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MEIOFAUNAL EFFECTS ON NUTRIENT FLUXES  
AND PROFILES IN MARINE SEDIMENTS.

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Being a thesis submitted for the degree of Doctor  
of Philosophy in the University of Glasgow.

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## SUMMARY

The main objective of my work has been to assess the effects of meiofauna on fluxes of dissolved nutrients through the sediment-water interface and on nutrient profiles in sediment porewaters. This work has been carried out using a combination of laboratory experiments and field surveys. My laboratory work has concerned the effects of meiofauna on interfacial nutrient fluxes under a range of biological, physical and chemical conditions. My field work has concerned the correlations between porewater nutrient profiles and various biological, physical and chemical parameters in two very different environments.

Manual chemical methods have been developed for the analysis of silicate, phosphate, sulphate, nitrate and ammonia on two millilitres of sample. The smear-ratio direct counting method for soil micro-organisms has been modified for use on marine sediments.

Modified diffusion cells have been developed for studying interfacial fluxes in marine sediments in the laboratory. These cells have been used for all of my laboratory experiments.

The effects of macrofauna, meiofauna and micro-organisms have been compared. Meiofauna generally have the greatest effect on nutrient fluxes. Macrofauna may reduce the effects of meiofauna. Micro-organisms alone tend to have the least effect on fluxes.

The effects of meiofaunal type and density on nutrient fluxes have been examined. Nematodes and copepods, the most prevalent meiofaunal groups in my sediment, usually have the most effect on fluxes. Less prevalent groups of meiofauna may alter the direction and magnitude of fluxes. Changes in meiofaunal density have less effect than changes in types of meiofauna.

The effects of salinity, compaction, oxygen saturation and particle size range on fluxes in the presence of nematodes and

copepods have been examined. Those of salinity are generally greatest. Physical and chemical parameters are more important in determining fluxes from and to the overlying water. <sup>m</sup>meiofaunal factors are more important in determining transfer of nutrients within the sediment column.

A survey of seven deep-sea sites in the central Pacific ocean has been conducted , and correlations between the biological and chemical parameters measured and porewater nutrient concentrations have been calculated. Nutrient concentration is most strongly correlated with microorganism density, water content and metazoan meiofauna densities.

A survey of four sites in the Tamar estuary, Plymouth, has been conducted and correlations between the biological, chemical and physical parameters measured, and porewater nutrient concentrations calculated. Nutrient concentration is most strongly correlated with salinity, water content, meiofaunal and microbial density.

The relationship between nutrient fluxes and concentration profiles, and the biological, physical and chemical parameters I have measured have been discussed, as have the possible causes of meiofaunal effects on nutrient fluxes and the interaction between biological, physical and chemical parameters.

## GENERAL INTRODUCTION

During the last twenty years there has been increasing interest in the processes controlling the production and fate of biogenic materials in the sea (Smith, 1984). The main global reservoir of organic carbon is in the sea and the world biogeochemical cycles of carbon, nitrogen, phosphorous, sulphur and oxygen may all be regulated by the oceanic cycles of these elements (Svennson and Soderland, 1977). Any natural or anthropogenic changes in these cycles are likely, therefore, to have major implications for the world environment and hence for human populations.

The American "Global Ocean Flux Study" workshop (GOFS, 1984) was the first to compile the existing data on fluxes in the ocean in a form whereby gaps in our present knowledge could be defined. There were two main purposes of the Benthic Transformations working group of the GOFS project ~~were~~. The first of these was to understand the rates of, and controls on, the transfer of solid and dissolved materials between the overlying water column, bottom water and sediments. The second purpose was to understand changes in the material within the benthic boundary zone during and following deposition. These changes in deposited material within the benthic boundary zone are termed early diagenesis (Berner, 1976, 1980; Wilson et al, 1985).

The oceanic cycles of carbon, nitrogen, phosphorous, sulphur and oxygen play a major role in determining the global environment (Broeker, 1973; Svennson and Soderland, 1977; Ivanov, 1978; Bender et al, 1984). The flux (time dependent change in concentration) of dissolved material between sediments and overlying water may play a large part in defining the spatial and temporal distributions of seawater properties. This exchange of material between sediments

and overlying water may also form a damping system for overall seawater properties (Rowe et al, 1975; GOFs, 1984, 1986). For example, the rates of production/uptake of dissolved nutrients by marine sediments, especially in the inshore environment, may be a major factor determining rates of primary production in the overlying water column (Boynton and Kemp, 1975; Ivanov, 1978; Rowe et al, 1985). The limitation of primary production in the water column by the rate of nutrient regeneration from sediments is one form of what is termed benthic-pelagic coupling (Rowe et al, 1975). The effects of physical, chemical and biological factors on the production and fate of biogenic materials in the benthic boundary zone need, therefore, to be known if the effects of anthropogenic and natural changes in the marine environment are to be predicted (Broeker, 1971; Price, 1978, 1982; Aller, 1982; GOFs, 1984, 1986; Smith, 1984). The prediction of effects on the marine environment may also be applied retrospectively in order to interpret historical conditions in the world oceans, as preserved in the sedimentary record (Bender et al, 1984).

The sediment-water interface is a major site of organic matter breakdown (Balzer, 1987). The rate of transfer of material through the sediment-water interface may control the rate of benthic nutrient regeneration (Berner, 1976; de Wilde, 1976; Bender et al, 1984). A large amount of work has already been done on the modelling of fluxes at the sediment-water interface, especially with respect to the effects of physical and chemical factors (e.g. Dugdale, 1977; Lerman, 1977; Billen and Vanderborght, 1978; Berner, 1980; Krom and Berner, 1980; Boatman and Murray, 1982; Goloway and Bender, 1982; Moore, 1984; Nyffeler et al, 1986; Balzer et al, 1987). In general the effects of biological parameters on fluxes

and early diagenesis have been studied far less than the effects of physical and chemical parameters. This is probably due to two factors, firstly the difficulty in controlling biological parameters during experimental studies and secondly the high variability of most biological effects (Berner, 1976; de Wilde, 1976).

The main factors which have been shown to affect the flux of dissolved and solid materials at the sediment-water interface are reviewed in table a. This table is based on some of the broader reviews of factors affecting fluxes. I have divided the factors affecting nutrient fluxes into primary, secondary and tertiary factors. Primary factors are affected by secondary factors, which are in turn affected by tertiary factors. For example nutrient fluxes are affected by dissolved material and water flow due to sediment-column growth (a primary factor). This primary factor is affected by compaction of the sediment and entrapment of water within the sediment (secondary factors). Compaction of the sediment is affected by the source of the sedimentary material, sediment binding, permeability and particle size range (tertiary factors).

Most studies on biological parameters have concerned the effects of animals on the physical structure of sediments, principally <sup>at</sup> binding and bioturbation, and on the production/breakdown of organic matter. The biota involved in these studies have generally been micro-organisms and burrowing macrofauna and megafauna (Fenchel and Harrison, 1975; Petr, 1977; Day, 1978; Gust and Harrison, 1981; Hines et al, 1982; Roman, 1983; Kristensen, 1984).

The most studied aspects of micro-organism effects on interfacial fluxes have been microbial breakdown of organic matter and production/use of dissolved nutrients (Fenchel and Harrison,



Table a. Review of factors which have been shown to affect nutrient fluxes across the sediment-water interface. References indicated by numbers and listed at end of table.

=====		
Primary factors	Secondary factors	Tertiary factors.
=====		
Dissolved material and water flow due to sediment -column growth. (1)		
	Compaction (7)	Material source and composition
		Permeability
		Sediment binding
		Particle size range
	Entrapment of water (3, 5)	Size of pore-spaces
		Particle size range
		Chemical trans- formations
Dissolved material and porewater flow due to groundwater pressure (1)		
	Permeability (8)	Burrows
		Tortuosity
		Sediment binding
		Particle size range
	Tidal fluctuations (8)	
	Seasonal fluctuations (8)	
Molecular diffusion fluxes in pore-water (1, 5, 7)		
	Temperature (2)	Seasonal variation
		Weather

table a. continued.

Primary factors	Secondary factors	Tertiary factors
=====		
		Emersion/immersion times
	Electrical potential of ion (1, 2, 4, 8, 10)	Complexation
		Enzymes
		Eh/pH
	Mean-free path (tortuosity) (1, 2, 3, 10)	Burrows
		Compaction
		Flux of solid material
		Microbial binding
		Faunal binding
		Particle size range
	Surface action (2, 3, 6, 11)	Organic films
		Binding site numbers
		Transformations
		Sorption
		Ion concentration
		Biological activity
		Eh/pH
		Tortuosity
Mixing of sediment and water at the interface (1, 5)		
	Turbulent mixing (5, 7, 10, 12)	Wave/current strength
		Weather
		Season

Table a. continued.

Primary factors	Secondary factors	Tertiary factors
=====		
		Particle size range
		Cohesion of sediment
		Faecal pellets
		Microbial binding
		Faunal binding
		Burrows
	Irrigation (3, 8, 10)	Burrow type and density
		Faunal activity
		Water currents/waves
	Bioturbation (3, 8, 9, 10)	Faunal size/density
		Depth of penetration
		Faunal activity
		Food availability
		Season/weather
		Immersion/emersion times
		Active transport
Sedimentation flux of solids (1, 8)		
	Physical factors (7, 8)	Wave/current conditions
		Proximity to land
		Proximity to rivers
		Water column production
	Biodeposition/ bioerosion (3, 10)	Bioturbation

Table a. continued.

Primary factors	Secondary factors	Tertiary factors
		Faunal types/ activities
	Flocculation (6, 8)	Salinity
	Microbial binding (10)	

References for table a.

- (1) Lerman, 1978
- (2) Duursma and Bosch, 1970
- (3) Petr, 1977
- (4) Burton, 1978
- (5) Bricker, 1978
- (6) Lal, 1978
- (7) Elderfield, 1978
- (8) Day, 1978
- (9) Aller, 1982
- (10) Lee and Swartz, 1980
- (11) Lion et al, 1982
- (12) Webb and Theodor, 1972

1975; Billen and Vanderborght, 1978; Day, 1978; Martens, 1978; Aller and Yingst, 1980; Hines et al, 1982). Micro-organisms have also been shown to affect sediment pore-size, and hence permeability, by the production of extracellular secretions. Mucopolysaccharide secretions may bind sediment particles, decreasing the effective pore-size of the sediment (Aspiras et al, 1971; Rheinheimer, 1974; Day, 1978; deBoer, 1981). Extracellular enzymes secreted by micro-organisms may digest existing binding, increasing sediment pore-size (Rheinheimer, 1974; Fletcher, 1978).

Most of the macrofaunal effects on interfacial fluxes which have been studied are related either to the formation and maintenance of burrows or to feeding activity (Petr, 1977; Aller, 1978a, 1982; Kristensen, 1984; Matisoff et al, 1985). The formation of burrows, in addition to relocating sediment particles, ventilates the sediment (Anderson and Meadows, 1978; Day, 1978; Gust and Harrison, 1981; Meadows, 1986). This ventilation is primarily caused by water circulation through burrows either actively, due to feeding or respiratory currents, or passively, due to induced flow in relict (unoccupied) burrows (Webb and Theodor, 1968; Gust and Harrison, 1981; Hines et al, 1982; Waslenchuk et al, 1983; Ray and Aller, 1985). Burrows in sediment also decrease the <sup>mean diffusion distance</sup> ~~distance an ion must diffuse in order to pass~~ between the interstitial water and the water column (tortuosity) and hence increase diffusion rates (Lerman, 1978; Berner, 1980). Many macrofaunal burrows are lined with mucous or are constructed of mucous-bound sediment particles (Barnes, 1980). These mucous-bound tubes may have diffusion properties very different from that of the bulk sediment. In areas of high burrow density, the rate of diffusion of ions through the burrow lining may be the main factor

limiting diffusion from the sediment as a whole (Gust and Harrison, 1977; Schink and Guinasso, 1977; Aller, 1980, 1983; Koop and Griffiths, 1982; Officer, 1982; Waslenchuk et al, 1983; Kristensen, 1984).

Feeding by macrofauna causes a wide range of effects on sediment structure (Day, 1978; Tenore and Rice, 1980). Deposit feeding causes cycling of sediment particles, which, depending on the mode of feeding, can either homogenise the sediment column or create zones of reworked particles within the column (stratification) (Aller, 1978a, 1982; Yingst and Rhoads, 1980; Hines et al, 1982). Stratification also occurs due to the production of faecal pellets by infauna, epifauna and pelagic animals (Hargrave and Wilson, 1975; Pomeroy, 1980; Wilson et al, 1985). These faecal pellets often form micro-environments within the sediment column, for example, many pellets become highly reduced environments within oxidised sediment columns (Jorgensen, 1977; Anderson and Meadows, 1978; Ivanov, 1978).

Meiofauna are defined as infaunal and epifaunal organisms which will pass a 500  $\mu\text{m}$  sieve and be retained on a 35  $\mu\text{m}$  sieve. Although this classification is based on size, the meiofauna contains a fairly well defined group of organisms. These organisms are mainly metazoan infauna plus a few protozoan, coelenterate and platyhelminthe groups (Swedmark, 1964; Hulings and Gray, 1971). A further division of the meiofauna into temporary meiofauna (mixobenthos) and permanent meiofauna is also often made. Temporary meiofauna consist largely of juvenile forms of larger organisms, mainly oligochaetes and polychaetes (Hulings and Gray, 1971). There are a large number of reviews of the meiofauna in the literature. Details of the composition and taxonomy of the meiofauna may be found in McIntyre (1964), Swedmark (1964), Gerlach (1971), Hulings

and Gray (1971) and Heip et al (1985). Details on the general ecology of the meiofauna can be found in McIntyre (1964); Coull (1973), Fenchel (1978), Coull and Bell (1979) and Hicks and Coull (1983).

Meiofauna may affect interfacial fluxes directly or indirectly. Direct effects include breakdown of organic matter, bioturbation, and possibly active transport of dissolved material (Chua and Brinkhurst, 1973; Coull, 1973; Hargrave, 1975; Gerlach, 1978; McLachlan, 1978; Stewart, 1979; Pomeroy, 1980; Yingst and Rhoads, 1980; Fricke and Flemming, 1983; Hennig et al, 1983; Hockin, 1983; Nicholas, 1984; Gray, 1985; Jensen, 1987 ). Meiofauna may also cause some direct effects due to the ventilation of sediments (Cullen, 1973; Fenchel and Harrison, 1975; Yingst and Rhoads, 1980; Hines et al, 1982; Fricke and Hemming, 1983; Nicholas, 1984; Varon and Thistle, 1988; Yingst and Rhoads, 1980). Very few meiofauna form permanent burrows (Hulings and Gray, 1971; Chandler and Fleeger, 1984) but many are burrowers, moving sediment particles and creating temporary burrows (Cullen, 1973; Yingst and Rhoads, 1980; Bell, 1983). In cohesive sediments these burrows may form an important, if temporary, ventilation system. This is particularly true of sediments which have low macrofaunal densities and are subject to little disturbance, such as in the deep-sea (Gerlach, 1971; Coull, 1972; Thiel, 1983; Heip et al, 1984; Gooday, 1988). In these environments the presence of a large number of very small burrows, which have high surface area to volume ratios, may greatly increase the effective surface area of the sediment.

Meiofauna in sediments may cause changes in microbial production or activity due to selective and non-selective deposit feeding often on preferred types of micro-organisms

(Gerlach, 1971, 1978; Coull, 1973; Fenchel and Harrison, 1975; Hargrave, 1975; Hennig et al, 1975; Boucher and Chamroux, 1976; McLachlan, 1978; Martens, 1978; Stewart, 1979; Aller and Yingst, 1980; Alongi and Tietjen, 1980; Tenore and Rice, 1980; Yingst and Rhoads, 1980; Koop and Griffiths, 1982; Nicholas, 1984; Alongi, 1985; Carman and Thistle, 1985; Gray, 1985; Balzer et al, 1987 Decho and Fleeger, 1988; Meyers et al, 1988). For example, marine nematodes in the laboratory have been reported as consuming up to  $1 \times 10^6$  bacteria per day (Nicholas, 1984). Meiofauna can also influence the productivity and activity of macrofauna (Bell, 1980; Bell and Coull, 1980; Tenore and Rice, 1980; Reise, 1983). This is particularly relevant in sediments containing deposit feeding macrofaunal species and in situations where meiofauna may influence the settling of juvenile macrofauna (Reise and Ax, 1979; Bell and Coull, 1980; Reise, 1983; Watzin, 1983). Macrofauna in sediments may influence bacterial activity in similar ways to meiofauna and may also influence meiofauna behaviour and densities (McIntyre, 1969; Yingst and Rhoads, 1980; Fricke and Flemming, 1983; Reise, 1983; Alongi, 1985)

The breakdown of organic matter in sediments by microbial action is the main source of nutrients regenerated from sediments (Correll et al, 1975; Lyons and Fitzgerald, 1978; Aller and Yingst, 1980; Hennig et al, 1983; Balzer, 1984; Balzer et al, 1987).

Micro-organisms are also major consumers of nutrients in sediments (Correll et al, 1975; Fenchel and Harrison, 1975; Hargrave, 1975; Jorgensen, 1977; Aller and Yingst, 1980; Hennig et al, 1983; Balzer, 1984). Any changes in the activity of the microbial population of the sediment will, therefore, affect nutrient fluxes through the sediment. Meiofauna and macrofauna in sediments affect the activity of the microbial population and may therefore affect



nutrient fluxes indirectly. The effects of deposit feeding species on microbial production are dependent on the site of feeding within the sediment column. Certain species tend to feed at particular positions within the sediment-column, depending on where their preferred microbial types are found (Coull, 1973; Hargrave, 1975; Boucher and Chamroux, 1976; McLachlan, 1978; Alongi and Tietjen, 1980; Alongi, 1985; Carman and Thistle, 1985; Balzer et al, 1987; Decho and Fleeger, 1988; Meyers et al, 1988). The effects of meiofauna and macrofauna on nutrient fluxes are likely, therefore, to be determined by the types of meiofauna present and on the stratification of micro-organisms within the sediment column.

There has been relatively little work done concerning the effects of meiofauna on fluxes across the sediment-water interface (Hennig et al, 1976; Day, 1978; Wormald and Stirling, 1979; Hockin, 1983; Gray, 1985). The small body of work which does exist indicates that meiofauna may be as important as macrofauna and micro-organisms in determining fluxes (Gerlach, 1971; Koop and Griffiths, 1982; Frithsen, 1984). In some environments, such as some deep-sea areas and organically polluted estuarine muds, the number, biomass and productivity of the meiofauna exceeds that of macrofauna (Koop and Griffiths, 1982; Hockin, 1983; Heip et al, 1984). In these areas the effects of meiofauna may be especially important.

The main objective of my work has been to assess the effects of meiofauna on the flux of nutrients across the sediment-water interface under a range of physical and chemical conditions. This work has been carried out using a combination of laboratory experiments and field surveys. The reason for this approach was to try and relate nutrient fluxes under a range of controlled

conditions in the laboratory, to observed concentrations of nutrients in the porewater of natural sediments. Section one of my thesis contains modified methods for nutrient analysis and porewater extraction. These methods are suitable for examining the effects of meiofauna on nutrient fluxes and concentrations on a smaller scale than that used by previous workers. Section one also contains the methods I have used for micro-organism counting, meiofaunal extraction and meiofaunal preservation.

All of my meiofaunal work has concerned taxa rather than species. There were three reasons for this. Firstly, many of the species of meiofauna found in British waters and many of the deep-sea genera are undescribed (Hulings and Gray, 1971). The second reason is that the division of meiofauna between feeding types may be more important than between species (Nicholas, 1984; Jensen, 1987). Thirdly, my laboratory experiments have involved the use of live animals. Identification of the animals used in these experiments to species level would have been impossible until after completion of the experiments. Species composition could not, therefore, have been controlled without the use of single species cultures. Single species cultures were not used as this would have involved maintaining the culture under laboratory conditions and the animals would not, therefore, have come from a natural environment.

My field survey work has been carried out in two very different environments. The first of these was the Tamar estuary, Plymouth, Devon, the results from which are given in section 4. The second part of my field work was carried out on samples from the Pacific ocean between Tahiti and Hawaii, the results of which are given in section 3. In both of these field surveys I investigated the relationship between a range of biological, physical and

chemical parameters in the sediments and the concentrations of dissolved nutrients in the interstitial water.

My laboratory experiments have concerned the effects of meiofauna on nutrient fluxes under a range of physical and chemical conditions. The materials for these laboratory experiments were collected from a muddy-sand beach in the Firth of Clyde, Scotland.

The lack of obvious correlation between the three environments I have sampled presents some difficulties for the comparison of my field and laboratory data. Both of my field studies were carried out as parts of multi-disciplinary studies, involving workers from different institutions. My participation in these multi-disciplinary studies precluded a field study of the site from which I obtained the samples for my laboratory work. The two field studies, however, enabled me to examine material from environments which would otherwise have been inaccessible to me.

I have attempted to compare the factors related to nutrient flux/concentration in my laboratory and field studies despite their lack of obvious correlation. This comparison was to examine how the processes controlling nutrient flux/concentration change between these environments. The results of this comparison between my field and laboratory studies and the implications of the similarities and differences in the factors regulating nutrient fluxes are described in the general discussion.

SECTION ONE - METHODS.

- (i) Nutrient analysis
- (ii) Micro-organism numbers
- (iii) Meiofaunal preservation
- (iv) Meiofaunal extraction
- (v) Porewater extraction

## NUTRIENT ANALYSES.

### Introduction

A large volume of water (over 400 ml) is necessary for conventional nutrient analyses on phosphate, sulphate, silicate, nitrate and ammonium in seawater (eg Strickland and Parsons, 1972; Parsons et al, 1984). When working with sediment porewaters this volume is rarely available. Resolution considerations, especially near the sediment-water interface, often limit the volume of sediment available (Hesslein, 1976; Robbins and Gustinis, 1976; Bricker, 1978; Smith, 1984). Thus, if small sediment samples are being processed, even with efficient extraction methods, there is a need for small scale analytical methods (Presley, 1971; Smith, 1984).

Many workers have described the use of autoanalysers capable of using very small sample volumes (eg Pugh, 1976; Blackburn and Henriksen, 1983; Hennig et al, 1983; Smith et al, 1983). The range of manual chemical methods for small volumes is, however, limited.

Presley (1971) described methods for single analyses of ammonium, silicate, phosphate and sulphate on approximately 4 ml of porewater. Bremner and Shaw (1955), Conway (1962) and Bremner (1965) describe methods for single analyses of ammonium and nitrate on 2 ml of sample. The methods presented here represent a combination of these techniques, scaled down to allow a single analysis of each of the above nutrients on 2 ml of sample. This volume should be readily available even from very cohesive sediments. These analyses require little specialised equipment and are suitable for use in the laboratory or onboard ship. Using these methods I regularly process 20 samples a day for all five nutrients.

The phosphate and silicate analyses are both colourimetric.

Presley (1971) scaled down the methods of Strickland and Parsons (1972) by using smaller volumes of more dilute reagents. Both of these analyses are based on the production of a highly coloured reduced molybdate complex. Details of the chemistry of the reactions can be found in Strickland and Parsons (1972) and Parsons et al (1984). The methods presented here have been scaled down to work with 250  $\mu$ l of sample each.

The sulphate analysis of Presley (1971) is a gravimetric one, based on the precipitation of sulphate as its insoluble barium salt. The modifications introduced here are from Vogel (1961). These increase the precision of the method when working with 500  $\mu$ l of sample.

The nitrate and ammonium analyses of Bremner and Shaw (1955), Conway (1962) and Bremner (1965) all involve the use of Conway diffusion cells. The basis of this method is the diffusion of ammonia from the sample into an indicator solution with a very high affinity for ammonia. This results in an equilibrium between the sample and the indicator. This equilibrium is shifted further towards the indicator by the addition of a basic suspension to the sample. When equilibrium is attained the indicator is titrated against standard acid to obtain the ammonium concentration. Nitrate analysis is similarly performed after reduction to ammonia. The techniques reported here have been modified according to Gasser (1963) and scaled down to allow analysis of dissolved ammonia and nitrate on a total of 1ml.

## Materials and methods

### Phosphate analysis

#### Reagents

##### Ammonium Molybdate solution:

A  $2\text{g l}^{-1}$  solution of analytical grade ammonium molybdate ( $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24}\cdot 4\text{H}_2\text{O}$ ). This solution is stable indefinitely if stored in a plastic bottle.

##### Sulphuric acid solution:

10ml of 98% analytical sulphuric acid ( $\text{H}_2\text{SO}_4$ , specific gravity 1.98) diluted to 1 litre.

##### Ascorbic acid solution:

A  $3.5\text{g l}^{-1}$  solution of analytical ascorbic acid ( $\text{CH}_2\text{OHCHOHCHCOH}=\text{COH}-\text{COOH}$ ). This solution is stable indefinitely if frozen in small vials and only thawed as necessary.

##### Potassium Antimonyl-Tartrate solution:

A  $0.09\text{g l}^{-1}$  solution of analytical grade potassium antimonyl-tartrate ( $\text{KSbC}_4\text{H}_4\text{O}_7\cdot 1/2\text{H}_2\text{O}$ ). This solution is stable for many months.

##### Phosphate standard:

A  $1.433\text{g l}^{-1}$  solution of analytical potassium hydrogen phosphate ( $\text{KH}_2\text{PO}_4$ ). This is a 1000 part per million (ppm) stock standard which is stable indefinitely providing no biological growth occurs.

The standard phosphate is made up in artificial seawater (25g of sodium chloride ( $\text{NaCl}$ ) and 8g of magnesium sulphate heptahydrate ( $\text{MgSO}_4\cdot 7\text{H}_2\text{O}$ ) in 1 litre of distilled water). All other solutions are made up using distilled water.

##### Mixed Reagent:

The ammonium molybdate, sulphuric acid, ascorbic acid and potassium antimonyl-tartrate solutions are mixed together in a ratio of 2:5:2:1 respectively. The mixed reagent must be used

within a few hours.

#### Phosphate Standards and blanks:

Stock phosphate solution is diluted with artificial seawater to give an appropriate range of standards. Blank solutions consist of artificial seawater. The blank solutions allow for turbidity and phosphate in the reagents.

#### Method

250  $\mu$ l of each standard, sample and blank are pipetted into 2ml plastic vials, followed by 250  $\mu$ l of mixed reagent. The vials are then sealed and shaken to mix.

The colour develops fully in 10 minutes and is stable for up to 4 hours. After this time a slow increase in absorbancy occurs. The absorbancy of the solutions is measured in a spectrophotometer at 885nm using 1cm pathlength semi-micro cells (total volume 750  $\mu$ l).

The standards ( blank corrected ) should form a straight line through the origin. Phosphate levels in the samples are obtained using a regression line calculated from the standards.

#### Sulphate analysis

##### Reagents

Hydrochloric acid:

10N analytical grade hydrochloric acid (HCl).

Barium Chloride solution:

A 20%w/v barium chloride ( $\text{BaCl}_2$ ) solution diluted to 7% w/v with distilled water.

Blanks: Distilled water

##### Method

500  $\mu$ l of the test solutions and blanks are pipetted into 50ml



conical flasks containing 4.5ml of distilled water. Dilution of the samples to 10% seawater concentration gives the best percentage theoretical yield (table 1.1).

The samples are then acidified by the addition of 50 $\mu$ l of 10N hydrochloric acid and are heated to incipient boiling point on a hotplate. This serves to remove any carbonate from the solution as carbon dioxide. The carbonate would otherwise precipitate with the barium sulphate. If the sample is acidified too strongly, full precipitation of the barium sulphate does not take place (Vogel, 1961).

Three ml of barium chloride solution is then added to the solution with swirling to mix. This addition must be done slowly to prevent co-precipitation of other barium salts (Vogel, 1961).

The flasks are incubated at incipient boiling for 1 hour to allow full precipitation of the barium sulphate. The solutions are then slowly cooled to room temperature. When the solutions are cool, the barium sulphate is collected by vacuum filtration through Whatman GF/F glass fibre filters (nominal retention 0.7 $\mu$ m) with repeated washing. These filters must be washed three times with distilled water, dried at 60°C and weighed before use.

The filters are then dried at 60°C overnight and re-weighed. The weights of barium sulphate produced are corrected for the blanks and used to calculate the concentration of sulphate in the original solution.

### Silicate analysis

#### Reagents

Standard silicate solution:

A 0.680g l<sup>-1</sup> solution of sodium silicofluoride (Na<sub>2</sub>SiF<sub>6</sub>) in distilled water (=100ppm stock solution). This solution is stable

% Seawater concentration	% yield	Coefficient of variation (%)
100	105.63	1.908
50	99.42	1.309
20	90.36	2.207
10	99.97	0.939
5	94.94	1.274

Table 1.1. The effect of dilution of a sample of artificial seawater , prior to sulphate analysis, on the % yield of sulphate and the coefficient of variation of three replicate samples. % yield = (observed yield/theoretical yield) x 100.

indefinitely if stored in a plastic bottle.

Molybdate reagent:

A  $8\text{g l}^{-1}$  solution of ammonium molybdate  $((\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O})$  in 0.3N Hydrochloric acid (HCl). This solution should be stored out of direct sunlight.

Metol-Sulphite solution:

A  $10\text{g l}^{-1}$  solution of metol (p-methylaminophenol sulphate,  $(\text{HO}-\text{C}_6\text{H}_4-\text{NH}-\text{CH}_3)_2-\text{H}_2\text{SO}_4$ ) in a  $12\text{g l}^{-1}$  solution of anhydrous sodium sulphite  $(\text{Na}_2\text{SO}_3)$ . This solution should be filtered through a Whatman no.1 filter paper, stored in a clean glass bottle and remade monthly.

Oxalic acid solution:

50g of oxalic acid dihydrate  $((\text{COOH})_2 \cdot 2\text{H}_2\text{O})$  shaken with 500ml of distilled water to form a saturated solution. The solution should be stored over the remaining crystals and decanted for use.

Sulphuric acid solution:

50% solution of analytical grade sulphuric acid  $(\text{H}_2\text{SO}_4)$ .

Artificial Seawater: As for phosphate analysis

Reducing solution:

Metol-sulphite, oxalic acid, sulphuric acid and distilled water mixed in the ratio 5:3:3:4. This solution should be remade daily.

Silicate standards and blanks:

Stock silicate solution diluted with Artificial seawater to give a suitable range of standards. Blank solution consists of artificial seawater. The blank allows for both turbidity and silicate in the reagents.

### Method

250  $\mu\text{l}$  of sample, standard and blank are pipetted into 2ml plastic vials, followed by 250  $\mu\text{l}$  of molybdate solution. The tubes are shaken and allowed to stand for 10 minutes. 250  $\mu\text{l}$  of reducing

solution is then added. The tubes are shaken and allowed to stand. The colour develops fully in 1 hour and is stable for up to 4 hours.

The absorbancy of the solutions is measured in a spectrophotometer at 810nm in 1cm pathlength semi-micro cells which have a total volume of 750  $\mu$ l. The standards should form a straight line passing through the origin. Silicate levels in the samples are obtained using a regression line calculated from the standards.

### Nitrate and Ammonium analysis

#### Reagents

Mixed indicator:

0.330g of bromocresol green and 0.165g of methyl red dissolved in 500ml of 95% ethanol.

titanium III sulphate:

A 15% w/v solution of technical grade titanium III sulphate ( $\text{Ti}_2(\text{SO}_4)_3$ ) in 24% sulphuric acid (available from BDH chemicals ltd).

Iron II sulphate solution:

A  $15\text{g l}^{-1}$  solution of analytical grade iron II sulphate ( $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$ ) in distilled water.

Standard sulphuric acid:

0.005N sulphuric acid diluted from standard (ConVol) concentrate.

Magnesium oxide suspension:

A 10% w/v suspension of magnesium oxide (MgO) in distilled water. The magnesium oxide must be ground finely, furnace at  $600^\circ\text{C}$  for 3 hours and stored in a desiccator containing potassium hydroxide pellets. This procedure removes any carbonate present. The suspension should be remade daily and stored in a sealed container until required.

### Sulphamic acid solution:

A  $20\text{g l}^{-1}$  solution of analytical grade sulphamic acid ( $\text{NH}_2\text{SO}_3\text{H}$ ) in distilled water. This solution should be stored at below  $10^\circ\text{C}$  and renewed weekly.

### Standard Ammonium and Nitrate solution:

0.36636 g of ammonium sulphate ( $(\text{NH}_4)_2\text{SO}_4$ ) and 0.16306 g of potassium nitrate ( $\text{KNO}_3$ ) dissolved in 1 litre of distilled water. If pure, dry reagents are used this solution contains  $100\text{ mg l}^{-1}$  each of ammonia and nitrate. The solution is stable indefinitely if refrigerated.

### Boric acid indicator:

20g of boric acid ( $\text{H}_3\text{BO}_3$ ) dissolved in 1 litre of 1:4 ethanol:distilled water. To this is added 20ml of mixed indicator solution. This solution should be stored tightly stoppered and renewed monthly. This solution has a very high affinity for ammonia (approx.  $500\text{ }\mu\text{g ml}^{-1}$ ).

### titanium III / Iron II sulphate mixture:

Titanium III sulphate and iron II sulphate solutions mixed 1:1. This solution should be used immediately.

### Method

#### Ammonium:

500  $\mu\text{l}$  of the sample is pipetted into the outer chamber of a Conway cell (figure 1.1), followed by 250  $\mu\text{l}$  of sulphamic acid solution. The ground glass rim of the cell is lightly greased and the lid slid firmly into place. The samples are allowed to stand to allow the sulphamic acid to quantitatively reduce any nitrite present to nitrogen.

After five minutes 250  $\mu\text{l}$  of Boric acid indicator solution is pipetted into the inner chamber through the hole in the dish lid.

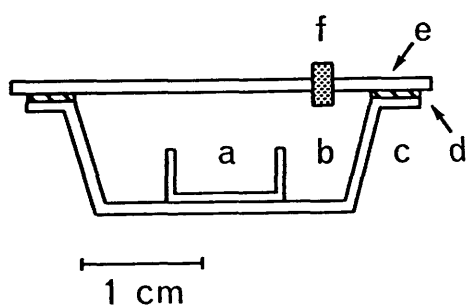


Figure 1.1. Transverse section of a Conway diffusion cell. a = inner chamber; b = outer chamber; c = borosilicate glass base with ground glass rim; d = silicon grease seal; e = perspex lid; f = neoprene stopper.

250  $\mu\text{l}$  of magnesium oxide suspension is then added to the outer chamber, the lid being sealed immediately with a lightly greased neoprene stopper. The addition of magnesium oxide decreases the solubility of ammonia in the sample, thus aiding the diffusion process.

The dishes are then placed on an oscillating table in an incubator at  $30^{\circ}\text{C}$  to allow diffusion of the ammonia into the boric acid solution. The rate of diffusion is dependent on the temperature of incubation, ammonia diffusing faster at higher temperatures. If the temperature is too high, however, there is an appreciable loss of efficiency due to the decrease in ammonia solubility in the boric acid indicator (Conway, 1962). The temperature of  $30^{\circ}\text{C}$  I used is a good compromise between rapid diffusion and low ammonia loss. 24 hours was found to be sufficient for the levels of ammonia found in the porewater samples.

At the end of this time the dishes are opened and the boric acid indicator is titrated against the standard sulphuric acid. The acid is dispensed using a micrometer glass syringe which has 0.05  $\mu\text{l}$  precision. The endpoint of this titration is a permanent change from pale green to pale pink. Ammonium concentration is calculated on the basis of 1 ml of standard acid being equivalent to 0.07 mg of ammonia (Bremner, 1965).

#### Nitrate:

This is assessed as nitrate plus ammonium. The procedure is the same as above, with one exception. Immediately before addition of the magnesium oxide suspension, 250  $\mu\text{l}$  of the titanium III / iron II sulphate solution is added. This solution quantitatively reduces nitrate to ammonium (Gasser, 1963).

Nitrate concentration is calculated on the basis of 1 mole of nitrate being reduced to 1 mole of ammonium.

Standards and blanks:

A range of standards are run in parallel to the samples in each analytical run. These provide a check on the efficiency of the diffusion. Blank solutions consist solely of the reagents.



## Results

The methods presented here have been tested against spectrophotometer reference standard solutions diluted with artificial seawater. The results are shown in table 1.2. These results represent average values for concentrations ranging from near zero to double the levels generally found in porewaters. All of the analyses gave results within 2 % of the reference standard concentrations. The coefficients of variation of three replicate analyses are also shown in table 1.2. These variations were less than 3% for all of the nutrients.

Nutrient	Mean % of Analytical Standard Conc.	s.d.	Coefficient of variation (%)
$\text{SO}_4^{2-}$	99.97(a)	0.9387	0.939
$\text{PO}_4^{3-}$	98.13	2.6691	2.720
$\text{NH}_4^+$	98.97	2.7741	2.803
$\text{NO}_3^-$	101.08	1.8983	1.878
$\text{SiO}_4^{4-}$	99.87	2.3130	2.316

Table 1.2. Mean percentages of analytical standard concentration and coefficients of variation of three replicates for each of the nutrient analyses. (a)= at 10% seawater concentration.

## Discussion

The techniques reported here probably do not represent the ultimate in miniaturisation of manual chemical analyses. I have, however, used them for all of my nutrient samples and have found them convenient and easy to use.

Smaller scale techniques for sulphate do exist (eg Hwang and Dasgupta, 1984). These techniques can give more accurate results for very low sulphate levels but they are laborious to use on large numbers of samples. Many of them are also subject to considerable salt interference. The gravimetric analysis of sulphate used here is a rapid and sensitive method for use on marine and estuarine samples.

Conway (1962) reports that the presence of seawater salts affects the diffusion of ammonia. This effect, however, increases the efficiency of the diffusion process. Full details of interference effects of various ions are given in Conway (1962).

The Conway dishes need to be agitated regularly for the first four to six hours of diffusion. This is to prevent gel formation by the titanous sulphate and magnesium oxide mixture. The presence of a gel decreases the efficiency of the initial rapid diffusion. After four hours the formation of a gel is less important (Bremner, 1965). I have found a continuously oscillating table to be the most convenient way of agitating the dishes. The agitation can, however, be carried out hourly by hand with no apparent loss of diffusion efficiency.

The Conway dishes need to be incubated at a constant temperature. This is to prevent condensation on the inner surface of the dish lids which decreases the recovery of ammonia. A full account of the effects of temperature on the rate of the diffusion process is given by Conway (1962).

