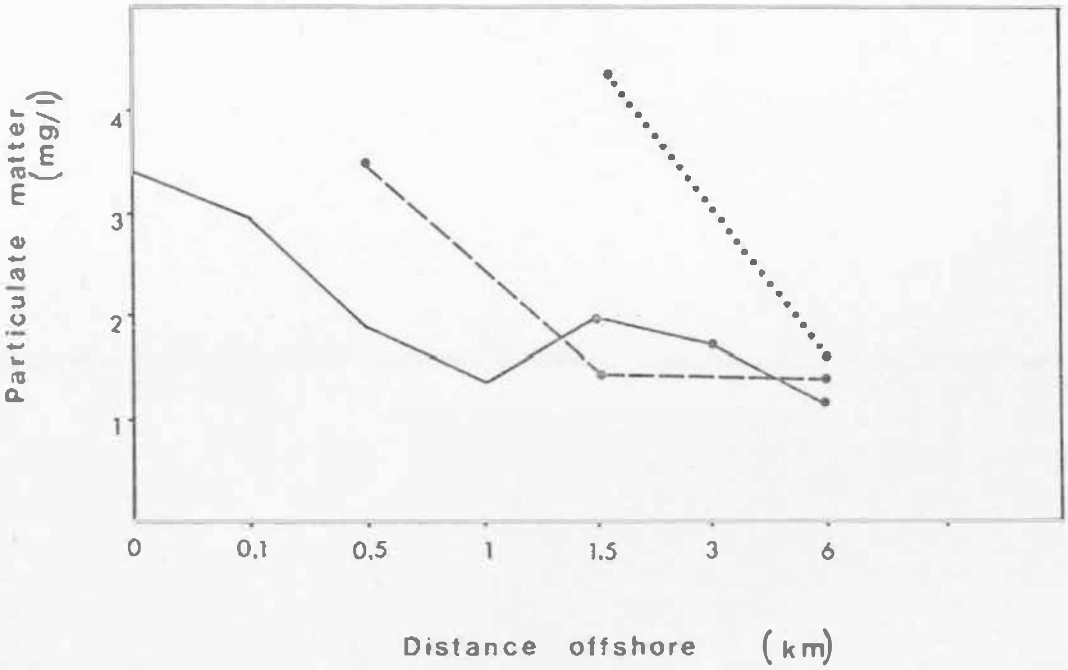

Figure 48. September False Bay transect : Dry mass (mg/l) of total particulate matter at 2 metres (————), 6 metres (— — — —) and 15 metres (•••••••••••).

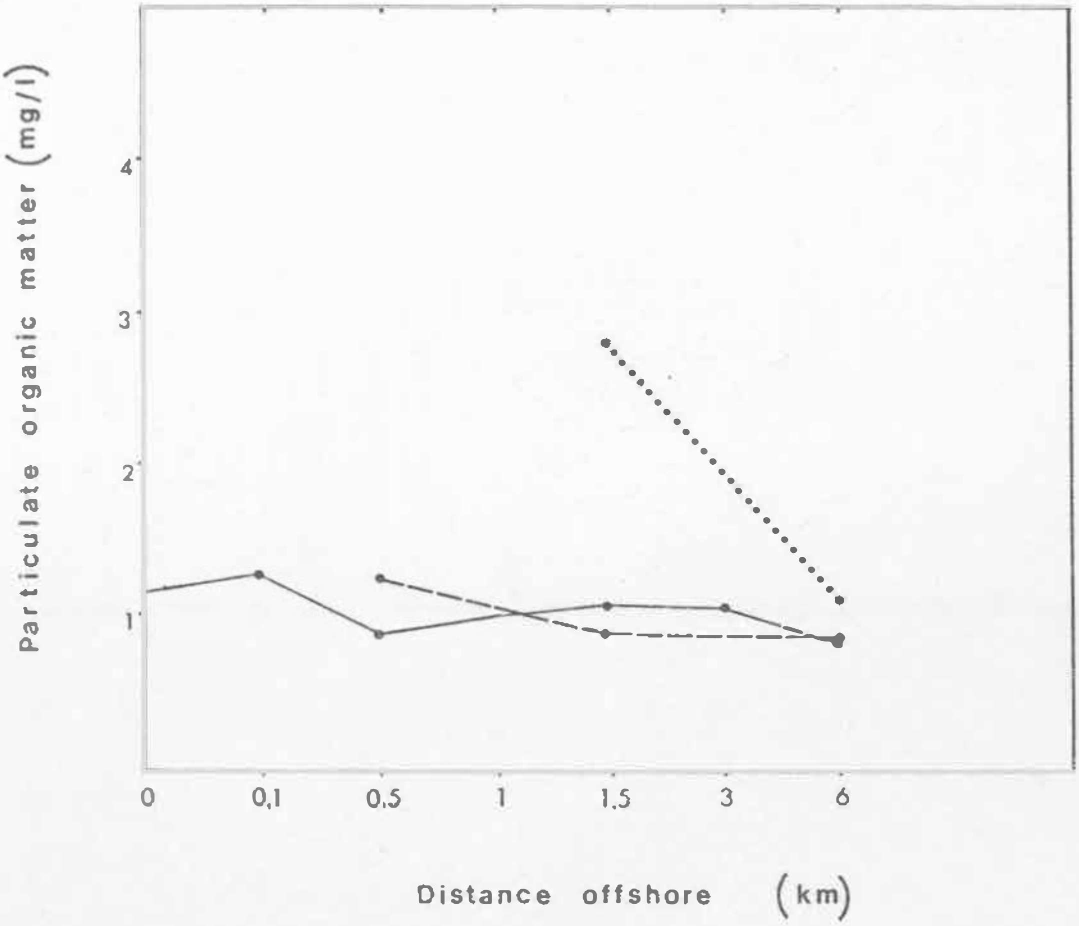

Figure 49. September False Bay transect : Dry mass (mg/l) of total particulate organic matter at 2 metres (———), 6 metres (– – – –) and 15 metres (••••••••••).