## SMEAR-RATIO METHOD FOR MICRO-ORGANISM COUNTING.

### Introduction

There are many methods in the literature for enumeration of micro-organisms in sediments. These methods are usually based on either viable organism counts or on direct counting. Viable organism methods include Colony Forming Unit (cfu) counts (Alexander, 1965; Jones, 1979) and isotopic labelling of active micro-organisms (Meyer-Reil, 1978; Hoppe, 1976). Direct counting methods include the use of light or fluorescence microscopy and a counting chamber or electron microscopy (Frankel, 1970; Jones, 1979). For certain groups of organisms other methods exist such as chlorophyll analysis for photoautotrophs (Parsons et al, 1984; Stanier et al, 1981).

Colony forming unit counts tend to underestimate numbers of micro-organisms. This is due to two factors, firstly the presence of non colony forming micro-organisms and organisms which are unable to grow under the incubation conditions, and secondly chains or clumps of micro-organisms forming single colonies (Cruikshank et al, 1975; Jones and Mollison, 1948; Wood, 1967). Colony forming unit counts also suffer from the disadvantage that they must be carried out soon after the sample is collected.

Labelled Substrate uptake counts are usually low because some organisms are unable to use the labelled substrate added (Hoppe, 1976).

Direct counting can overestimate numbers of micro-organisms. This is due to the presence of dead and metabolically inactive organisms which are counted by the technique (Wood, 1967). Direct counting can also be difficult due to the need to quantify the volume of sample being examined (Wood, 1967). One common method for this is the use of a Haemocytometer. With this however the depth of

the field of view (usually 0.1mm) sometimes means that organisms are obscured by other particulates (Jones and Mollison, 1948). Direct counting can also be carried out using membrane filtered samples. This method, however, suffers from the same effect at high organism densities (Jones, 1979). Direct counting methods such as the haemocytometer can be used on samples which have been preserved immediately after collection.

Thornton and Gray (1934) described a method called the Smear-ratio technique. In this technique, they mixed a known volume of bacterial suspension with a known volume and concentration of a suspension of solid particles. A smear of this mixture was taken on a microscope slide, stained and examined under oil immersion. The numbers of bacteria in the original suspension could then be assessed using the ratio of bacteria to added particles in each field of view.

Thornton and Gray's (1934) requirements for the added particles were that the particles should be of the same order of size as the bacteria and should be easily recognisable under the microscope. For this they used a coarse filtered suspension of Indigotin (a solid dye) particles. These particles were not, however, regular in size and were often difficult to identify and count under the microscope. Thornton and Gray's method was later adapted by Frederick (1965). Frederick used a suspension of latex beads which were regular in size ( $1.2\mu$  diameter) and shape. The beads did not stain and were easily distinguished from micro-organisms under the microscope. Latex beads were also used by Peterson and Frederick (1979). Both of these studies were on soil micro-organisms.

The purpose of my experiments was to determine the extraction and counting conditions needed to apply the Smear-ratio technique

to intertidal sediments. An initial trial of the conditions used by Frederick (1965) and Peterson and Frederick (1979) was carried out. The results of this trial were very variable probably because of aggregation of the beads and micro-organisms and non-quantitative retention of the beads and micro-organisms on the slides.

In order to determine the optimum extraction and smear conditions a range of methods were compared. Two extraction methods and two smear methods were used, giving four treatments in all.

## Materials and methods

The sediment used was a mud from Langbank which was stored under aerated seawater until required. Samples of approximately 1.5g wet weight with no overlying water were weighed into two glass 20 ml universal tubes. The treatments used were:

### Treatment 1

Artificial seawater (Tropic Marin salts in distilled water, sterile filtered, 35%) was added to the sediment in the ratio of  $5\text{mlg}^{-1}$  of sediment. The samples were then sealed and shaken vigorously for 10 minutes using a Griffin Flask Shaker.

After agitation the tubes were removed from the shaker and allowed to stand for 30 seconds to allow sediment particles to settle. A 1ml aliquot of the supernatant was then removed and added to an equal volume of 0.01% agar (Difco Bacteriological Agar no.1, sterile filtered) followed by 1ml of latex bead suspension (diameter  $1.091\mu\pm 0.0082\mu\text{m}$   $85.83 \times 10^6\text{ml}^{-1}$ , Sigma chemical co., diluted in sterile filtered seawater). A few drops of Formaldehyde (sterile filtered) were also added to fix the micro-organisms.

The mixture was shaken well and smears were prepared using Frederick's (1965) method. A few drops of the mixture were placed on a clean microscope slide. These were spread thinly and evenly and allowed to air dry in a dust free atmosphere. The slides were then stained over a boiling water bath by flooding their surface with sterile filtered 5% aqueous Rose Bengal. The stain was reapplied as necessary to prevent the slides drying. After 15 minutes the slides were rinsed clean of any excess stain by repeated dipping in distilled water. They were then dried over the water bath and allowed to cool in a dessicator.

When cool the slides were covered with dry coverslips and examined under oil immersion at 1000 x magnification (field of view

= 0.9782 mm<sup>2</sup>). The micro-organisms were stained red by the Rose Bengal. The number of micro-organisms and latex beads in each of 10 random fields of view was recorded for each slide.

#### Treatment 2

The extraction was carried out using 10ml of bead suspension, 1ml of 0.05% w/v agar solution, 0.1ml of 40% formaldehyde and 0.1ml of 1% Teepol (detergent) solution to reduce aggregation. This mixture is ready for smearing immediately following extraction.

Smears were prepared and examined as above but without allowing the sediment to settle before removal of the smear sample.

#### Treatment 3

The extraction method from treatment 1 and the smear method from treatment 2 were used in this treatment.

#### Treatment 4

The extraction method from treatment 2 and the smear method from treatment 1 were used in this treatment.

Two replicate extractions were prepared for each treatment. Five smears were prepared from each extraction. Ten randomly placed fields of view were examined on each slide. The numbers of beads and micro-organisms and beads in each field of view were noted. This gave 100 fields of view for each treatment.

The number of micro-organisms g<sup>-1</sup> of sediment was calculated, for each treatment, as :

$$N = B.y \frac{\{ C \}}{\{ P \}}$$

Where N=micro-organisms g<sup>-1</sup> of sediment , C=micro-organisms in field of view , P=beads in field of view , y=beads per ml of original suspension , B=ml of bead suspension added per gramme of sediment .



## Results

The ratios of micro-organisms to beads for each of the replicate extractions, and pooled ratios for each of the treatments are given in tables 1.3 and 1.4 respectively. Pooled ratios were calculated using the counts from all 100 of the fields of view on both of the replicates. The coefficients of variation of the ratio of beads to micro-organism numbers are in the order Treatment 1 > 3 > 4 > 2. The relationship between number of beads and micro-organisms in each of the fields of view are shown in figures 1.2-1.5. If both beads and micro-organisms are distributed randomly on the slides, the plot of bead against micro-organism numbers should be linear. Treatment 2 gave the <sup>best</sup> straight line fit between numbers of beads and numbers of micro-organisms.

The significance of the regression lines calculated for the bead and micro-organism count are in the order treatment 1 < 3 < 4 < 2. Treatments 2 and 4 showed less aggregation of beads and micro-organisms than did treatments 1 and 3. Treatments 2 and 3 gave no problems during counting despite the presence of sediment particles on the smears.

Treatment (replicate)	Ratio of beads mean	to micro-organisms (C/P) s.d.	coefficient of variation (%)
--------------------------	------------------------	----------------------------------	---------------------------------

=====			
1(1)	22.3722	21.7861	97.3802
1(2)	13.8391	12.1216	87.5895
2(1)	8.2579	1.5942	19.3052
2(2)	8.2217	1.3748	16.7216
3(1)	13.9791	13.0939	93.6677
3(2)	12.1776	9.4937	77.9604
4(1)	6.3661	3.8600	60.6337
4(2)	7.5067	5.0386	67.1214
=====			

Table 1.3. Ratios of beads (C) to micro-organisms (P), mean standard deviation and coefficient of variation, for each of the replicate treatments

Treatment	Ratio of beads to micro-organisms.		
	mean	s.d.	Coefficient of variation (%)
1	18.3508	18.3941	100.2523
2	8.2168	1.5486	18.8467
3	13.1555	11.6225	88.3463
4	6.9157	4.5032	65.1151

Table 1.4. Pooled ratios of micro-organisms to beads (mean, standard deviation and coefficient of variation) for each of the treatments.

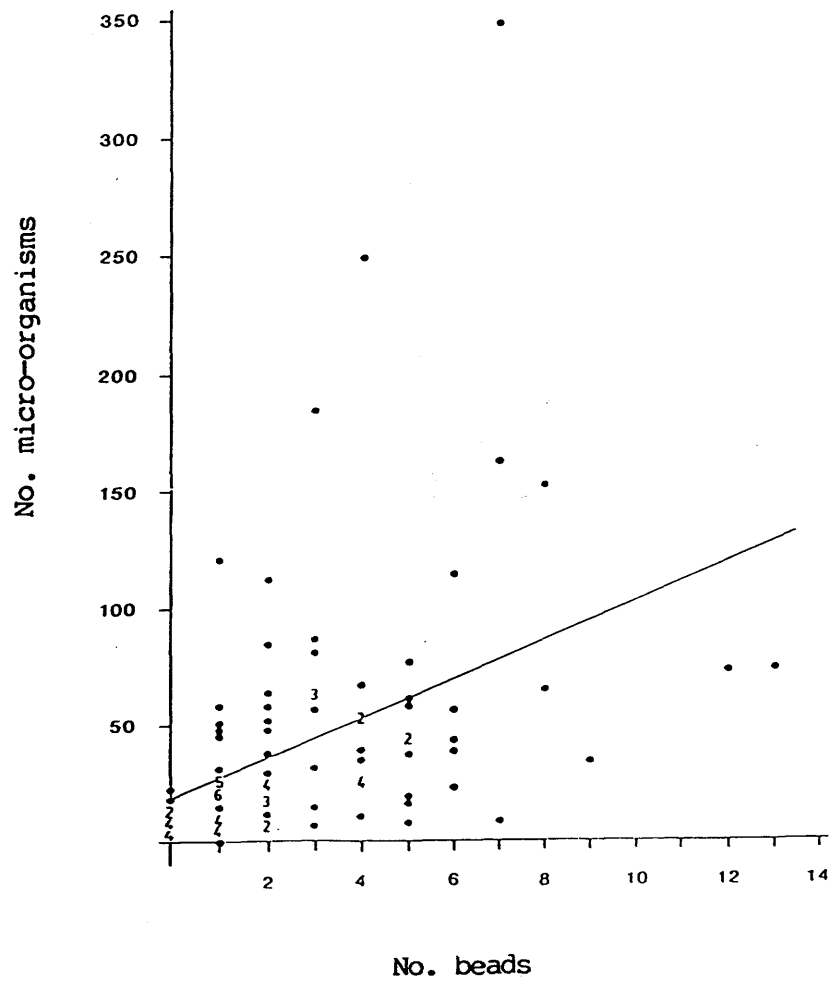


Figure 1.2. Treatment 1. Relationship between number of beads and number of micro-organisms in each field of view.

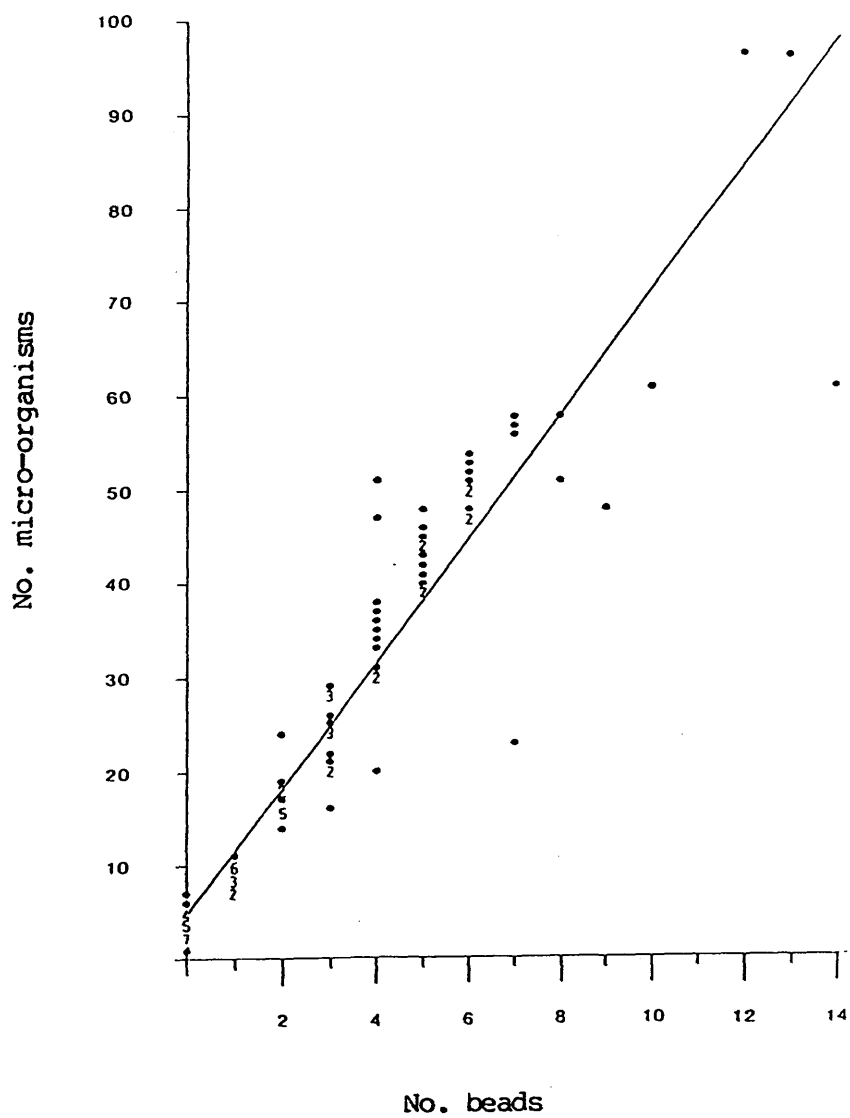


Figure 1.3. Treatment 2. Relationship between number of beads and number of micro-organisms in each field of view.

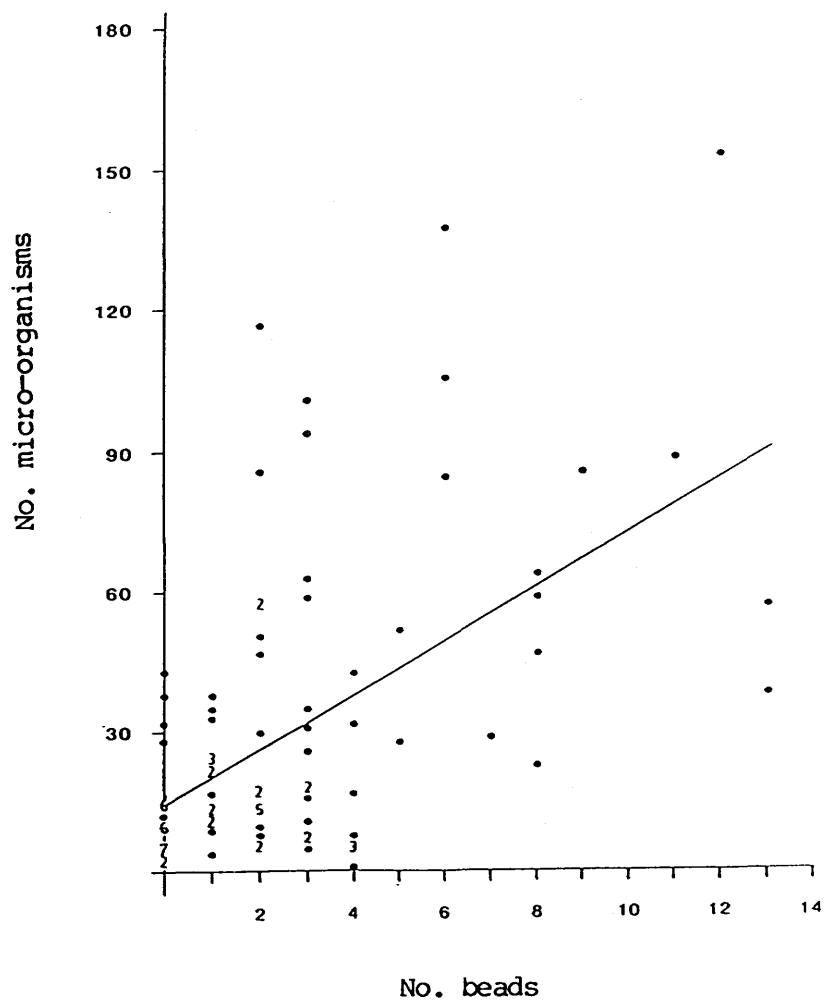


Figure 1.4. Treatment 3. Relationship between number of beads and number of micro-organisms in each field of view.

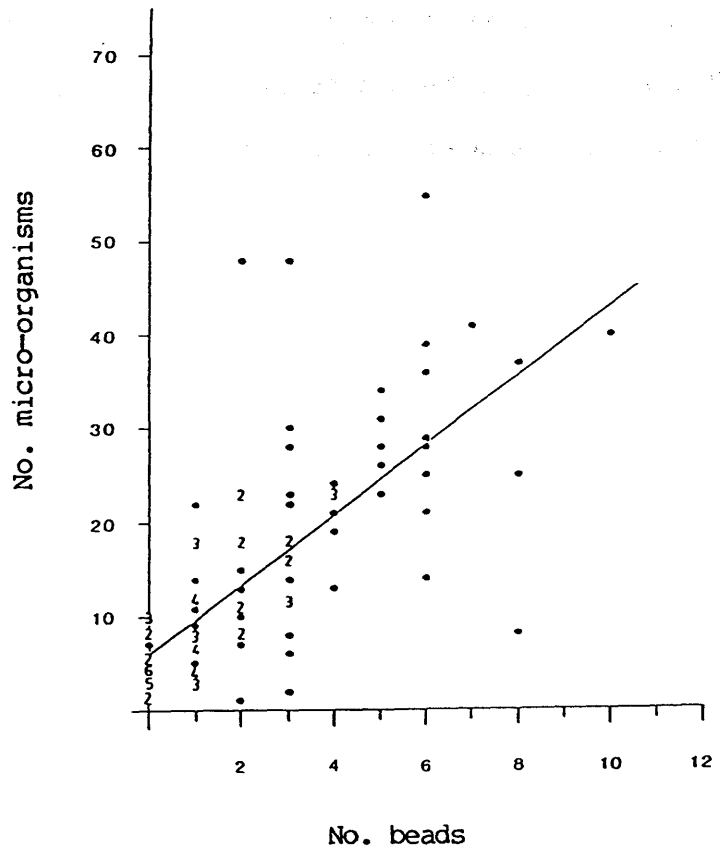


Figure 1.5. Treatment 4. Relationship between number of beads and number of micro-organisms in each field of view.

## Discussion

The extraction and smear method used in treatment two gives a lower coefficient of variation (18.85%) than that of Peterson and Frederick (1979) (32.1%), and also less than that of four replicate plate counts (20 - 30%, Jones, 1979). The reduced scatter in treatments 2 and 4 may be due to improved retention of beads and micro-organisms by the increased agar concentration. The presence of a detergent may also have improved the extraction of micro-organisms from the sediment particles.

Some of the remaining scatter may be due to occasional large micro-organisms, such as diatoms, which tended to give low C/P ratios. This problem was also reported by Peterson and Frederick (1979).

The conditions used in treatment 2 gave the lowest scatter and were adopted as standard for all further smear-ratio counts.



### MEIOFAUNAL PRESERVATIVE COMPARISON.

The aim of this experiment was to compare the effects of three preservatives and one anaesthetic on the numbers of different types of meiofauna that can be extracted from sediment samples.

#### Materials and Methods

The anaesthetic used was a solution of magnesium chloride. The three preservatives used were unbuffered formalin, buffered formalin and Steedmans solution.

Sediment samples were collected from Ardmore between mid and low tide level. Eight sample bottles of 5.5cm diameter ( $23.758 \text{ cm}^2$  area) were pushed gently into the sediment to a depth of 10cm. This gives a sample volume of  $237.58 \text{ cm}^3$ . The bottles were then dug out of the sediment and 125 ml of preservative or anaesthetic was added. Each of the four solution was added to two bottles. The bottles were sealed and shaken, and packed in wet sand to minimise any temperature changes during transport to the laboratory.

The samples containing live animals ( $\text{MgCl}_2$  anaesthetic) were extracted using the decantation technique. Details of this method are given in section 1. This extraction was carried out immediately on return to the laboratory. The other samples were stored at  $4^\circ\text{C}$  and extracted later using the same technique.

All counting was done on samples stained with Rose Bengal under a binocular microscope at 30x magnification. A compound microscope was used for identification as necessary.

**Steedmans solution:** A stock solution of Steedmans preservative was made up as follows (Lincoln and Sheals, 1979).

Propylene phenoxetol (1-Phenoxy Propan-2-ol)	50 ml
Propylene glycol (Propane-1,2-diol)	450 ml
100% commercial Formalin (40% Formaldehyde solution)	500 ml
Sodium B-glycerophosphate	26.32 g

This solution was diluted 1 to 9 with filtered seawater immediately before use.

**Buffered Formalin:** This solution consisted of 100 ml of commercial Formalin, 900 ml of distilled water, 4 g of sodium hydrogen phosphate and 6.5 g of sodium dihydrogen phosphate mixed thoroughly. The solution should have a pH of approximately 7.

**Unbuffered Formalin:** This solution consisted of 100ml of commercial Formalin diluted to 1 litre with distilled water. The solution usually has a pH of 5 - 5.8.

**Magnesium chloride anaesthetic:** This anaesthetic consisted of 70.4 g of analytical grade  $MgCl_2$  dissolved in 1 litre of distilled water. The solution is isotonic with seawater.

## Results

The numbers of each type of meiofauna extracted from the samples are shown in tables 1.5-1.8. The numbers of each meiofaunal taxon extracted from the four treatments were compared using students t-tests. The results of the t-tests are shown in tables 1.9-1.12.

In general the largest numbers of organisms were extracted from the  $MgCl_2$  anaesthetised samples (live animal extraction), followed by Steedmans solution, buffered formalin and unbuffered formalin (table 1.13). This order of extraction efficiency may change for certain types of meiofauna. For example the largest number of turbellarians were extracted from Steedmans solution, followed by magnesium chloride, unbuffered formalin and buffered formalin (table 1.14).

Meiofaunal type	sample one	sample two	Mean	s.d.
Nematodes	12736	12921	12828.5	92.5
Foraminiferans	121	137	129.0	8.0
Polychaetes	47	72	59.5	12.5
Oligochaetes	107	124	115.5	8.5
Copepods	29	37	33.0	4.0
Ostracods	53	43	48.0	5.0
Eggs	163	156	159.5	3.5
Tardigrades	7	8	7.5	0.5
Bivalves/Brachiopods	6	7	6.5	0.5
Turbellarians	5	8	6.5	1.5
Ciliates	12	14	13.0	1.0

Table 1.5. Numbers of each Meiofaunal type in the two replicate samples using  $\text{MgCl}_2$  anaesthetic (results are expressed as numbers per  $237.58 \text{ cm}^3$  of sediment, see materials and methods).

Meiofaunal type	sample one	sample two	Mean	s.d.
Nematodes	9418	9563	9490.5	72.5
Foraminiferans	90	92	91.0	1.0
Polychaetes	41	46	43.5	2.5
Oligochaetes	73	91	82.0	9.0
Copepods	19	21	20.0	1.0
Ostracods	35	33	34.0	1.0
Eggs	102	133	117.5	15.0
Tardigrades	3	2	2.5	0.5
Bivalves/Brachiopods	3	4	3.5	0.5
Turbellarians	7	4	5.5	1.5
Ciliates	7	6	6.5	0.5

Table 1.6. Numbers of each Meiofaunal type in the two samples preserved with unbuffered Formalin (results are expressed as numbers per  $237.58 \text{ cm}^3$  of sediment, see materials and methods).

Meiofaunal type	sample one	sample two	Mean	s.d.
Nematodes	9872	10012	9942.0	70.0
Foraminiferans	97	99	98.0	1.0
Polychaetes	46	42	44.0	2.0
Oligochaetes	89	86	87.5	1.5
Copepods	26	22	24.0	2.0
Ostracods	34	41	37.5	3.5
Eggs	119	124	121.5	2.5
Tardigrades	4	6	5.0	1.0
Bivalves/Brachiopods	7	3	5.0	2.0
Turbellarians	2	3	2.5	0.5
Ciliates	4	3	3.5	0.5

Table 1.7. Numbers of each Meiofaunal type found in the two samples preserved with buffered Formalin (results are expressed as numbers per 237.58 cm<sup>3</sup> of sediment, see materials and methods).

Meiofaunal type	sample one	sample two	Mean	s.d.
Nematodes	11324	11417	11370.5	46.5
Foraminiferans	121	112	116.5	4.5
Polychaetes	49	55	52.0	3.0
Oligochaetes	97	108	102.5	5.5
Copepods	27	31	29.0	2.0
Ostracods	39	45	42.0	3.0
Eggs	145	137	141.0	4.0
Tardigrades	7	8	7.5	0.5
Bivalves/Brachiopods	11	7	9.0	2.0
Turbellarians	9	10	9.5	0.5
Ciliates	13	12	12.5	0.5

Table 1.8. Numbers of each Meiofaunal type found in the two samples preserved with Steedmans solution (results are expressed as numbers per 237.58 cm<sup>3</sup> of sediment, see materials and methods).

Treatment	unbuffered formalin	buffered formalin	Steedmans solution
=====			
<u>CILIATES</u>			
MgCl <sub>2</sub>	t=6.5 0.02 < p < 0.05	t=9.5 0.01 < p < 0.2	t=0.5 0.6 < p < 0.7
unbuffered formalin		t=3.0 0.05 < p < 0.1	t=6.0 0.02 < p < 0.05
buffered formalin			t=10.0 0.001 < p < 0.01
-----			
<u>OSTRACODS</u>			
MgCl <sub>2</sub>	t=14.0 0.001 < p < 0.01	t=10.5 0.001 < p < 0.01	t=6.0 0.02 < p < 0.05
unbuffered formalin		t=3.5 0.05 < p < 0.1	t=8.0 0.01 < p < 0.02
buffered			t=4.5 0.02 < p < 0.05
-----			
<u>EGGS</u>			
MgCl <sub>2</sub>	t=42.0 p < 0.001	t=38.0 p < 0.001	t=18.5 0.001 < p < 0.01
unbuffered formalin		t=4.0 0.05 < p < 0.1	t=23.5 0.001 < p < 0.01
buffered formalin			t=19.5 0.001 < p < 0.01
=====			

TABLE 1.9. t-tests comparing the number of organisms extracted from the different treatments (e.g. Ciliates: MgCl<sub>2</sub> vs. unbuffered formalin, t=6.5). In all cases n=2.



Treatment	unbuffered formalin	buffered formalin	Steedmans solution
=====			
<u>TARDIGRADES</u>			
MgCl <sub>2</sub>	t=5.0 0.02 < p < 0.05	t=2.5 0.1 < p < 0.2	t=0.0 p=1.0
unbuffered formalin		t=2.5 0.1 < p < 0.2	t=5.0 0.02 < p < 0.05
buffered formalin			t=2.5 0.1 < p < 0.2
-----			
<u>BIVALVES/BRACHIOPODS</u>			
MgCl <sub>2</sub>	t=3.0 0.05 < p < 0.1	t=1.5 0.2 < p < 0.3	t=2.5 0.1 < p < 0.2
unbuffered formalin		t=1.5 0.2 < p < 0.3	t=5.5 0.02 < p < 0.05
buffered formalin			t=4.0 0.05 < p < 0.1
-----			
<u>TURBELLARIANS</u>			
MgCl <sub>2</sub>	t=1.0 0.4 < p < 0.5	t=4.0 0.05 < p < 0.1	t=3.0 0.05 < p < 0.1
unbuffered formalin		t=3.0 0.05 < p < 0.1	t=4.0 0.05 < p < 0.1
buffered formalin			t=7.0 0.01 < p < 0.02
=====			

Table 1.10. t-tests comparing the number of organisms extracted from different treatments (e.g. Tardigrades:MgCl<sub>2</sub> vs. unbuffered formalin t=5.0). n=2 in all cases.

Treatment	unbuffered formalin	buffered formalin	Steedmans solution
=====			
<u>NEMATODES</u>			
MgCl <sub>2</sub>	t=3338.0 p < 0.001	t=2886.5 p < 0.001	t=1458.0 p < 0.001
unbuffered formalin		t=451.5 p < 0.001	t=1880.0 p < 0.001
buffered formalin			t=1428.5 p < 0.001
-----			
<u>FORAMINIFERANS</u>			
MgCl <sub>2</sub>	t=38.0 p < 0.001	t=31.0 0.001 < p < 0.01	t=12.5 0.001 < p < 0.01
unbuffered formalin		t=7.0 0.01 < p < 0.02	t=25.5 0.001 < p < 0.1
buffered formalin			t=18.5 0.001 < p < 0.1
-----			
<u>POLYCHAETES</u>			
MgCl <sub>2</sub>	t=16.0 0.001 < p < 0.1	t=15.5 0.001 < p < 0.1	t=7.5 0.01 < p < 0.2
unbuffered formalin		t=0.5 0.6 < p < 0.7	t=8.5 0.01 < p < 0.02
buffered formalin			t=8.0 0.01 < p < 0.02
=====			

Table 1.11. t-tests comparing number of organisms extracted from different treatments. (e.g. Nematodes: MgCl<sub>2</sub> vs. unbuffered formalin t=3338.0). n=2 in all cases.

Treatment	unbuffered formalin	buffered formalin	Steedmans solution
=====			
<u>OLIGOCHAETES</u>			
MgCl <sub>2</sub>	t=33.5 p < 0.001	t=28.0 0.001 < p < 0.01	t=13.0 0.001 < p < 0.01
unbuffered formalin		t=5.5 0.02 < p < 0.05	t=20.5 0.001 < p < 0.01
buffered formalin			t=15.0 0.001 < p < 0.01
-----			
<u>COPEPODS</u>			
MgCl <sub>2</sub>	t=13.0 0.001 < p < 0.01	t=9.0 0.01 < p < 0.02	t=4.0 0.05 < p < 0.1
unbuffered formalin		t=4.0 0.05 < p < 0.1	t=9.0 0.01 < p < 0.02
buffered formalin			t=5.0 0.02 < p < 0.05
=====			

Table 1.12. t-tests comparing number of organisms extracted from different treatments. (e.g. Oligochaetes: MgCl<sub>2</sub> vs. unbuffered formalin t=33.5). n=2 in all cases.

Treatment	MgCl <sub>2</sub>	unbuffered formalin	buffered formalin	Steedmans solution
=====				
Nematodes	100	73.9798	77.4993	88.6347
Foraminiferans	100	70.5426	75.9690	90.3101
Polychaetes	100	73.1092	73.9496	87.3950
Oligochaetes	100	70.9957	75.7576	88.7446
Copepods	100	60.6061	72.7273	87.8788
Ostracods	100	70.8333	78.1250	87.5000
Eggs	100	73.6677	76.1755	88.4013
Tardigrades	100	33.3333	66.6667	100
Bivalves/Brachiopods	72.2222	38.8889	55.5556	100
Turbellarians	68.4211	36.8421	26.3158	100
Ciliates	100	50.0000	26.9231	96.1538
=====				
Mean %	94.6039	59.3453	64.1513	92.2744
standard deviation	11.4754	15.6445	18.7316	5.2622
=====				

Table 1.13. Numbers of each type of meiofauna extracted from the four treatments expressed as a percentage of the maximum number extracted.

Meiofaunal organism	MgCl <sub>2</sub>	unbuffered formalin	buffered formalin	Steedmans solution
Ciliates	1	3	4	2
Ostracods	1	4	3	2
Eggs	1	4	3	2
Tardigrades	1=	4	3	1=
Bivalves/Brachiopods	2	4	3	1
Turbellarians	2	3	4	1
Nematodes	1	4	3	2
Foraminiferans	1	4	3	2
Polychaetes	1	4	3	2
Oligochaetes	1	4	3	2
Copepods	1	4	3	2
Modal values	1	4	3	2

**Table 1.14.** Table showing the order of extraction of highest numbers of each meiofaunal type from each of the four treatments. For example, number of ciliates extracted from MgCl<sub>2</sub> samples > number from Steedmans > numbers from unbuffered formalin > number from buffered formalin. (Modal value = most common value).

## Discussion

The number of meiofauna that could be extracted from Ardmore sand was highest in unpreserved samples. This lack of preservation, however, means that even for resilient taxa such as nematodes, samples cannot be stored for more than 2-3 days before extraction and counting. Samples collected for quantitative analysis of soft taxa such as ciliates and turbellaria need to be extracted much sooner after collection - usually within hours if quantitative data is required (Hulings and Gray, 1971; Lincoln and Sheals, 1979).

Slightly fewer animals were extracted from sediment samples preserved with Steedmans solution. Preservation in Steedmans solution may, however, be the preferred method as it is often impossible to extract and count meiofauna from collected samples immediately after collection.

Unbuffered formalin is acidic and tends to degrade calcareous matter as well as causing brittleness in soft bodied animals. Buffered formalin also causes brittleness but the degradation of calcareous structures is avoided (Lincoln and Sheals, 1979; Swedmark, 1971). Steedmans solution is buffered by sodium B-glycerophosphate thus avoiding damage to calcareous material. It also has the advantage of combining formalin fixation and preservation with the softening action of propylene phenoxetol and propylene glycol.

It is possible that larger differences between the four preservation methods would have been found if the samples had been stored for a longer period. Some of these differences would be caused by the progressive dissolution of calcareous structures by the unbuffered formalin. There would also be some effect due to animals becoming progressively more brittle in formalin, thus tending to be more easily damaged by the extraction procedure.

Differences in extraction efficiency caused by long-term storage were not, however, examined as the period of storage used in this experiment was comparable with that which would be used for routine samples.

## MEIOFAUNAL EXTRACTION METHODS.

### Decantation

A sediment sample was placed in a large container with an equal volume of filtered seawater and stirred into suspension. The heavier sediment particles were then allowed to settle for five to ten seconds following which the supernatant was decanted through a 45  $\mu\text{m}$  sieve. This supernatant contained animals which, because of their lower density, had not settled with the sediment particles.

The seawater from the first extraction was retained, returned to the sediment, and the extraction repeated. Four extractions were usually necessary to obtain extraction efficiencies of over 95%. After the extractions the animals were back-washed off the sieve with clean seawater or preservative solution.

Extraction efficiency was determined by examination of the residual sediment. This was performed whenever a new sediment type was used and also periodically for any series of samples (Hulings and Gray, 1971).

This method is suitable for live or preserved material. Animals in live samples may be anaesthetised by using solutions of chloral hydrate or magnesium chloride (6% w/v) for the extraction.

There are several potential problems with this method. These include damage to animals during stirring, the time-consuming nature of the extraction and the presence of sand grains in the final sievings.



### Elutriation

This method, like decantation, relies on the different densities of animals and sediment. A sample of sediment was placed in a separating funnel (figure 1.6) which had a water supply attached to its base and an outlet at its top leading to a sieve. Seawater was pumped upwards through the sediment in the separating funnel. The water flow was adjusted so that the sediment particles were fluidised and lifted  $2/3^{\text{rds}}$  of the way up the funnel before falling back. The animals, having a lower density, were carried over onto the sieve by the water flow.

The elutriator that I built for extracting live animals from Ardmore sand for the flux experiments was a closed circuit system (figure 1.7, plate 1.1). This system had a seawater tank containing a submerged pump. The outlet from this pump was connected via a series of flow splitters to eight separating funnels. An excess pressure by-pass from the pump was used for coarse control of the water flow to the funnels. This was mainly used to compensate for the sample size, smaller samples requiring lower water pressures. A pair of taps under each funnel were used for fine adjustment of the flow rate. These taps also enabled any or all of the funnels to be run simultaneously. Each of the separating funnels was connected to a separate sieve, the elutriating water draining through the sieves back into the storage tank. Individual funnels were removed by switching the water flow off under the funnel and removing the funnel from the support frame.

Elutriation for 20-25 minutes usually produced an extraction efficiency of over 99% (tested as for the decantation technique). Thus, if samples were staggered by five minutes when the elutriator was set-up, by the time the eighth sample was running the first sample could be removed. This made the elutriator very time-

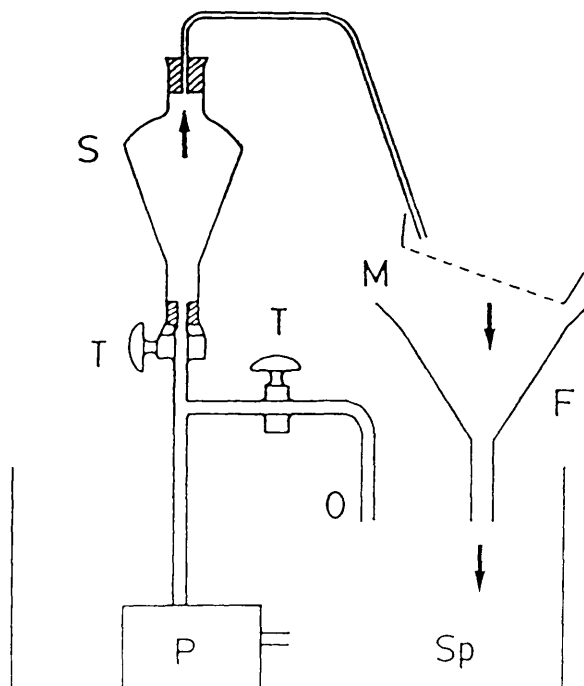
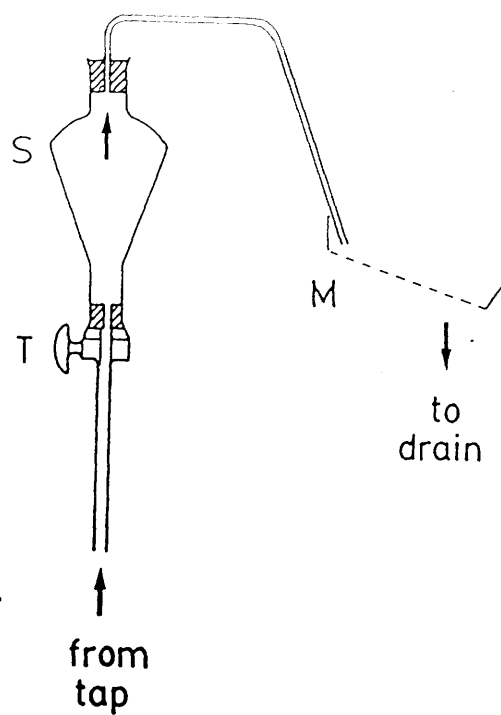


Figure 1.6. (Top) Single elutriator attached to tap-water supply.

Figure 1.7. (Bottom) Closed circuit elutriator.

S = separating funnel; T = tap; M = 45  $\mu$ m mesh sieve; F = funnel;

Sp = sump; P = pump. Arrows indicate direction of water flow.

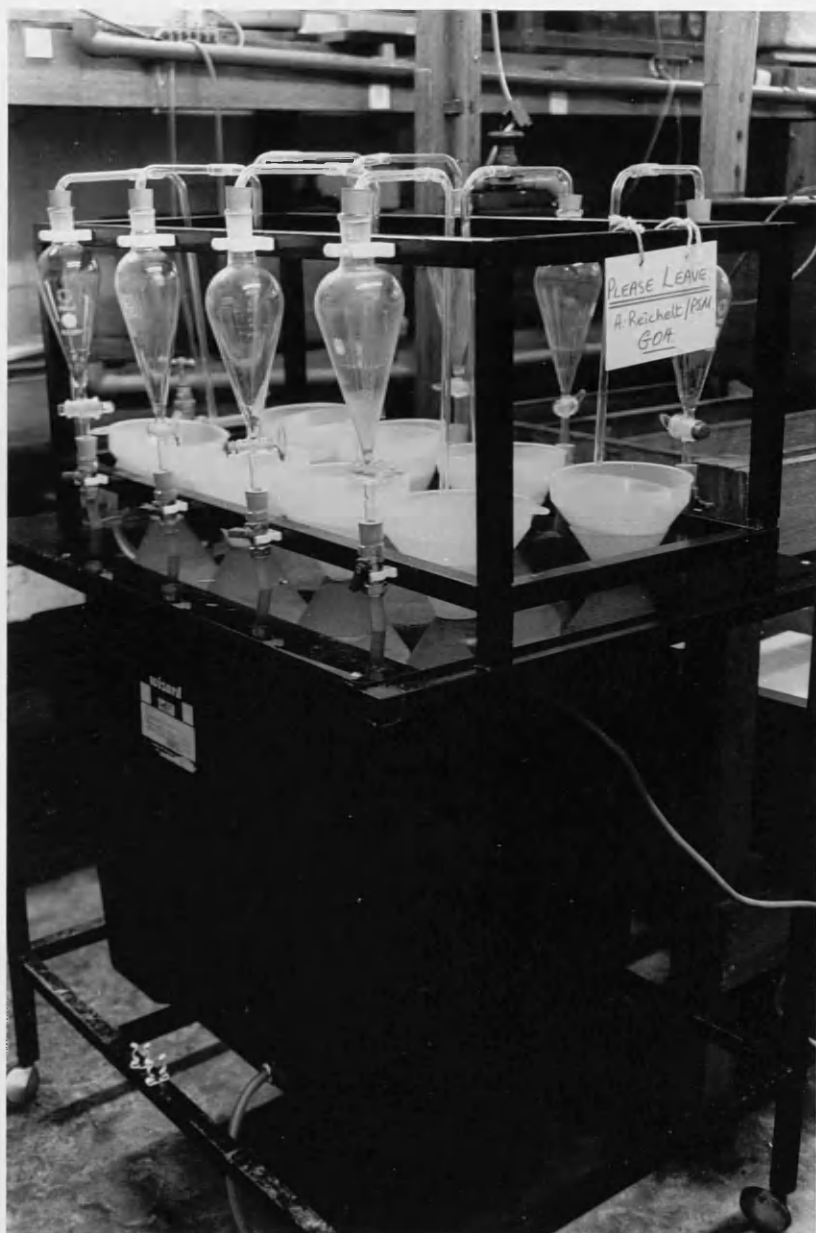


Plate 1.1. Closed circuit elutriator used for meiofaunal extraction.

efficient for large numbers of samples.

The only disadvantage I have encountered with this method is the need for mains electricity to run the pump. This limitation means that closed-circuit elutriation cannot be carried out in the field. Animal damage during extraction is negligible and very few sand grains are carried over onto the sieves.

The elutriation technique and the decantation technique are both suitable for either live or preserved material. The extraction efficiency for live samples is improved by anaesthetisation of the animals before extraction. In general extraction is easiest when most sediment particles are over 125  $\mu\text{m}$  diameter because few particles of this size and over are carried over onto the sieves during extraction.

### Ludox density-difference flotation.

This method was developed by de Jonge and Bouwman (1977) and is based on the difference in density between organic matter and sediment particles. Early flotation media included carbon tetrachloride (Dillon, 1964) and solutions of saccharose (Heip et al, 1974). Neither of these methods were entirely suitable for regular use. Carbon tetrachloride produces highly toxic fumes and is not water miscible, and saccharose solutions are prone to bacterial growth. Ludox-TM is a commercial colloidal silica suspension with a specific gravity of  $1.39 \text{ gcm}^{-3}$  and can be diluted with distilled water to produce a suitable specific gravity before use.

A  $5 \text{ cm}^3$  sample of sediment was drained on a  $45 \mu\text{m}$  sieve and rinsed with distilled water to remove as much salt as possible. This was necessary because Ludox produces an insoluble precipitate if mixed with seawater. The sediment sample was then washed into a 500 ml beaker containing 250 ml of 25 % v/v Ludox. This dilution produces a medium with a specific gravity of  $1.0975 \text{ gcm}^{-3}$ . The mixture of Ludox and sediment was then stirred into suspension with a magnetic stirrer. When the sediment was evenly dispersed the stirrer was switched off. The beaker was then covered with tinfoil and left for 24 hours for the sample to separate.

During the 24 hour separation period the animals and other organic matter floated to the surface of the Ludox suspension. This was due to the lower density of animals and organic matter compared with sediment particles. The sediment particles, having a density higher than  $1.0975 \text{ gcm}^{-3}$ , sank to the base of the beaker. For example silica has a specific gravity of approximately 1.67.

At the end of the separating period the supernatant from the beaker was decanted through a  $45 \mu\text{m}$  sieve, the Ludox being retained

for re-use. The material retained on the sieve was then rinsed with distilled water to remove any residual Ludox and transferred to Steedmans solution. This supernatant fraction contained most of the animals from the sediment sample.

The residual sediment in the beaker was also rinsed onto a 45  $\mu\text{m}$  sieve and preserved in Steedmans solution. This fraction contained some of the heavier animals, including some ostracods and foraminifera.

In general the extraction efficiency of Ludox extraction was high, ranging from 90 - 99 % depending on the proportion of heavy-bodied animals in the sample. Ludox extraction is, however, a slow procedure, with samples having to be left for 24 hours to separate. Ludox is highly toxic because it contains dissolved chemicals that prevent the colloidal silica from precipitating. This means that Ludox extraction is only suitable for preserved samples. Despite the limitations of extraction time and its unsuitability for live animal samples, Ludox is an efficient method for removing a high proportion of the animals from muddy sediment samples.

SEDIMENT PRESSES FOR POREWATER EXTRACTION- construction and use.Introduction.

My field sampling work has involved analysis of the concentrations of various dissolved chemical species in the porewaters of muddy sediments. The apparatus which I used for the Tamar estuary samples (section 4) could not remove porewater from very cohesive sediment samples. Robbins and Gustinis (1976) have described simple sediment presses powered by compressed air, suitable for field and laboratory use. The presses which I have used have been developed from their design.

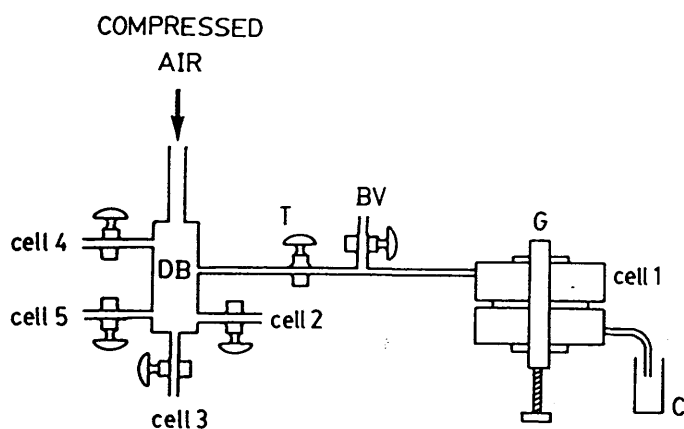
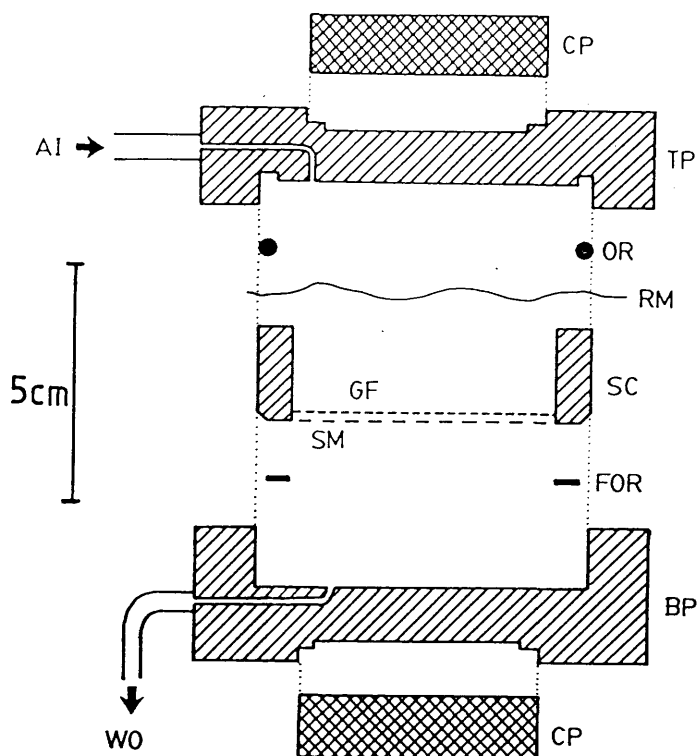
An exploded view of one of my sediment press cells is shown in figure 1.8. The cell essentially consists of two nylon plates enclosing a sediment cartridge. The top plate is connected to a 50 - 90 p.s.i. compressed air supply. The compressed air is used to press a rubber membrane onto the surface of the sediment sample. This pressure reduces the volume of the sediment section by decreasing the size of the interstices. The porewater displaced by this decrease in volume drains through a glass fibre filter into a collection vessel.

The arrangement of sediment presses I have used consists of five press cells connected to a common air supply (figure 1.9, plate 1.2). Each cell is connected to the air supply via a bleed valve and an air tap. Using this arrangement any or all of the cells can be operated independently of each other.

Method.

- (1) A GF/A grade glass fibre filter is inserted into the sediment cartridge.
- (2) The sediment sample to be squeezed is placed on top of the GF/A filter, taking care to minimise the amount of air trapped within the sediment sample.
- (3) The flat O-ring is inserted into the base plate of the filtration cell.
- (4) The sediment cartridge is inserted into the base plate on top of the flat O-ring.
- (5) The rubber membrane is placed on top of the sediment cartridge and the portion of its upper surface resting on the edges of the sediment cartridge is lightly silicone greased.
- (6) The top O-ring is lightly silicone greased and inserted into the groove on the lower face of the top plate.
- (7) The top plate is placed over the sediment cartridge, the clamp plates are inserted and the cell is sealed using firm hand pressure on a G-clamp (figure 1.9, plate 1.2).
- (8) The outlet tube is placed into a water collection vessel, the bleed valve is closed and the air tap opened. This procedure starts the squeezing of the sediment section.
- (9) When the sediment section has been drained of water the air tap is closed, the water drain tube is removed from the collection vessel and the bleed valve is opened. This allows all the air above the rubber membrane to decompress. The cell can then be disassembled in reverse order.





**Figure 1.8.** (Top) Exploded view of a single squeezing cell. CP = aluminium clamp plate; AI = air inlet; TP = nylon top-plate; OR = o-ring seal; RM = rubber membrane; GF = glass fibre filter; SC = sediment cartridge; SM = stainless steel mesh; FOR = flat o-ring seal; BP = nylon base-plate; WO = water outlet.

**Figure 1.9.** (Bottom) Single filtration cell connected to air distribution system. DB = air distribution box; T = tap; BV = bleed valve; G = G-clamp; C = water collection vessel.

# Discussion

I have used these squeezing cells for all of the sediment samples I collected from the deep-sea (see Table 1). The cells can remove a large proportion of the interstitial water from these sediments very quickly, the squeezing times for single sediment sections always being less than 10 minutes. On 30 ml of extracted porewater.

The sediment press cells used for porewater extraction.



Plate 1.2. Sediment press cells used for porewater extraction.

Foreground - disassembled cell. Left to right; twin air tap system, base plate, flat o-ring, sediment cartridge, rubber membrane, top-plate, aluminium clamp-plate. Background - assembled cell with collection vessel in position.

### Discussion

I have used these squeezing cells for all of the sediment samples I collected from the deep-sea (section 3). The cells can remove a large proportion of the interstitial water from these cohesive sediments very quickly, the squeezing times for single sediment sections always being less than 10 minutes for 20 ml of extracted porewater.

The sediment presses could also be used for the removal of porewater from anoxic sediments without aeration. This would be achieved by sectioning the sediment cores into the cells, and squeezing the sediment, in a glove box filled with nitrogen and using compressed nitrogen for the squeezing.

**SECTION TWO - FLUX EXPERIMENTS.**

## Introduction.

In the last twenty years there has been increasing interest in the effects of various environmental factors on the flux of materials between marine sediments and the water column (GOFS, 1984, 1986; Smith, 1984). Experimental studies of these effects have been carried out in both in situ and, to a lesser extent, in shipboard and landbased laboratories. The landbased studies have included both the measurement of fluxes through the interface of 'undisturbed' sediment cores collected from the field and also the use of artificial (not field-collected) sediment columns.

Most of the studies of fluxes under in situ field conditions have involved the use of benthic chambers. The various types of benthic chambers which have commonly been used are described by Zeitzschel (1980). In the intertidal and shallow (<30 m) subtidal regions these chambers have generally been placed and sampled by hand using SCUBA equipment where necessary (Rowe et al, 1975; Stewart, 1975; Hartwig, 1976; Nixon et al, 1980; Zeitzschel, 1980; Balzer, 1984; Balzer et al, 1987; Boucher and Boucher-Rodini, 1988). The advances in deep-sea submersible, deep-water free vehicle and remote underwater manipulator technology in recent years have now made similar in situ experimental work possible in deeper water. Some of the sampling/monitoring equipment now being used incorporates sampling grabs to retain the sediment under the chamber at the end of the deployment. These grabs allow the measured fluxes to be related directly to the physical, chemical and biological parameters of the sediment enclosed by the sampler (Hargrave and Connolly, 1978; Zeitzschel, 1980; Boynton and Kemp, 1985; Simon, 1988).

A second area of flux studies on natural sediments which has received a large amount of attention is the laboratory study of

fluxes across the interface of sediment cores collected from the field (Vanderborght and Billen, 1975; Blake and Leftley, 1977; Jorgensen, 1977; Nixon et al, 1980; Blackburn and Henriksen, 1983; Hennig et al, 1983; Balzer, 1984; Boaden and Elhag, 1984; Raaphorst and Brinkman, 1985). Many of these studies have been carried out in conjunction with profiling of related parameters within the sediment column.

The fluxes of a wide range of chemical parameters have been studied in the field. Much of this work has concerned the flux of dissolved oxygen across the interface as a measure of sediment community oxygen consumption (Rowe et al, 1975; Smith et al, 1978; Nixon et al, 1980; Balzer, 1984; Boaden and Elhag, 1984; Boynton and Kemp, 1985; Balzer et al, 1987). There have also been studies on the transfer of dissolved metals and inorganic and organic nutrients through the interface (Correll et al, 1975; Rowe et al, 1975; McLachlan, 1978; Smith et al, 1978; Blackburn and Henriksen, 1983; Balzer, 1984; Boynton and Kemp, 1985; Gray, 1985; Balzer et al, 1987; Boucher and Boucher-Rodoni, 1988; Simon, 1988)

There have been comparatively few attempts to correlate measured fluxes across the interface of field sediments with biological and physical parameters within the sediments. Most of the flux data quoted in the literature is for bulk sediment samples, no related biological or physical data being given (Rowe et al, 1975; Stewart, 1975; Blackburn and Henriksen, 1983; Balzer, 1984; Balzer et al, 1987; Goeyens et al, 1987; Boucher and Boucher-Rodoni, 1988; Simon, 1988). Most of the work that has been done on the relationship between biological parameters and fluxes in field sediments has concerned the effect of micro-organisms and, to a lesser extent, macrofauna (Stewart, 1975; Vanderborght and

Billen, 1975; Blake and Leftley, 1977; Jorgensen, 1977; Smith et al, 1978; Koop and Griffiths, 1982; Blackburn and Henriksen, 1983; Hennig et al, 1983; Owens and Stewart, 1984; Balzer et al, 1987; Boucher and Boucher-Rodoni, 1988). In contrast there is little information on the relationship between meiofauna and chemical fluxes in the field (McLachlan, 1978; Smith et al, 1978; Koop and Griffiths, 1982; Hennig et al, 1983; Boaden and Elhag, 1984; Gray, 1985; Boucher and Boucher-Rodoni, 1988).

The work which has been done concerning the relationship between measured fluxes and physical factors within field sediments has generally been concerned with the effects of sediment pore size and the effects of water flow both above and through the sediment column (Rhoads et al, 1975; Vanderborght and Billen, 1975; McLachlan, 1978; Balzer et al, 1987; Simon, 1988).

The most studied factors in field sediments with respect to interfacial fluxes have been the levels of various chemical parameters (Rhoads et al, 1975; Stewart, 1975; Hartwig, 1976; Lee et al, 1977; McLachlan, 1978; Hennig et al, 1983; Balzer, 1984; Owens and Stewart, 1984; Balzer et al, 1987). The chemical factors studied have included the rates of nutrient addition to sediments, pollutant loading, Eh and pH, sulphate reduction rates and nitrogen transformation rates (Blake and Leftley, 1977; Smith et al, 1978; Koop and Griffiths, 1982; Blackburn and Henriksen, 1983; Gray, 1985; Raaphorst and Brinkman, 1985; Balzer et al, 1987; Goeyens et al, 1987; Simon, 1988).

There have been considerably fewer laboratory flux studies on artificially manipulated field sediments than on 'undisturbed' field sediments. This is probably due to the difficulty in creating and maintaining artificial sediment columns in the laboratory and also the difficulty in relating sediment systems manipulated in the

laboratory to field sediments (Pugh, 1976; Kristensen, 1984; Smith, 1984; Seitzinger and Nixon, 1985).

In general, laboratory flux studies have, like field studies, studied the effects of bulk sediment on dissolved chemical concentrations in the overlying water or the effects of macrofauna and micro-organisms on dissolved chemical fluxes (Aller, 1978a; Wormald and Stirling, 1979; Kristensen, 1984; Matisoff et al, 1985). Most of the laboratory studies have tested the effects of various types of micro-organisms on the rates of nitrogen, sulphur and carbon cycling through sediments and on the oxygen consumption of sediments (Fillos, 1977; Lee et al, 1977; Wormald and Stirling, 1979; Matisoff et al, 1985).

The laboratory flux studies have included investigations on a wider range of physical factors than the field studies. The factors studied in the laboratory include sediment layering, particle/pore size and sediment disturbance (Aller, 1978a; Krom and Berner, 1980).

Artificial manipulation of field sediment columns in the laboratory has been used to separate the effects of micro-organisms on fluxes from those of larger sediment biota (Wormald and Stirling, 1979; Frithsen, 1984; Kristensen, 1984; Matisoff et al, 1985). This work has involved the selective enrichment of micro-organisms and also the use of antibiotics to remove any effects due to bacteria (Wormald and Stirling, 1979; Hennig et al, 1983; Seitzinger and Nixon, 1985). Some of this work has included separation of meiofaunal effects from those of macrofauna and micro-organisms (Wormald and Stirling, 1979; Hennig et al, 1983; Frithsen, 1984).

Much of the large scale artificial sediment column work has



been done using the MERL (Marine Ecosystems Research Laboratory) micro- and meso-cosms at the University of Rhode Island. These have been designed so that the water flow within and above a sediment column can be regulated to simulate natural conditions (Frithsen, 1984; Seitzinger and Nixon, 1985). Other workers have also used artificial columns with and without water flow to simulate field conditions (Pugh, 1976; Fillos, 1977; Aller, 1978a; Wormald and Stirling, 1979; Krom and Berner, 1980; Hennig et al, 1983; Kristensen, 1984; M<sup>^</sup>atisoff et al, 1985; Raaphorst and Brinkman, 1985; Roman et al, 1988).

There is also some literature on the effects of macro-faunal burrows on nutrient flux, and on the flow of water through sediments which will affect nutrient flux (Kristensen, 1984; Ray and Aller, 1985). This work has been carried out using natural burrows with and without animals and also artificial burrows with and without animals.

Another approach has been to use diffusion cells. Krom and Berner (1980) investigated the flux of dissolved sulphate, ammonium and phosphate between two samples of anoxic mud. One of the sediment samples was low in ammonium and phosphate but high in sulphate, the other was low in sulphate but high in ammonium and phosphate. The two samples were sealed into the chambers of the diffusion cells, separated by a filter paper to prevent sediment movement. Krom and Berner then studied the flux of nutrients between the two samples by following changes in porewater concentration of the nutrients with time.

Diffusion cells were also used by Aller (1983) to study the flux of dissolved silicate and ammonium across the burrow linings of eight species of marine macro-invertebrates. In Aller's work two well mixed chambers of known volume and initial solute

concentration were separated by burrow linings. Aller calculated the fluxes across the linings as the change in concentration in the chambers with time.

My work has involved the use of a modified form of the diffusion cell. Two chambers of the diffusion cell are separated by a thin layer of sediment supported on a nylon mesh (figure 2.2). This layer simulates the interfacial sediment of a sedimentary column. The pore size of the nylon mesh ( $35\ \mu\text{m}$ ) on which the sediment rests is greater than the pore size of the sediment. The mesh should therefore have little or no effect on the flux of dissolved material through the sediment layer.

The chambers on either side of the sediment layer contain seawater. The upper chamber is open to the atmosphere but protected from dust by a loose-fitting lid. The lower chamber is totally filled with water so that transfer of material to it can only occur through the sediment layer. The upper chamber simulates the lower portion of a water column. The lower chamber and the sides of the sediment layer are masked to prevent any effects due to light. The lower chamber simulates the presence of a larger volume of interstitial water at the base of the layer of sediment. There will be no diagenetic changes within this chamber. This assumption is reasonable because the lower chamber is isolated from the atmosphere and contains no sediment.

The advantage of my diffusion cell technique compared to a longer sediment column is that it allows interfacial effects to be separated from those occurring deeper in the sediment column. The large volume of water at the base of the sediment section also allows smaller volumes of sediment to be used than would be necessary if the sediment porewater were being sampled. The small

volume of the sediment section also eliminates some of the problems associated with meso- and macro-scale variability in sediment structure, for example uneven sediment thickness and uneven particle size distribution.

The work reported in this section consists of three experiments using diffusion cells. In these experiments I have looked at the effect of fixed levels of various biological, physical and chemical factors on the flux of five nutrients through the sediment-water interface. In the first experiment I have compared the effects of macrofauna, meiofauna and micro-organisms at natural densities. In the second experiment I have examined the effects of various densities of selected meiofaunal taxa. These taxa have been used both singly and in combination. In the third experiment I have examined the effects of various physical and chemical factors on fluxes in the presence of meiofauna. In each of the experiments I have examined the changes in nutrient concentration in the overlying and underlying water of diffusion cells with time. The changes in nutrient concentration with time have been used to calculate the flux through the sediment-water interface in order to compare the relative effects of each of the parameters studied.

## MATERIALS AND METHODS.

### 1) Comparison of macrofaunal, meiofaunal and micro-organism effects on nutrient fluxes.

Three treatments were used in this experiment. These were sediment containing only micro-organisms, sediment with micro-organisms and meiofauna and sediment containing micro-organisms, meiofauna and macrofauna. Each treatment was run in triplicate.

The top 5 cm of sand from the low intertidal region of Ardmore beach, Firth of Clyde, Scotland (plate 2.1; figure 2.1, site a) was collected and gently homogenised by hand. This sediment was returned to the laboratory, where it was split into four portions each of about 3 litres volume. Two portions of the sediment were stored at 10°C in an aquarium under aerated seawater to keep the animals and micro-organisms within them alive. Twelve subsamples of 3-4 g each were removed from a third portion of the original sediment. These subsamples were used for percentage water and organic matter analyses. Six subsamples were also taken for the analysis of initial micro-organism density using the smear-ratio method described in section 1. The remaining sediment from the third portion was used to assess the densities of macrofauna and meiofauna in the original sediment.

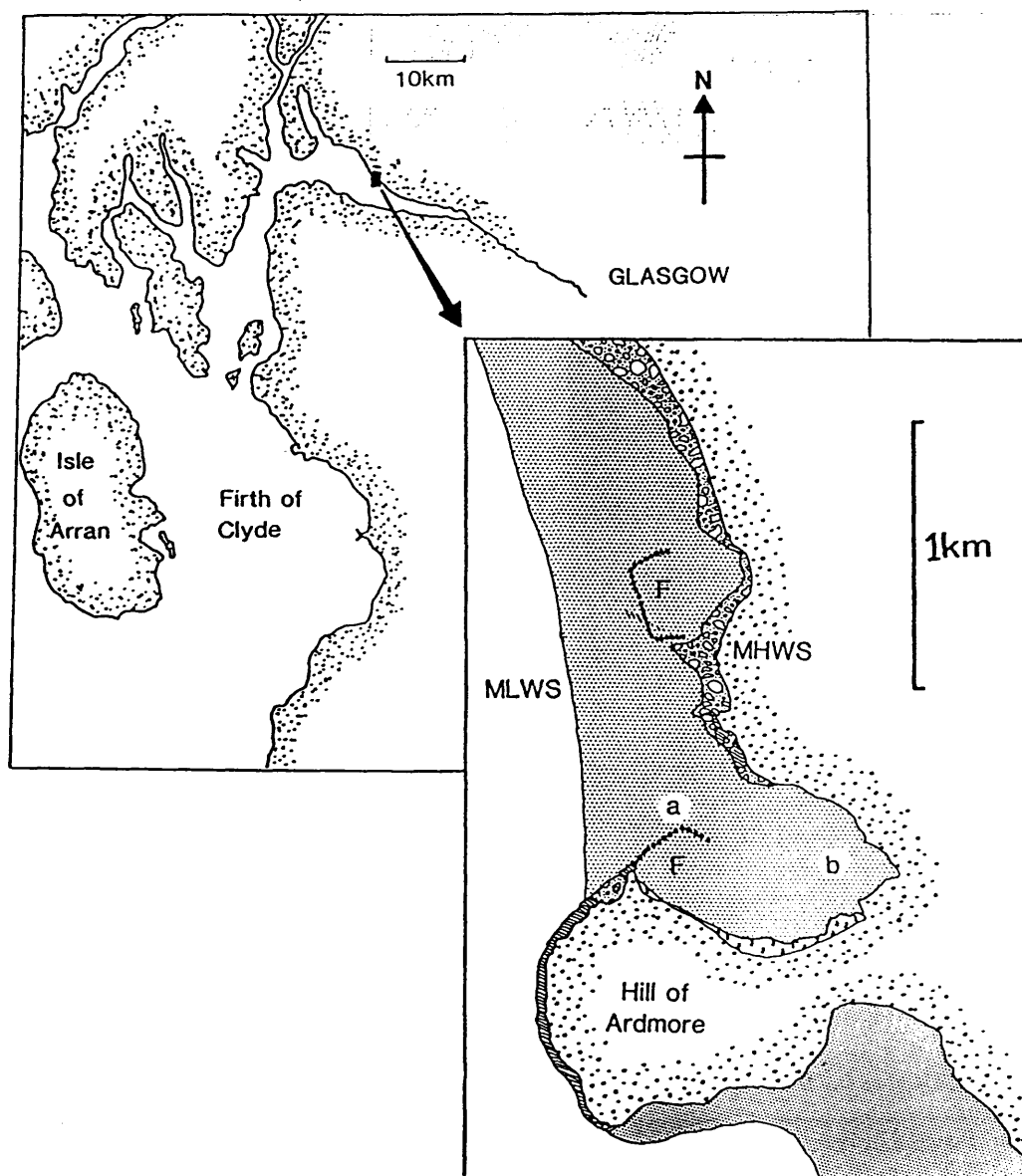
The densities of macrofauna were assessed by wet sieving the sediment through a 500  $\mu\text{m}$  mesh, the animals retained on the mesh being transferred to 10% formalin and stained with Rose bengal. The macrofauna were later sorted and identified under a dissecting microscope. The sediment passing the 500  $\mu\text{m}$  sieve was then elutriated as described in section 1. The elutriate was used for the assessment of initial meiofaunal densities. Meiofauna were counted under a dissecting microscope, a compound microscope was used for



Plate 2.1. Ardmore beach, Firth of Clyde. Low tide area.



Plate 2.2. Ardmore beach, Firth of Clyde. High tide area.



**Figure 2.1.** Map of Ardmore beach, Firth of Clyde, Scotland. a, b = sampling sites (see text); F = old fish yairs.

identification as necessary.

The twelve samples of sediment for water and organic matter content were weighed, dried at 60°C for 24 hours, cooled in a desiccator and reweighed. The water content was calculated as;

$$\% \text{ water} = \frac{\text{wet weight} - \text{dry weight}}{\text{dry weight}} \times 100$$

(B.S.1377)

The sediment samples were then muffle-furnaced at 250°C for 24 hours, cooled in a desiccator and reweighed. These conditions are sufficient to remove all of the organic matter without significantly affecting the inorganic portion of the sediment. The organic matter content was calculated as;

$$\% \text{ organic matter} = \frac{\text{dry weight} - \text{furnaced weight}}{\text{dry weight}} \times 100$$

The fourth portion of the original sediment was used to produce a sediment containing natural densities of micro-organisms but no macro- or meiofauna using the method of Krumbein (1970). This portion was wet sieved through a 500  $\mu\text{m}$  mesh and allowed to settle in seawater. The sediment was then elutriated using the equipment described in section 1. This elutriation was to remove the meiofauna. The sediment was then allowed to settle fully prior to autoclaving at 121°C, 20 p.s.i. for 10 minutes. This autoclaving was to kill any remaining meiofauna and eggs in the sediment.

A suspension of bacteria was produced by shaking one of the two stored portions of sediment with an equal volume of seawater for 15 minutes. This suspension was then filtered through a 10  $\mu\text{m}$  pore size membrane filter to remove any larger organisms. The

seawater passing the filter was then added to the autoclaved sediment along with 250 ml of seawater nutrient broth. The nutrient broth consisted of Oxoid Nutrient Broth made up in 25 ‰ seawater and autoclaved. This mixture was stored at 20° C in a 12 hours day / 12 hours night regime to allow the bacteria to recolonise the sediment. Bacterial numbers in this re-innoculated sediment were assessed daily using the smear-ratio technique described in section 1. This incubation was continued for four days after which the density of micro-organisms in the treated sediment was within the range of that normally found in the initial sediment samples. The sediment was then drained of overlying water and gently rinsed with 35  $\mu$ m filtered seawater to remove any remaining nutrient broth. This sediment was then gently re-homogenised.

The flux cells used in this experiment are shown in figure 2.2. The cells were initially filled with 2 litres of sterile filtered seawater. The treated sediment was introduced through the overlying water. Small volumes of sediment (10-20 ml) were held just below the water surface so that they dispersed into the water column and settled onto the mesh at the base of the overlying water chamber. Larger sediment particles, settling faster through the water column, ensured that no smaller sediment particles passed through the mesh. 250 ml of the re-innoculated sediment was introduced into each cell. This produced a layer approximately 5 cm thick and gave a sediment volume : water volume ratio of 0.125. The cells were then left at 10°C overnight to allow the sediment to settle fully.

Meiofauna were removed from one of the portions of the original sediment which had been stored in aerated seawater using the elutriation technique described in section 1. The meiofauna were



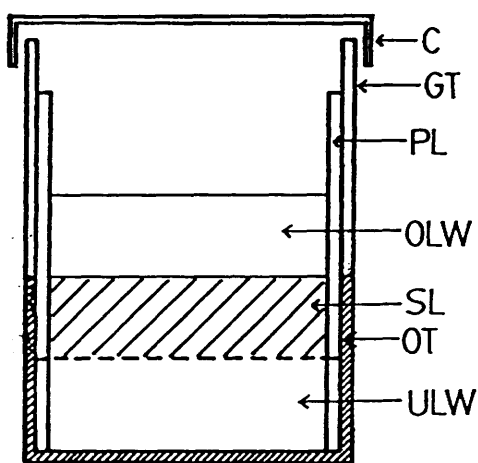


Figure 2.2. Diagrammatic cross-section of a flux cell. C = loose fitting transparent cap; GT = glass tube; PL = plastic liner; OLW = overlying water; SL = sediment layer resting on 35  $\mu\text{m}$  mesh; OT = opaque tube; ULW = underlying water.

transferred to six of the nine flux cells without further sorting. This was done by transferring a portion of the homogenised elutriate containing the animals which came from 250 ml of the original sediment (i.e. one twelfth of the total volume of elutriate) into the overlying water of the flux cells. Macrofauna from the second portion of the original sediment which had been stored in aerated seawater were then added to three of the flux cells. They were removed from the stored sediment by wet sieving through a 500  $\mu\text{m}$  sieve and then gently introduced by hand onto the surface of the sediment in the cells. The cells were left for 12 hours to allow the meiofauna and macrofauna to burrow and acclimatise. The overlying water was aerated continuously after the animals were introduced.

At the beginning of the experiment any macrofauna remaining on the surface of the sediment were removed. This was to ensure that no dead or seriously damaged animals had been introduced to the cells. A layer of liquid paraffin was then poured onto the surface of the outer chamber, isolating it from the atmosphere.

The flux cells were sampled non-destructively over a period of 72 hours. Water samples were removed from the outer (underlying) and inner (overlying) chambers of each of the nine cells after 0, 24, 48 and 72 hours. The water samples were withdrawn using acid washed disposable syringes. The underlying water was sampled using a syringe with an hypodermic needle attached. This was to prevent contamination of the water sample with liquid paraffin. Three 2.5 ml water samples were removed from each chamber of each cell at each sampling time. These water samples were filtered through 0.22  $\mu\text{m}$  membrane filters into 2.5 ml plastic snap-cap vials. The water samples were then stored in a deep-freeze prior to analysis. Nutrient analysis on these water samples was carried out using the

small scale methods described in section 1.

At each sampling time the pH and percentage oxygen saturation of the overlying and underlying water in each cell was measured. The pH was measured using an EIL combination electrode, dissolved oxygen was measured using a flow-through oxygen electrode calibrated for oxygen saturation.

At the end of the 72 hour period of the nutrient sampling the cells were disassembled. The volume of water remaining in each cell was measured. Samples of sediment were taken from each cell for assessment of the micro-organism densities. The remaining sediment was then preserved with its own volume of 10% formalin. This sediment was used for an assessment of final animal types and densities. The densities were assessed as above for the pre-experiment samples.

## 2) The effect of meiofaunal type and density.

In this experiment the changes in nutrient concentration in three replicates each of thirteen treatments were monitored at four time intervals over a period of 28 days. The treatments used consisted of low, medium and high densities each of nematodes, copepods, nematodes plus copepods and whole (unsorted) meiofauna plus a control containing no meiofauna. The medium density of animals used corresponded to the natural density of animals at Ardmore beach at the time of collecting. The low density treatments contained half the number of animals in the medium density. The high density contained twice the numbers of animals in the medium density.

The sediment used in this experiment was collected from the

same site as that used in the previous experiment. Only the top 2 cm of sediment was collected for this experiment. The collected sediment was stored at 10°C under aerated seawater. Meiofauna were removed from 500 ml of the sediment using the closed circuit elutriator described in section 1. These meiofauna were used for practice at handling and transferring single animals without damaging them. The sediment remaining after elutriation was autoclaved at 121°C, 20 p.s.i. for 10 minutes to kill any remaining meiofauna and eggs. The sterilised sediment was re-innoculated in the same way as that used for the previous experiment.

The flux cells were filled with approximately 16 ml of sterile filtered seawater. The bulk re-innoculated sediment was then sub-cored using a 5 ml plastic syringe, the anterior end of which had been removed. Two cm<sup>3</sup> of sediment was added to each of the flux cells by extruding the sediment from the syringe and slicing it off with a spatula. This gave a sediment volume : water volume ratio of 0.125. The sediment was allowed to settle through the water column onto the nylon mesh attached to the inner sleeve of the flux cells. Once the sediment had been added to the cells they were stored at 10°C as above until needed.

The animals to be used in the experiment were extracted from the original bulk sediment by elutriation after 500µm sieving to remove any macrofauna. This was done the evening before the animals were introduced to the flux cells, the animals being stored in aerated seawater at 10°C overnight. The flux cells were set-up on alternate days over the course of a week, a fresh batch of animals being elutriated for each days set-up. Animals were sorted into the cells using a 10 µl fixed-volume pipette. This meant that single animals could be transferred rapidly and easily without causing them mechanical damage.

The whole meiofauna treatments were prepared in the same way as the meiofauna treatments in the previous experiment. The volume of homogenised elutriate added to each experimental cell was such that it contained the meiofauna from two ml of sand for the medium (natural) density, one ml for the low density and four ml for the high density.

A total of 156 cells were set-up in batches of 52, these batches contained a random selection of treatments and incubation times. This randomisation was to minimise any systematic errors due to variations in animal handling and time of set-up.

Flux cells were destructively sampled after 0, 7, 14 and 28 days. The covers of the cells were removed (figure 2.2), the overlying water was drawn off with a syringe and its exact volume noted. This water was sterile filtered through a 0.22  $\mu\text{m}$  GSWP membrane filter into three 2.5 ml plastic snap-cap vials.

The sediment in the cells was then removed from the cells by gently removing the whole inner sleeve. The nylon mesh was backwashed with dilute Steedmans solution (see section 1.) to transfer the sediment into a 7 ml glass bijou bottle.

The water remaining in the cells, which had been underlying the sediment, was then removed with a syringe and treated in the same way as the overlying water. All of the water samples were stored in a deep-freeze for later analysis using the small scale techniques described in section 1.

The meiofauna in the preserved sediment were counted after Rose Bengal staining without prior extraction. This was possible because of the small volume of sediment used in this experiment. This counting was to assess any changes in meiofaunal density over the course of the experiment.