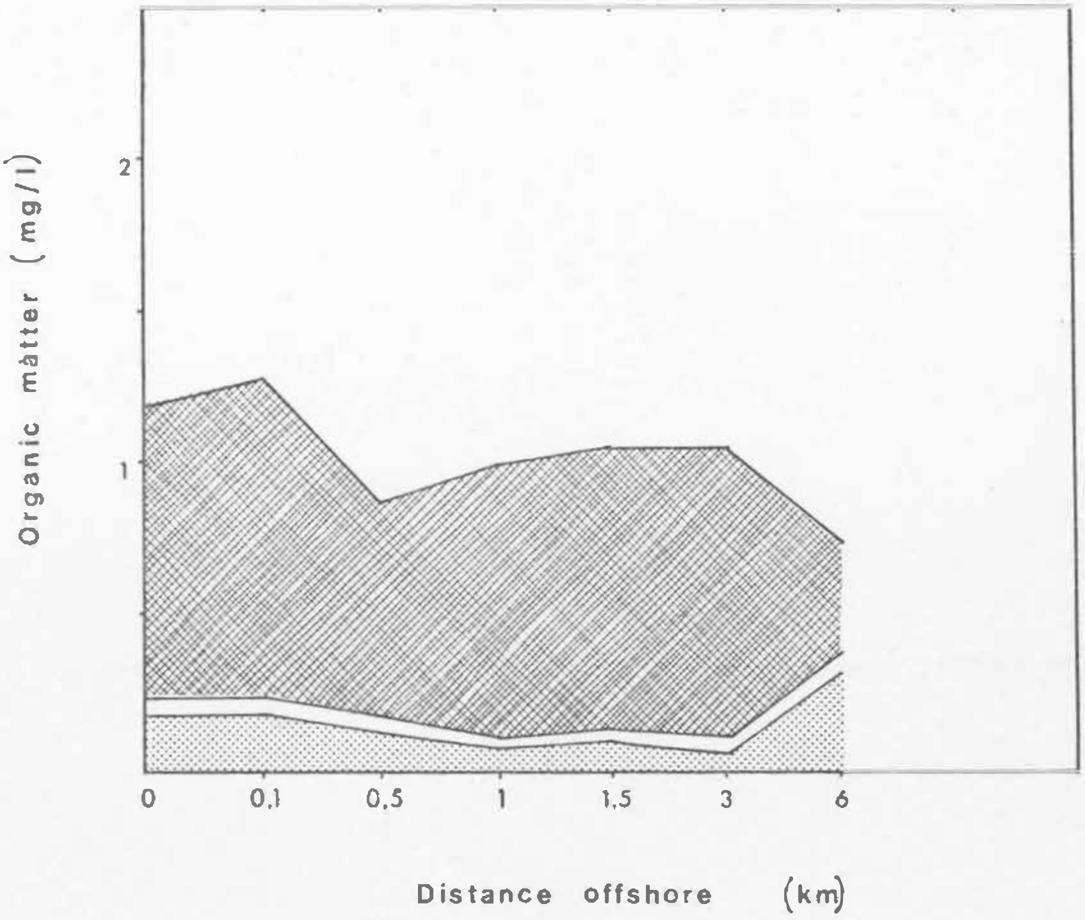

Figure 50. September False Bay transect : Spatial variation in the composition of particulate organic matter at 2 metres.

☐ bacterial organic matter
░ phytoplankton organic matter
▩ detrital organic matter

CHAPTER 5

DISCUSSION

5.1 : INTRODUCTION

In False Bay it is possible to recognise two ecosystems. The inshore ecosystem, as at Dalebrook, is characterised by large seaweed communities (McQuaid, in prep.). In the deeper waters towards the mouth of the bay one encounters the offshore system. Here the influence of the macrophytes is reduced and the phytoplankton assumes greater importance, particularly in the south-eastern sector where the upwelling of nutrient-rich waters stimulates phytoplankton production (Tromp and Horstman, in press).

The complex hydrographic conditions that exist in the bay (Atkins, 1970a) make it impossible to define boundaries between these two systems. Furthermore, it is difficult to determine the origin of dissolved materials and particulate organic matter in suspension over the reef. An understanding of the hydrography of the bay is therefore necessary to account for temporal and spatial differences in dissolved inorganic nutrients, phytoplankton and bacterial standing stocks and detrital loads in the water in the vicinity of Dalebrook.

5.2 : HYDROGRAPHY OF FALSE BAY

Atkins (1970a) describes the configuration of False Bay as neither that of a shallow bay, such as an estuary, nor a wide one where deep sea conditions predominate. The result is that the temperature and current patterns are somewhat complex.

The water off the bay is a mixture of that from the warm Agulhas current and the colder South Atlantic Ocean. In spring and summer, under the influence of southerly winds, warm surface waters from the Agulhas bank enter the bay. The surface currents are slow, about 0,2 knots, and generally follow a clockwise pattern (Fig. 51) round the bay (Atkins, 1970b). The water enters along the west coast and is driven northwards to Glencairn and then eastwards along the northern shores past Dalebrook. Due to solar heating in the shallow waters along this section of coast, the temperatures may exceed 20°C (Fig. 22). The water moves down the east coast and out of the bay past Cape Hangklip. The nutrient concentrations in this surface water are low (Tromp and Horstman, in press) which is confirmed by the results from the September transect (Fig. 45), and any primary production is governed by the rate of nutrient regeneration at the surface. At Dalebrook in spring, summer and early autumn (October to April) concentrations of nitrates (Fig. 3, 23) and silicates (Fig. 5) in solution were low.