### 3) The effects of various physical and chemical factors.

In this experiment the effects on nutrient fluxes of five levels each of five treatments was compared over a period of 28 days. The treatments used were: salinity, particle size range, compaction, partial pressure of oxygen and animal type/density. The animal type/density treatment was included as a control for comparison with the previous experiments.

The salinities used were 5, 15, 25, 35 and 45 ‰, these were chosen to bracket the range 14.6 - 32.2 ‰ found naturally at Ardmore (personal observation). The natural level for salinity was taken as 25 ‰. The particle size ranges used were: natural, silt (<63  $\mu\text{m}$ ), very fine sand (63-125  $\mu\text{m}$ ), fine sand (125-250  $\mu\text{m}$ ) and medium sand (250-500  $\mu\text{m}$ ) (BS 1377). Over 90 % of the particles found at Ardmore are within these size ranges. The levels of compaction used were; very low, low, natural, high and very high. This range of compactions corresponds to 0.4 - 6.2 x the natural shear strength of undisturbed Ardmore sediment. The partial pressures of oxygen ( $p\text{O}_2$ ) used corresponded to concentrations of 0, 5.2, 10.4, 14.9 and 21 %  $\text{O}_2$  in the air over the flux cells. These levels were chosen to represent the range of conditions from anaerobic to oxygen-saturated surface sediments found at Ardmore. The animal treatments used were: high densities of nematodes and copepods separately, natural and high densities of nematodes plus copepods and a control with no meiofauna. Each of the five factors (salinity, particle size, compaction,  $p\text{O}_2$ , animal type/density) was examined separately. In each treatment the factors not being examined were used at natural levels. For example, in the 50 ‰ salinity treatment, natural Ardmore sediment was used at natural

compaction and 21 % oxygen. The non-animal factor treatments were all carried out using natural densities of nematodes plus copepods in the sediment.

The sediment used in this experiment was collected from Ardmore beach. Part of the sediment was collected from site a (figure 2.1) and part from site b (plate 2.2; figure 2.1). The latter site was used in addition to site a because it contained a larger proportion of fine sediment than site a. All of the sediment was collected from the top 2 cm. The collected sediment was stored at 10°C under aerated seawater until required.

The first sediment treatment consisted of wet-sieving a portion of the sediment collected from both sites through 500  $\mu\text{m}$ , 250  $\mu\text{m}$ , 125  $\mu\text{m}$  and 63  $\mu\text{m}$  sieves. This was to produce the four treated particle size ranges. These sieved sediments were then sterilised along with a larger volume sediment which had been 500  $\mu\text{m}$  sieved and elutriated as in the previous experiment. The sterilization and re-innoculation conditions used were the same as those used in the previous experiment. The treated bulk (sieved and unsieved) sediment was stored under aerated seawater until needed.

120 ml of sterile filtered artificial seawater was added to each of the flux cells. In all of the non-salinity treatments this seawater was at a concentration of 25‰. The artificial seawater used in all of the cells was made from Tropic Marin seawater salts with dissolved nutrient stock solution added such that the final concentration of nutrients was the same in all of the treatments. Fifteen ml of sediment was then added to each of the cells. This produced a sediment volume : water volume ratio of 0.125. The sediment used in all of the non-particle size treatments consisted of the re-innoculated unsieved Ardmore sediment. The sediment was

introduced through the water column using a 20 ml syringe, the anterior end of which had been removed. The sediment in all of the cells was compacted by gentle vibration of the whole cell on a rotamixer. The vibration times used for compaction of the sediment in the compaction treatments were; very low compaction = 0 seconds, low compaction = 15 seconds, natural compaction = 30 seconds, high compaction = 45 seconds and very high compaction = 60 seconds. These vibration times produced initial shear strengths of between 0.105 and 0.85 kNm<sup>-2</sup>. The 30 second compaction time was used for all of the non-compaction treatments.

The meiofauna were introduced to the cells immediately after compaction of the sediment. The meiofauna used were elutriated from the site a sediment which had been stored under aerated seawater. These animals were sorted by hand into the cells using a 10  $\mu$ l pipette as in the previous experiment. The cells were then covered and maintained at 10°C during the experiment.

The pO<sub>2</sub> treatments were run inside double-chambered glove bags. These bags were connected to supplies of pre-mixed gas supplied by British Oxygen Company. The 0 % oxygen treatment was connected to a cylinder of pure nitrogen. The 5.2, 10.4 and 14.9 % oxygen treatments were connected to cylinders containing the appropriate ratio of oxygen to nitrogen. The 21 % oxygen treatments were left open to the atmosphere, but covered in the same way as the non-pO<sub>2</sub> treatments to prevent dust contamination. The double chambered glove bags allow cells being sampled to be removed from the bag without contamination of the rest of the bag by the outside atmosphere. This is done by transferring the cells being sampled into the outer chamber of the bag using the gloves fitted into the bags. The inner chamber is then sealed, the outer chamber opened and the cells removed. The outer chamber can then be resealed and



purged with the appropriate gas mixture before the inner chamber is unsealed.

A total of 300 cells were set-up for this experiment, each treatment being run in triplicate. The cells were set-up on five consecutive days, 60 cells being set-up each day. The cells set-up on each day consisted of a random selection of treatments and incubation times. This was to reduce the effects of any systematic errors.

Flux cells were destructively sampled after 0, 7, 14 and 28 days. The covers of the cells were removed and the overlying water drawn off with a syringe taking care not to disturb the sediment surface. This water was sterile filtered through a 0.22  $\mu\text{m}$  GSWP membrane filter directly into 2.5 ml snap-cap vials. A subsample of approximately 0.5 ml was immediately taken from each vial and its salinity measured using a refractometer.

The shear strength of the sediment was then measured with Geonor cone shear apparatus. All of the shear strength measurements were performed using a 60.11 g cone with an angle of 60°. The measurement is carried out by locating the cone within the body of the apparatus. The height of the body is then adjusted such that the tip of the cone is just touching the sediment surface. The release button is then pressed, allowing the cone to drop. The penetration of the cone into the sediment can then be measured from the scale on the body. The shear strength ( $T_j$ ) is calculated as;

$$T_j = \frac{K \times Q}{h^2} \quad \text{kNm}^{-2}$$

where;  $K = 0.225$  (cone constant)  
 $Q$  = cone weight in grams  
 $h$  = cone penetration in mm

(Hansbro, 1957)

After the shear strength was measured the sediment was removed from the cells by removing the whole inner chamber. The sediment was then backwashed into a 25 ml bijou bottle with Steedmans solution. The meiofauna in these sediment samples were <sup>La</sup> ~~at~~ter extracted using the elutriator described in section 1. The animals were then stained with Rose Bengal and counted under a binocular microscope.

The water remaining in the cells, which had been underlying the sediment, was then drawn off and filtered as above. The salinity of the water in each vial was also measured with a refractometer as above. The overlying and underlying water samples were stored in a deep-freeze prior to analysis using the small scale techniques described in section 1.

## Results

### 1) Comparison of macrofaunal, meiofaunal and micro-organism effects on nutrient fluxes.

The whole sediment collected from Ardmore contained 28.5909 % water (sd = 0.6052) and 3.0546 % organic matter (sd = 1.9082). Numbers of micro-organisms per gram of sediment for each of the treatments are shown in table 2.1. The densities of meiofauna and macrofauna in each of the cells are shown in tables 2.2 and 2.3 respectively. The numbers of each type of organism in the replicate cells have been compared using t-tests. There were no significant differences in density between cells for the micro-organisms, meiofauna or macrofauna.

During the experiment the pH of the overlying water of all cells was constant at 7.1. Dissolved oxygen concentrations in the treatments are shown in table 2.4. The dissolved oxygen concentration in the underlying water of all cells decreased slightly during the experiment. The lowest concentration reached was 90.1 % saturation after 72 hours.

The nutrient concentrations in the overlying and underlying water of each of the three treatments at each sampling time are shown in appendix 2.1 tables 1-5. These values are mean concentrations of the three replicates of each treatment.

The fluxes of each nutrient in each treatment have been calculated by regressing the concentration of each nutrient against time (days). These regressions were carried out separately for the overlying and underlying water chambers. Regressions were carried out using the original data and transformed data. The transformations used were  $\sqrt{y}$ ,  $\log_{10}y$  and  $-1/y$ . The regression lines calculated for each of the transformed and untransformed data sets were compared and the best-fit regression chosen. The best-fit

Sediment	micro-organisms $\times 10^8 \cdot g^{-1}$	
	mean	sd
Natural Ardmore	1.6724	0.2324
Micro-organism treatment	1.5987	0.1867
Meiofauna treatment	1.6386	0.3182
Macrofauna plus meiofauna treatment	1.5828	0.1822

Table 2.1. Densities of micro-organisms in natural Ardmore sediment and in each of the treatments used in flux experiment 1. n=100 in all cases.

Meiofaunal taxon	Meiofauna only	Macrofauna plus meiofauna.
Nematodes	23.3333 (1.1547)	24.6667 (0.5774)
Copepods	5.6667 (2.0817)	4.3333 (0.5774)
Polychaetes	3.3333 (2.6458)	4.6667 (1.1547)
Oligochaetes	4.0000 (2.0817)	3.0000 (1.0000)
Ostracods	5.3333 (3.2146)	2.3333 (1.1547)
Turbellarians	3.6667 (1.1547)	5.0000 (1.0000)
Ciliates	2.0000 (3.2146)	3.6667 (2.6458)
Gastrotrichs	6.3333 (2.6458)	4.3333 (1.1547)

Table 2.2. Flux experiment 1. Densities of meiofauna (number ml<sup>-1</sup>; mean, (sd)) in the meiofauna only and macrofauna plus meiofauna treatments. n=3 in all cases.

Species	mean	sd
<u>Nereis diversicolor</u>	1.3333	0.5774
<u>Scoloplos armiger</u>	3.6667	1.5275
<u>Pygospio elegans</u>	28.3333	4.5040
<u>Bathyporeia pelagica</u>	2.3333	0.5774
<u>Hydrobia ulvae</u>	1.3333	1.1547
<u>Eteone sp.</u>	1.3333	0.5774
<u>Macoma balthica</u>	2.0000	1.0000

Table 2.3. Flux experiment 1. Numbers of macrofauna 50 ml<sup>-1</sup> in the macrofauna plus meiofauna treatment. n=3 in all cases.

Treatment/ Chamber	Time (days)	0	1	2	3
<b>Micro-organisms only</b>					
	O	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)
	U	100 (0.0)	100 (0.0)	97.2 (2.5893)	90.1 (3.6545)
<b>Meiofauna only</b>					
	O	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)
	U	100 (0.0)	100 (0.0)	98.5 (1.9835)	96.2 (3.8547)
<b>Macrofauna plus meiofauna</b>					
	O	100 (0.0)	100 (0.0)	100 (0.0)	100 (0.0)
	U	100 (0.0)	100 (0.0)	97.2 (3.2134)	95.4 (3.8558)

Table 2.4. Flux experiment 1. Percentage saturation (mean, (sd)) of oxygen in the overlying (O) and underlying (U) water of each of the treatments at each sampling time. n=3 in all cases.

regression was taken to be the regression with the largest value for the correlation coefficient. This series of regression analyses gave 30 best fit regressions (three treatments x two water chambers x five nutrients). Of the 30 regressions only three were non-significant. These were the regressions of: phosphate concentration against time for the underlying water of the micro-organisms treatment; sulphate concentration against time for the underlying water of the micro-organisms treatment; and sulphate concentration against time for the overlying water of the macrofauna plus meiofauna treatment. The coefficients of the best-fit regression lines for each of the nutrients in each treatment are given in appendix 2.2 tables 1-5.

Comparison of the overall slope of the regression lines, which is the nutrient flux, was not possible. This was because some of the best-fit regression lines were for transformed data. In order to compare the flux between treatments it was necessary to calculate the flux at a single time in all of the treatments and then compare these values. This was achieved by differentiating the best-fit regression equations and then substituting a single value of  $x$  (time) to obtain an instantaneous flux. For example, an equation of the form  $-1/y = mx + c$  can be rearranged to give  $y = -1/(mx + c)$ . If the latter is differentiated with respect to  $x$  this gives  $dy/dx = m/(m^2x^2 + 2mxc + c^2)$ . The value of  $x$  chosen for substitution was  $x=0$ . The flux calculated using  $x=0$  represents the initial flux. In the above example this gives  $dy/dx = m/c^2$  at  $x=0$ . The use of an initial flux value should remove variations in fluxes caused by progressive changes in nutrient concentration in the overlying and underlying water by examining the flux at the time when there was the least variation in nutrient concentration



between cells.

The initial fluxes ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ ) of each nutrient in each treatment are given in table 2.5. The fluxes of silicate, phosphate and ammonia were all positive for the overlying water and negative for the underlying water. This means that dissolved silicate, phosphate and ammonia were moving from the underlying water chamber into the overlying water chamber during the experiment. The fluxes of sulphate and nitrate were all negative for the overlying water and positive for the underlying water. This means that dissolved sulphate and nitrate were moving from the overlying water into the underlying water.

The initial fluxes of each nutrient in each water chamber have been compared between treatments using t-tests. This was to determine which treatment had the greatest effect on nutrient flux. The results of these t-tests are given in appendix 2.3. A breakdown of the significant differences between treatments is given in table 2.6. Differences were only considered significant if they were significant differences between the initial fluxes calculated from two significant regression lines. Any significant differences calculated using initial fluxes from non-significant regression lines were not used.

Silicate fluxes in both the overlying and underlying water chambers were greatest in the meiofauna only treatments, followed by the macrofauna plus meiofauna treatments and then the micro-organism treatments (table 2.6). Phosphate fluxes in the overlying water chamber were greatest in the meiofauna only treatment followed by the macrofauna plus meiofauna treatment and then the micro-organism treatment. No significant differences were found between phosphate fluxes in the underlying water (table 2.6). The only significant difference in sulphate flux between treatments was

Nutrient	Treatment /chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	sd of m
=====			
SiO <sub>4</sub>	1/O	0.0996	0.0517
	1/U	-0.1407	0.0234
	2/O	1.4187	0.1028
	2/U	-1.3875	0.0401
	3/O	1.9726	0.0350
	3/U	-1.6285	0.0309
PO <sub>4</sub>	1/O	1.5007	0.3186
	1/U	-0.4478	0.3025
	2/O	0.8004	0.2571
	2/U	-1.1359	0.2298
	3/O	2.0660	0.4669
	3/U	-1.5902	0.3935
SO <sub>4</sub>	1/O	-125.2800	53.0350
	1/U	57.9250	6.0055
	2/O	-71.2000	49.0405
	2/U	72.8100	28.6685
	3/O	-201.0080	12.3412
	3/U	261.3200	39.7624
NO <sub>3</sub>	1/O	-4.6798	0.3307
	1/U	3.8023	0.1462
	2/O	-5.3368	0.1775
	2/U	5.0893	0.0812
	3/O	-0.0	0.0
	3/U	5.8250	0.1914
NH <sub>4</sub>	1/O	45.4750	1.3252
	1/U	-17.7625	0.0599
	2/O	25.2175	1.9181
	2/U	-7.5150	1.4523
	3/O	29.1390	0.1991
	3/U	-12.9500	1.3562
=====			

Table 2.5. Flux experiment 1. Initial fluxes of each nutrient in each treatment. 1 = micro-organisms only; 2 = macrofauna plus meiofauna; 3 = meiofauna only. O = overlying water chamber; U = underlying water chamber. Positive fluxes = out of sediment; negative fluxes = into sediment. n=3 in all cases.

Nutrient	Chamber.	Differences
<hr/>		
SiO <sub>4</sub>	O	3 > 2 > 1
	U	3 > 2 > 1
PO <sub>4</sub>	O	3 > 2 > 1
	U	none
SO <sub>4</sub>	O	none
	U	3 > 2
NO <sub>3</sub>	O	2 > 1 > 3
	U	3 > 2 > 1
NH <sub>4</sub>	O	1 > 3 > 2
	U	1 > 3 > 2
<hr/>		

Table 2.6. Flux experiment 1. Summary of significant differences in initial flux between treatments. 1 = micro-organisms only; 2 = macrofauna plus meiofauna; 3 = meiofauna only. O = overlying water chamber; U = underlying water chamber.

between the meiofauna and macrofauna plus meiofauna treatments in the underlying water, the meiofauna only treatment showing the greater flux (table 2.6). Nitrate fluxes in the overlying water chamber were greatest in the macrofauna plus meiofauna treatment, followed by the micro-organism treatment and then the meiofauna treatment. Nitrate fluxes in the underlying water chamber were greatest in the meiofauna only treatment, followed by the macrofauna plus meiofauna treatment and then the micro-organism treatment (table 2.6). Ammonia fluxes in both the overlying and underlying water chambers were greatest in the micro-organism treatment followed by the meiofauna treatment and then the macrofauna plus meiofauna treatment (table 2.6)

## 2) The effect of meiofaunal type and density.

The final densities of meiofauna in each of the treatments used in this experiment are shown in table 2.7. The initial and final densities of meiofauna in the nematode, copepod and nematode plus copepod treatments have been compared using t-tests. None of the faunal densities changed significantly during the experiment.

The nutrient concentrations in each of the treatments at each sampling time for the overlying and underlying water chambers are given in appendix 2.4 tables 1-5. Linear regression analysis has been performed on these concentrations at 0, 7, 14 and 28 days using the same method as for experiment 1. This gave a total of 130 best-fit regressions (13 treatments x two water chambers x five nutrients). Of these 130 regressions 46 were non-significant, indicating that there was no linear relationship between nutrient concentration and time. The coefficients of the best-fit regressions for each nutrient are given in appendix 2.5 tables 1-5.

Table 2.7. Flux experiment 2. Numbers of meiofauna  $\text{ml}^{-1}$  (mean, (sd)) of sediment at each sampling time. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; C = control (no meiofauna). L = low density; M = medium density; H = high density. n=3 in all cases.

Treatment	Taxon	Time (days)			
		0	7	14	28
WL	Nematodes	10.3333 (1.5275)	10.6667 (1.5275)	11.3333 (3.0551)	9.6667 (2.8868)
	Copepods	2.0000 (0.0000)	2.0000 (1.0000)	2.6667 (0.5774)	3.3333 (0.5774)
	Polychaetes	2.6667 (0.5774)	2.3333 (0.5774)	2.3333 (0.5774)	2.6667 (0.5774)
	Oligochaetes	2.3333 (0.5774)	1.6667 (0.5774)	1.6667 (0.5774)	2.6667 (1.5275)
	Gastrotrichs	2.0000 (1.0000)	1.0000 (1.0000)	3.0000 (0.5774)	1.3333 (0.5774)
	Ostracods	1.6667 (0.5774)	1.0000 (1.0000)	1.3333 (1.5275)	1.3333 (1.1547)
	Brachiopods	1.0000 (1.0000)	0.6667 (0.5774)	0.3333 (0.5774)	1.0000 (1.0000)
WM	Nematodes	20.6667 (1.5275)	19.3333 (1.5275)	20.0000 (3.6056)	23.0000 (4.5826)
	Copepods	4.0000 (1.0000)	3.6667 (0.5774)	4.3333 (1.5275)	6.0000 (1.0000)
	Polychaetes	3.0000 (1.0000)	2.6667 (0.5774)	3.0000 (1.0000)	3.3333 (1.5275)
	Oligochaetes	2.6667 (0.5774)	3.3333 (2.0817)	3.3333 (0.5774)	4.6667 (0.5774)
	Gastrotrichs	2.3333 (0.5774)	3.0000 (1.0000)	1.6667 (1.5275)	2.0000 (1.7321)
	Ostracods	2.6667 (0.5774)	3.3333 (0.5774)	3.3333 (1.5275)	3.0000 (0.0000)
	Brachiopods	1.3333 (0.5774)	1.6667 (0.5774)	4.0000 (1.0000)	3.0000 (1.0000)
WH	Nematodes	41.0000 (3.0000)	39.6667 (2.0817)	41.6667 (4.9329)	48.0000 (4.0000)
	Copepods	8.3333 (1.1547)	8.3333 (0.5774)	8.6667 (1.5275)	9.3333 (2.5166)
	Polychaetes	5.0000 (1.0000)	6.6666 (0.5774)	4.6667 (1.5275)	6.0000 (1.7321)
	Oligochaetes	4.3333 (1.5275)	7.6667 (1.5275)	4.6667 (0.5774)	5.6667 (3.2146)
	Gastrotrichs	3.0000 (1.0000)	4.0000 (1.0000)	2.0000 (1.0000)	4.3333 (0.5774)

Table 2.7. continued.

Treatment	Taxon	Time (days)			
		0	7	14	28
=====					
	Ostracods	4.0000 (1.0000)	3.0000 (1.0000)	1.6667 (1.5275)	4.6667 (1.5275)
	Brachiopods	1.3333 (0.5774)	3.3333 (1.5275)	3.0000 (0.0000)	3.0000 (1.0000)
NL	Nematodes	10.0000 (0.0000)	10.6667 (0.5774)	11.6667 (3.2146)	11.3333 (3.7859)
NM	Nematodes	20.0000 (0.0000)	22.0000 (2.6458)	19.6667 (3.7859)	22.0000 (5.2915)
NH	Nematodes	39.6667 (0.5774)	41.3333 (3.7859)	43.0000 (5.2915)	44.0000 (7.0000)
CpL	Copepods	2.0000 (0.0000)	2.6667 (0.5774)	2.6667 (1.1547)	4.0000 (1.0000)
CpM	Copepods	4.0000 (0.0000)	4.0000 (1.0000)	5.3333 (0.5774)	7.0000 (1.0000)
CpH	Copepods	8.0000 (0.0000)	8.6667 (1.5275)	8.6667 (1.5275)	9.6667 (0.5774)
NCpL	Nematodes	10.0000 (0.0000)	11.0000 (1.7321)	9.6667 (2.0817)	10.6667 (2.5166)
	Copepods	2.0000 (0.0000)	2.6667 (0.5774)	2.6667 (0.5774)	3.0000 (1.0000)
NCpM	Nematodes	19.6667 (0.5774)	20.0000 (2.6458)	19.6667 (4.0415)	22.3333 (5.5076)
	Copepods	4.0000 (0.0000)	3.6667 (0.5774)	5.3333 (0.5774)	5.6667 (1.5275)
NCpH	Nematodes	39.0000 (1.0000)	40.3333 (3.0551)	40.0000 (6.2450)	40.6667 (5.6862)
	Copepods	7.6667 (0.5774)	7.6667 (1.1547)	7.0000 (2.6458)	9.3333 (2.0817)
C	None	0	0	0	0
=====					

The initial flux has been calculated for each nutrient in each chamber of each treatment by differentiation of the linear regression as above. The initial fluxes ( $\mu\text{molm}^{-2}\text{day}^{-1}$ ) for each of the significant regressions are shown in table 2.8 - 2.12. These fluxes have been compared in two ways using t-tests. Firstly the fluxes have been compared between animal densities within a treatment, for example low density of nematodes compared with medium density of nematodes. The results of these comparisons are given in appendix 2.6 tables 1-20. The significant differences shown by these comparisons are summarised in table 2.13. Secondly the fluxes have been compared between treatments within a density, for example low densities of nematodes compared with low densities of copepods. The results of these comparisons are given in appendix 2.6 tables 21-35. The significant differences shown by these comparisons are summarised in table 2.14.

### 3) The effects of various physical and chemical factors.

The final densities of meiofauna in each of the treatments are shown in table 2.15. None of the treatments showed a significant change in meiofaunal density during the experiment. The final levels of each of the salinity and compaction treatments are shown in table 2.16. There was no significant change in salinity in any of the cells during the experiment. The compaction in the very-low compaction treatments increased slightly over the 28 days of the experiment.

The concentrations of each of the five nutrients in the overlying and underlying water chambers of each treatment at 0, 7, 14 and 28 days are given in appendix 2.7 tables 1-5. This nutrient data has been used for linear regression analysis as in experiment 1. The regression analysis gave a total of 250 best-fit

Treatment  
/chamber

$m_{t=0}$   
( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )

sd of m

WL / O	2.9612	0.5816
WL / U	-2.5858	0.5067
WM / O	3.6102	1.8313
WM / U	-0.0	0.0
WH / O	3.2751	1.4790
WH / U	-2.6989	0.9227
NL / O	3.7473	0.4082
NL / U	-1.0268	0.3824
NM / O	2.1752	0.5352
NM / U	-1.4823	0.3869
NH / O	0.3861	0.4218
NH / U	-1.8274	0.5801
CpL / O	1.8707	0.2717
CpL / U	-0.3042	0.4534
CpM / O	1.2370	0.5313
CpM / U	-0.5513	0.6947
CpH / O	2.6228	0.6938
CpH / U	-0.2426	0.6104
NCpL / O	2.7283	0.8424
NCpL / U	-2.6013	0.5683
NCpM / O	2.7854	0.7166
NCpM / U	-2.1604	0.6259
NCpH / O	2.2744	0.8192
NCpH / U	-1.6376	0.9101
Co / O	1.8010	0.5941
Co / U	-1.7543	0.4752

Table 2.8. Flux experiment 2. Initial fluxes of silicate in each treatment at each animal density. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna); O = overlying water chamber; U = underlying water chamber. n=3 in all cases.



Treatment  
/chamber

$m_{t=0}$   
( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )

sd of m

WL / O	0.8886	$9.2697 \times 10^{-2}$
WL / U	$6.3607 \times 10^{-2}$	0.3262
WM / O	-0.5953	0.2331
WM / U	-0.8220	0.3110
WH / O	$-7.4345 \times 10^{-2}$	0.2337
WH / U	-0.5006	0.2490
NL / O	0.1382	0.1862
NL / U	$8.7103 \times 10^{-2}$	0.2319
NM / O	0.1834	0.1173
NM / U	-0.1682	0.1533
NH / O	0.2608	0.2285
NH / U	-0.4806	0.2490
CpL / O	0.5058	0.2809
CpL / U	-0.4139	$9.3739 \times 10^{-2}$
CpM / O	-0.1439	0.1537
CpM / U	0.4430	0.2189
CpH / O	$-2.3838 \times 10^{-2}$	0.3146
CpH / U	0.1978	$9.8083 \times 10^{-2}$
NCpL / O	-0.2361	0.1753
NCpL / U	-0.2969	0.2530
NCpM / O	-0.4034	0.1430
NCpM / U	$-2.9212 \times 10^{-2}$	0.2327
NCpH / O	-0.5544	0.1500
NCpH / U	$-1.1189 \times 10^{-2}$	0.2590
Co / O	$6.7133 \times 10^{-2}$	0.1736
Co / U	0.2834	0.1187

**Table 2.9.** Flux experiment 2. Initial fluxes of phosphate in each treatment at each animal density. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna); O = overlying water chamber; U = underlying water chamber. n=3 in all cases.

Treatment /chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	sd of m
=====		
WL / O	$-4.8038 \times 10^2$	$4.1499 \times 10^2$
WL / U	$5.2984 \times 10^2$	$4.6675 \times 10^2$
WM / O	$-5.5739 \times 10^2$	$3.9726 \times 10^2$
WM / U	$5.4888 \times 10^2$	$3.9131 \times 10^2$
WH / O	$-1.7963 \times 10^3$	$3.5774 \times 10^2$
WH / U	$5.3414 \times 10^2$	$4.1935 \times 10^2$
NL / O	$2.4135 \times 10^2$	$5.2519 \times 10^2$
NL / U	$-3.1918 \times 10^2$	$3.7012 \times 10^2$
NM / O	$7.4722 \times 10^2$	$1.8852 \times 10^2$
NM / U	$-7.7817 \times 10^2$	$4.5103 \times 10^2$
NH / O	$9.1592 \times 10^2$	$5.5082 \times 10^2$
NH / U	$-1.1107 \times 10^3$	$3.5832 \times 10^2$
CpL / O	$-1.0343 \times 10^3$	$6.1406 \times 10^2$
CpL / U	$4.8822 \times 10^2$	$5.8907 \times 10^2$
CpM / O	$-3.8532 \times 10^2$	$5.6515 \times 10^2$
CpM / U	$8.4695 \times 10^2$	$5.3074 \times 10^2$
CpH / O	$-7.5588 \times 10^2$	$5.4522 \times 10^2$
CpH / U	$1.3891 \times 10^2$	$3.7111 \times 10^2$
NCpL / O	$-2.1215 \times 10^2$	$4.0802 \times 10^2$
NCpL / U	$4.0296 \times 10^2$	$3.1645 \times 10^2$
NCpM / O	$-1.3804 \times 10^3$	$3.7634 \times 10^2$
NCpM / U	$1.1258 \times 10^2$	$5.3902 \times 10^2$
NCpH / O	$-1.6498 \times 10^3$	$4.2749 \times 10^2$
NCpH / U	$4.8854 \times 10^2$	$3.6396 \times 10^2$
Co / O	$3.3042 \times 10^2$	$6.3353 \times 10^2$
Co / U	$-2.7550 \times 10^2$	$3.7460 \times 10^2$
=====		

**Table 2.10.** Flux experiment 2. Initial fluxes of sulphate in each treatment at each animal density. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna); O = overlying water chamber; U = underlying water chamber. n=3 in all cases.

Treatment  
/chamber

$m_{t=0}$   
( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )

sd of m

WL / O	-2.4931	0.5831
WL / U	2.1392	0.6525
WM / O	-5.9721	1.3341
WM / U	1.8950	0.7558
WH / O	-6.0270	2.1811
WH / U	3.7377	0.8866
NL / O	-0.2529	1.4528
NL / U	1.4827	0.5715
NM / O	-3.9426	0.7128
NM / U	1.4809	0.9903
NH / O	-4.3768	0.5223
NH / U	1.7284	0.7668
CpL / O	-0.6298	0.6868
CpL / U	0.7755	0.4062
CpM / O	-2.8686	1.2952
CpM / U	1.6545	0.7053
CpH / O	-2.1289	0.8838
CpH / U	2.4366	0.6736
NCpL / O	-3.4928	0.7521
NCpL / U	1.6429	0.5098
NCpM / O	-4.5007	0.6745
NCpM / U	3.7033	0.7920
NCpH / O	-4.8584	1.2467
NCpH / U	$2.755 \times 10^{-3}$	1.2397
Co / O	-1.8517	0.7933
Co / U	0.2335	0.8842

Table 2.11. Flux experiment 2. Initial fluxes of nitrate in each treatment at each animal density. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna); O = overlying water chamber; U = underlying water chamber. n=3 in all cases.

Treatment  
/chamber

$m_{t=0}$   
( $\mu\text{mol m}^{-2} \text{day}^{-1}$ )

sd of m

WL / O	11.0030	4.0531
WL / U	-5.2341	3.7354
WM / O	29.0040	54.5625
WM / U	-1.2598	0.3361
WH / O	1.4693	6.7903
WH / U	-24.9540	9.1911
NL / O	1.7452	4.6824
NL / U	-8.1961	2.5980
NM / O	4.9195	4.4917
NM / U	-4.2287	4.9519
NH / O	14.1432	3.7555
NH / U	-21.7085	5.6787
CpL / O	0.1395	4.5119
CpL / U	-20.6592	4.2513
CpM / O	5.0454	8.0127
CpM / U	-15.7489	6.2432
CpH / O	0.3170	5.8572
CpH / U	-19.1325	5.6526
NCpL / O	7.4320	11.4355
NCpL / U	-23.8148	5.8475
NCpM / O	12.8661	4.1306
NCpM / U	-26.0855	7.1834
NCpH / O	15.7102	7.0352
NCpH / U	-35.2069	9.2235
Co / O	4.1219	4.0677
Co / U	-3.0900	4.4972

Table 2.12. Flux experiment 2. Initial fluxes of ammonia in each treatment at each animal density. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna); O = overlying water chamber; U = underlying water chamber. n=3 in all cases.

Table 2.13. Flux experiment 2. Summary of significant differences in initial flux of each nutrient between animal densities within a treatment. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods. O = overlying water; U = underlying water.

Nutrient	Treatment	Chamber	Differences
SiO <sub>4</sub>	W	O	none
		U	low > medium high > medium
	N	O	low > medium > high
		U	none
	Cp	O	none
		U	none
	NCp	O	none
		U	none
PO <sub>4</sub>	W	O	low = negative flux medium = positive flux
		U	none
	N	O	none
		U	none
	Cp	O	none
		U	high, medium = positive flux low = negative flux
	NCp	O	none
		U	none
SO <sub>4</sub>	W	O	none
		U	none
	N	O	none
		U	none

Table 2.13. continued.

Nutrient	Treatment	Chamber	Differences
$\text{NO}_3$	Cp	O	none
		U	none
	NCp	O	none
		U	none
	W	O	medium > low high > low
		U	none
	N	O	none
		U	none
	Cp	O	none
		U	high > low
	NCp	O	none
		U	medium > low
$\text{NH}_4$	W	O	none
		U	high > medium
	N	O	none
		U	high > low high > medium
	Cp	O	none
		U	low > high
	NCp	O	none
		U	none

Table 2.14. Flux experiment 2. Summary of significant differences in initial flux between treatments at a single animal density. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; O = overlying water chamber; U = underlying water chamber.

Nutrient	Density	Chamber	Differences
SiO <sub>4</sub>	Low	O	N > Cp
		U	W > N NCp > W NCp > N
	Medium	O	W > Cp NCp > Cp
		U	N > W NCp > W
	High	O	W > N Cp > N NCp > N
		U	none
PO <sub>4</sub>	Low	O	none
		U	none
	Medium	O	N = positive flux W, NCp = negative flux
		U	Cp = positive flux N = negative flux
	High	O	none
		U	none
SO <sub>4</sub>	Low	O	none
		U	none
	Medium	O	NCp > N
		U	Cp = positive flux

N = negative flux

Table 2.14. continued.

Nutrient	Density	Chamber	Differences
NO <sub>3</sub>	High	O	N = positive flux W, Cp, NCp = negative flux Cp > W NCp > Cp
		U	none
	Low	O	none
		U	none
	Medium	O	W > N W > Cp
		U	NCp > W NCp > N NCp > Cp
	High	O	W > Cp N > Cp NCp > Cp
		U	W > N
NH <sub>4</sub>	Low	O	none
		U	Cp > N NCp > N
	Medium	O	none
		U	Cp > W Cp > N NCp > N
	High	O	none
		U	NCp > Cp



Table 2.15. Flux experiment 3. Densities of meiofauna (number  $\text{ml}^{-1}$ ; mean, (sd)) in each treatment at each sampling time. S = salinity ( $^{\circ}/_{\text{oo}}$ ); PS = particle size range (N = natural, Si = silt, VFS = very fine sand, FS = fine sand, MS = medium sand); C = compaction (VL = very low, L = low, N = natural, H = high, VH = very high);  $\text{O}_2$  = partial pressure oxygen (%); An = animals. n=3 in all cases.

Treatment/ level	Time (days) Taxon	0	7	14	28
S/5	Nematodes	20	19.3333	19.6667	22.3333
		(0.0)	(2.6458)	(1.5275)	(1.5275)
	Copepods	4	4.3333	3.6667	4.3333
		(0.0)	(1.1547)	(0.5774)	(1.5275)
S/15	Nematodes	20	22.0000	19.0000	21.3333
		(0.0)	(0.0000)	(1.0000)	(0.5774)
	Copepods	4	4.6667	3.6667	3.3333
		(0.0)	(1.5275)	(0.5774)	(2.0817)
S/25	Nematodes	20	18.6667	19.3333	21.0000
		(0.0)	(1.5275)	(0.5774)	(1.5275)
	Copepods	4	5.0000	6.3333	5.0000
		(0.0)	(1.0000)	(3.2146)	(1.5275)
S/35	Nematodes	20	18.3333	21.6667	20.3333
		(0.0)	(0.5774)	(1.5275)	(0.5774)
	Copepods	4	3.3333	3.6667	5.6667
		(0.0)	(2.6458)	(2.0817)	(3.2146)
S/45	Nematodes	20	21.6667	20.6667	21.0000
		(0.0)	(1.5275)	(0.5774)	(1.0000)
	Copepods	4	4.3333	4.6667	3.6667
		(0.0)	(3.2146)	(1.5275)	(0.5774)
PS/N	Nematodes	20	19.6667	22.3333	20.0000
		(0.0)	(0.5774)	(2.0817)	(1.5275)
	Copepods	4	5.0000	3.6667	4.3333
		(0.0)	(2.0817)	(1.5275)	(0.5774)
PS/Si	Nematodes	20	22.0000	19.6667	22.0000
		(0.0)	(1.5275)	(3.2146)	(1.5275)
	Copepods	4	3.6667	4.6667	3.3333
		(0.0)	(0.5774)	(3.2146)	(2.0817)

Table 2.15. continued.

Treatment/ level	Time (days) Taxon	0	7	14	28
PS/VFS	Nematodes	20	21.3333	22.6667	21.0000
		(0.0)	(3.2146)	(0.5275)	(0.5774)
	Copepods	4	3.6667	4.0000	4.3333
		(0.0)	(0.5774)	(0.5774)	(2.0817)
PS/FS	Nematodes	20	20.3333	18.6667	19.6667
		(0.0)	(2.6458)	(3.2146)	(0.5774)
	Copepods	4	3.3333	4.3333	4.0000
		(0.0)	(2.0817)	(0.5774)	(0.0000)
PS/MS	Nematodes	20	19.0000	21.3333	22.0000
		(0.0)	(0.5774)	(1.5275)	(1.5275)
	Copepods	4	4.0000	3.6667	4.6667
		(0.0)	(1.5275)	(2.0817)	(0.5774)
C/VL	Nematodes	20	18.6667	19.0000	21.3333
		(0.0)	(0.5774)	(2.0000)	(1.5275)
	Copepods	4	5.3333	4.3333	4.6667
		(0.0)	(2.0817)	(0.5774)	(1.5275)
C/L	Nematodes	20	21.3333	20.6667	21.0000
		(0.0)	(0.5774)	(2.0817)	(1.0000)
	Copepods	4	4.6667	4.3333	5.0000
		(0.0)	(3.2146)	(0.5774)	(0.5774)
C/N	Nematodes	20	21.6667	20.3333	19.3333
		(0.0)	(1.5275)	(3.2146)	(0.5774)
	Copepods	4	4.0000	4.6667	4.0000
		(0.0)	(2.6458)	(1.5275)	(1.0000)
C/H	Nematodes	20	22.0000	21.6667	18.6667
		(0.0)	(0.5774)	(2.0817)	(1.5275)
	Copepods	4	3.6667	4.3333	4.0000
		(0.0)	(2.6458)	(1.5275)	(1.0000)
C/VH	Nematodes	20	20.3333	18.6667	19.6667
		(0.0)	(1.5275)	(0.5774)	(3.2146)
	Copepods	4	4.3333	4.6667	3.6667
		(0.0)	(2.0817)	(2.6458)	(1.5275)
O <sub>2</sub> /O	Nematodes	20	20.6667	19.3333	21.0000
		(0.0)	(3.2146)	(1.5275)	(0.5774)
	Copepods	4	3.0000	3.6667	4.3333
		(0.0)	(1.0000)	(1.5275)	(2.0817)

Table 2.15. continued.

Treatment/ level	Time (days) Taxon	0	7	14	28
O <sub>2</sub> /5	Nematodes	20	21.0000	23.0000	21.3333
		(0.0)	(0.5774)	(2.6458)	(1.5275)
	Copepods	4	4.6667	3.6667	4.3333
		(0.0)	(3.7859)	(2.0817)	(0.5774)
O <sub>2</sub> /10	Nematodes	20	19.6667	19.3333	20.6667
		(0.0)	(3.7859)	(1.5275)	(3.2146)
	Copepods	4	3.6667	4.3333	4.6667
		(0.0)	(0.5774)	(2.6458)	(2.0817)
O <sub>2</sub> /15	Nematodes	20	18.6667	20.0000	18.6667
		(0.0)	(2.0817)	(0.5774)	(0.5774)
	Copepods	4	3.6667	4.0000	4.0000
		(0.0)	(1.5275)	(1.0000)	(1.5275)
O <sub>2</sub> /21	Nematodes	20	19.3333	18.6667	19.3333
		(0.0)	(0.5774)	(2.0817)	(2.6458)
	Copepods	4	4.6667	4.3333	4.6667
		(0.0)	(2.0817)	(0.5774)	(1.5275)
A/N	Nematodes	20	21.6667	19.6667	20.3333
		(0.0)	(0.5774)	(2.0817)	(1.5275)
A/Cp	Copepods	4	3.3333	4.6667	4.0000
		(0.0)	(2.6458)	(0.5774)	(0.5774)
A/NCp	Nematodes	20	21.3333	20.6667	19.3333
		(0.0)	(2.0817)	(1.5275)	(2.0817)
	Copepods	4	4.0000	4.0000	3.6667
		(0.0)	(1.0000)	(0.5774)	(1.5275)
A/W	Nematodes	21.3333	21.6667	23.3333	22.6667
		(0.5774)	(0.5774)	(0.5774)	(3.2146)
	Copepods	5.6667	4.3333	7.6667	5.3333
		(1.5275)	(1.5275)	(2.0817)	(1.5275)
	Polychaetes	3.6667	2.3333	3.0000	3.6667
		(2.0817)	(3.7859)	(0.5774)	(0.5774)
	Oligochaetes	2.3333	1.6667	2.0000	2.3333
		(0.5774)	(3.2146)	(2.0817)	(1.5275)
	Ostracods	3.6667	4.0000	5.6667	4.3333
		(0.5774)	(1.0000)	(2.0817)	(0.5774)
Turbellarians	8.3333	6.6667	9.3333	9.6667	
	(0.5774)	(1.5275)	(0.5774)	(2.0817)	
Ciliates	6.0000	5.6667	4.3333	6.3333	
	(1.0000)	(0.5774)	(2.6458)	(1.5275)	
Gastrotrichs	2.3333	1.3333	3.6667	3.3333	
	(0.5774)	(2.0817)	(0.5774)	(1.5275)	

Nominal salinity (‰)	Time (days)	0	7	14	28
5	O	4.89 (0.8502)	4.93 (1.0033)	5.12 (0.2301)	5.02 (0.9539)
	U	5.26 (0.1155)	5.12 (0.5503)	4.89 (0.7349)	5.24 (0.2417)
15	O	15.64 (0.7937)	15.43 (0.9857)	15.16 (0.4726)	14.98 (0.5942)
	U	15.58 (0.6010)	15.12 (1.0969)	15.24 (0.7616)	15.11 (0.4440)
25	O	25.23 (0.8888)	24.87 (0.4468)	25.35 (0.4189)	24.36 (0.6506)
	U	25.42 (0.2055)	25.18 (0.8824)	25.63 (0.4163)	25.42 (1.0817)
35	O	35.43 (0.4618)	34.86 (0.8718)	35.92 (0.5710)	35.27 (0.6503)
	U	35.18 (0.6872)	35.23 (0.4048)	34.87 (0.5053)	35.21 (1.2591)
45	O	45.67 (1.4012)	46.34 (1.0785)	44.52 (0.2097)	45.38 (1.0017)
	U	45.69 (0.9074)	46.21 (0.5011)	45.38 (0.6523)	45.72 (0.2490)

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Nominal shear  
strength level

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VL	0.0412 (0.0286)	0.0395 (0.0264)	0.0465 (0.0289)	0.0418 (0.0198)
L	0.0826 (0.0264)	0.0924 (0.0352)	0.0763 (0.0367)	0.0862 (0.0412)
N	0.1624 (0.0526)	0.1587 (0.0318)	0.1493 (0.0427)	0.1526 (0.0319)
H	0.3263 (0.0637)	0.3442 (0.0482)	0.3624 (0.0517)	0.3362 (0.0486)
VH	0.6127 (0.0625)	0.6029 (0.0524)	0.6243 (0.0496)	0.6218 (0.0528)

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Table 2.16. Salinity (‰, mean (sd)) in the salinity treatments and shear strength (kNm<sup>-2</sup>, mean (sd)) in the compaction treatments at each sampling time. n=3 in all cases.

regressions. A total of 25 of these 250 regressions were non-significant, indicating that there was no linear relationship between nutrient concentration and time. The coefficients of the best-fit regression lines for each nutrient are given in appendix 2.8 tables 1-5.

The initial fluxes ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ ) in each of the treatments have been calculated from the best-fit regression lines by differentiation of the best-fit regression lines as above. The initial fluxes calculated from significant regressions are shown in tables 2.17 - 2.21. These initial fluxes have been compared within a treatment, between levels of that treatment, using t-tests. For example, the initial flux in the 5‰ salinity treatment compared with that in the 15‰ salinity treatment. The results of these t-tests are given in appendix 2.9 tables 1-<sup>25</sup>~~35~~. The significant differences within <sup>t</sup>treatments are summarised in tables 2.22 - 2.26.

Table 2.17. Flux experiment 3. Initial fluxes of silicate in each level of each treatment. S = salinity (‰); PS = particle size (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high); O<sub>2</sub> = partial pressure of oxygen (%); A = animal (details as for table 2.8). positive flux = out of sediment; negative flux = into sediment. n=3 in all cases.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	$sd_m$
S/5	O	4.9684	0.7542
	U	-2.0855	1.4958
S/15	O	8.6259	1.2652
	U	-7.7347	1.0699
S/25	O	9.3016	2.3092
	U	-6.9017	2.4402
S/35	O	9.4666	2.4558
	U	0.0	0.0
S/45	O	1.6539	1.2866
	U	-3.1444	1.8962
PS/N	O	11.3118	0.9561
	U	-5.1395	2.1887
PS/Si	O	5.9822	0.7057
	U	0.0	0.0
PS/VFS	O	7.2101	0.5643
	U	-3.0325	0.5179
PS/FS	O	6.3349	10.0042
	U	0.0	0.0
PS/MS	O	7.8202	0.6708
	U	-3.2430	2.4574
C/VL	O	4.6910	1.2391
	U	-4.1539	1.0890
C/L	O	3.0747	0.6738
	U	-2.7903	1.3527

Table 2.17. continued.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	$s_{dm}$
C/N	O	7.0503	1.0159
	U	-1.2075	1.4413
C/H	O	1.1994	0.8291
	U	-0.8479	0.7606
C/VH	O	1.3419	0.9777
	U	-0.8900	0.9934
O <sub>2</sub> /0	O	-2.7792	1.1153
	U	-2.6240	0.8858
O <sub>2</sub> /5	O	-0.3503	1.0680
	U	$-4.852 \times 10^{-3}$	0.8206
O <sub>2</sub> /10	O	1.5065	0.9290
	U	-1.8207	0.8036
O <sub>2</sub> /15	O	0.8873	0.9209
	U	-0.7972	0.9546
O <sub>2</sub> /21	O	3.6736	0.9428
	U	-2.2689	2.3896
A/N	O	1.7276	0.5771
	U	-0.2973	0.6917
A/Cp	O	1.5885	0.9557
	U	-0.3906	0.5908
A/NCp	O	3.8310	0.5877
	U	-0.2840	0.7831
A/W	O	3.3024	0.8094
	U	-1.4808	0.8722
A/Co	O	3.2430	0.7193
	U	0.0	0.0

Table 2.18. Flux experiment 3. Initial fluxes of phosphate in each level of each treatment. S = salinity ( $^{\circ}/_{\infty}$ ); PS = particle size (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $O_2$  = partial pressure of oxygen (%); A = animal (details as for table 2.8). positive flux = out of sediment, negative flux = into sediment. n=3 in all cases.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	$s_{dm}$
S/5	O	7.6665	0.8954
	U	-7.7805	0.6866
S/15	O	8.0345	0.9621
	U	-8.4912	0.5227
S/25	O	10.3157	1.4352
	U	-9.3458	0.3189
S/35	O	17.2534	1.7655
	U	-13.4698	0.9824
S/45	O	13.8457	1.2173
	U	-8.5273	0.6960
PS/N	O	6.1216	0.7956
	U	-8.4704	0.3272
PS/Si	O	6.7377	0.9116
	U	-7.8474	0.6302
PS/VFS	O	7.4950	0.9832
	U	-11.5611	0.5242
PS/FS	O	4.0706	0.8434
	U	-6.4140	0.4895
PS/MS	O	4.3199	0.6141
	U	-8.5318	0.6248
C/VL	O	7.2302	1.0096
	U	-10.0199	0.5208
C/L	O	7.0134	0.6872
	U	-11.6725	0.3119



Table 2.18. continued.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	$s_d$
C/N	O	9.5748	1.0786
	U	-8.4386	0.4675
C/H	O	6.6742	1.0126
	U	-9.0271	0.6572
C/VH	O	4.5622	0.8096
	U	-8.0454	0.6423
O <sub>2</sub> /0	O	1.4143	0.5156
	U	-0.6667	0.2415
O <sub>2</sub> /5	O	4.9671	0.6514
	U	-1.0180	0.2532
O <sub>2</sub> /10	O	5.0667	0.7932
	U	-3.1752	0.5562
O <sub>2</sub> /15	O	5.9392	1.1074
	U	-1.7890	0.2622
O <sub>2</sub> /21	O	9.2283	1.0637
	U	-2.0006	0.2231
A/N	O	9.8902	0.7703
	U	0.0	0.0
A/Cp	O	8.0010	1.1741
	U	-8.0395	0.5119
A/NCp	O	9.6553	1.2839
	U	-8.5285	0.6117
A/W	O	10.8094	1.2046
	U	-9.5352	0.5227
A/Co	O	6.9570	0.8011
	U	-6.5949	0.5882

Table 2.19. Flux experiment 3. Initial fluxes of sulphate in each level of each treatment. S = salinity (‰); PS = particle size (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $O_2$  = partial pressure of oxygen (%); A = animal (details as for table 2.8). positive flux = out of sediment; negative flux = into sediment. n=3 in all cases.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	$s_{dm}$
S/5	O	$-1.6280 \times 10^3$	$1.0511 \times 10^3$
	U	$2.0052 \times 10^3$	$6.2656 \times 10^2$
S/15	O	$-5.0217 \times 10^2$	$8.2853 \times 10^2$
	U	$4.9811 \times 10^2$	$9.0583 \times 10^2$
S/25	O	$-1.1476 \times 10^3$	$7.4483 \times 10^2$
	U	$7.4367 \times 10^2$	$7.5471 \times 10^2$
S/35	O	$-1.1032 \times 10^3$	$7.5006 \times 10^2$
	U	$5.7114 \times 10^2$	$6.9348 \times 10^2$
S/45	O	$-1.8590 \times 10^3$	$9.1222 \times 10^2$
	U	$2.0636 \times 10^3$	$7.3292 \times 10^2$
PS/N	O	$-8.3114 \times 10^2$	$9.1426 \times 10^2$
	U	$3.6884 \times 10^2$	$5.8384 \times 10^2$
PS/Si	O	$-1.0244 \times 10^3$	$7.4309 \times 10^2$
	U	$3.1813 \times 10^3$	$8.7474 \times 10^2$
PS/VFS	O	$-8.3434 \times 10^2$	$6.9049 \times 10^2$
	U	$3.0197 \times 10^3$	$6.3731 \times 10^2$
PS/FS	O	$-4.7416 \times 10^2$	$6.1848 \times 10^2$
	U	$1.6042 \times 10^3$	$6.4632 \times 10^2$
PS/MS	O	$-2.1871 \times 10^3$	$2.1592 \times 10^3$
	U	$1.1037 \times 10^3$	$5.9862 \times 10^2$
C/VL	O	$-1.6449 \times 10^3$	$6.6492 \times 10^2$
	U	$3.6114 \times 10^3$	$8.1284 \times 10^2$
C/L	O	$-2.4636 \times 10^3$	$4.9182 \times 10^2$
	U	$-4.5335 \times 10^2$	$6.4893 \times 10^2$

Table 2.19. continued.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2} \text{day}^{-1}$ )	$s_d$ ( $\mu\text{mol m}^{-2} \text{day}^{-1}$ )
C/N	O	$-2.2950 \times 10^3$	$6.5102 \times 10^2$
	U	$3.1758 \times 10^3$	$6.7683 \times 10^2$
C/H	O	$-2.4054 \times 10^3$	$8.2126 \times 10^2$
	U	$2.0752 \times 10^3$	$7.2682 \times 10^2$
C/VH	O	$-2.2726 \times 10^2$	$8.2010 \times 10^2$
	U	$4.3841 \times 10^3$	$6.6898 \times 10^2$
O <sub>2</sub> /0	O	$-6.2016 \times 10^2$	$5.3705 \times 10^2$
	U	$-1.4452 \times 10^3$	$7.558 \times 10^2$
O <sub>2</sub> /5	O	$-2.1437 \times 10^3$	$5.1360 \times 10^2$
	U	$-3.4554 \times 10^2$	$6.9700 \times 10^2$
O <sub>2</sub> /10	O	$-1.0003 \times 10^3$	$7.2100 \times 10^2$
	U	$2.1900 \times 10^3$	$6.9892 \times 10^2$
O <sub>2</sub> /15	O	$-4.3847 \times 10^2$	$7.9767 \times 10^2$
	U	$1.8210 \times 10^3$	$8.7590 \times 10^2$
O <sub>2</sub> /21	O	$-2.1014 \times 10^3$	$1.0988 \times 10^3$
	U	$2.4856 \times 10^3$	$6.2336 \times 10^2$
A/N	O	$-3.9128 \times 10^2$	$1.0235 \times 10^2$
	U	$2.9863 \times 10^3$	$2.8642 \times 10^2$
A/Cp	O	$-2.3575 \times 10^3$	$8.4251 \times 10^2$
	U	$7.7128 \times 10^2$	$4.8154 \times 10^2$
A/NCp	O	$-2.3736 \times 10^3$	$6.5669 \times 10^2$
	U	$2.3083 \times 10^3$	$8.0237 \times 10^2$
A/W	O	$-1.4307 \times 10^3$	$9.2065 \times 10^2$
	U	$4.1331 \times 10^3$	$9.2792 \times 10^2$
A/Co	O	$-2.9381 \times 10^3$	$7.7157 \times 10^2$
	U	$-5.2629 \times 10^2$	$7.6489 \times 10^2$

Table 2.20. Flux experiment 3. Initial fluxes of nitrate in each level of each treatment. S = salinity (‰); PS = particle size (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high); O<sub>2</sub> = partial pressure of oxygen (%); A = animal (details as for table 2.8). positive flux = out of sediment, negative flux = into sediment. n=3 in all cases.

Treatment	Chamber	$m_{t=0}^{sd_m}$ ( $\mu\text{mol m}^{-2} \text{day}^{-1}$ )	
S/5	O	-2.0222	1.1083
	U	0.4942	0.7399
S/15	O	-1.7369	1.0818
	U	-0.1044	0.6516
S/25	O	-0.6781	0.9108
	U	0.5614	0.7152
S/35	O	-1.5424	0.4795
	U	1.5542	0.5769
S/45	O	-0.9965	0.7706
	U	-1.4561	0.6183
PS/N	O	-5.9505	1.0354
	U	0.5741	0.8216
PS/Si	O	-0.8441	1.4539
	U	-0.9099	0.8164
PS/VFS	O	-2.3588	0.6822
	U	2.4960	0.6930
PS/FS	O	-2.1416	1.0936
	U	0.3195	0.9762
PS/MS	O	-0.8440	0.5086
	U	0.3990	0.8075
C/VL	O	-5.7019	0.8134
	U	-0.2419	0.3071
C/L	O	-0.9050	0.8962
	U	1.7509	0.7686

Table 2.20. continued.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2} \text{ day}^{-1}$ )	$s_{dm}$
C/N	O	-6.5805	0.8082
	U	1.8022	0.7173
C/H	O	-2.7516	0.9112
	U	2.9816	0.8505
C/VH	O	-0.7268	1.0377
	U	0.2583	0.7627
O <sub>2</sub> /0	O	-0.3339	1.0975
	U	3.0842	0.7132
O <sub>2</sub> /5	O	-0.9450	0.9279
	U	1.9628	1.0219
O <sub>2</sub> /10	O	-1.2383	1.2137
	U	0.5526	0.8432
O <sub>2</sub> /15	O	-1.2230	1.4582
	U	4.3527	0.8212
O <sub>2</sub> /21	O	-2.1375	1.2487
	U	0.2491	0.6361
A/N	O	-2.8223	0.7015
	U	0.1719	0.7366
A/Cp	O	-1.3638	1.1308
	U	1.6906	0.4563
A/NCp	O	-2.1424	1.2260
	U	0.6493	0.8294
A/W	O	-2.5700	0.8979
	U	0.8758	0.7292
A/Co	O	-2.4686	0.9247
	U	1.0237	0.6354

Table 2.21. Flux experiment 3. Initial fluxes of ammonia in each level of each treatment. S = salinity (‰); PS = particle size (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $O_2$  = partial pressure of oxygen (%); A = animal (details as for table 2.8). positive flux = out of sediment; negative flux = into sediment. n=3 in all cases.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	$s_d m$
S/5	O	22.9131	13.7681
	U	-12.4956	3.8319
S/15	O	19.4998	4.2995
	U	-30.2114	2.7108
S/25	O	35.6083	13.7790
	U	-46.1526	7.5701
S/35	O	28.8645	4.5801
	U	-14.5384	3.2473
S/45	O	16.2139	2.1064
	U	-23.3033	3.3384
PS/N	O	26.0390	4.0128
	U	-24.5960	3.8155
PS/Si	O	11.4324	3.1468
	U	-28.8213	2.8762
PS/VFS	O	29.0118	4.1275
	U	-23.2445	3.4595
PS/FS	O	18.7620	3.8454
	U	-12.4248	4.8692
PS/MS	O	20.9397	4.2019
	U	-8.3325	10.3365
C/VL	O	22.5671	3.7555
	U	-8.2768	3.1862
C/L	O	20.5367	2.5419
	U	-6.5243	6.2439

Table 2.21. continued.

Treatment	Chamber	$m_{t=0}$ ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )	$s_d$ m
C/N	O	9.8530	2.5001
	U	-4.7630	4.1802
C/H	O	16.4836	3.8315
	U	-3.8624	3.1827
C/VH	O	-1.8382	3.0435
	U	-6.5671	2.9030
O <sub>2</sub> /0	O	16.1953	2.3528
	U	-46.1262	5.6249
O <sub>2</sub> /5	O	22.4152	7.8818
	U	-41.1835	6.3187
O <sub>2</sub> /10	O	14.4997	2.9387
	U	-39.7267	4.1827
O <sub>2</sub> /15	O	24.3511	4.2112
	U	-38.5160	3.5974
O <sub>2</sub> /21	O	9.8235	3.5449
	U	-35.1424	7.9264
A/N	O	4.5413	3.5633
	U	-15.8267	5.4323
A/Cp	O	10.1831	3.3420
	U	-11.6241	6.4418
A/NCp	O	7.7528	3.4998
	U	-28.0648	5.6232
A/W	O	20.5073	3.5122
	U	-16.5571	8.2438
A/Co	O	6.4323	3.5370
	U	-9.4315	7.9267

Table 2.22. Flux experiment 3. Summary of the significant differences in initial flux between the different levels of a each treatment. S = salinity (‰); PS = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high); O<sub>2</sub> = partial pressure of oxygen (%); A = animal (W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna)).

=====			
Nutrient	Treatment	Chamber	Difference
=====			
SiO <sub>4</sub>	Salinity	O	15 > 5
			25 > 5
			35 > 5
			5 > 45
			15 > 45
			25 > 45
			35 > 45
		U	15 > 5
			15 > 35
			15 > 45
			25 > 35
			45 > 35
	Particle size	O	N > Si
			N > VFS
			N > MS
			MS > Si
		U	N > Si
			N > FS
	Compaction	O	VFS > Si
			VFS > FS
			N > VL
			VL > H
			VL > VH
			N > L
			L > H
			L > VH
			N > H
			N > VH



Table 2.22. continued.

Nutrient	Treatment	Chamber	Difference
		U	VL > N VL > H
O <sub>2</sub>		O	10 > 0 15 > 0 21 > 0 21 > 10 21 > 15
		U	None
Animal		O	NCp > N W > N Co > N NCp > Co
		U	W > Co

Table 2.23. Flux experiment 3. Summary of the significant differences in initial flux between the different levels of a each treatment. S = salinity (‰); PS = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high); O<sub>2</sub> = partial pressure of oxygen (%); A = animal (W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna)).

=====			
Nutrient	Treatment	Chamber	Difference
=====			
PO <sub>4</sub>	Salinity	O	25 > 5
			35 > 5
			45 > 5
			35 > 15
			45 > 15
			35 > 25
			45 > 25
			35 > 45
		U	25 > 5
			35 > 5
			35 > 15
			35 > 25
	Particle size	O	N > FS
			N > MS
			Si > FS
			Si > MS
			VFS > FS
			VFS > MS
		U	VFS > N
			N > FS
			VFS > Si
			Si > FS
	Compaction	O	VFS > FS
			VFS > MS
			MS > FS
			N > VL
			VL > VH
			N > L
			N > VH
			N > H

Table 2.23. continued.

Nutrient	Treatment	Chamber	Difference
			N > VH
			H > VH
		U	L > VL
			VL > N
			VL > H
			L > N
			L > H
			L > VH
O <sub>2</sub>		O	5 > 0
			10 > 0
			15 > 0
			21 > 0
			21 > 5
			21 > 10
			21 > 15
		U	10 > 0
			10 > 5
			10 > 15
			15 > 0
			15 > 5
			10 > 21
			21 > 0
			21 > 5
Animal		O	N > Co
			W > Cp
			NCp > Co
			W > C
		U	Cp > N
			NCp > N
			W > N
			Co > N
			W > Cp
			Cp > Co
			NCp > Co
			W > C

Table 2.24. Flux experiment 3. Summary of the significant differences in initial flux between the different levels of a each treatment. S = salinity ( $^{\circ}/_{\infty}$ ); PS = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $O_2$  = partial pressure of oxygen (%); A = animal (W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna)).

Nutrient	Treatment	Chamber	Difference
SO <sub>4</sub>	Salinity	O	None
		U	5 > 35 45 > 35
	Particle size	O	None
		U	Si > FS MS > Si VFS > FS MS > VFS
	Compaction	O	None
		U	VL > L N > L H > L VH > L VH > H
	O <sub>2</sub>	O	5 > 0 5 > 15
		U	10 > 0 15 > 0 0 > 21
	Animal	O	Cp > N NCp > N Co > N
		U	N > Cp NCp > Cp W > Cp W > NCp

Table 2.25. Flux experiment 3. Summary of the significant differences in initial flux between the different levels of a each treatment. S = salinity ( $^{\circ}/_{\infty}$ ); PS = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $O_2$  = partial pressure of oxygen (%); A = animal (W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna)).

Nutrient	Treatment	Chamber	Difference
NO <sub>3</sub>	Salinity	O	None
		U	5 > 45
			25 > 45
			35 > 45
	Particle size	O	N > Si
			N > VFS
			N > FS
			N > MS
		U	N > VFS
			VFS > FS
			VFS > MS
	Compaction	O	VL > L
			VL > H
			VL > VH
			N > L
			H > L
			N > H
			N > VH
			H > VH
		U	L > VL
			N > VL
			H > VL
O <sub>2</sub>		O	None
		U	0 > 21
			15 > 5
			15 > 21

Table 2.25. continued.

=====			
Nutrient	Treatment	Chamber	Difference
=====			
	Animal	O	None
		U	NCp > N
			NCp > Cp
			NCp > Co
=====			

Table 2.26. Flux experiment 3. Summary of the significant differences in initial flux between the different levels of a each treatment. S = salinity (‰); PS = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high); O<sub>2</sub> = partial pressure of oxygen (%); A = animal (W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; Co = control (no meiofauna)).

Nutrient	Treatment	Chamber	Difference
NH <sub>4</sub>	Salinity	O	35 > 45
			15 > 5
			25 > 15
			25 > 35
			25 > 5
			15 > 35
			25 > 45
			45 > 5
			15 > 45
			45 > 35
	Particle size	O	N > Si
			VFS > Si
			FS > Si
			MS > Si
			VFS > FS
		U	N > FS
			Si > FS
			VFS > FS
	Compaction	O	VL > N
			L > N
			H > N
		U	L > VL
			N > VL
			H > VL
O <sub>2</sub>		O	15 > 0
			0 > 21
			5 > 21
			15 > 10
			15 > 21

Table 2.26. continued.

=====			
Nutrient	Treatment	Chamber	Difference
=====			
		U	None
Animal	O	O	W > N
			W > Cp
			W > NCp
			W > Co
		U	NCp > N
			NCp > Cp
			NCp > Co
=====			



## Discussion.

The sediment-water interface is an area of intense biological, physical and chemical activity (Berner, 1976, 1980; de Wilde, 1976; Novitsky, 1983; Balzer, 1984). It has been described as the major site of organic matter production and breakdown (de Wilde, 1976; Novitsky, 1983; Balzer, 1984; Balzer et al, 1987). For example, Novitsky (1983) has described bacterial activity at the sediment-water interface at a rate several orders of magnitude higher than in the overlying water column and a factor of two higher than that one cm into the sediment. Macrofauna and meiofauna are also concentrated towards the sediment-water interface in many sediments (Gerlach, 1978; Reise, 1983).

Many early diagenetic changes are associated with the sediment surface and the nepheloid (sediment-laden) layer of the water column (Berner, 1976; 1980). The sediment-water interface has also been described as being the major source of nutrients entering the water column and deeper sediment (Raaphorst and Brinkman, 1985) although other authors have reported the source of nutrients to be regeneration from deeper sediment layers and the overlying water (Berner, 1976; Suess, 1976).

In this discussion I shall first briefly review the literature concerning field and laboratory flux studies. I shall then discuss the directions and magnitudes of fluxes I have found, followed by the results of each of my experiments. Finally I shall discuss some of the potential problems with the use of diffusion cells.

## Field Flux Studies.

The majority of nutrient flux studies have concerned fluxes through the interface of field sediments (Hartwig, 1976; Cantelmo, 1983; Balzer, 1984; Balzer et al, 1987) or the calculation of

fluxes using interstitial water-concentration data (Pugh, 1976; Aller, 1980; Aller and Yingst, 1980). Some of these studies have been concerned with the measurement of biological parameters, mainly bacterial production/density (Billen, 1978; Smith et al, 1978; Aller and Yingst, 1980; Blackburn and Henriksen, 1983; Balzer, 1984; Balzer et al, 1987) but also some macrofaunal effects (Smith et al, 1978; Aller, 1980; Blackburn and Henriksen, 1983) and some meiofaunal effects (Smith et al, 1978; Aller and Yingst, 1980; Blackburn and Henriksen, 1983; Cantelmo, 1983). The majority of the field studies of nutrient fluxes in the literature, however, concern fluxes from/into bulk sediment, no attempt being made to correlate fluxes with sediment parameters (e.g. Hartwig, 1976; Nixon et al, 1980; Boynton and Kemp, 1983; Owens and Stewart, 1984; Seitzinger and Nixon, 1985; Goeyens et al, 1987; Boucher and Boucher-Rodoni, 1988).

#### Laboratory Flux Studies.

In general there have been fewer laboratory studies of nutrient fluxes than there have been field studies. A higher proportion of the laboratory studies have attempted correlations between levels of biological, physical and chemical parameters in the sediments and nutrient fluxes (Pugh, 1976; Aller, 1978a; Wormald and Stirling, 1979; Cantelmo, 1983; Hennig et al, 1983; Kristensen, 1984). Biological factors affecting nutrient fluxes which have been studied in the laboratory include macrofaunal density/biomass (Aller, 1978a; Kristensen, 1984; Matisoff and Fischer, 1985), meiofauna (Wormald and Stirling, 1979; Cantelmo, 1983; Hennig et al, 1983) and bacterial/algal density, biomass and activity (Cantelmo, 1983; Hennig et al, 1983; Balzer, 1984; Balzer

et al, 1987). Very few of the field and laboratory studies on factors affecting nutrient fluxes have concerned the effects of physical and chemical factors.

A summary of the nutrient fluxes reported by other authors is given in table 2.27. Most of these fluxes are of nitrate, ammonium and phosphate. Most of the references concerned with silicate and sulphate have involved the measurement of interstitial-water concentration profiles rather than fluxes. References quoting fluxes calculated from interstitial-water concentrations have been omitted from table 2.27 due to the problems associated with calculating fluxes from non-dynamic data (Billen and Vanderborght, 1978).

#### Directions and Magnitudes of Fluxes.

The silicate fluxes in my experiments were generally positive for the overlying water and negative for the underlying water, corresponding to a flux of silicate out of the sediment (tables 2.5, 2.8, 2.17). Balzer (1984) also reports positive fluxes of silicate. The magnitude of the silicate fluxes reported by Balzer (1984), however, is two orders of magnitude higher than in my experiments. One possible reason for this difference is that Balzer's work was carried out on organically enriched subtidal muddy sediments which have higher micro-organism numbers and detrital input. The prime source of silicate regenerated from sediments is the breakdown of silica diatom frustules. Sediments from Ardmore beach, where my experimental sediments were collected, contain fairly low numbers of relict diatom frustules. A second possible reason for the difference between Balzer's (1984) work and my experiments may, therefore, be differences in the diatom frustule content of the sediments.

Flux ( $\mu\text{mol m}^{-2}\text{day}^{-1}$ )					
SiO <sub>4</sub>	PO <sub>4</sub>	SO <sub>4</sub>	NO <sub>3</sub>	NH <sub>4</sub>	Reference
—	—	+ve	—	-ve	Aller (1978a)
—	>740	—	—	1623 (anoxic)	Balzer (1984)
2078	63	—	—	476 (oxic)	Balzer (1984)
—	—	—	—	28 → 50	Blackburn and Henriksen (1983)
—	—	—	—	<2880	Boucher and Boucher-Rodoni (1988)
—	—	—	—	35 → 820	Boynton and Kemp (1985)
—	-438 → 502	—	—	-720 → 647	Hartwig (1976)
—	-192 → 144	—	-1824 → 144	2280	Kristensen (1984)
—	2.25	—	—	— (field)	Nixon et al (1980)
—	2.76	—	—	— (lab)	Nixon et al (1980)
—	—	—	—	3.8 → 46.5	Owens et al (1984)
—	—	—	—	-6744 → 4536	Seitzinger and Nixon (1985)
—	—	—	—	-20 → -690	Simon (1988)
—	-0.2 → 45.5	—	-1 → -118	—	Smith et al (1978)
—	48 → 1200	—	3.6 → 20.9	24 → 9600	Zeitschel (1980)

**Table 2.27.** Summary of some of the direct flux measurements reported in the literature on field and laboratory sediments. Positive fluxes are out of the sediment, negative fluxes into the sediment. Note - this table excludes fluxes calculated indirectly from interstitial water concentration data (Billen and Vanderborght, 1978).

The fluxes of phosphate in my experiments were generally positive for the overlying water and negative for the underlying water, corresponding to a flux out of the sediment (tables 2.5, 2.9, 2.18). Most of the fluxes reported by other workers (table 2.27) also show regeneration of phosphate from sediments into the overlying water column. The magnitude of the phosphate fluxes in my experiments is at the lower end of the range reported by other workers (Hartwig, 1976; Smith et al, 1978; Nixon et al, 1980; Zeitzschel, 1980; Balzer, 1984; Kristensen, 1984). This may be due to differences in sediment type between my experiments and those of other workers, most of the fluxes reported in the literature being for muddy sediments.

The only sulphate flux information in the literature which has been calculated directly is that of Aller (1978a). He quotes sulphate fluxes as being positive for the overlying water but gives no details of the rate of sulphate production by sediments. Most of the sulphate fluxes I measured were negative for the overlying water and positive for the underlying water, corresponding to a flux of sulphate into the sediment (tables 2.5, 2.10, 2.19).

The nitrate fluxes reported in the literature are highly variable ranging from  $-1824$  to  $+1114$   $\mu\text{mol m}^{-2} \text{d}^{-1}$  (Kristensen, 1984) ~~to  $-6744$  to  $+4536$   $\mu\text{mol m}^{-2} \text{d}^{-1}$  (Seitzinger and Nixon, 1985).~~ The nitrate fluxes I measured were generally negative for the overlying water and positive for the underlying water, corresponding to a flux into the sediment (tables 2.5, 2.11, 2.20). The magnitudes of the nitrate fluxes I found were far less variable than those of other authors (Hartwig, 1976; Smith et al, 1978; Zeitzschel, 1980; Kristensen, 1984; Seitzinger and Nixon, 1985; Boucher and Boucher-Rodoni, 1988; Simon, 1988). This may reflect the variability of field measurements of fluxes compared with

laboratory measurements.

The ammonia fluxes I measured were generally positive for the overlying water and negative for the underlying water, corresponding to a flux out of the sediment (tables 2.5, 2.12, 2.21). Positive fluxes of ammonia were also found by other workers (Zeitzschel, 1980; Blackburn and Henriksen, 1983; Balzer, 1984; Kristensen, 1984; Owens and Stewart, 1984; Boynton and Kemp, 1985; Boucher and Boucher-Rodoni, 1988; Simon, 1988). Simon (1988) also reports that the direction of ammonia fluxes varies with the extent of tidal scour of the sediment surface. During periods of resuspension of sediment Simon (1988) reports negative fluxes of ammonia (into the sediment) and positive fluxes during calm periods (out of the sediment). Hartwig (1976) and Smith et al (1978) also report some negative fluxes of ammonia but do not relate it to tidal scour.

#### Comparison of Macrofaunal, Meiofaunal and Micro-organism Effects on Nutrient Fluxes.

In my first experiment the meiofauna treatments generally showed the greatest fluxes, followed by the macrofauna plus meiofauna treatment and then the micro-organisms only treatment (table 2.6). The increase in flux caused by the presence of meiofauna in the sediment may be due to several factors. These factors include active transport of dissolved nutrients (Hargrave, 1975; Boucher and Chamroux, 1976; Gerlach, 1978; Stewart, 1979; Yingst and Rhoads, 1980; Hennig et al, 1983; Nicholas, 1984; Jensen, 1987); Breakdown of organic matter (Coull, 1973; Hargrave, 1975; Gerlach, 1978; Tenore and Rice, 1980; Yingst and Rhoads, 1980; Koop and Griffiths, 1982); bioturbation and consequent exchange of porefluids with the water column (Cullen, 1973; Fenchel

and Harrison, 1975; Yingst and Rhoads, 1980; Hines et al, 1982; Fricke and Flemming, 1983; Nicholas, 1984; Varon and Thistle, 1988); and also effects on microbial productivity and activity (Fenchel and Harrison, 1975; Hargrave, 1975; Gerlach, 1978; Lerman, 1978; Martens, 1978; Tenore and Rice, 1980; Yingst and Rhoads, 1980; Hennig et al, 1983; Nicholas, 1984; Balzer et al, 1987).

There is a large amount of literature concerning the effects of micro-organisms on nutrient concentration and the effects of meiofauna on microbial productivity and activity (see above). This literature indicates that the interaction between meiofauna and micro-organisms may be the main cause of meiofaunal effects on nutrient fluxes.

Micro-organisms in sediments may cause nutrient fluxes through two major activities. These are production and consumption of nutrients. For example, sulphate reducing bacteria such as Desulphovibrio spp. consume sulphate and produce hydrogen sulphide. In anaerobic conditions hydrogen sulphide reacts with iron oxides, which are common in sediments, to produce iron sulphides. These sulphides are insoluble and precipitate onto sediment particles, giving anaerobic sand its characteristic grey-black colour (Reeburgh, 1978; Postgate, 1984).

The microbial flora of sediments shows strong vertical zonation related to the position of suitable physical and chemical conditions (ZoBell, 1946; Zajic, 1969; Reeburgh, 1978; Meadows and Tait, 1985). Zonation of micro-organisms within sediments may lead to a vertical zonation of chemical reactions (Redford, 1958; Krauskopf, 1979; Berner, 1980; Levinton, 1982)

The addition of macrofauna to the meiofauna in my first experiment reduced the nutrient fluxes compared with the meiofauna

only treatment. In my experiments the macrofauna had no effect on meiofaunal density. The changes in flux associated with macrofauna plus meiofauna compared with meiofauna alone must either be due to direct macrofaunal effects on fluxes or due to macrofaunal effects on meiofaunal behaviour.

Macrofauna may cause effects on nutrient fluxes directly in the same ways as meiofauna, due to active transport (Yingst and Rhoads, 1980; Aller, 1983; Kristensen, 1984; Matisoff et al, 1985); breakdown of organic matter (Gerlach, 1978; Tenore and Rice, 1980; Yingst and Rhoads, 1980); bioturbation (McIntyre, 1969; Fenchel and Harrison, 1975; Aller, 1978a, 1983; Yingst and Rhoads, 1980; Hines et al, 1982; Matisoff et al, 1985; Ray and Aller, 1985); or effects on microbial productivity and activity (McIntyre, 1969; Hargrave, 1975; Gerlach, 1978; Nixon et al, 1980; Tenore and Rice, 1980; Yingst and Rhoads, 1980; Balzer et al, 1987).

The effects of macrofaunal bioturbation are likely to be considerably greater than those of meiofauna, even when the macrofauna are at a much lower density than the meiofauna, as they were in my experiments (Cullen, 1973). The macrofauna may, therefore, reduce the extent of fluxes by exchanging and homogenising the overlying water, underlying water and porewater.