5.2.1 : Upwelling and nutrient replenishment

Tromp and Horstman (in press) found that during spring and summer there

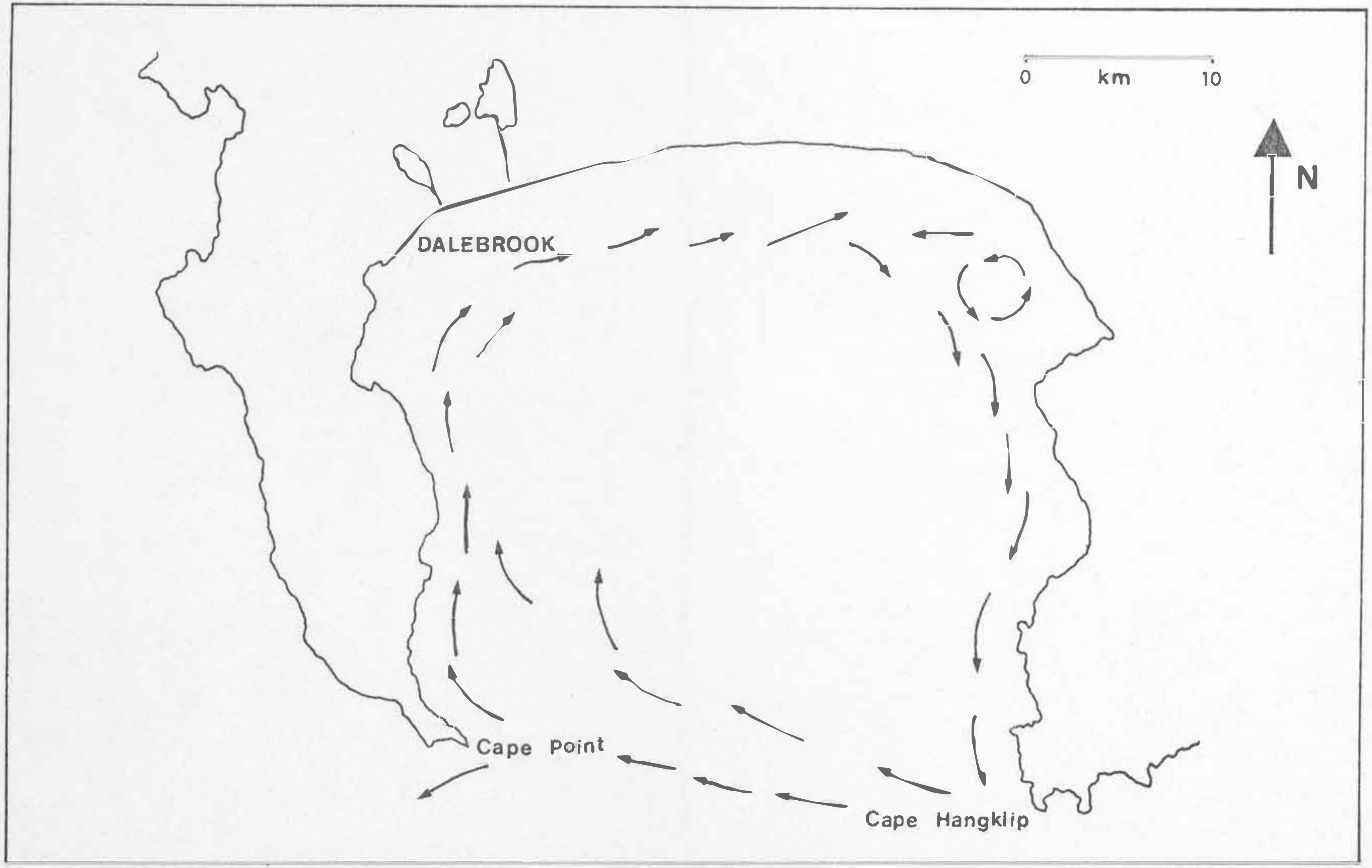

Figure 51. Current patterns in False Bay (after Atkins, 1970b).

is substantial replenishment of nutrients in the mouth of False Bay. Below the nutrient-depleted surface waters they encountered a colder body of water, rich in inorganic nutrients. These two water masses were separated by a distinct thermocline. The action of strong south-easterly winds in the Cape Hangklip area, where the coastline runs diagonally across the path of the wind, is sufficient to break up this stratification and causes the upwelling of the rich sub-surface waters. Nitrate and silicate concentrations exceeding 20 μg at/l were recorded at the surface and these stimulated considerable phytoplankton production.

The topography of the bay is such that it is deepest at its southern entrance (approximately 90 metres) and shelves gradually towards the northern shores. Three kilometres off the Dalebrook coast the water is less than 20 metres deep. This would appear to preclude the penetration of nutrient-rich, sub-surface waters close inshore off Dalebrook. Furthermore, the angle of the coastline relative to the prevailing winds is also not conducive to any wind-induced upwelling near the reef. Any nutrient enrichment in the area is therefore dependent on the influx of surface waters originating from upwelling sites such as at Cape Hangklip. Cram (1970) has found that the south-easterly wind causes a drift of upwelled water into the centre of the bay. Dalebrook is approximately 30 kilometres from Hangklip; this distance, coupled with the slowness of the surface currents and the general pattern of water movement in the bay, suggests that if this upwelled water mass is able to penetrate so close inshore, the nutrient content will have been greatly reduced by phytoplankton uptake and dilution by mixing with adjacent waters.

In summer there is evidence that nutrient-rich water may be driven inshore over the reef at Dalebrook. In December a body of water, rich in nitrates (9 µg at N/l; Fig. 3) and silicates (18 µg at Si/l; Fig. 5) was encountered at the offshore station. There was a marked temperature difference between stations, with a colder body of water present at the offshore station. The results of the April False Bay transect confirmed the observations of Cram (1970), who traced the movement of upwelled water into the centre of False Bay, and indicate that Dalebrook is not totally isolated from the effects of upwelling. The nitrate concentrations were relatively low (< 4 µg at/l; Fig. 37) along the transect and similarly the chlorophyll levels over the reef (3 µg/l; Fig. 38). However, in the waters beyond the reef, chlorophyll concentrations were in the region of 10 µg/l (Fig. 38) and a value of 19 µg/l was recorded in a *Nitschia* bloom only 0,5 km offshore. In this particular situation the phytoplankton standing stocks have escalated at the expense of the nutrients.

With the onset of winter there is a change in weather patterns and winds blow mainly from the north-west - offshore at Dalebrook. This has a number of important effects. There are heavy rainfalls over the Cape Peninsula resulting in an increase in the outflow of fresh water from Sandvlei and Zeekoevlei (Fig. 1) into the bay. Variations in the cyclic pattern of surface waters moving in a clockwise direction round the bay are evident (Atkins, 1970b). The influence of the warmer Agulhas bank water in False Bay and adjacent coastal areas is reduced (Shannon, 1966). Using drift cards, Duncan and Nell (1969) found that there is a southerly trend in the surface currents off the Cape south coast in winter, with cold water rounding Cape Point from the west. These factors, together with a decrease in the effects of solar warming, explain the occurrence of lower water temperatures at Dalebrook in winter (13°C; Fig. 29).