Macrofaunal effects on meiofaunal behaviour have been described by a number of authors (e.g. McIntyre, 1969; Yingst and Rhoads, 1980; Fricke and Flemming, 1983; Reise, 1983; Alongi, 1985). The detailed effects of macrofauna on meiofauna are very variable (Yingst and Rhoads, 1980; Reise, 1983; Alongi, 1985) and depend on the exact species, densities and activities of the macrofauna and meiofauna present. Macrofauna may, for example, cause meiofauna to feed at positions in the sediment which are below their optimal requirements (e.g. the presence of particular microbial types or



densities) or the macrofauna may change the position in the sediment at which the optimal requirements are found (Gerlach, 1978; Yingst and Rhoads, 1980).

#### The Effects of Meiofaunal Type and Density.

The effects of meiofaunal type and density on nutrient fluxes in my experiments were very variable (tables 2.13, 2.14 and 2.22-2.26). There has been no comparable work to mine reported in the literature. None of the published studies of meiofaunal effects on nutrient fluxes have attempted to control the densities and types of meiofauna (Wormald and Stirling, 1979; Cantelmo, 1983; Hennig et al, 1983) although there is some work on nitrogenous excretion by meiofauna at various densities (Gray, 1985).

In my experiments the whole meiofauna and nematode plus copepod treatments generally showed higher fluxes than the copepod, nematode and control treatments at any single density. This effect may be due to differences in the behaviour of meiofauna caused by the presence of other taxa or due to differences in absolute density of animals. The latter is because the nematode plus copepod treatment consisted of nematodes and copepods at the same individual densities as in the separate treatments, their combined density being the sum of the individual densities. For example the high density of nematodes plus copepods was equivalent to the high nematode treatment (40 animals) plus the high copepod treatment (8 animals), giving a total of 48 animals.

The presence of mixtures of taxa may change the behaviour of meiofauna in a number of ways. These include predation on other meiofauna (McIntyre, 1969; Watzin, 1983; Nicholas, 1984); competition for food resources and production of new food resources

(e.g. faecal pellets) (McIntyre, 1969; Coull, 1973; Boucher and Chamroux, 1976; Gerlach, 1978; Yingst and Rhoads, 1980; Carman and Thistle, 1985; Decho and Fleeger, 1988; Meyers et al, 1988) and changes in the physical and chemical nature of the sediments (McIntyre, 1969; Coull, 1973; Yingst and Rhoads, 1980; Fricke and Flemming, 1983; Hockin, 1983). Changes in meiofaunal density may also alter the behaviour of meiofauna in similar ways to changes in the taxa present (Coull, 1973; Gerlach, 1978; Yingst and Rhoads, 1980).

In my experiments changes in meiofaunal density did not alter the nutrient flux in a consistent way. For example silicate fluxes were greater at low and high densities of whole meiofauna than at medium density. The silicate flux also decreased with increasing nematode density (table 2.13). In some of the treatments the direction of the nutrient flux was altered by changes in faunal density. For example the overlying water phosphate flux was positive at medium densities of whole meiofauna but negative at low densities (table 2.13). The variability of the effects of meiofaunal density on fluxes may reflect a range of interactions between individuals of various meiofaunal taxa and also between meiofauna and food resources. For example meiofauna feeding on faecal pellets may affect nutrient fluxes by selectively consuming sulphate reducing bacteria, producing faecal pellets with a much reduced bacterial population suitable either for colonisation by other sulphate reducers or for increased growth of the bacteria remaining. This type of ingestion, recolonisation and re-ingestion has been described as "harvesting" or "gardening" of micro-organisms (Coull, 1973; Gerlach, 1978; Yingst and Rhoads, 1980). Both of the latter effects will tend to increase the rate of sulphate consumption as the numbers of bacteria increase

(Jorgensen, 1977; Tenore and Rice, 1980). This situation is analogous to the continuous culture of micro-organisms, where organisms are removed from the culture in order to maintain an exponential growth of the population (Yingst and Rhoads, 1980). In contrast, however, as the number of meiofauna feeding in a limited volume of sediment increases, the rate at which individual pellets are re-consumed will also increase. This process may keep the densities of bacteria in pellets at a very low level due to the short time between re-ingestions for re-colonisation of the faecal pellets and colony growth by sulphate reducers. The presence of small numbers of bacteria which are regularly "harvested" will tend to keep the rate of sulphate consumption low (Jorgensen, 1977). This situation is analogous to a continuous culture system with a removal rate such that the population is kept below the exponential growth phase (Lynch and Poole, 1979 p.46; Yingst and Rhoads, 1980).

#### The effects of Various Physical and Chemical Factors.

The effects of various physical and chemical parameters on nutrient flux in the presence of meiofauna were more regular than the effects of changes in meiofaunal types and densities. This may be due to the use of a single faunal composition (natural densities of nematodes plus copepods) in all of the physical and chemical factor treatments. The fluxes of silicate and phosphate in the overlying water were generally higher at salinities of 15, 25 and 35 ‰ than at 5 and 45 ‰. Salinities of 15-35 ‰ are more normal on Ardmore beach than 5 and 45 ‰, which represent extremes encountered at periods of heavy rainfall and rapid evaporation respectively. The underlying water fluxes of silicate, phosphate, nitrate and ammonia showed similar patterns, the

greatest flux being associated with intermediate salinities. This pattern of decrease in flux at extremes of salinity may reflect changes in meiofaunal activity (Coull, 1973). Sulphate and nitrate fluxes in the overlying water were not affected by salinity. Sulphate fluxes in the underlying water were greatest at very low and very high salinity. This increase in sulphate flux and decrease in flux of other nutrients at extremes of salinity may be due to meiofaunal feeding patterns being regulated by the salinity of the overlying water. At times of inundation of sediments with freshwater and times of high evaporation meiofauna tend to migrate away from the sediment-water interface (Harris, 1972b; Coull, 1973). This migration may mean that the meiofauna are bioturbating the sediment at a different point in the sediment column and are feeding on different populations of micro-organisms, producing a different effect on nutrient fluxes.

The effect of particle size on nutrient fluxes in the presence of meiofauna is difficult to assess. The meiofauna used in these experiments were all collected from a muddy-sand beach and are probably in a sub-optimal habitat if placed in a sediment with a different particle size range. This effect is reflected in the fact that in most cases the nutrient flux was greatest in those treatments containing natural Ardmore sediment. In general the silt and very fine sand treatments showed fluxes similar to those in the unsorted (natural) sediment. The fine sand treatments generally showed fluxes slightly lower than the silt and very fine sand treatments. The lowest fluxes were generally associated with medium sand.

The problems of relating fluxes to particle size range are compounded by the difference in sediment composition between the various size ranges. The smaller particle size ranges tend to

contain a higher proportion of organic matter than do the larger ones. This difference may well cause changes in micro-organism activity. The smaller particle size ranges also have a higher surface area for a given sediment volume than do the larger particle size ranges. Smaller particle size ranges therefore have larger areas open for microbial colonisation. The smaller particle size ranges will also have smaller pore-spaces than will the larger ones, increasing the degree of physical disturbance of the sediment caused by meiofaunal movement (Crisp and Williams, 1971). The natural sediment, containing a wider range of particle sizes, will probably have smaller pore-spaces than the larger of the sorted particle size ranges (Berner, 1980). The reduced pore-spaces in the finer sorted sediments will probably restrict the activity of species which move through the interstices in the sediment. Species of meiofauna which intentionally move sediment particles, either by their locomotion or feeding, will probably be less affected by changes in the size of the interstices.

The degree of compaction of the sediment had a great effect on nutrient fluxes. In general the fluxes of silicate, phosphate, nitrate and ammonia were greatest in the normal compaction treatment, followed by the very low compaction treatment and the very high compaction treatment. The low and high compaction treatments showed lower fluxes than the very low or normal treatments. At lower compactions the size of the porespace will be greater than at higher compactions. This will tend to increase the diffusion rates of chemical species in the porewater by decreasing the tortuosity (average distance an ion must move to travel from the porewater into the water column) of the sediment (Lerman, 1978; Berner, 1980). The reduction of diffusion rates at higher

compaction will tend to limit the flow of microbial end-products out of the sediment and will also reduce the rate of supply of dissolved nutrients to the micro-organisms. Increases in the pore size will also tend to decrease the rate of physical sediment disturbance by meiofauna and hence reduce the physical exchange of porewater with overlying or underlying water (Cullen, 1973). The reduction in flux associated with compactions either side of the natural compaction may reflect a summation of the effects of increasing tortuosity and physical water exchange at increasing sediment compaction.

The effects of oxygen concentration on nutrient flux were very variable between nutrients. Silicate fluxes were not generally affected by oxygen concentration, the same being true of ammonia fluxes in the underlying water and nitrate fluxes in the overlying water. Phosphate fluxes in the overlying water were higher at higher oxygen concentrations. In the underlying water, however, they were greatest at 10 % oxygen followed by oxygen concentrations of 15 and 21 % and then the 5 and 0 % concentrations. Fluxes of sulphate and nitrate in the underlying water were greatest at 10 and 15 % oxygen concentrations and lower at 0 and 21 %. Ammonia fluxes in the overlying water were greater at below atmospheric oxygen (highest flux at 15% O<sub>2</sub>) and lowest at atmospheric concentration.

At lower oxygen concentrations meiofauna tend to concentrate towards the sediment-water interface (McLachlan, 1978). Aller and Yingst (1980) report 100 % mortality of meiofauna in anaerobic sediments after 6 days. Some meiofauna have, however, been reported as being facultative anaerobes, being able to change their metabolic processes to survive in low oxygen environments such as those found in organically enriched muds (Coull, 1973). I have

encountered no problems with meiofaunal survival under low oxygen and anerobic conditions, the densities of meiofauna not changing significantly over 28 days.

The activity of many micro-organisms is also affected by oxygen concentration. At high oxygen concentrations micro-organisms which are obligate anaerobes will be restricted to anaerobic micro-environments, such as faecal pellets (Jorgensen, 1977), whilst at low oxygen concentrations they will be able to grow throughout the sediment column. Similarly the activity of obligate aerobes will be restricted by low oxygen concentrations and enhanced by higher concentrations. The effects of oxygen concentration on nutrient fluxes may reflect a combination of changes in microbial activity and in the activity of meiofauna.

The effects of animal type on nutrient fluxes in this experiment were similar to those found in my second experiment concerning the effects of meiofaunal type and density. In general the greatest fluxes were associated with the presence of whole meiofauna and nematodes plus copepods, the fluxes associated with nematodes alone, copepods alone and the control (no meiofauna) being lower.

#### Potential Problems with Diffusion Cells.

There are some potential problems with the diffusion cell technique. These are related to physical changes in the sediment, changes in biological processes and chemical changes.

The major physical changes in the sediment are associated with the introduction of sediment into the cells and the consequential disruption of sediment micro-structure. This occurs with the creation of any artificial sediment column. Problems associated

with changes in sediment compaction should not have occurred in my work because of the thin layer of sediment used. Other aspects of sediment structure, for example the presence of reduced micro-environments within oxidised regions, will be destroyed during pre-treatment of the sediment. These micro-structures, many of which are transient in the field, will however rapidly reform within the sediment layer before and during the experiment (Jorgensen, 1977). The depth layering of algal and bacterial populations within the sediment will also rapidly reform (Anderson and Meadows, 1978; Joint et al, 1982).

The layer of sediment used in my experiments was thin compared with the depth of a natural sediment column. This presents a second potential problem in terms of animal migration and survival. Many meiofauna show marked vertical migrations related to tidal cycles and feeding behaviour (Harris, 1972a; McLachlan, 1978; Joint et al, 1982). The range of migration can be up to 10 cm (Harris, 1972a; Joint et al, 1982). The range of sediment thicknesses used in my experiments was one to five cm. This depth is smaller than the migration range of many meiofauna and may therefore have altered their behaviour. The underlying water in my cells was examined in all of the experiments to determine whether any meiofauna had migrated through the mesh below the sediment. No meiofauna were found in any of the underlying water chambers.

Another potential problem with the diffusion cell technique was the survival of animals in a limited volume of sediment during the experiments. The changes in meiofaunal density within cells were, therefore, tested before the experiments were carried out. In all cases the minimum survival rate was over 90% for a 42 day incubation, the maximum being 140 % due to the presence of gravid copepods. No significant changes in relative density of the various



meiofaunal taxa were found. Since all of the flux experiments I carried out were over a maximum of 28 days, no major problems due to decreases in meiofaunal density were anticipated. The densities of each meiofaunal taxon in the flux cells were re-assessed at the end of each experiment for the calculation of meiofaunal density effects on nutrient flux.

The possible problems associated with the chemistry of the cells are mainly related to the limited volume of overlying water and the lack of a continuing sediment column below the interfacial sediment layer. The cells are a sealed system, with no water exchange and so there may be a problem with limited nutrient supplies. The introduction of a flow-through system, whilst it would provide a more constant supply of nutrients in the overlying water, would also introduce problems due to possible sediment resuspension and contamination of the cells (Boucher and Chamroux, 1976).

The limited supply of nutrients in my flux cells combined with the lack of a continuing sediment column also means that the flux through the sediment section may tend towards a steady state. This should lead to no net flux through the interface (Bernier, 1980). If this is the case then transformation of the flux:time relationship to a straight line allows the peak flux (at the start of the experiment) to be calculated.

A comparison between the results of these experiments and those of my field work has been made in the general discussion. In my general discussion I have also discussed in more detail the possible implications of meiofaunal effects on nutrient fluxes under a range of physical and chemical conditions in terms of effects on nutrient regeneration and oceanic productivity.

SECTION THREE - PACIFIC DEEP-SEA SURVEY.

## Introduction.

The cruise of H.M.S. Challenger between 1873 and 1876 collected samples from 362 stations at approximately 200 mile intervals from all over the worlds oceans. These samples provided the first evidence of the existence of faunal activity in sediments from depths of up to 5500 m. Amongst these samples were the first deep-Pacific samples. Since the voyage of the Challenger there has been considerable interest in the physical, chemical and biological environment of the deep-sea worldwide (Mills, 1983).

This introduction is divided into three parts. The first of these concerns manganese nodules in the Pacific ocean, the second concerns the effect of surface-water productivity on benthic productivity, the third section concerns the fauna of the seabed and its effects on nutrient re-cycling.

The main interest of those workers sampling the sediments of the central Pacific abyssal plain has been in factors affecting the density of manganese nodules. These nodules from the Pacific were first studied by the Challenger expedition. Data on the distribution of manganese nodules is, however, still patchy.

In general the highest densities of manganese nodules are found in areas with low rates of sediment accumulation and hence tend to be areas away from the continental margins, beneath the central oceanic gyres. The highest densities of nodules from the Pacific have been found in siliceous oozes with a sediment accumulation rate of  $<3 \text{ mm } 10^{-3} \text{ years}$  (Cronan, 1980).

The dissolved metals from which manganese nodules are formed come from four main sources. These sources are submarine volcanism, continental run-off, cosmic material (meteoritic dust) and diagenetic redistribution of elements (Cronan, 1974). There is now a large amount of interest in the effects of biological and

physico-chemical factors on the rates and modes of manganese nodule genesis. This work is also applicable to interpretation of the history of the deep-sea environment because the nodules collected represent a record of historical biological and physico-chemical ~~cond~~itions.

Much of the more recent sampling of sediments from the worlds oceans has been carried out by the Deep Sea Drilling Project (DSDP). Three legs of the DSDP cruise have sampled central Pacific ocean sediments. These were legs 7 - 9, sites 61 - 84. These samples were long, drilled cores in which the top 1-5 metres of sediment was often lost. The results of the DSDP sampling are, therefore, not applicable to studies of early diagenesis in sediments, except as a comparison with historical conditions. The geophysical properties of surface sediments from the central Pacific ocean have, more recently, been studied by Scripps Institution of Oceanography using a combination of piston, gravity and box cores. In general, however, the central regions of the Pacific ocean are still among the least studied areas of the worlds oceans (Marshall, 1979).

The two major oceanic gyres found in the central Pacific are the southern equatorial and northern equatorial gyres. Beneath these surface currents are strong undercurrents, often less than 100 metres below the water surface. The areas contained within these central oceanic gyres are oligotrophic zones of low surface productivity ( $< 100\text{mg C.m}^{-2} \text{ day}^{-1}$ ) (Marshall, 1979).

Many studies of manganese nodule genesis and diagenesis within sediments rely on the dating of sediments which may be very difficult in areas with a low deposition rates. The low surface water productivity is one of the major reasons for the low

sedimentation rate in the central Pacific (Osmond, 1981). Much of the dating of buried sediments is carried out using micro-fossils of benthic or planktonic foraminifera, with the dates of appearance or disappearance of a single species often being the reference points. Deeper sediments are often also dated using paleomagnetic data. Neither of these two methods is applicable when the sediments being considered are near to the sediment-water interface, as these sediments are often still being disturbed by biological activity (Osmond, 1981).

The productivity of the abyssal plains is related to the supply of organic material into the ecosystem. The main source of new organic matter to the sediments of the abyssal plains, away from continental margins, is in the form of detritus from the surface waters. The main forms of this detritus are faecal pellets, animal carcasses and phytodetritus (Marshall, 1979; Lochte and Turley, 1988 ). Much of the material sedimenting out of the surface water is consumed by mid-water organisms before reaching the bottom. These mid-water organisms, however, also contribute to the detrital 'rain' by the production of more faecal material. A second source of new organic matter in some regions of the seafloor, around the areas of hydro-thermal vents, is primary production by chemosynthetic bacteria (Jannasch and Wirsen, 1983; Grassle, <sup>1986</sup>1983). In general this hydrothermal productivity is restricted to fairly small areas of the seabed.

The surface productivity of the central Pacific gyres is, as mentioned above, very low. The productivity of the seabed below these oligotrophic waters is correspondingly low. Bacterial production in the central Pacific has been estimated to be  $4 - 480 \text{ ng C.1000 cm}^{-3} \text{ day}^{-1}$  (Jannasch and Wirsen, 1983). This is a factor of 10-1000 lower than would be expected for continental shelf

areas.

Much of the work on the fauna of the deep-Pacific has been carried out using subsamples from grabs and boxcores of sediments. The studies of meiofauna from the central Pacific have revealed very diverse but very variable communities (Thiel, 1983). The first meiofauna collected by the Challenger expedition consisted of a few ostracods and a large number of foraminifera (Brady, 1960). Since then improvements in sampling gear have permitted the collection of almost undisturbed samples of sediment. These samples have shown that, although slightly fewer taxa of meiofauna are to be found in the deep-sea, many of the taxa show greatly increased numbers of species compared with shallow-water areas (Thistle, 1979; Thiel, 1983). Often these species are highly localised, being present in only single samples (Thistle, 1979).

The deep-sea meiofauna tends to be dominated by nematodes and, in some regions, foraminifera (Marshall, 1979; Thiel, 1983). The density of meiofauna found in central Pacific sediments is generally a factor of 2 lower than that found under comparable conditions in the Atlantic. This difference may be due to the differences in productivity between the Atlantic and Pacific surface waters. The density and biomass of meiofauna in deep-sea sediments is also usually less than half that found in shallow-water. This difference is probably also related to differences in the supply of organic matter to the sediments.

In general the meiofauna of deep-sea sediments are concentrated at the sediment-water interface, over 90 % of the animals being found in the top 5 cm of sediment. Central oceanic deep-sea sediments tend to be well oxygenated, unlike shallow-water muds. The concentration of meiofauna at the interface is probably,

therefore, related to the supply of organic carbon as a food source (Thiel, 1983).

The level of biological activity within the sediments of the seafloor also determines what proportion of the detrital material is broken down into inorganic nutrients. The infauna of the sediments is responsible for the initial breakdown of larger organic particles. The shredding of organic debris by infauna produces a larger surface area for bacterial colonisation (Pomeroy, 1980). The rate of subsequent bacterial digestion of organic matter in the deep-sea is slow relative to that in shallow waters. This is partly due to the lower numbers of bacteria in the deep-sea than in shallow-water sediments. Another reason for the low rate of breakdown of organic matter in the deep-sea is the lower metabolic rate of bacteria at high pressure (Jannasch and Wirsen, 1983; Lochte and Turley, 1988; Suess, 1988).

Some of the nutrients produced by breakdown of organic matter on the seafloor are retained within the sedimentary column and undergo subsequent diagenetic reactions during burial. The nutrients not retained in the sediment porewater are eventually recycled to the surface waters and are thus made available to primary producers. The processes whereby nutrients are transported from the bottom-water into the euphotic zone include bottom currents, upwelling currents and storm mixing. It is the movement of large quantities of nutrients from deep water into the surface water that is partly responsible for the spring phytoplankton bloom. The organic material produced by this bloom is now being investigated as a possible major source of detrital matter for the deep-sea in the form of phytodetritus (Lochte and Turley, 1988).

Some work has been done on the relationship between sediment community oxygen consumption and rates of nutrient exchange in

Pacific sediments (e.g Goloway and Bender, 1982; Smith et al, 1983). There is, however, little literature on the relationships between nutrient concentration profiles in these sediments and profiles of other physical, chemical and biological parameters.

The samples used in this section were collected aboard the Scripps Institution research vessel Thomas Washington<sup>S</sup> during the third leg of the Crossgrain cruise led by Dr. David Cronan of Imperial College London. There were two main purposes to this cruise. The first of these was to study the spatial variability of manganese nodules and sediments in the central Pacific between Tahiti and Hawaii. The second purpose of the cruise was to look at the relationships between various biological, physical and chemical parameters in the sediments. My work has been concerned with the latter part of the project.



### Materials and methods

The samples used in this section were collected by myself and James Waterworth whilst aboard the Scripps Institute research vessel "Thomas Washington" between the 8<sup>th</sup> and 22<sup>nd</sup> of May 1987. The sediments sampled were from the southern Central Pacific Ocean at a latitude of between 01° 20' S and 07° 57' S and at a longitude of between 157° 18' W and 159° 49' W. The depths from which sediments were collected ranged from 5098 to 5657 metres.

The exact positions, cruise reference numbers and water depths of each of the stations sampled are shown in table 3.1. The positions of each of the stations in relation to each other are shown in figure 3.1 (general Pacific Ocean) and figure 3.2 (ships course).

At each station one spade-box core was collected using a Hessler-Sandia Mk IV Spade Box Corer (Ocean Instruments, San Diego). This spade-box corer is illustrated in plate 3.1. The box-core was then subsampled (plate 3.2) in the order shown in table 3.2. We collected 1 core for numbers of macrofauna, meiofauna and micro-organisms and 2 cores for interstitial nutrient concentrations and interstitial dissolved metal concentrations.

Other workers also collected subcores for sediment-bound metal concentrations (Imperial College London), sediment particle size and water content, Eh, pH and bioturbation (P.S. Meadows and A. Tufail).

The subcores for nutrient/metal concentrations and faunal numbers were transferred to the cold room (5°C) immediately after removal from the box core.

The depths at which the cores for faunal numbers, nutrients and water content were sectioned are shown in figure 3.3. The cores were clamped upright and extruded using a plunger (figure 3.4.)

Station number	Cruise reference	Latitude	Longitude	Depth (m)	Date
1	CRGN 49	07°56.43 S	159°20.11 W	5657	08/05/87
2	CRGN 64	06°46.53 S	159°21.61 W	5272	11/05/87
3	CRGN 76	05°22.65 S	158°04.42 W	5155	13/05/87
4	CRGN 83	04°44.45 S	158°50.00 W	5098	14/05/87
5	CRGN 91	03°49.10 S	159°48.80 W	5120	16/05/87
6	CRGN 102	02°26.29 S	157°36.40 W	5132	18/05/87
7	CRGN 109	01°19.30 S	158°36.40 W	5229	19/05/87
8	CRGN 128	05°39.21 S	157°18.43 W	5298	22/05/87

Table 3.1. Cruise reference numbers, latitude, longitude, water depth and sampling date (GMT) for each of the boxcore stations.

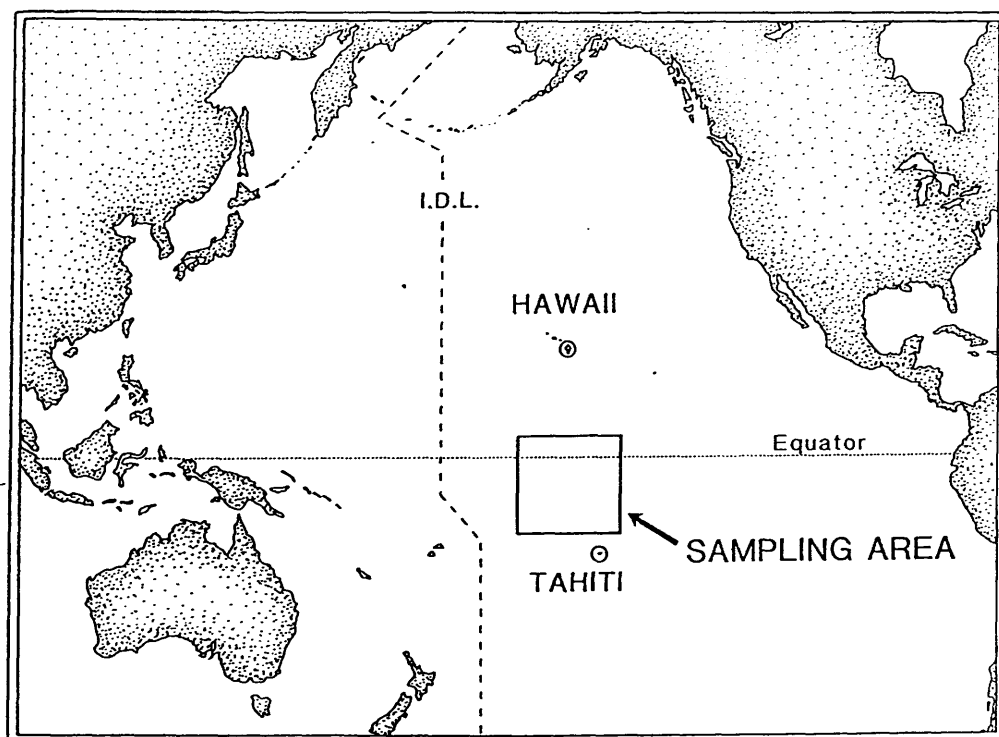


Figure 3.1. General map of the Pacific Ocean showing the position of our sampling area. I.D.L. = International Date Line.

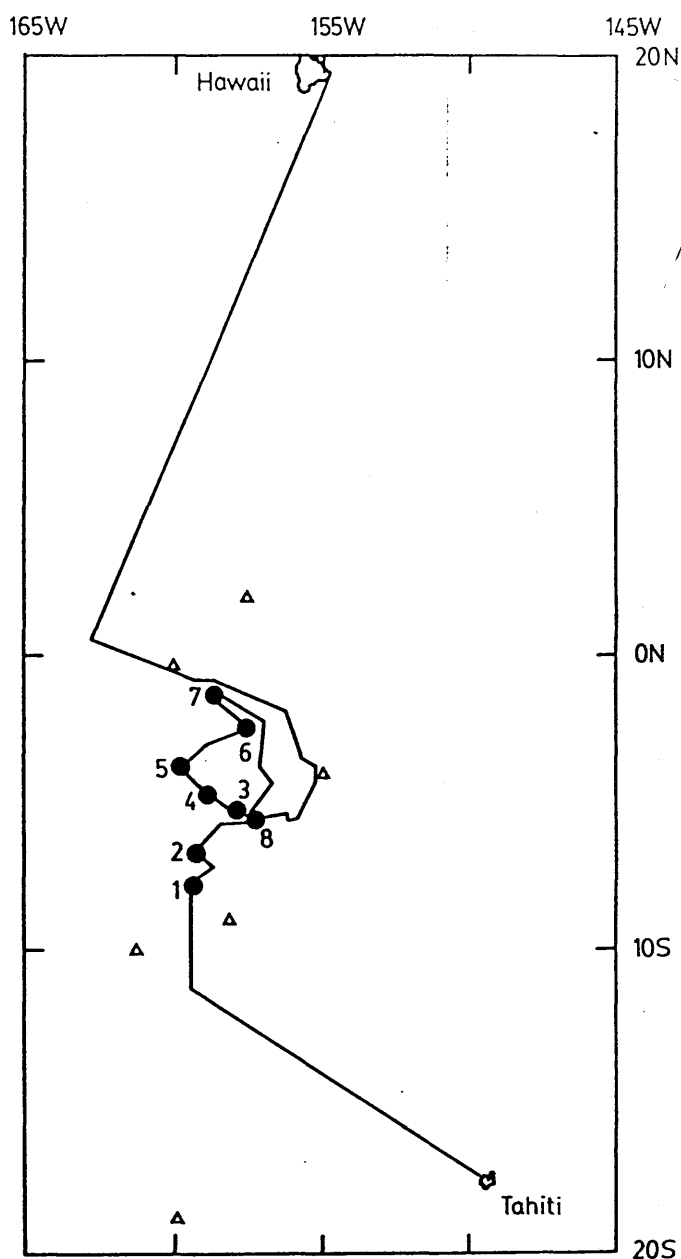


Figure 3.2. Plot of the ship's course between Tahiti and Hawaii. Numbered circles = sampling stations; Open triangles = islands / atolls.



Plate 3.1. Hessler-Sandia Mk IV Boxcorer on the deck of the RV Thomas Washington.



Plate 3.2. Plastic subcores in position in a boxcore.

- 
- 1) Boxcore removed from spade-box corer.
  - 2) Overlying water from boxcore siphoned-off and retained.
  - 3) Depth of boxcore measured.
  - 4) Boxcore photographed with reference card and colour charts.
  - 5) Surface nodules removed with forceps.
  - 6) Vane shear strength profile measured.
  - 7) Plastic subcores inserted, sediment surface marked on core, cores labelled.
  - 8) Side of boxcore opened, any nodules removed from side of boxcore.
  - 9) syringe-cores of sediment taken for metal analysis (by ICL)
  - 10) Subcores dug-out, capped and photographed as necessary.
  - 11) Subcores transfered to laboratory/cold room.
- 

Table 3.2. Order of treatments used for the boxcore once onboard ship.

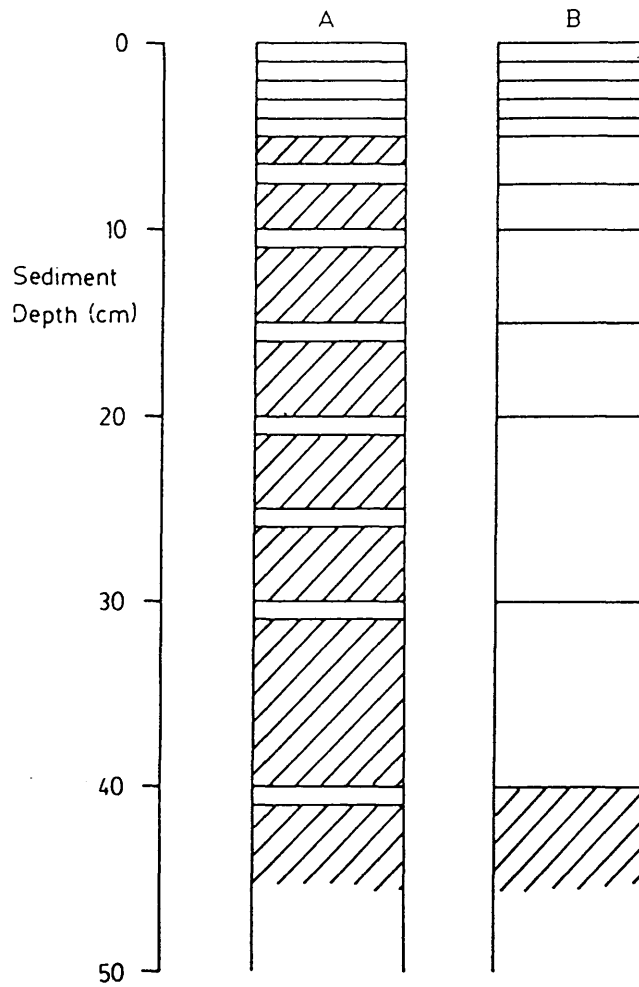
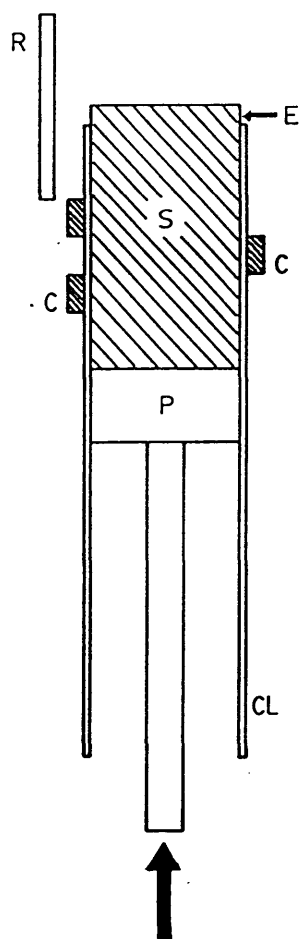


Figure 3.3. Sampling depths for each of the parameters measured. Core A = dissolved nutrients/metals, micro-organism numbers and water content. Core B = meiofaunal numbers. Hatched sediment = unused.



**Figure 3.4.** Core extrusion set-up. CL = core liner; P = plunger; C = clamp; S = sediment; E = extruded sediment; R = ruler.



#### Micro-organism number samples.

These were removed from the nutrient cores immediately after sectioning. Two ml of sediment was transferred to a 2.5 ml snap-top vial and preserved with 0.5 ml of 20% formalin. These samples were then stored in the coldroom on board ship and re-refrigerated until being analysed. This was to prevent any evaporation from the vials.

Numbers of micro-organism per gram of sediment were assessed using the smear-ratio method described in section 1. The number of micro-organisms per gram wet weight of sediment was converted to numbers per gram dry weight using the sediment water content calculated as a percentage of the wet weight.

#### Meiofauna/macrofauna samples.

Two 25 ml sediment samples were collected from each of the depths sampled (figure 3.3). For the surface samples (0-5 cm) this was the whole sediment section. For the deeper samples (5-40 cm) this was a vertical subsample covering the whole depth range of the section.

These samples were stored in 30 ml plastic universal containers and preserved with 5 ml of 20% formalin. The samples were kept in the coldroom on board ship.

The meiofauna and macrofauna were extracted from the sediment by Ludox density-difference flotation as described in section 1. Three 5 ml subsamples of the preserved bulk sediment were extracted for each depth section. This extraction gave two fractions, a heavy sediment-rich sample, and a light organic fraction. Both fractions of the extracted sediment subsamples were then stained with Rose Bengal and the metazoans counted under a binocular microscope. A

compound microscope was used for identification as necessary. The extracted samples were then sieved through a 150  $\mu\text{m}$  and a 100  $\mu\text{m}$  sieve to give three size fractions (35-100, 100-150 and 150-500  $\mu\text{m}$ ). The foraminifera in these fractions were then counted separately and the counts pooled. This re-sieving reduces the size-range of animals under observation and thus makes the counting simpler.

Benthic foraminifera were distinguished from planktonic foraminifera using the descriptions and illustrations of Barker (1960) and advice given by Dr. A. Gooday from the Institute of Oceanographic Sciences. Living foraminifera contained pink-stained protoplasm within the test.

#### Water content samples.

These samples were collected by P.S. Meadows and A. Tufail at the same depths as the Smear-ratio samples. The samples were taken from within the main core of sediment, avoiding the sediment in contact with the plastic core. One 2.5 ml vial of sediment was collected from each depth sampled. Subsequent analysis of these samples was carried out by myself.

In the laboratory these sediment samples were homogenised gently and divided into three subsamples. The subsamples were placed onto pre-weighed foil, reweighed and oven dried at 60° C for 24 hours. The foils were then allowed to cool in a desiccator and then re-weighed. The water contents were calculated as % dry weight (B.S.1377). The water content as % wet weight was also calculated in order to convert the smear-ratio counts to micro-organism numbers per gram dry weight.

#### Dissolved nutrient/metal samples.

These samples were collected using two sediment cores. Both cores were sectioned within 30 minutes of the cores being transferred to the cold room. This was 2 - 4 hours after the boxcore was brought inboard. The sediment samples from the whole of both cores were sectioned using the set-up shown in figure 3.4 into screw-top plastic tubs which were then sealed until the porewater was extracted.

Porewater was extracted from the sediment sections using a sediment squeezing apparatus. The details of this method are given in section 1. The water samples collected from the cores were then taken-up in a syringe and filtered through a  $0.22\mu\text{m}$  membrane filter which had been pre-rinsed in porewater from the same water sample. Samples were filtered directly into 2.5 ml plastic snap-top vials. Five of these vials were collected from each of the sediment sections. In general 20 ml of porewater was collected from each of the sediment sections, the remaining porewater was used for pre-rinsing the membrane filters. The squeezing time required to extract this volume of ~~extracted~~ porewater was less than 10 minutes for all of the sediment sections, most sections being squeezed in less than one minute.

The porewater vials were stored in a deep-freeze on board ship and packed in ice for air travel back to the U.K. The samples were kept frozen in a deep-freeze until required for analysis. Two of the vials of extracted porewater were used for dissolved metal analysis, three vials being used for dissolved nutrient analysis.

Dissolved nutrient analysis was carried out on return to Glasgow using the small-scale methods described in section 1.

The dissolved metal analysis was performed using the Inductively Coupled Plasma Atomic Emission Spectrophotometer

(ICPAES, Applied Research Laboratories model 34000C) at the Royal School of Mines, Imperial College London.

Prior to analysis one ml of the water samples was diluted with nine ml of 1N Hydrochloric acid. This dilution reduces the extent of interference due to excess sodium in the solution and ensures that all of the metal present is in solution. The samples were then run through the ICPAES with 6 reagent blanks and 11 standard solutions at a range of concentrations. Thirteen of the samples were run in duplicate in order to determine the analytical precision of both the equipment and of the analytical run. The samples were run in a random order to reduce any systematic errors.

Two analytical runs are needed in order to cover all of the elements of interest. The first analytical run used the GEN-5 calibration. This calibration allows concentrations of lithium, sodium, potassium, magnesium, calcium, strontium, barium, iron and zinc to be measured. The second analytical run used the SALT-1 calibration. This calibration allows the concentrations of phosphorous, sulphur, boron, silicon and arsenic to be measured. The detection limits and analytical precision for each of the elements in the two analytical runs are given in table 3.3. The machine detection limits are determined by the concentration of the elements in the lowest standard solution. The effective detection limit for an element is taken to be twice the standard deviation on replicate analyses of a single sample. The analytical precision is calculated as the mean of the percentage difference between replicate analyses of a single sample (R. Hodgkinson pers. comm.).