5.3 : INORGANIC NUTRIENTS

Inshore there is obviously competition between the macrophytes and the phytoplankton for nutrient resources. The former are at a considerable advantage, as their longer life-span enables them to survive periods of nutrient shortage and possibly to build up stores of nutrients when the concentrations in solution are in excess of their immediate requirements. Phytoplankton cells, although displaying high surface area to volume ratios, have extremely short life-spans and are very dependent on the prevailing nutrient concentrations in the water.

5.3.1 : Ammonia

There was no obvious seasonal pattern in the concentrations of ammonia in solution over the reef. Levels, ranging from 2 to 4 µg at NH_3 - N/l (Table 2), fell into the range 0 - 5 µg at/l quoted by Williams (1975) for the world ocean. Hutchings (unpublished data) has recorded values from 1 to 4 µg at/l in the nutrient-rich inshore waters off the Cape west coast, rising to well over 10 µg at/l near dense aggregations of zooplankton or benthic animals. Ammonia is released principally through excretion and it is somewhat surprising that the values over the Dalebrook reef, where there is considerable animal activity, were not higher. In this regard it is interesting to note the elevated concentrations (Fig. 45) over the large bed of *Choromytilus meridionalis*, 1,5 km offshore on the September False Bay transect. The slightly higher levels on outgoing tides (Table 2) were possibly the result of excretion by animals on the reef, and this suggestion is supported by the results from the April transect (Fig. 37) where there was a drop in the ammonia concentration as one moved off the end of the reef into open water.

Ammonia has received little attention in comparison to the alternative sources of inorganic nitrogen and other nutrients regarding its role in phytoplankton production. Parsons et al. (1977) cite Eppley et al. (1969) who found that certain phytoplankton species take up ammonia preferentially as a source of nitrogen, presumably because it may be used directly for amino acid synthesis through transamination, while nitrates and nitrites must first be reduced. It is possible that a similar situation exists for the macrophytes, which may involve the uptake of much of the excreted ammonia.

5.3.2 : Nitrates

Although the phytoplankton requires a number of essential inorganic nutrients, the supplies of nitrates are invariably utilised in a greater proportion relative to phosphates and silicates (Parsons, et al., 1977). Throughout the summer and autumn, nitrate concentrations on the reef were generally less than 1 µg at N/l (Fig. 3, 23); such levels are considered to limit phytoplankton production (Strickland, 1960). As mentioned in section 5.2.1, there was evidence of some nitrate replenishment from richer, offshore waters.

There are no immediately apparent reasons as to why concentrations of nitrates over the reef were higher in winter (Fig. 3, 30). Tromp and Horstman (in press) have been unable to detect any upwelling in winter.

It is possible that the increased flow of fresh water into False Bay via Sandvlei, together with effluent from the sewerage works on Zeekoevlei, might have some influence. Grindley (pers. comm.) has encountered diatom blooms in the discoloured waters emerging from these two vleis which suggests that they are rich in nutrients. In May, August and September I observed plumes of this dirty water hugging the coast and travelling from Sandvlei in the opposite direction to the general water flow in the bay, past Dalebrook towards Kalk Bay. The May monthly sampling coincided with the appearance of such a plume at Dalebrook and this might account for the high concentrations of all four nutrients recorded on the reef.

5.3.3 : Phosphates

Summer levels of orthophosphates (Fig. 23) were little different from those recorded in winter (Fig. 30), rarely dropping to a level which might be considered limiting. Concentrations were slightly higher in outgoing water, suggesting that there is some regeneration of this nutrient on the reef.

It is interesting to compare nitrate and phosphate concentrations with values from a kelp bed on the west coast of the Cape Peninsula, which is strongly influenced by the upwelling of nutrient-rich, Benguela current water close inshore (Andrews et al., in press; Field et al., in press). The latter workers recorded nitrate values ranging from less than 1 µg at/l up to 18 µg at/l after a period of upwelling. Nitrate concentrations higher than 10 µg at/l (Fig. 3) were extremely rare over the Dalebrook reef; however, mean phosphate concentrations at Dalebrook, 1,5 μg at/l (Table 2), were little different from those recorded in the kelp bed.

5.3.4 : Silicates

Marked seasonal trends were evident in the concentrations of silicates in solution (Fig. 5), and like nitrates, these were highest in winter. In summer, silicates, although not as depleted as nitrates, were generally low, considering that the phytoplankton was dominated by diatoms which have a high requirement for silica. Tromp and Horstman (in press) commonly recorded values exceeding 20 μg at/l off the mouth of False Bay in summer. In December there was strong evidence of silicate replenishment from richer offshore waters, with values of 20 μg at Si/l recorded at the offshore reef station. Mean annual concentrations over the reef were 5 - 8 μg at Si/l (Table 2), which were close to the lowest levels recorded by Field et al. (in press) in a Cape west coast kelp bed. Hutchings (unpublished data) has found that on the west coast levels tend to rise as high as 20 μg at/l after strong westerly winds as sediment is lifted up and mixed through the water column. In the shallow waters round the Dalebrook reef, where the sediment is easily stirred up, one would expect silicates to be continually entering solution and to regularly approach values of 20 μg at/l.

Fielding (unpublished data) has compared the summer and winter production rates of the four most important seaweed species at Dalebrook. In view of the seasonal variation in the availability of nitrates and silicates over the reef it is interesting to note that he found production rates were higher in summer in all four species.

To summarise, phosphates rarely fell to levels which might be considered limiting to phytoplankton production and are possibly regenerated on the reef. There is good evidence that much of the ammonia in solution is autochthonous, rather than imported from offshore. The higher nitrate and silicate concentrations in incoming water and at the offshore station suggest that these nutrients are being imported from richer, offshore waters. Over the reef they are possibly taken up by the macrophytes to be exported from the reef ecosystem in the detrital fraction. Mineralisation and regeneration will then occur elsewhere.

The influence of sewerage and fresh waters might account for the higher nitrate and silicate concentrations in winter and the appearance of a body of water rich in all four nutrients over the reef in May.

5.4 : PHYTOPLANKTON BIOMASS AND PRODUCTION

From October through to April, the nitrate concentrations (Fig. 3, 23) over the reef were generally low. It is not surprising, therefore, that the phytoplankton stocks were also low during this period (Fig. 6, 24). The influences of upwelling on chlorophyll concentrations at Dalebrook have already been discussed (Section 5.2.1). Chlorophyll levels were highest at the offshore station and on incoming tides (Fig. 7). Primary production experiments (Table 4) revealed that very little phytoplankton production took place in the vicinity of the reef in summer. This means that in summer most of the phytoplankton present over the reef was produced offshore. Griffiths (unpublished data) has monitored levels of particulate matter in suspension over the large beds of *Choromytilus meridionalis* at Bailey's Cottage, 2 kilometres north-east of Dalebrook. She found that the numbers of phytoplankton cells increased after a strong onshore wind. All this is strong evidence that in spring and summer the onshore wind-driven currents may advect phytoplankton from offshore into the intertidal waters on the north-west coast of False Bay. Here they will make a large, albeit infrequent, contribution to the food requirements of the filter feeders on the shore.

In winter the water over the reef was richer in nitrates (Fig. 3, 30) and silicates (Fig. 5, 30) which accounts for the higher chlorophyll levels (Fig. 31). Griffiths (unpublished data) also recorded large numbers of phytoplankton cells at Bailey's Cottage in May, July and August. Bailey's Cottage lies between Sandvlei and Dalebrook and is therefore also influenced by the plumes of discoloured water moving along the coast from the mouths of Sandvlei and Zeekoevlei. In view of the higher nutrient concentrations at Dalebrook in winter, it is possible that some autochthonous phytoplankton production may take place, but this unlikely to approach that by the large seaweed community on the reef.

Although phytoplankton biomass may be dependent on the concentrations of nutrients in solution a number of days before, the series of cross correlations calculated for each daily sampling programme failed to reveal any lagged relationships. This is not surprising on an exposed shoreline, such as Dalebrook, where one water mass is unlikely to remain over the reef for a sufficiently long period of time for such relationships to be apparent.

5.5 : PARTICULATE MATTER

There were significant monthly differences in the dry mass of TPM and POM in suspension over the reef (Table 8); levels appeared to be slightly higher in winter than summer. This trend was more marked in the daily sampling programme, where the mean summer values of TPM and POM were 2,1 mg/l and 1,4 mg/l (Fig. 26) respectively and equivalent winter values of 3,5 mg/l and 1,6 mg/l (Fig. 33). This is strange in that the water over the reef is generally calmer in winter when the wind blows offshore (Fig. 29). McQuaid (in prep.) has found that the biomass of *Gigartina hystrix* and *Gelidium pristoides*, the two most important seaweeds at Dalebrook, is highest in summer. They enter a senescent phase in late autumn, with the biomass falling to its lowest levels in winter. This means that considerable amounts of macrophyte material are released as particulate organic detritus during the winter, which might account for these seasonal differences. The influence of water with high seston loads from Sandvlei and Zeekoevlei must also not be discounted.

Although the dry mass of POM rarely dropped below 1 mg/l, this value was low in relation to other South African inshore environments. Field et al. (in press) recorded a mean dry mass of POM of over 2 mg/l in a kelp bed; they also found that peaks in the mass of TPM coincided with the largest swells. Schleyer (1979) working in the extremely turbulent, Natal waters, recorded mean annual particulate organic carbon values of 3,5 mg/l which is probably equivalent to well over 5 mg POM/l. Bailey's Cottage is more exposed than Dalebrook and Griffiths (unpublished data) recorded a mean dry mass of POM of 5 - 6 mg/l, ranging as high as 10 mg/l. She encountered large amounts of sand in suspension, in the region of 12 mg/l.

At Dalebrook approximately 75% of the POM was smaller than 100 µm with little change along the transect line. At Bailey's Cottage this value was only 60% (Griffiths, unpublished data), again probably the result of greater turbulence retaining larger particles in suspension. By comparison Mullin (1965) working in the oceanic waters of the Indian Ocean found that 75% of the particulate organic carbon in surface waters was smaller than 33 µm.

The analysis of variance (Table 8) indicated that there were no spatial or tidal differences in the amount of particulate matter at each of the three stations on the reef. This does not mean that there was no movement of material into and out of the system. Unlike an estuary where the tidal influence merely causes the water to flow in and out of the system and where this water movement can be quantified, exposed coastal areas such as Dalebrook are subject to considerable lateral movements of water. This is clearly evident when observing plumes of dirty water, no more than 150 metres wide, moving along the coast past Dalebrook from Sandvlei. Such movements will result in the transport of particulate matter parallel to the coast with large, undetected gains or losses for the Dalebrook reef ecosystem.

5.6 : DETRITUS

The role of detritus in aquatic ecosystems has received considerable attention in the last decade. Judging from the literature, there appear to be few aquatic environments in which the amount of living particulate matter in suspension exceeds that of detritus. The only possible exceptions are regions of coastal upwelling, such as the Benguela system off the Cape west coast, where phytoplankton stocks may reach 50 µg chlorophyll a/l which is equivalent to 7 mg organic matter/l (Andrews et al., in press). During these blooms, conditions capable of supporting the high rates of primary production are invariably short-lived and mortality rates escalate as nutrient concentrations fall.

In this study the amount of detritus has been estimated as the difference between total POM and the sum of phytoplankton and bacterial organic matter. This procedure has a number of shortcomings, for the biomass of microzooplankton has not been considered and the results are dependent on the carbon : chlorophyll ratio of the phytoplankton. This value is a function of temperature, nutrient concentration, illumination and species composition and may fluctuate between 15 and 130 (Strickland, 1960). In this study a value of 60 has been selected on the grounds that at Dalebrook the nutrient concentrations were low and the light intensities high. However, the contribution by phytoplankton to the POM was generally so low (see Fig. 21, 27, 34) that any change in the carbon : chlorophyll ratio was unlikely to have influenced the results substantially. Only in the April transect (Fig. 43) was this potential error possibly important. A further difficulty results from the presence of chlorophyll degradation products, which absorb light at wave lengths similar to chlorophyll (Strickland, 1960). Again, in view of the low chlorophyll concentrations over the reef, absorbance by these degradation products was believed to be negligible.