Calibration/ Element	Machine detection limit	Effective detection limit	Analytical precision (+ %)
=====			

GEN-5 calibration.

Lithium	0.030	0.034	14.0815
Sodium	0.500	5.976	2.1600
Potassium	1.000	0.708	3.5523
Magnesium	1.000	0.318	2.5046
Calcium	0.600	0.290	2.6792
Strontium	0.030	0.012	2.1085
Barium	0.050	0.010	13.3954
Iron	0.400	0.106	5580.5462*
Zinc	0.100	0.086	63.3323

SALT-1 calibration.

Phosphorous	0.400	0.234	239.9415
Sulphur	1.000	2.552	2.4931
Boron	0.050	0.174	12.6623
Silicon	0.500	0.174	12.6623
Arsenic	0.500	0.332	236.6831

Table 3.3. Machine detection limits, effective detection limits and analytical precision for the elements analysed using the ICPAES. Machine detection limits = lowest standard concentration; effective detection limit = 2 x standard deviation on the 13 samples run in duplicate; analytical precision = mean of the percentage difference between replicate analyses for the duplicate samples. \* = high due to Fe concentrations being close to detection limit. All units  $\text{mg l}^{-1}$

## Results

Successful boxcores were collected from seven stations. At station three the boxcore lid failed to shut completely, allowing the surface of the boxcore to be eroded during ascent. The sediment from this boxcore was not used for the work reported here.

Photographs of the boxcores collected at stations 1,2,4,5,6,7 and 8 are shown in plates 3.3 - 3.9. These photographs contain Kodak colour and black and white exposure charts. These were included in order to give a standard colour range for reference purposes.

The depths of the sediment cores collected from each station with the types of sediment and weights and types of manganese nodules in each boxcore are shown in table 3.4. All of the boxcores were collected from below the Carbonate Compensation Depth (C.C.D.), this is the depth at which the rate of dissolution of carbonate exceeds the rate of burial of deposited material due to continued sedimentation (Berner, 1980). Sediments from above the C.C.D. tend to be lighter in colour due to the presence of large numbers of calcareous Foraminiferan tests (calcareous oozes), those from below the C.C.D. tend to be dark red or brown siliceous oozes. The changes in sediment colour associated with the C.C.D. are shown in plate 3.10. Some of the sediment below the surface of the boxcore in stations 5, 6 and 7 was, however, calcareous (plates 3.11, 3.12 and 3.13. The presence of calcareous sediments below the C.C.D. may be due to several processes, including rapid deposition and burial of calcareous material and fluctuations in the level of the C.C.D. due to sea-level changes (on geological time scales).

## Micro-organism numbers.

The numbers of micro-organisms per gram dry weight of sediment



Plate 3.3. Station one boxcore surface.



Plate 3.4. Station two boxcore surface.



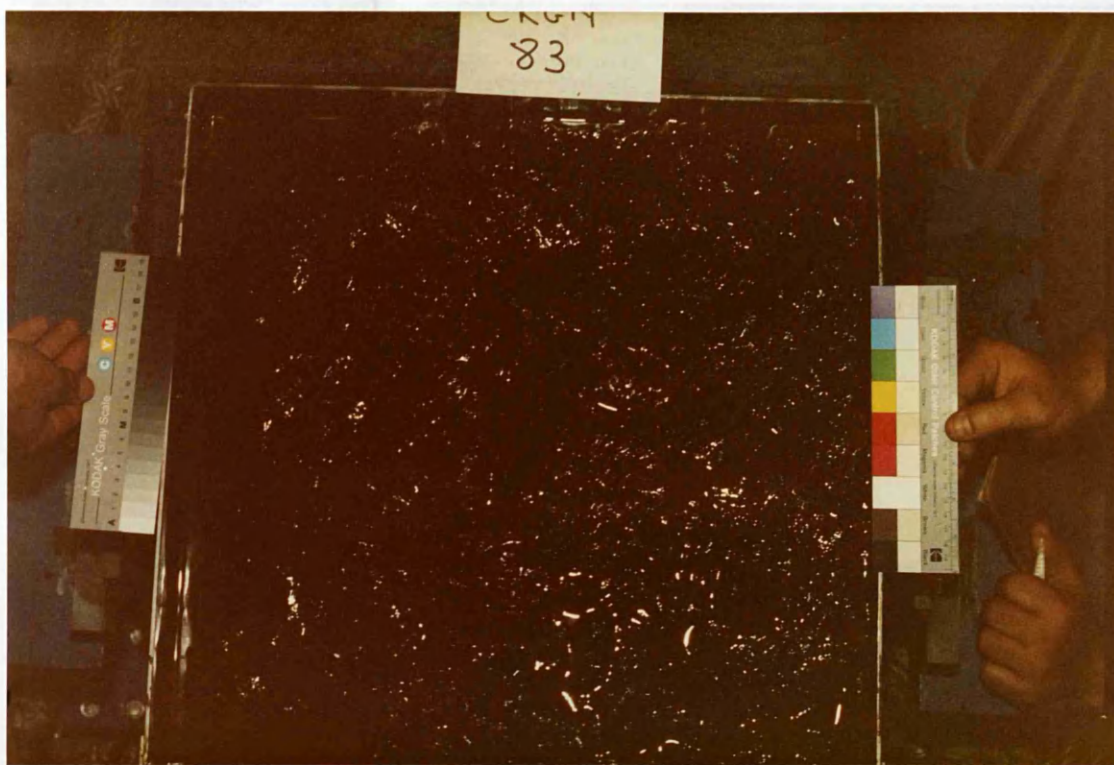


Plate 3.5. Station four boxcore surface.



Plate 3.6. Station five boxcore surface.





Plate 3.7. Station six boxcore surface.

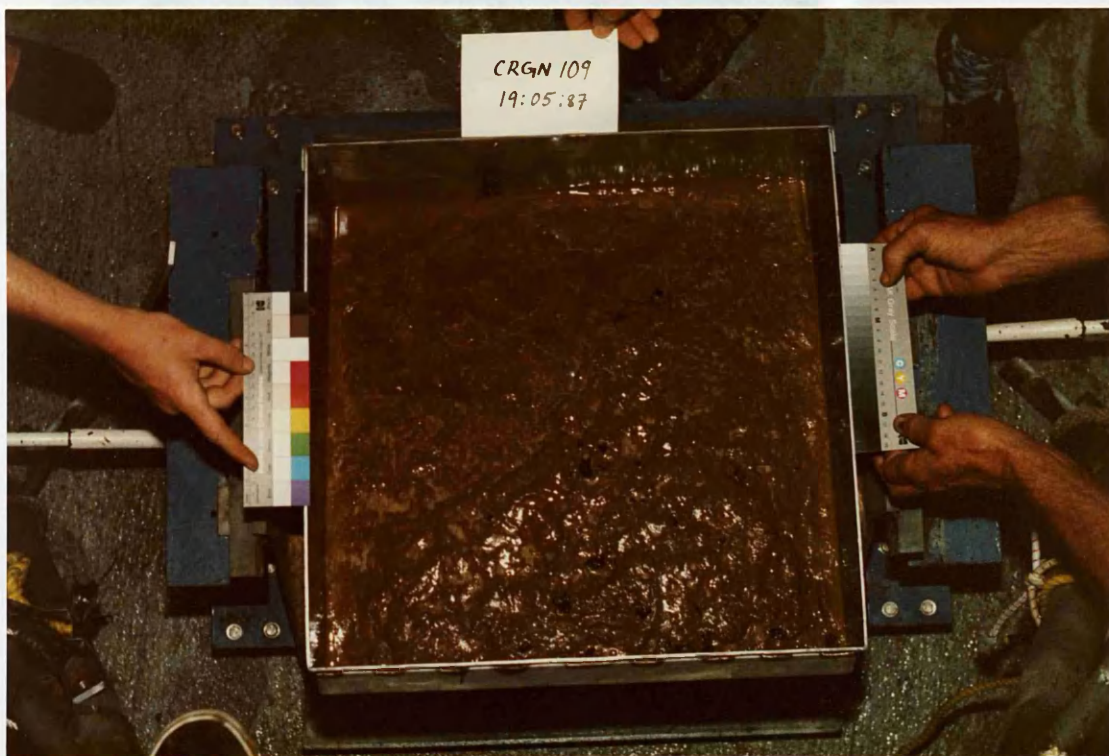


Plate 3.8. Station seven boxcore surface.

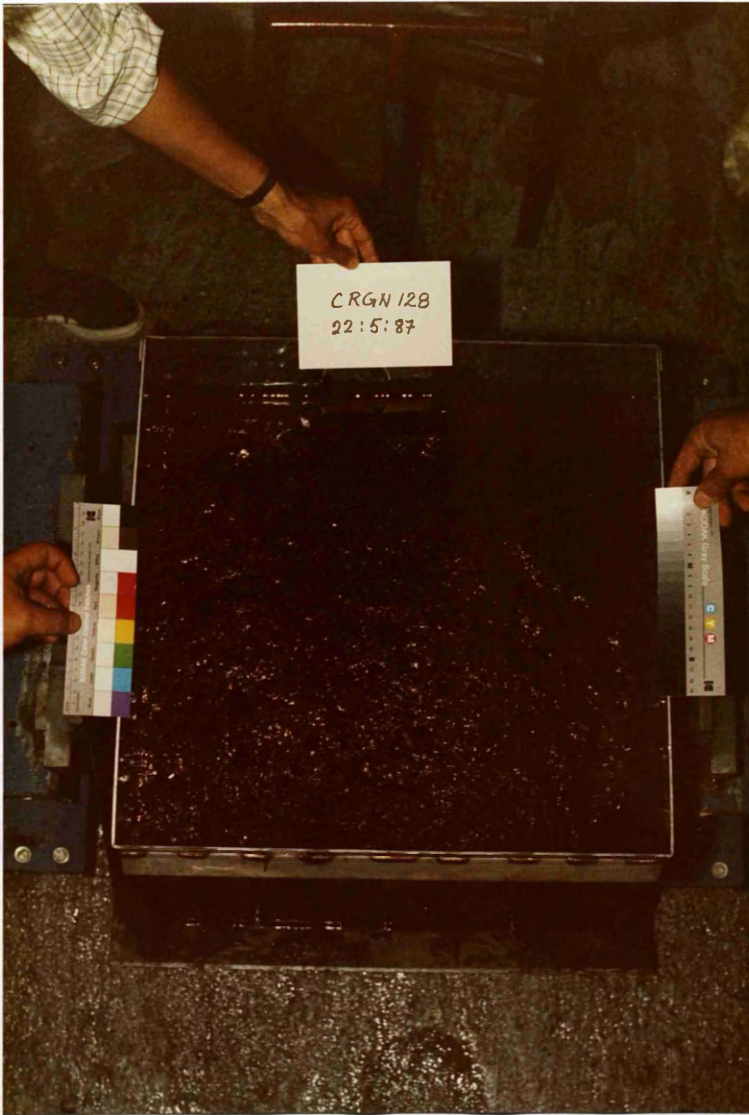


Plate 3.9. Station eight boxcore surface.

Station number	Sediment type	Nodule weight (kg)	Nodule type.
1	Red/brown clay unbanded	1.2	r, s-m
2	Brown clay unbanded	0.022	r, s
4	Brown clay unbanded	1.6	r, s-m
5	Brown clay overlaying calcareous ooze	0.84	r, s-m
6	Brown clay overlaying calcareous ooze	2.15	r, m
7	Brown clay overlaying calcareous ooze	0.11	r, s
8	Brown clay unbanded	1.1	r, s & m

Table 3.4. Types of sediment, weights of nodules and types of nodules at each of the stations sampled. r = rough nodules, s = small (<2.5 cm), m = medium (2.5 - 7.5 cm).



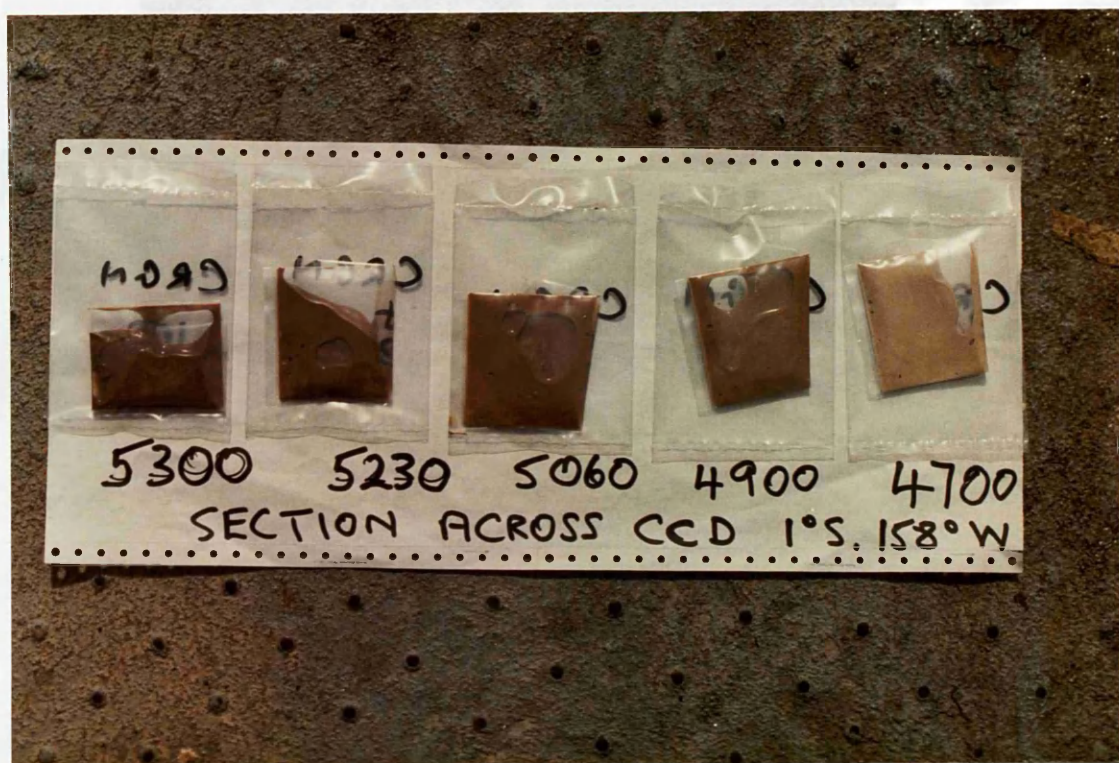


Plate 3.10. Changes in colour associated with the Carbonate Compensation Depth (CCD). Lighter samples contain more carbonate and are from above the CCD. Darker samples, from below the CCD, are mainly siliceous.

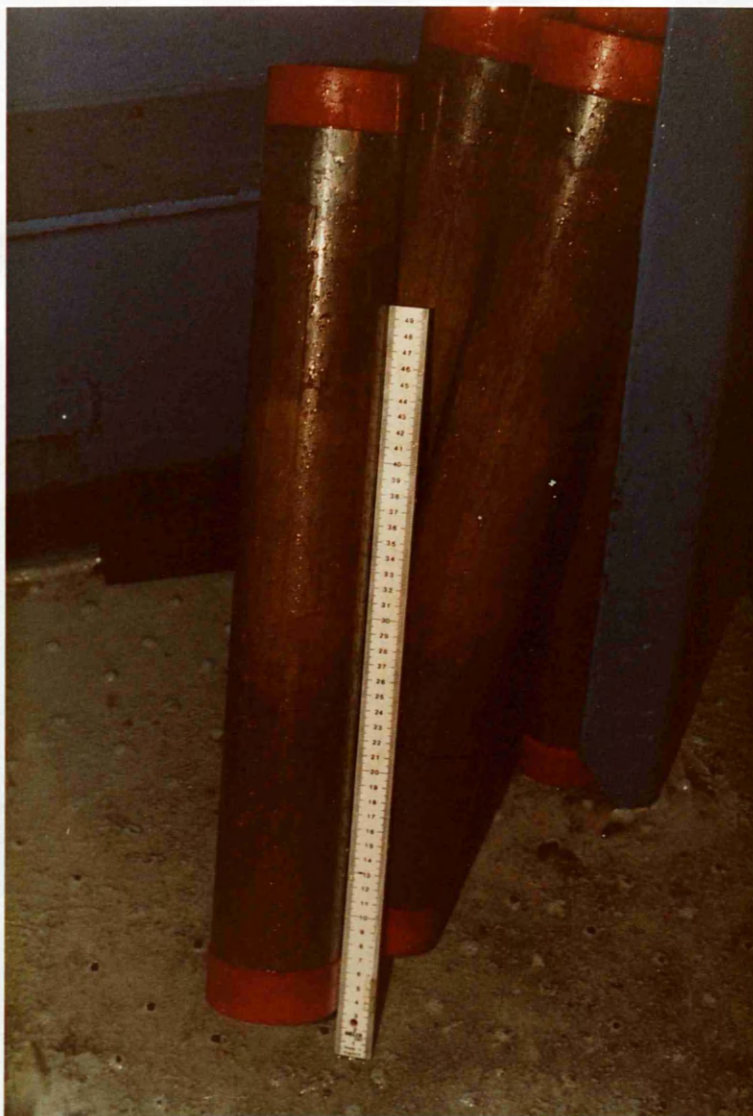


Plate 3.11. Station five. Sediment layering in the subcores.

Plate 3.12. Station six. Sediment layering in the subcores.



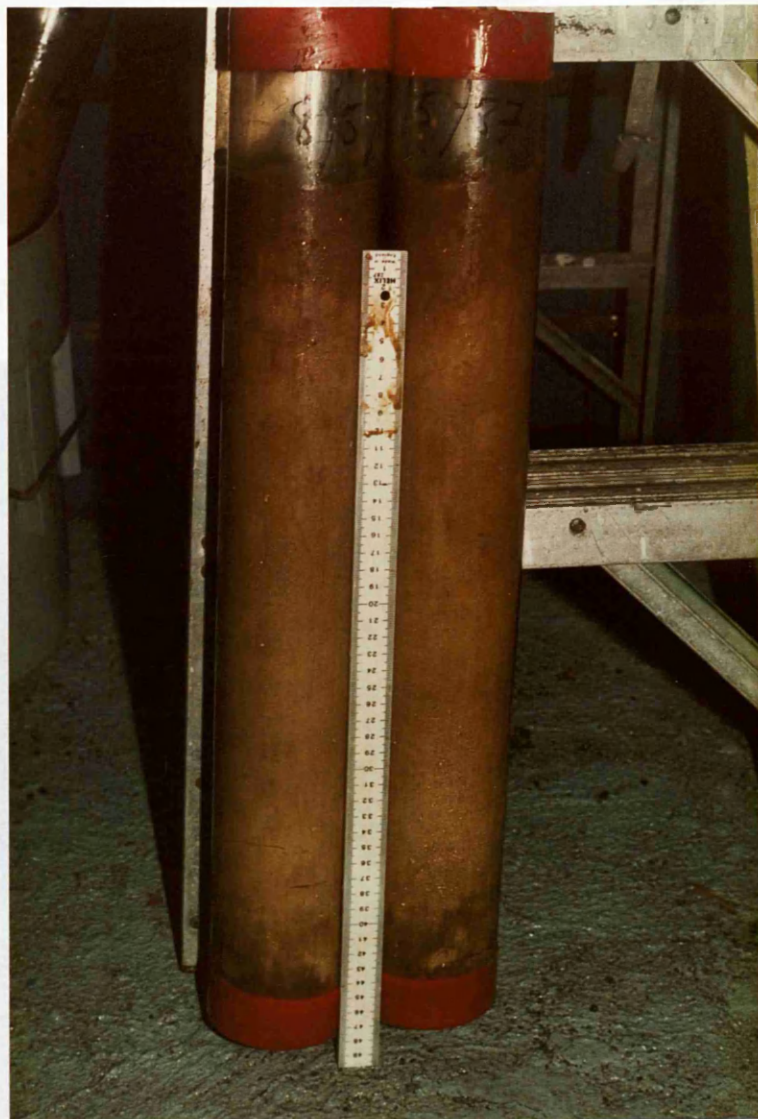


Plate 3.12. Station six. Sediment layering in the subcores.

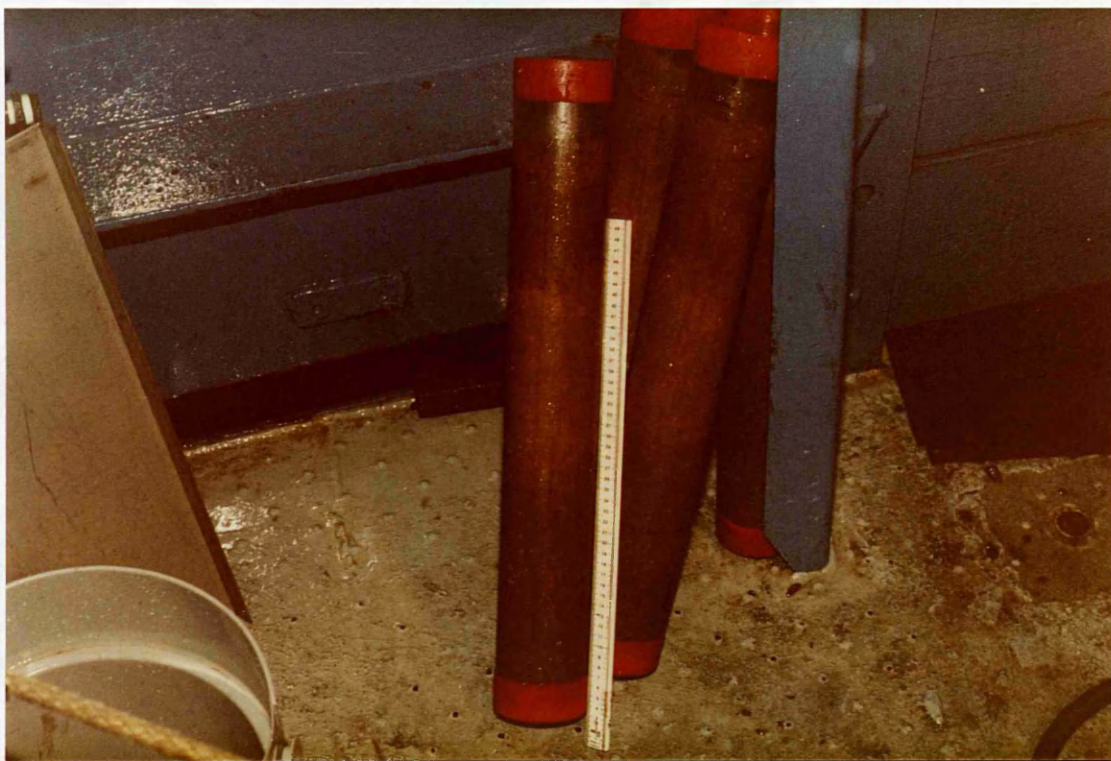


Plate 3.13. Station seven. Sediment layering in the subcores.

(mean and s.d.) for stations 1,2,4,5,6,7 and 8 are shown in tables 3.5-3.11. Depth profiles of these densities have been plotted alongside the meiofaunal densities for comparison in figures 3.5, 3.7, 3.9, 3.11, 3.13, 3.15 and 3.17. The densities of micro-organisms have been converted from numbers per gram wet weight of sediment using the data from the water content samples. The profiles for stations 6 and 7 are incomplete. This is due to the absence of a water content sample for the 40-41 cm depth section.

In general the micro-organisms densities decreased exponentially from the surface into the core, the density at 30-40 cm being 1.75-9.5 % of the surface count. Regression lines were fitted to the depth profiles of micro-organisms. These lines were fitted to the original data and to three sets of transformed data. The transformations used were square root,  $\log_{10}$  and negative reciprocal. The negative reciprocal transformation gave the best fit for all stations. The coefficients of the regression lines and the correlation coefficients are given in table 3.12. The lines are significant for all stations.

#### Meiofauna numbers.

The densities (numbers per ml of sediment) of each taxon of meiofauna (mean and sd) for each of the depth samples are shown in tables 3.13-3.19 for stations 1,2,4,5,6,7 and 8 respectively. Profiles of foraminiferan and metazoan numbers with depth into the sediment have been plotted alongside the respective micro-organism densities for comparison and are shown in figures 3.6, 3.8, 3.10, 3.12, 3.14, 3.16 and 3.18 for stations 1,2,4,5,6,7 and 8 respectively.

The meiofaunal numbers generally showed an exponential decline into the sediment, the maximum depth to which meiofauna were found



Sediment depth (cm)	micro-organism numbers ( $\times 10^6 \text{ g}^{-1}$ )		%surface
	mean	sd	
00 - 01	7.3701	0.0708	100.00
01 - 02	4.8412	0.0329	65.69
02 - 03	4.1437	0.0288	56.22
03 - 04	2.0877	0.0230	28.33
04 - 05	1.8531	0.0247	25.14
6.5 - 7.5	1.3279	0.0199	18.02
10 - 11	1.0460	0.0257	14.19
15 - 16	0.7838	0.0322	10.63
20 - 21	0.6634	0.0165	9.00
25 - 26	0.4415	0.0098	5.99
30 - 31	0.3328	0.0091	4.52
40 - 41	0.0225	0.0226	3.05

Table 3.5. Numbers of micro-organisms per gram dry weight of sediment for each depth sample at station 1 (mean, sd, % surface count). n=3 for all depth samples.

Sediment depth (cm)	micro-organism numbers ( $\times 10^6 \text{ g}^{-1}$ )		%surface
	mean	sd	
00 - 01	5.8202	0.0454	100.00
01 - 02	3.9827	0.0178	68.43
02 - 03	4.0279	0.0283	69.21
03 - 04	2.8491	0.0090	48.95
04 - 05	1.8909	0.0161	32.49
6.5 - 7.5	1.3158	0.0079	22.61
10 - 11	1.0520	0.0079	18.07
15 - 16	0.8840	0.0065	15.19
20 - 21	0.7491	0.0139	12.87
25 - 26	0.4905	0.0040	8.43
30 - 31	0.3904	0.0170	6.71
40 - 41	0.2411	0.0082	4.14

Table 3.6. Numbers of micro-organisms per gram dry weight of sediment for each depth sample at station 2 (mean, sd, % surface count). n=3 for all depth samples.

Sediment depth (cm)	micro-organism numbers ( $\times 10^6 \text{ g}^{-1}$ )		%surface
	mean	sd	
00 - 01	10.8993	0.0294	100.00
01 - 02	8.2486	0.0342	79.82
02 - 03	6.7949	0.0273	62.34
03 - 04	5.1367	0.0394	47.13
04 - 05	4.5711	0.0639	41.94
6.5 - 7.5	2.4861	0.0252	22.81
10 - 11	1.8201	0.0087	16.70
15 - 16	1.3105	0.0217	12.02
20 - 21	0.8004	0.0227	7.34
25 - 26	0.6968	0.0284	6.39
30 - 31	0.5277	0.0413	4.84
40 - 41	0.4935	0.0261	4.53

Table 3.7. Numbers of micro-organisms per gram dry weight of sediment for each depth sample at station 4 (mean, sd, % surface count). n=3 for all depth samples.

Sediment depth (cm)	micro-organism numbers ( $\times 10^6 \text{ g}^{-1}$ )		%surface
	mean	sd	
00 - 01	7.8470	0.0385	100.00
01 - 02	6.5893	0.0276	83.97
02 - 03	5.6836	0.0259	72.43
03 - 04	5.8100	0.0215	74.04
04 - 05	3.6077	0.0228	45.98
6.5 - 7.5	2.2749	0.0213	28.99
10 - 11	1.7142	0.0215	21.85
15 - 16	1.4620	0.0300	18.63
20 - 21	1.3150	0.0277	16.76
25 - 26	1.0800	0.0288	13.76
30 - 31	0.8354	0.0219	10.65
40 - 41	0.7398	0.0263	9.43

Table 3.8. Numbers of micro-organisms per gram dry weight of sediment for each depth sample at station 5 (mean, sd, % surface count). n=3 for all depth samples.

Sediment depth (cm)	micro-organism numbers ( $\times 10^6 \text{ g}^{-1}$ )		%surface
	mean	sd	
00 - 01	7.1947	0.0568	100.00
01 - 02	4.7609	0.0266	66.17
02 - 03	3.6653	0.0341	50.94
03 - 04	2.9543	0.0332	41.06
04 - 05	1.7701	0.0270	24.60
6.5 - 7.5	1.2570	0.0133	17.47
10 - 11	0.7882	0.0257	10.96
15 - 16	0.5623	0.0096	7.82
20 - 21	0.3246	0.0178	4.51
25 - 26	0.2315	0.0092	3.22
30 - 31	0.1264	0.0115	1.76
40 - 41	n/a	n/a	n/a

**Table 3.9.** Numbers of micro-organisms per gram dry weight of sediment for each depth sample at station 6 (mean, sd, % surface count). n/a = not available due to lack of water content sample. n=3 for all depth samples.

Sediment depth (cm)	micro-organism numbers ( $\times 10^6 \text{ g}^{-1}$ )		%surface
	mean	sd	
00 - 01	7.4203	0.0248	100.00
01 - 02	4.9615	0.0276	66.86
02 - 03	3.4371	0.0470	46.32
03 - 04	2.2977	0.0186	30.96
04 - 05	1.4939	0.0320	20.13
6.5 - 7.5	1.6422	0.0285	22.13
10 - 11	0.7016	0.0128	9.46
15 - 16	0.4766	0.0173	6.42
20 - 21	0.3504	0.0158	4.72
25 - 26	0.2926	0.0143	3.94
30 - 31	0.1699	0.0248	2.29
40 - 41	n/a	n/a	n/a

Table 3.10. Numbers of micro-organisms per gram dry weight of sediment for each depth sample at station 7 (mean, sd, % surface count). n/a = not available due to lack of water content sample. n=3 for all depth samples.

Sediment depth (cm)	micro-organism numbers ( $\times 10^6 \text{ g}^{-1}$ )		%surface
	mean	sd	
00 - 01	4.7628	0.0272	100.00
01 - 02	3.7614	0.0185	78.97
02 - 03	2.7792	0.0264	58.35
03 - 04	1.9071	0.0151	40.04
04 - 05	1.7466	0.0153	36.67
6.5 - 7.5	1.3169	0.0260	27.65
10 - 11	0.8050	0.0235	16.90
15 - 16	0.4645	0.0098	9.75
20 - 21	0.3020	0.0135	6.34
25 - 26	0.2140	0.0111	4.49
30 - 31	0.1941	0.0080	4.08
40 - 41	0.1482	0.0102	3.11

Table 3.11. Numbers of micro-organisms per gram dry weight of sediment for each depth sample at station 8 (mean, sd, % surface count). n=3 for all depth samples.

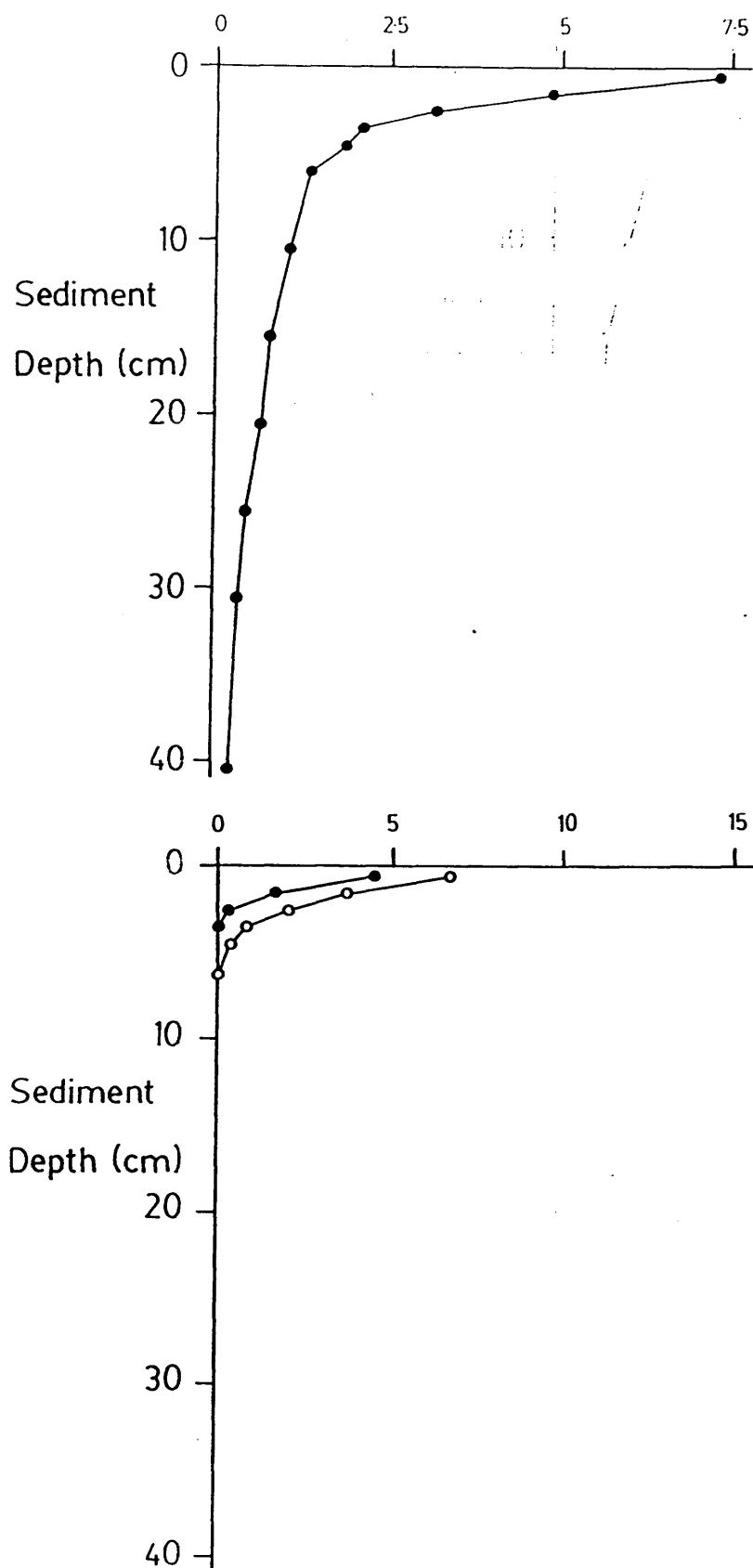


Figure 3.5. (Top) Micro-organism numbers  $\times 10^6 \text{ g}^{-1}$  dry weight for each sediment depth at station 1.

Figure 3.6. (Bottom) Meiofaunal numbers  $\text{ml}^{-1}$  for each sediment depth at station 1. Open circles = metazoans, solid circles = foraminifera.



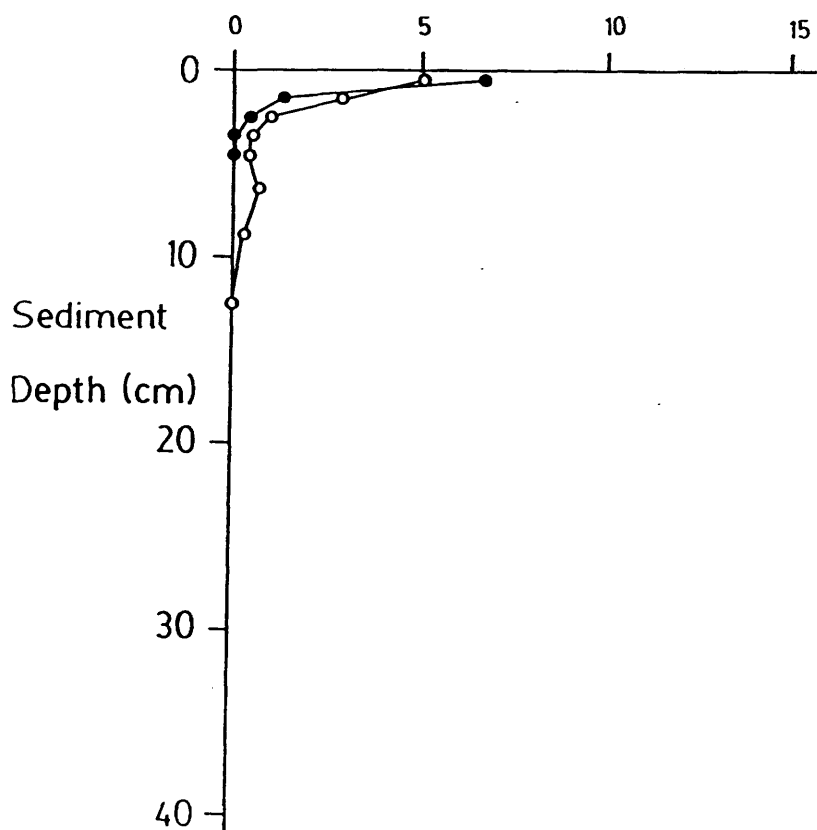
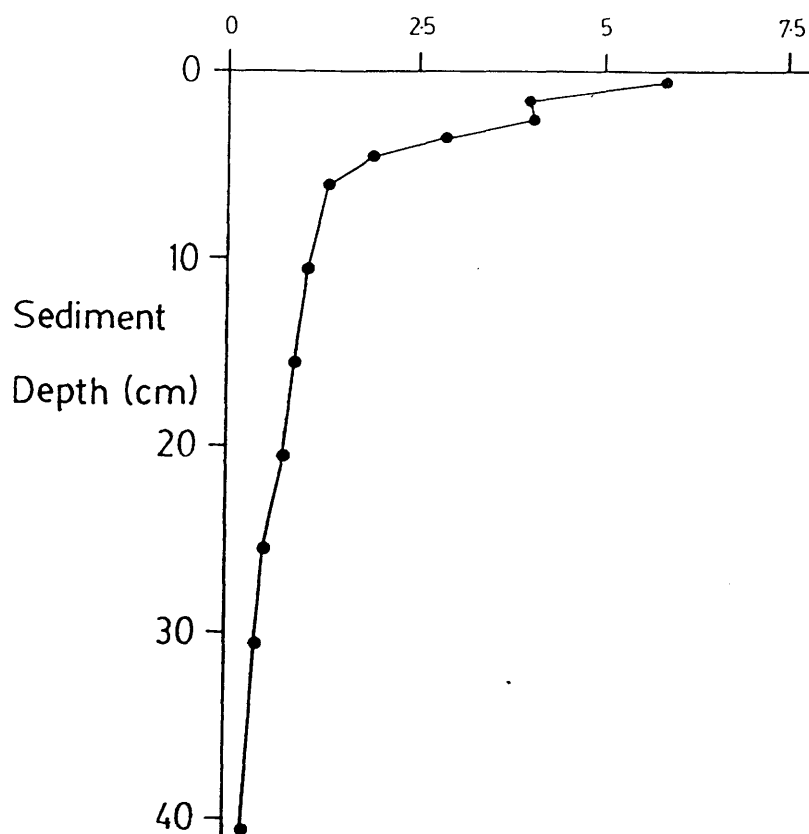


Figure 3.7. (Top) Micro-organism numbers  $\times 10^6 \text{ g}^{-1}$  dry weight for each sediment depth at station 2.