Methods currently used to separate planktonic and detrital organic matter are based on the measurement of biochemical components specific to all living organisms such as albumen (Lenz, 1977) or adenosine triphosphate - ATP (Holm-Hansen and Booth, 1966). ATP has an advantage over chlorophyll in that it is absent from dead cells and detritus. It also occurs in fairly uniform concentrations in micro-organisms, regardless of environmental stress (Holm-Hansen, 1972) making the determination of microbial biomass fairly accurate. Although the analytical procedure is relatively quick and suited to the processing of large numbers of samples, it was impractical in terms of the available apparatus.

These limitations should not be allowed to detract from the dominance of the seston by detritus (Fig. 21). Mann (1976), in reviewing the role of marine macrophytes in the food web, states that in systems approaching steady state, 90% or more of the production enters detrital, rather than grazing food chains. There is a well-established macrophyte community at Dalebrook. The water over the reef is very shallow and the prevailing wind is onshore. This combination of factors will ensure the erosion and abrasion of considerable amounts of macrophyte material. Considering that the phytoplankton stocks in the vicinity of the reef were low, much of the detritus in suspension was probably of macrophyte origin.

The amount of detritus in suspension over the reef never dropped below 0,5 mg/l. The analysis of variance (Table 8) has shown that tides and localities had no significant effect on the dry mass of POM in the water. Chlorophyll concentrations were slightly higher in the incoming water and at the offshore station, which, by difference, means that there was fractionally more detritus in the outgoing water and at the inshore station. In the April transect (Fig. 43) there was a high detrital load over the reef which fell in the waters beyond the reef and remained more or less constant along the transect. All this suggests that the reef is a source of some of the detritus in suspension.

5.7 : MICROSCOPIC EXAMINATION

Under the microscope most of the detritus appeared as old aggregates, with a low incidence of fresh, clearly-identificable macrophyte and phytoplankton detritus. This suggests that import from surrounding areas provides the bulk of non-living material over the reef. Diving at Dalebrook and on other exposed coastlines it is not uncommon to find large amounts of macrophyte material being swept over the reef as macroscopic debris. This debris tends to collect in recesses on the reef where there is a sufficient reduction in water movement. Fenchel (1970) has monitored the decomposition of organic detritus from the turtle grass, *Thalassia testudinum*. He found that the detritus is colonised by a large microbial community consisting mainly of bacteria, fungi, actinomycetes, small flagellates and to a lesser extent, ciliates. This attracts detritus feeders which consume the micro-organisms and at the same time decrease the particle size of the detritus. This means that by the time it enters suspension as particles of 200 μm and smaller, the detritus has undergone considerable modification. This process may take several days, during which time the material may be carried some distance from its source. It is, therefore, not surprising that only a small fraction of the detritus is identifiable as being macrophytic.

The fractionally greater detrital loads inshore and on the outgoing tide may be largely accounted for by the higher numbers of faecal pellets at the inshore and middle stations, and their absence from the offshore station on the incoming tide.

A problem that is common to all studies of particulate matter is that the actions of sampling and filtering tend to break up the delicate flocculent aggregates and chains of phytoplankton cells. This gives a false impression of the particle size distribution. Mucus strands with entrapped material, often several millimetres long, were observed in suspension under calm conditions. These strands were particularly common in the phytoplankton bloom in the April transect. The strands were extremely delicate, hence their reference in the literature as marine "snow", and it was not surprising that they were never seen in the turbulent water over the reef or under the microscope.

5.8 : PARTICLE SIZE DISTRIBUTION

The particle size spectra produced by the Coulter Counter showed an almost logarithmic decrease in the numbers of particles with increasing particle size, a feature noted by Sheldon and Parsons (1967), Zeitzschel (1970) and Field et al. (in press). However, particles ranging in diameter from 10 to 30 μm were present in high concentrations, and those particles which contributed the greatest volume were around 15 μm in diameter (Fig. 20).

A striking feature of all the curves (Fig. 14 - 19) was the decline in the concentration of particles approximately 60 μm and bigger. At first this was thought to be an artifact, the result of processing small volumes (< 5 ml) of sample through the instrument. However, increasing the sample volume to 15 - 20 ml did not alter the shape of the curves obtained. It would appear that this effect is real but it is difficult to explain, as the gravimetric analysis revealed that 25% of particulate matter was retained by a 100 μm mesh net. Zeitzschel (1970), working in the Gulf of California, also recorded a sharp decline in particle volume at diameters of approximately 65 μm.

Concentrations of particles 5 μm in diameter, the lower limit of measurement, were fairly high. It would be profitable to extend the range of particles measured down to sizes approaching bacterial cells. Coulter Counter tubes are available with both smaller and larger apertures, but accurate dilutions with particle-free seawater are necessary when using a 70 μm or 100 μm tube.

The particle size spectra revealed that when the POM comprised almost entirely detritus, there tended to be an even distribution of particles of diameters 6 to 40 µm. The height of the curve was dependent on the amount of detritus present, i.e. high in May (Fig. 16) and low in September (Fig. 19). A peak in the curve indicated an increase in the number of particles over a fairly narrow size range. This appeared to coincide with chlorophyll concentrations exceeding 2 µg/l; it was usually over the particle size range of 10 to 20 µm (Fig. 14, 18) and was probably due to the presence of an increase in the numbers of uniform sized phytoplankton cells in the sample. Very few phytoplankton cells were visible in the May samples (Fig. 16) and yet chlorophyll concentrations were extremely high (Fig. 6). The particle size spectra for these samples showed a peak at 6 µm. It is therefore highly likely that there were large numbers of naked, ultraplankton which burst when dried on the filters prior to microscopic examination.

Zeitzschel (1970) analysed the quantity, composition and distribution of suspended particulate matter in the Gulf of California. Using the Coulter Counter he found that particulate volume of particles 2 - 150 µm in diameter was significantly correlated with such parameters as seston dry mass, particulate carbon, phytoplankton carbon and chlorophyll a. Similar correlations between particle volume and chlorophyll a and the < 100 µm fractions of the TPM and POM were evident in this study in both the summer (4.2.1) winter (4.2.2) daily sampling and the April transect (4.3.1).

It would appear that the bulk of the POM lies within a size range suitable for ingestion by filter feeding animals on the reef. However, this suggestion can only be confirmed when more is known of the particle size requirements of the filter feeders on the reef.

5.9 : THE ROLE OF BACTERIA

It has been suggested (Saunders, 1972), that the reason why detrital stocks exceed those of living organic matter, is that much of the material is refractory and cannot be broken down and utilised as an energy substrate by heterotrophs. Plant material consists largely of structural polysaccharides or other structural polymers, e.g. lignin. The ability to hydrolyse such compounds is rare among animals, and when ingested, these compounds usually pass unchanged through the digestive system. Hylleberg Kristensen (1972) investigated the activity of digestive carbohydrases in 22 shallow-water, marine invertebrates. Only one case of moderate alginase activity was found.

Another important characteristic of macrophytes is a low nitrogen and phosphorous content. Mann (1972) cites Russell-Hunter (1970) who states that, with the exception of ruminants, all animals of all trophic levels so far investigated have adult nutritional requirements for protein which correspond to a C : N ratio of less than 17. Both bacteria and phytoplankton with ratios in the region of 6 (Strickland, 1960; Mann, 1972) handsomely meet these requirements. Niell (1976) has investigated 24 species of benthic, intertidal algae and found that their C : N ratios are much higher, with values for some brown algae in excess of 17. Similarly the carbon : phosphorous ratios are very high in macrophytes (~ 200) compared with micro-algae (~ 30) and bacteria (~ 27) (Spector, 1956; cited by Mann, 1972). Unfortunately no values are available for the POM in suspension over the reef.

Bacteria display a number of properties which make them the primary decomposers in aquatic ecosystems. These micro-organisms possess the enzyme systems necessary to hydrolyse structural plant compounds. They are able to assimilate organic matter, nitrates and phosphates in solution and at the same time decompose nutrient-poor plant tissue. Complexes consisting of detrital particles and colonising bacteria are a rich source of the essential nutrients readily available to the filter feeders.

Newell (1965) and Hargrave (1975 and references cited therein) have demonstrated that in many detritus feeders, little of the ingested material is digested; it is the attached micro-organisms which are assimilated. A cyclic phenomenon is established, whereby the detritus and faecal matter are recolonized by bacteria and these particles re-enter the food web. It is possible that a similar situation exists for the filter feeding animals at Dalebrook, which may explain why much of the detritus was old and unidentifable.

The numbers of bacteria in the water over the reef were high, 4 - 16 x 10^5 cells/ml. Mazure (1978) and Field et al. (in press) reported similar values from a kelp bed on the west coast of the Cape Peninsula. Schleyer (1979) recorded an annual mean of 19 x 10^5 cells/ml in Natal littoral waters. He found that 90% of the cells were cocci whose volume was an order of magnitude smaller than the mean bacterial volume (0,1 - 0,4 μm^3) at Dalebrook. This meant that although bacterial counts from Dalebrook were lower than those from Natal waters, the bacterial biomass was higher.

In this study it was found that, on average, only 5% of the bacteria were attached to particles, though this still constituted a large number of cells (0,3 x 10^5 cells/ml). Ferguson and Rublee (1976), Mazure (1978) and Schleyer (1979) found a higher incidence of attached cells - close to 20% of the total number of cells. In this study the colonised particles were generally small aggregates, around 15 µm, or films smaller than 5 µm. Occasionally larger detrital aggregates (20 to 60 µm) were found with up to 150 attached bacteria. It was not possible to estimate the abundance of these particles in such a small sample, but they certainly constituted a rich nutritional source for filter feeding animals on the reef.

Wiebe and Pomeroy (1972) found that more than 50% of the recognizable cells in freshly-taken samples were coccoid in shape and often very small. When incubated there was a marked decrease of cocci and an increase in rod forms. They suggested that the small cocci, free-living in natural populations, are dormant. Ferguson and Rublee (1976) found that 80% of the cells were small cocci. They concluded that these cells, with their high surface area to volume ratios, were better suited to using dilute nutrients than the larger rods.

Schleyer (1979) monitored the assimilation of C^{14} labelled glucose by bacteria, 90% of which were free-living coccoid forms. The results showed that these cells were not dormant and accounted for most of the glucose assimilated. In this study the samples collected over the reef on the April transect were dominated by rods. It was not uncommon to find two rods attached, possibly due to recent cell division, and it is unlikely that these cells were dormant. The bacterial population in the offshore waters of the September transect was largely small cocci. It is feasible that these cells were close to a dormant state, as there was neither a large macrophyte nor phytoplankton population in the immediate vicinity to provide the necessary nutrients. Mazure (1977) found the bacteria within a kelp bed were dominated by rods, but tiny cocci were most common 1 km and further offshore.

Although the daily sampling (Fig. 25, 32) showed that there was considerable day-to-day variation in the numbers of unattached bacteria, the results supported the seasonal trends evident in Figure 8, where the densities were highest in late summer. Mazure (1978) has found that the seasonal cycle in bacterial biomass correlated with that of the phytoplankton. At Dalebrook, where the phytoplankton stocks were extremely small, it is not surprising that no such correlation was evident. In the daily sampling programmes correlations were sought between bacterial densities, both free and attached, and the < 100 µm fraction of the POM in suspension on the day of sampling and up to four days before. There was no indication that the bacteria were dependent on the amount of POM present.

In view of the high incidence of free bacteria in the water, there must be a large source of dissolved organic matter to supply these cells with the necessary metabolites. There is considerable evidence that macrophyte communities provide this material. Mann (1972) cites Sieberth and Jensen (1969) and Khailov and Burlakova (1969) who found that under experimental conditions seaweeds released up to 40% of the products of gross photosynthesis in soluble form. Fielding (unpublished data) found that the production rates of the four most important seaweeds at Dalebrook were higher in summer than winter. This may account for the peak in numbers of free bacteria (Fig. 8) in late summer.

However, the increase in the numbers of free bacteria at the offshore station parallels the trend shown by the phytoplankton and appears to contradict the concept of DOM given off by the macrophytes and animals on the reef, providing a rich bacterial growth medium. There is no obvious explanation as to why the numbers of attached cells should be highest at the inshore station. Inshore the water is the most turbulent over the reef and it is possible that this movement increases the chances of a bacterial cell being brought into contact with a detrital particle.

Zobell and Feltham (1937) have shown that *Mytilus* can survive and grow on a bacterial diet. They used cultured bacteria which tend to be larger than those occurring naturally and at a concentration of at least 5 x 10^8 cells/ml, which is considerably in excess of the densities at Dalebrook. Experiments have shown that a variety of filter feeders can feed directly on planktonic bacteria of concentrations between 0,02 and 0,2 mg/l dry weight (Sorokin, 1971). These include cladocerans, sponges and some polychaetes. Fenchel and Jørgensen (1977) add tunicates and some lamellibranchs to this list. At Dalebrook bacterial concentrations fluctuated between 0,05 and 0,18 mg organic matter/l with a mean of 0,09 mg/l, which corresponds to a dry weight of close to 0,1 mg/l.

So it would appear that there is sufficient bacterial biomass to support filter feeders, provided they are able to extract the free bacteria from the water.

There is an important consideration that must not be overlooked. Unless the filter feeders are able to remove the individual bacterial cells from the water, then these micro-organisms, with their large numbers and rapid metabolic rates, will respire much of the assimilated DOM and represent a substantial energy sink.

5.10 : DISSOLVED ORGANIC MATTER

Concentrations of DOM are believed to be an order of magnitude greater than particulate matter in seawater (Wangersky, 1965; Parsons, 1975). Schleyer (1979) recorded mean dissolved and particulate organic carbon values of 14,8 mg/l and 3,5 mg/l respectively in the littoral waters of Natal. Rates of DOM production in Dalebrook waters are expected to be high due to macrophytic activity and the release of DOM during digestion, excretion and senescence all along the food web. Ogura (1975) has found the concentration of DOM in coastal waters of Japan to be about 2,7 mg/l, 24% of which was of low molecular weight (< 500).

It is these compounds, amino acids, peptides, lipids and carbohydrates which constitute the substrate for bacterial metabolism. Jannasch and Pritchard (1972) have evidence that in certain natural waters the concentrations of these compounds may not be high enough for efficient uptake by micro-organisms. Williams (1975) agrees in part with this concept but adds that as soon as the concentrations of these assimilable organic compounds increase, they are rapidly reduced to their microgram amounts by microbial uptake.

Velimorov et al. (in press) have found that the laminarian seaweeds *Ecklonia maxima* and *Laminaria pallida*, common on the southern shores of False Bay, release approximately 75% of the dissolved organic fraction as mannitol, a low molecular weight, acyclic polyol. In incubation experiments bacterial numbers rose from 10^5 cells/ml to

10^9 cells/ml within five hours, and the concentrations of mannitol dropped rapidly. Andrews et al. (1971) and others have recorded bacterial assimilation efficiencies for glucose of as much as 65% and even as high as 80% for certain amino acids. At Dalebrook it would appear that the large numbers of unattached bacteria are converting a substantial fraction of the primary photosynthate and secondarily produced, dissolved organic materials into microbial protoplasm.

The DOM also comprises larger, more complex compounds such as polysaccarides and proteins, many of which may be resistant to bacterial decomposition. Khailov and Finenko (1969) state that these compounds exhibit high surface activity with the result that they are easily adsorbed on to particle surfaces. These authors believe that bacteria are only able to decompose these surfactants after their adsorption on to particulate matter. Not only do detrital aggregates provide such a substrate but inorganic particles may also be involved.

While organic decomposition basically involves a reduction in particle size, it is believed that this adsorption phenomenon might form the basis for a process whereby particles are created and enlarged *in situ* (Riley, 1970; Parsons, 1975). Observations and experiments referred to by Riley (1970) indicate that particulate matter may be formed on air-water interfaces and within the water column by aggregations of smaller particles, together with adsorption of colloidal and dissolved organic matter. Parsons (1975) states that bacteria are almost certainly involved and the secretion of bacterial slimes will tend to trap other particles.

A large number of bacteria attached to particles, especially in July and August, were found embedded in tiny films of mucus whose extremities were hardly visible. It is possible that much of this is secreted by the bacterial cell and initiates particle formation and the bacterial clumping response which has been observed by Seki (1971). It seems that the POM and DOM are not merely intermediary steps in the breakdown of living matter into inorganic elements, but may be involved in the "creation" of new particles and an increase in the size of existing ones.

5.11 : CONCLUDING REMARKS

The large, rocky shore ecosystem at Dalebrook lies on the north-west coast of False Bay, where it is exposed to wave action and considerable water movement in to and out of the system. The benthic fauna is dominated by filter feeders, rather than grazers, and therefore particulate organic matter in suspension probably constitutes the most important energy input to the system.

The mass of POM rarely dropped below 1 mg/l and 60 - 90% of this was detritus. Much of this detritus was thought to originate from the large, intertidal seaweed community, however microscopic examination showed that most of the detrital particles were in an advanced state of decomposition and there was little fresh, easily identifiable plant material. This suggests that the particles undergo substantial modification, and in the process much of the autochthonous detritus may be exported from the system.

There were large numbers of bacteria in suspension. The majority of these were found free in suspension, where they were possibly metabolising the DOM released by the macrophytes and other members of the reef community. Macrophyte detritus is of limited nutritional value to the filter feeders. However, protein enrichment was provided by significant numbers of colonising bacteria.

For a large part of the year (October to April) concentrations of nitrates and silicates were low. Consequently there was little autochthonous phytoplankton production and chlorophyll concentrations over the reef were low. There was strong evidence of nutrient replenishment during this period, together with the influx of large phytoplankton stocks from offshore. This phenomenon appears to be associated with upwelling of nutrient-rich water in the south-eastern sector of the bay, under the influence of strong south-easterly winds.

It is difficult to account for the higher nitrate, silicate and chlorophyll concentrations in the winter (May to August). The effects of sewerage effluent and increased fresh water outflow a few kilometres from Dalebrook must be examined. In winter some autochthonous phytoplankton production will take place, but this is unlikely to approach that of the macrophyte community.

At Dalebrook, detritus is the largest source of organic input to the reef ecosystem, as the biomass of phytoplankton appears to be unable to support the large filter feeding community.

CHAPTER 6

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CHAPTER 7

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