Figure 3.8. (Bottom) Meiofaunal numbers  $\text{ml}^{-1}$  for each sediment depth at station 2. Open circles = metazoans, solid circles = foraminifera.

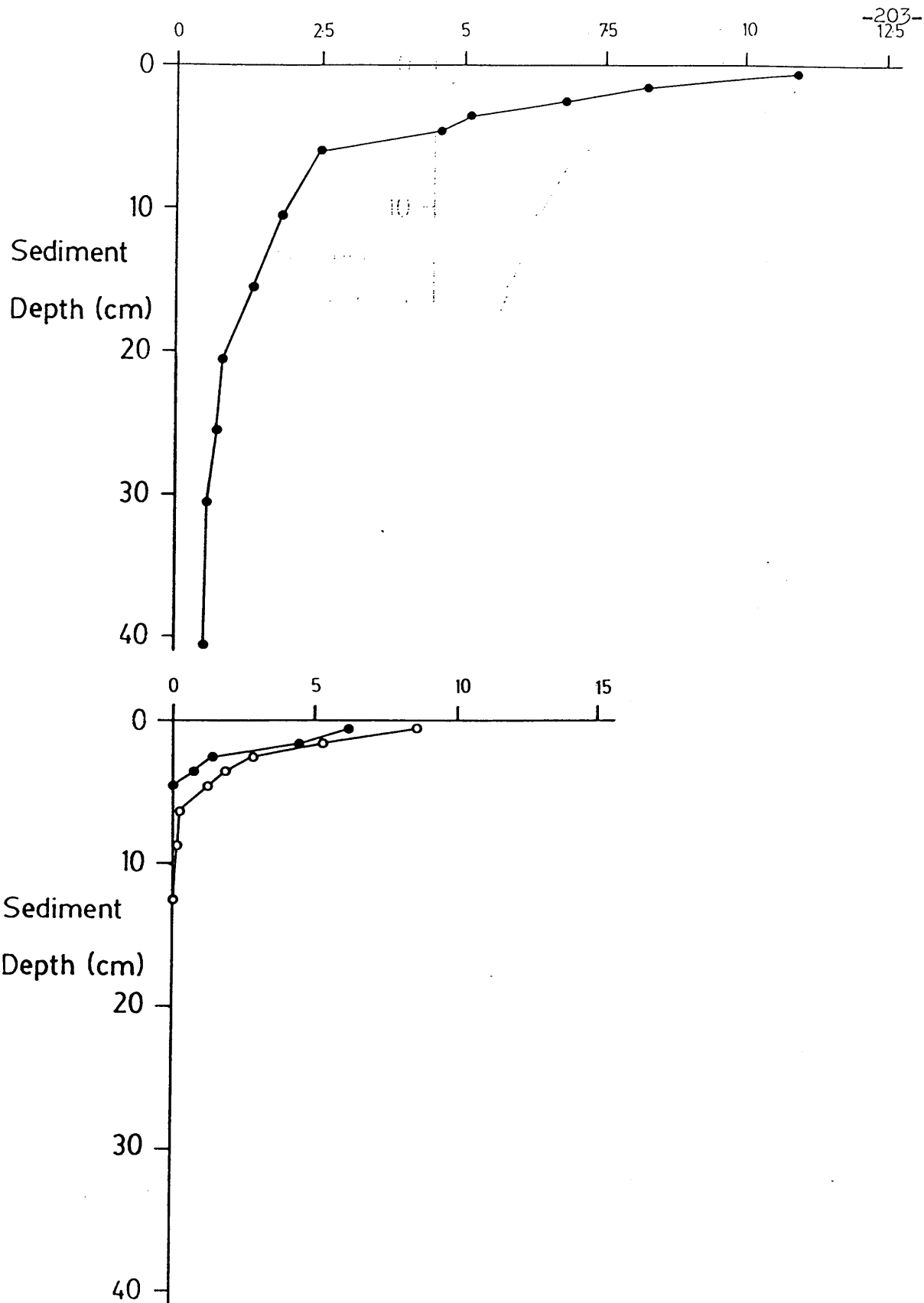


Figure 3.9. (Top) Micro-organism numbers  $\times 10^6 \text{ g}^{-1}$  dry weight for each sediment depth at station 4.

Figure 3.10. (Bottom) Meiofaunal numbers  $\text{ml}^{-1}$  for each sediment depth at station 4. Open circles = metazoans, solid circles = foraminifera.

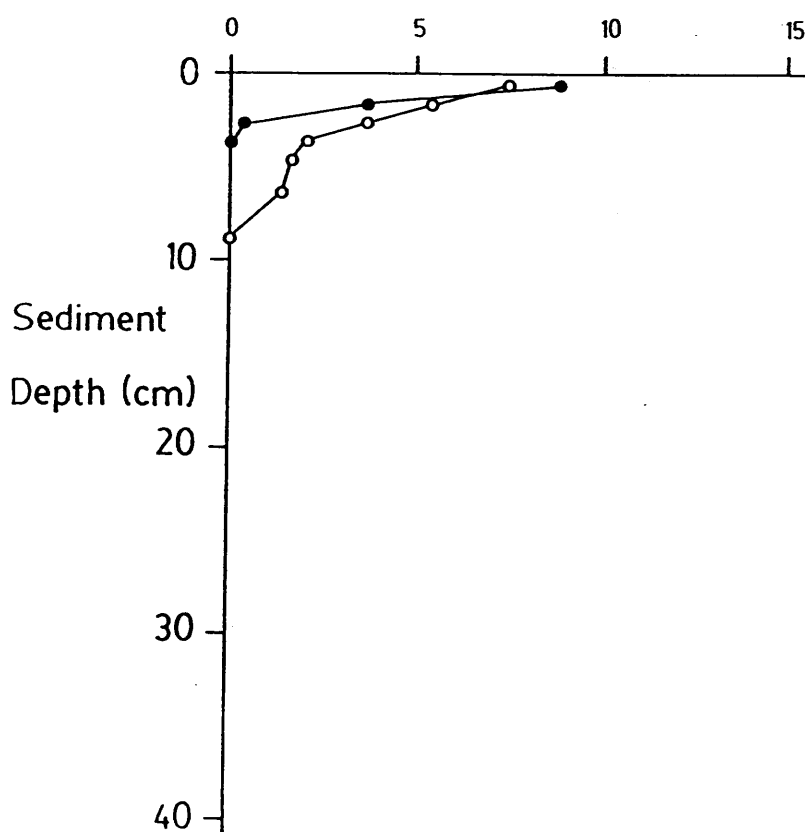
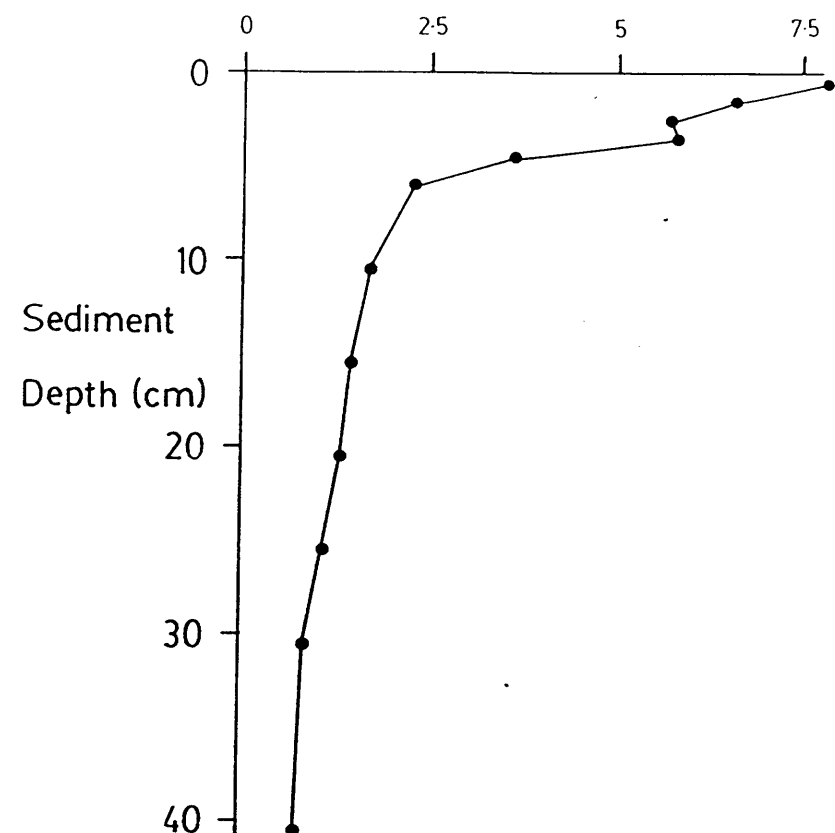


Figure 3.11. (Top) Micro-organism numbers  $\times 10^6 \text{ g}^{-1}$  dry weight for each sediment depth at station 5.

Figure 3.12. (Bottom) Meiofaunal numbers  $\text{ml}^{-1}$  for each sediment depth at station 5. Open circles = metazoans, solid circles = foraminifera.

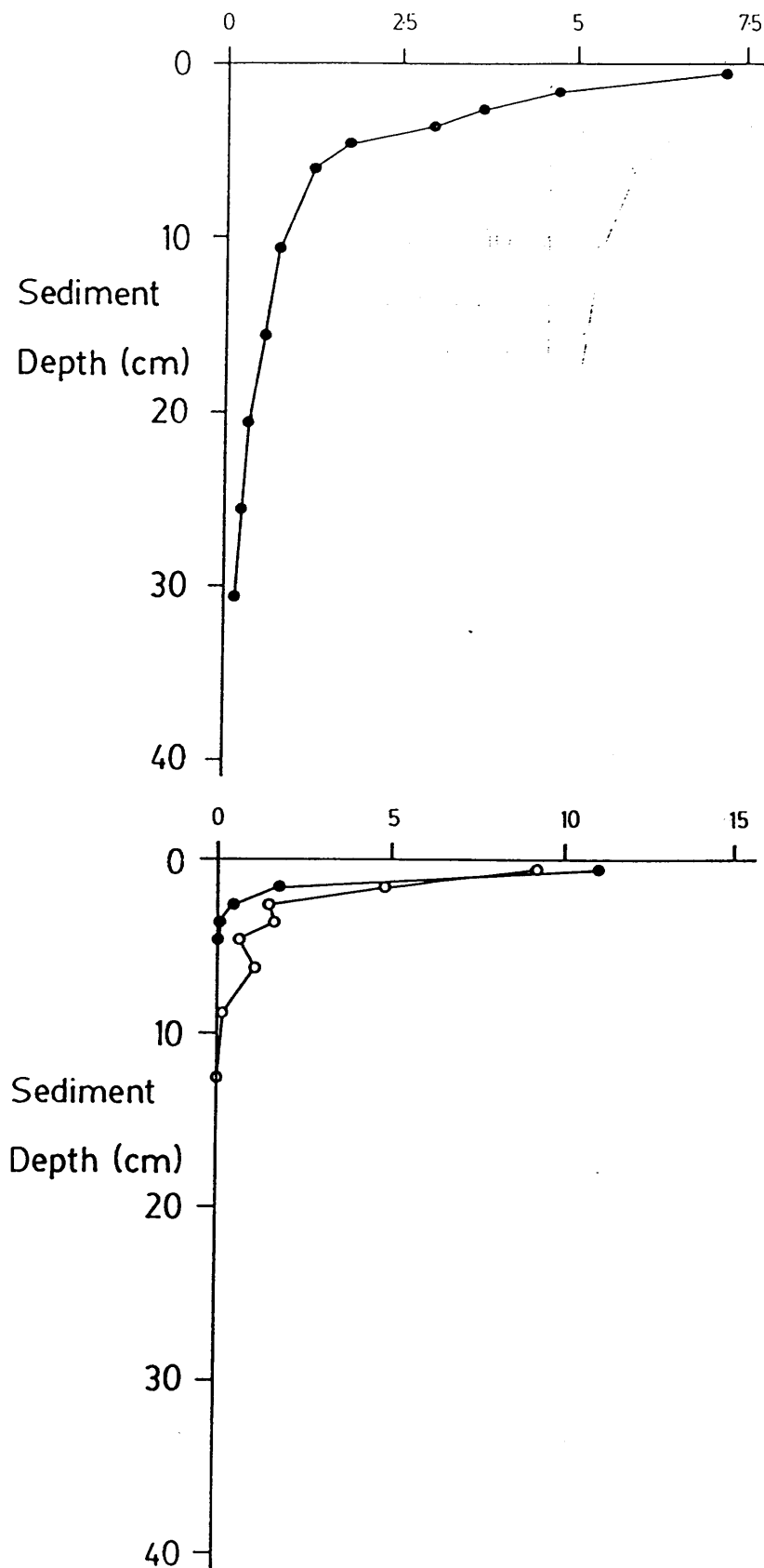


Figure 3.13. (Top) Micro-organism numbers  $\times 10^6 \text{ g}^{-1}$  dry weight for each sediment depth at station 6.

Figure 3.14. (Bottom) Meiofaunal numbers  $\text{ml}^{-1}$  for each sediment depth at station 6. Open circles = metazoans, solid circles = foraminifera.

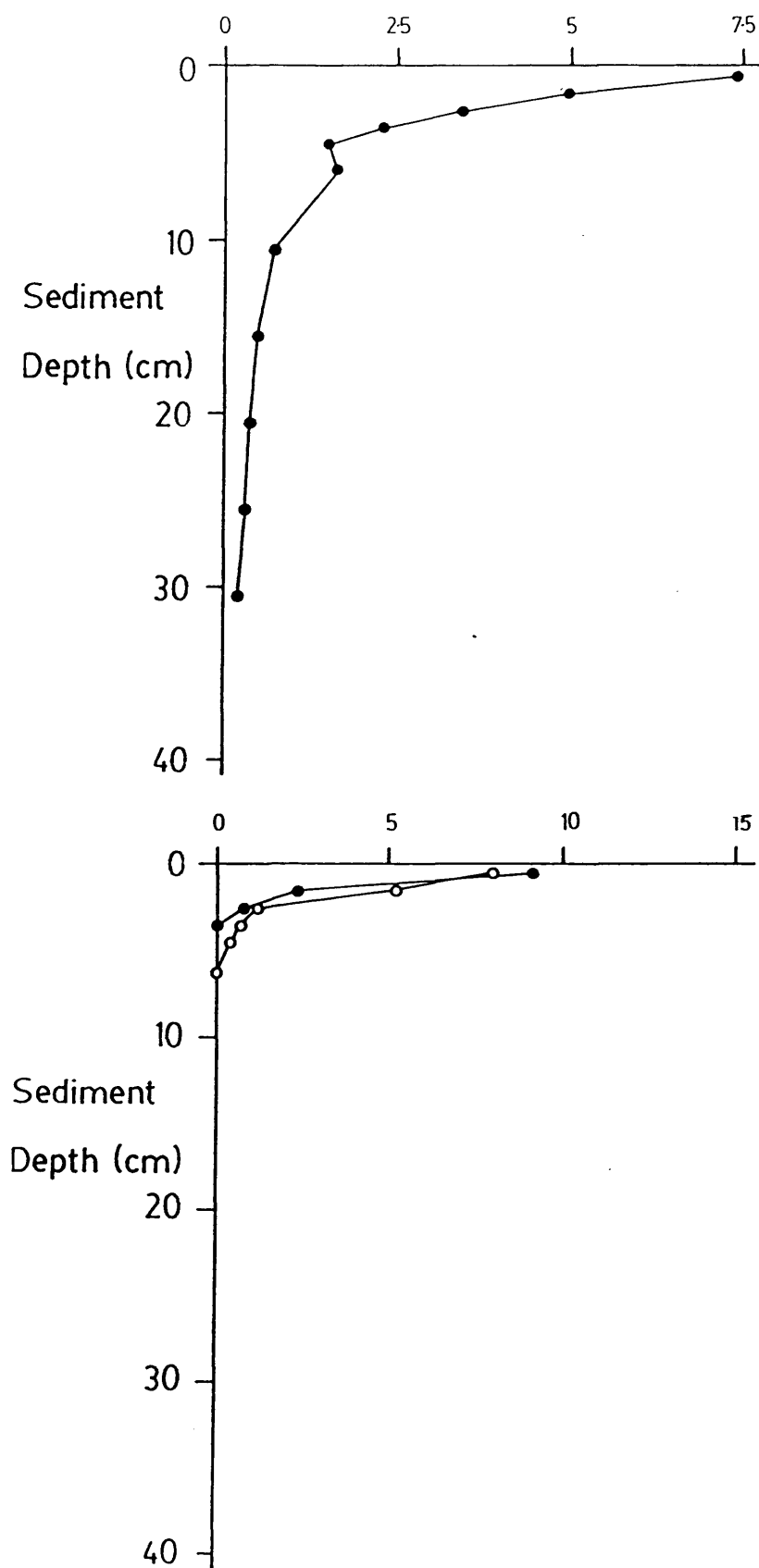


Figure 3.15. (Top) Micro-organism numbers  $\times 10^6 \text{ g}^{-1}$  dry weight for each sediment depth at station 7.

Figure 3.16. (Bottom) Meiofaunal numbers  $\text{ml}^{-1}$  for each sediment depth at station 7. Open circles = metazoans, solid circles = foraminifera.

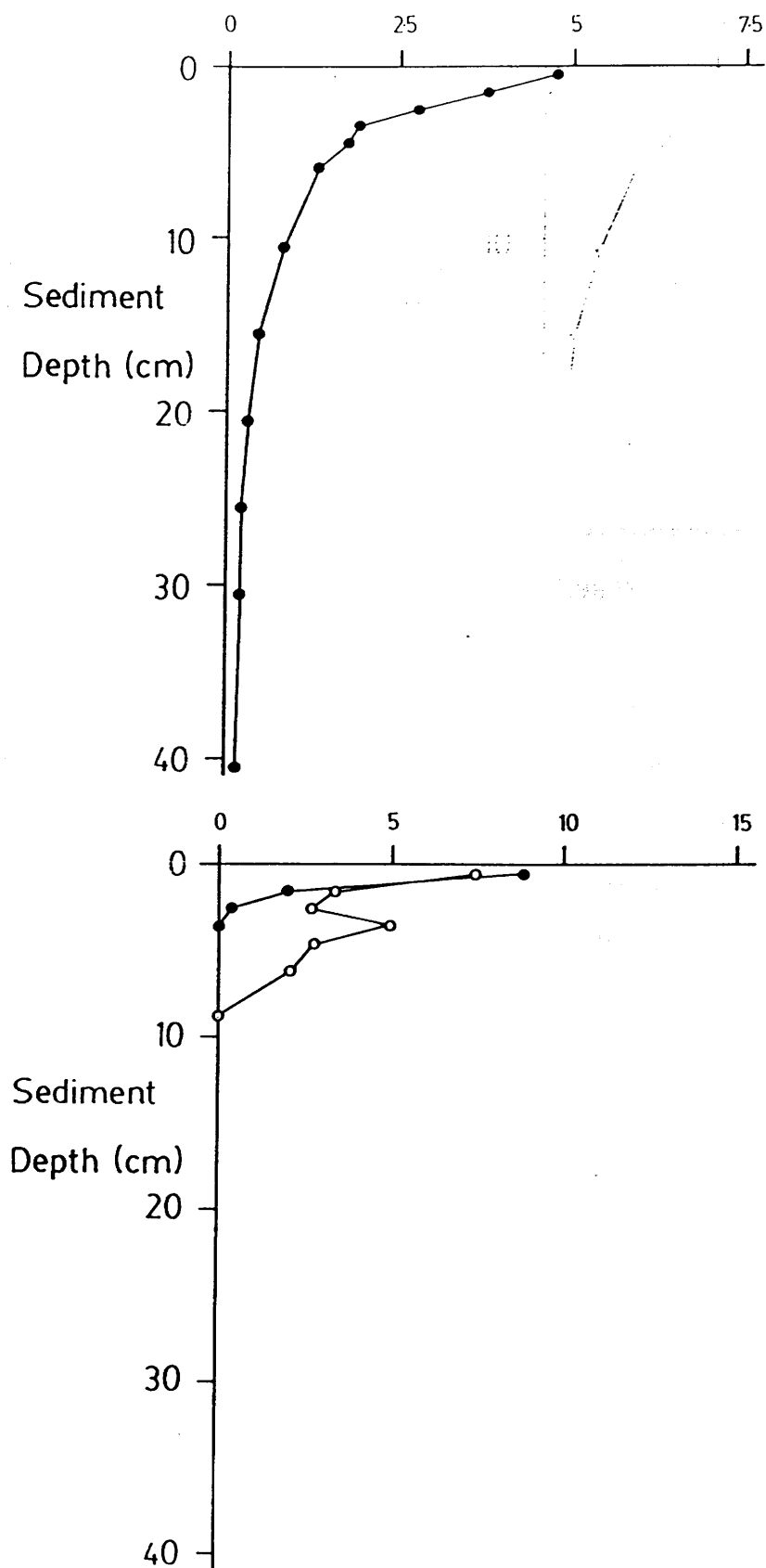


Figure 3.17. (Top) Micro-organism numbers  $\times 10^6 \text{ g}^{-1}$  dry weight for each sediment depth at station 8.

Figure 3.18. (Bottom) Meiofaunal numbers  $\text{ml}^{-1}$  for each sediment depth at station 8. Open circles = metazoans, solid circles = foraminifera.

Station number	m	c	r	p
1	-0.00983	-0.00012	0.9803	p<0.001
2	-0.00883	-0.00175	0.9721	p<0.001
4	-0.00538	-0.00339	0.9884	p<0.001
5	-0.00339	-0.01266	0.9829	p<0.001
6	-0.02165	0.05014	0.9365	p<0.001
7	-0.01674	0.02028	0.9690	p<0.001
8	-0.01727	0.01519	0.9894	p<0.001

Table 3.12. Regression coefficients for the regressions on micro-organisms densities after  $-1/x$  transformation. ( $y=mx + c$ ,  $y$ =micro-organism density  $\times 10^5$ ,  $x$ =sediment depth, cm,  $r$ =correlation coefficient.

Sediment depth (cm)	Meiofaunal taxon	Number ml <sup>-1</sup>	
		mean	sd
00 - 01	Foraminiferans	4.4667	1.2220
	Nematodes	5.2667	0.6110
	Copepods	0.2667	0.1155
	Nauplii	1.0000	0.2000
	Oligochaetes	0.0667	0.1155
	Tardigrades	0.1333	0.1155
	Metazoans	6.7333	0.4163
	Total	11.2000	1.6371
01 - 02	Foraminiferans	1.6000	0.2000
	Nematodes	2.9333	0.7024
	Copepods	0.1333	0.2309
	Nauplii	0.5333	0.3055
	Polychaetes	0.0667	0.1155
	Metazoans	3.6667	0.6110
	Total	5.2667	0.8083
02 - 03	Foraminiferans	0.2667	0.1155
	Nematodes	1.7333	0.4163
	Copepods	0.0667	0.1155
	Nauplii	0.2000	0.2000
	Metazoans	2.0000	0.2000
	Total	2.2667	0.1155
03 - 04	Nematodes	0.6667	0.3055
	Copepods	0.1333	0.2309
	Total	0.8000	0.2000
04 - 05	Nematodes	0.3333	0.1155

Table 3.13. Numbers of each meiofaunal taxon (mean and sd) at each sediment depth at station 1. n=3 for all depth samples.



Sediment depth (cm)	Meiofaunal taxon	Number ml <sup>-1</sup>	
		mean	sd
=====			
00 - 01	Foraminiferans	6.6667	1.0066
	Nematodes	3.9333	0.4163
	Copepods	0.4667	0.4163
	Nauplii	0.4000	0.4000
	Polychaetes	0.1333	0.1155
	Tardigrades	0.1333	0.2309
	Metazoans	5.0667	0.5033
	Total	11.7333	0.9866
01 - 02	Foraminiferans	1.3333	0.5033
	Nematodes	2.0667	0.4163
	Copepods	0.4000	0.3464
	Nauplii	0.4000	0.2000
	Metazoans	2.8667	0.7024
	Total	4.2000	0.7211
02 - 03	Foraminiferans	0.4667	0.1155
	Nematodes	0.8000	0.4000
	Nauplii	0.2000	0.2000
	Metazoans	1.0000	0.5292
	Total	1.4667	0.6110
03 - 04	Foraminiferans	0.0667	0.1155
	Nematodes	0.5333	0.3055
	Total	0.6000	0.3464
04 - 05	Nematodes	0.4667	0.3055
05 - 7.5	Nematodes	0.4667	0.1155
	Nauplii	0.2667	0.3055
	Total	0.7333	0.2309
7.5 - 10	Nematodes	0.3333	0.2309
=====			

Table 3.14. Numbers of each meiofaunal taxon (mean and sd) at each sediment depth at station 2. n=3 for all depth samples.

Sediment depth (cm)	Meiofaunal taxon	Number ml <sup>-1</sup>		
		mean	sd	
=====				
00 - 01	Foraminiferans	6.1333	1.1015	
	Nematodes	7.2000	1.6000	
	Copepods	0.6000	0.2000	
	Nauplii	0.5333	0.6110	
	Polychaetes	0.0667	0.1155	
	Tardigrades	0.1333	0.1155	
	Kinorhynchs	0.0667	0.1155	
Metazoans	8.6000	1.5875		
Total	14.7333	0.6110		
01 - 02	Foraminiferans	4.4667	1.1015	
	Nematodes	4.5333	0.8327	
	Copepods	0.5333	0.3055	
	Nauplii	0.2000	0.2000	
	Metazoans	5.2667	0.7024	
Total	9.7333	1.6289		
02 - 03	Foraminiferans	1.4000	0.4000	
	Nematodes	2.2000	0.6000	
	Copepods	0.2000	0.2000	
	Nauplii	0.3333	0.2309	
	Polychaetes	0.0667	0.1155	
	Metazoans	2.8000	0.4000	
Total	4.2000	0.4000		
03 - 04	Foraminiferans	0.7333	0.4163	
	Nematodes	1.7333	0.5033	
	Copepods	0.1333	0.1155	
	Metazoans	1.8667	0.4163	
Total	2.6000	0.0000		
04 - 05	Nematodes	1.1333	0.3055	
	Nauplii	0.1333	0.2309	
	Total	1.2667	0.4163	
05 - 7.5	Nematodes	0.2667	0.3055	
7.5 - 10	Nematodes	0.1333	0.2309	
=====				

Table 3.15. Numbers of each meiofaunal taxon (mean and sd) at each sediment depth at station 4. n=3 for all depth samples.

Sediment depth (cm)	Meiofaunal taxon	Number ml <sup>-1</sup>	
		mean	sd
=====			
00 - 01	Foraminiferans	8.7333	1.4742
	Nematodes	5.5333	1.8148
	Copepods	0.7333	0.4163
	Nauplii	0.7333	0.3055
	Polychaetes	0.2667	0.2309
	Tardigrades	0.1333	0.1155
	Metazoans	7.4000	1.6371
	Total	16.1333	0.8083
01 - 02	Foraminiferans	3.6667	0.5033
	Nematodes	4.8000	1.3115
	Copepods	0.0667	0.1155
	Nauplii	0.4667	0.3055
	Metazoans	5.3333	1.0066
	Total	9.0000	1.5545
02 - 03	Foraminiferans	0.3333	0.2309
	Nematodes	2.9333	0.6429
	Nauplii	0.6667	0.3055
	Polychaetes	0.0667	0.1155
	Metazoa	3.6667	0.4163
	Total	4.0000	0.2000
03 - 04	Nematodes	1.8667	0.3055
	Copepods	0.2000	0.2000
	Total	2.0667	0.5033
04 - 05	Nematodes	1.4667	0.3055
	Copepods	0.0667	0.1155
	Nauplii	0.1333	0.2309
	Total	1.6667	0.3055
05 - 7.5	Nematodes	1.4000	0.7212
=====			

Table 3.16. Numbers of each meiofaunal taxon (mean and sd) at each sediment depth at station 5. n=3 for all depth samples.

Sediment depth (cm)	Meiofaunal taxon	Number ml <sup>-1</sup>		
		mean	sd	
=====				
00 - 01	Foraminiferans	10.9333	1.4742	
	Nematodes	6.8667	1.2220	
	Copepods	1.1333	0.6429	
	Nauplii	0.8000	0.4000	
	Polychaetes	0.1333	0.1155	
	Kinorhynchs	0.1333	0.1155	
	Ostracods	0.0667	0.1155	
Metazoans	9.1333	2.2121		
Total	20.6667	0.8327		
01 - 02	Foraminiferans	1.7333	0.4163	
	Nematodes	3.2667	0.5033	
	Copepods	1.0000	0.5292	
	Nauplii	0.4000	0.2000	
	Polychaetes	0.1333	0.1155	
	Metazoans	4.8000	0.6000	
Total	6.5333	0.4163		
02 - 03	Foraminiferans	0.4667	0.3055	
	Nematodes	1.2667	0.4163	
	Copepods	0.0667	0.1155	
	Nauplii	0.1333	0.1155	
	Metazoans	1.4667	0.4163	
Total	1.9333	0.1155		
03 - 04	Foraminiferans	0.0667	0.1155	
	Nematodes	1.4667	0.3055	
	Copepods	0.0667	0.1155	
	Nauplii	0.1333	0.1155	
	Metazoans	1.6667	0.1155	
Total	1.7333	0.2309		
04 - 05	Nematodes	0.6000	0.4000	
05 - 7.5	Nematodes	0.9333	0.3055	
	Nauplii	0.1333	0.1155	
Total	1.0667	0.1155		
7.5 - 10	Nematodes	0.1333	0.1155	
=====				

Table 3.17. Numbers of each meiofaunal taxon (mean and sd) at each sediment depth at station 6. n=3 for all depth samples.

Sediment depth (cm)	Meiofaunal taxon	Number ml <sup>-1</sup>	
		mean	sd
=====			
00 - 01	Foraminiferans	9.0667	1.4048
	Nematodes	7.0000	1.1136
	Copepods	0.2000	0.3464
	Nauplii	0.4667	0.5033
	Oligochaetes	0.1333	0.1155
	Ostracods	0.1333	0.1155
	Metazoans	7.9333	0.7024
	Total	17.0000	2.1071
01 - 02	Foraminiferans	2.3333	0.4163
	Nematodes	3.6667	0.5033
	Copepods	0.2667	0.2309
	Nauplii	0.3333	0.3055
	Polychaetes	0.2000	0.3464
	Metazoans	4.4667	0.4163
	Total	6.8000	0.0000
02 - 03	Foraminiferans	0.7333	0.4163
	Nematodes	0.6000	0.4000
	Nauplii	0.5333	0.5033
	Metazoans	1.1333	0.4163
	Total	1.8666	0.4163
03 - 04	Nematodes	0.6667	0.4619
04 - 05	Nematodes	0.3333	0.4163
=====			

Table 3.18. Numbers of each meiofaunal taxon (mean and sd) at each sediment depth at station 7. n=3 for all depth samples.

Sediment depth (cm)	Meiofaunal taxon	Number ml <sup>-1</sup>	
		mean	sd
=====			
00 - 01	Foraminiferans	7.8667	0.7572
	Nematodes	5.8000	0.5292
	Copepods	0.6000	0.5292
	Nauplii	0.6000	0.2000
	Polychaetes	0.0667	0.0115
	Oligochaetes	0.1333	0.1155
	Tardigrades	0.1333	0.1155
	Kinorhynchs	0.1333	0.1155
	Metazoans	7.4667	0.0262
	Total	15.3333	0.7024
01 - 02	Foraminiferans	1.9333	0.4163
	Nematodes	2.3333	0.4163
	Copepods	0.6000	0.2000
	Nauplii	0.3333	0.4163
	Ostracods	0.1333	0.1155
	Metazoans	3.4000	0.8718
	Total	5.3333	0.7024
02 - 03	Foraminiferans	0.3333	0.3055
	Nematodes	1.5333	0.3055
	Copepods	0.6667	0.3055
	Nauplii	0.3333	0.4163
	Polychaetes	0.1333	0.1155
	Metazoans	2.6667	0.3055
	Total	3.0000	0.6000
03 - 04	Nematodes	3.4667	1.3013
	Copepods	1.0667	0.3055
	Nauplii	0.4000	0.2000
	Total	4.9333	1.0066
04 - 05	Nematodes	1.3333	0.5033
	Copepods	1.1333	0.5033
	Nauplii	0.2000	0.2000
	Oligochaetes	0.0667	0.1155
	Total	2.7333	0.2309
05 - 7.5	Nematodes	0.6667	0.2309
	Copepods	0.2000	0.2000
	Total	0.8667	0.4163
=====			

Table 3.19. Numbers of each meiofaunal taxon (mean and sd) at each sediment depth at station 8. n=3 for all depth samples.

being 10 cm (at stations 2, 4 and 6). In general only nematodes were found in the deepest meiofauna-containing section (except at station 8 where copepods were also found). Foraminifera were absent in samples from below 4 cm.

The density of foraminifera in the surface sediment was generally higher than that of the metazoan taxa. In the sediment sections below 1 cm, however, the density of metazoan taxa was generally greater than that of the foraminifera. These differences in density between metazoans and foraminifera have been tested using paired t-tests. For each station the paired t-test was repeated twice, once including the 0-1 cm section and once excluding it. The results of these tests are shown in table 3.20.

Most of the living foraminifera found in the samples were of the agglutinating form, with tests composed of sediment particles and very small manganese nodules (micro-nodules). Small numbers of foraminifera with secreted, siliceous, tests were also found. Details of the differences between the major divisions of the foraminifera are given by Brady (1960).

Regression lines have been fitted to the density-depth profiles of meiofauna using total meiofaunal numbers, numbers of metazoans, numbers of foraminiferans and number of nematodes. These regression lines were fitted after negative reciprocal transformation of the original data. This transformation gave the best straight line fit for all stations. No other single taxon was present in sufficient density to allow the calculation of a separate regression line. The coefficients of the calculated regression lines are shown in table 3.21. The regression lines are significant for all of the sub-divisions of the meiofauna at all of the stations.

All of the meiofauna samples were examined for macrofauna

Station number		t-value	n	p	M/F relationship.	
=====						
1	I	-2.791	36	0.0315	M > F	*
	E	-2.260	33	0.0734	NS	
2	I	-0.0981	36	0.3643	NS	
	E	-3.778	33	0.0129	NS	
4	I	-3.655	36	0.0106	M > F	*
	E	-3.842	33	0.0121	M > F	*
5	I	-2.208	36	0.0693	NS	
	E	-3.846	33	0.0121	M > F	*
6	I	-1.436	36	0.2010	NS	
	E	-2.978	33	0.0309	M > F	*
7	I	-0.974	36	0.3678	NS	
	E	-1.618	33	0.1666	NS	
8	I	-2.757	36	0.0330	M > F	*
	E	-3.376	33	0.1980	NS	
=====						

**Table 3.20.** Paired t-tests comparing metazoan density (M) with foraminiferan density (F) at each station. I=including 0-1 cm section, E=excluding 0-1 cm section. NS = not significant. \* = significant at  $0.01 < p < 0.05$ .



Station number	Group	m	c	r	p
=====					
1	T	-0.12748	-0.04973	0.9423	p<0.001
	M	-0.15958	0.00140	0.9905	p<0.001
	F	-0.18559	-0.01802	0.9859	p<0.001
	N	-0.15289	-0.04383	0.9925	p<0.001
2	T	-0.07705	-0.17019	0.8276	p<0.001
	M	-0.06027	-0.27171	0.8871	p<0.001
	F	-0.22477	-0.07366	0.9757	p<0.001
	N	-0.05660	-0.32326	0.9000	p<0.001
4	T	-0.11263	0.05104	0.9706	p<0.001
	M	-0.08278	-0.08479	0.9576	p<0.001
	F	-0.21137	0.06510	0.9445	p<0.001
	N	-0.08000	-0.11520	0.9592	p<0.001
5	T	-0.10513	0.05390	0.9397	p<0.001
	M	-0.09757	0.01063	0.9198	p<0.001
	F	-0.32277	0.12870	0.9581	p<0.001
	N	-0.09345	-0.02581	0.9116	p<0.001
6	T	-0.09425	-0.04223	0.9295	p<0.001
	M	-0.07482	-0.13245	0.9407	p<0.001
	F	-0.24037	-0.01279	0.9742	p<0.001
	N	-0.07107	-0.17375	0.9466	p<0.001
7	T	-0.12979	-0.04336	0.9349	p<0.001
	M	-0.16252	-0.00779	0.9864	p<0.001
	F	-0.29790	0.10170	0.9793	p<0.001
	N	-0.15260	-0.07551	0.9550	p<0.001
8	T	-.09633	0.05940	0.8538	p<0.001
	M	-0.8813	0.00560	0.8056	0.001<p<0.01
	F	-0.30709	0.06320	0.9905	p<0.001
	N	-0.09591	-0.06035	0.9203	p<0.001
=====					

table 3.21. Coefficients for the regression lines ( $y=mx + c$ ,  $y$ =meiofaunal density,  $x$ =sediment depth) calculated for the meiofauna data after  $-1/x+1$  transformation. T=total meiofauna, M=metazoans, F=foraminiferans, N=nematodes.

during the counting procedure. No macrofaunal metazoans were found in the sediment samples from any of the stations. Some of the foraminifera were  $> 500 \mu\text{m}$  (the conventional limit for macrofauna). These larger foraminifera have been included with the foraminifera  $< 500 \mu\text{m}$ .

A fine floc was present in the surface sediment samples from all stations after Ludox extraction. This floc was similar to samples of phytodetritus obtained from the Atlantic ocean (A. Gooday, pers. comm.). More detail on the possible importance of this floc material is given in the discussion.

#### Water content.

Depth profiles of sediment water content for stations 1, 2, 4, 5, 6, 7 and 8 are shown in figures 3.19-3.25. The vertical lines in these graphs represents the depth range over which the sample was collected. The means and standard deviations of this water content data are given in appendix 3.1 tables 1-7. In general the water content of the sediment decreased with sediment depth. In some stations, for example in stations 4 and 5, figures 3.21 and 3.22, the pattern is disrupted over part of the length of the core. This disruption may be related to changes between siliceous and calcareous sediment.

#### Metal concentrations.

The concentrations of each of the metals measured by the ICPAES analyses are shown in appendix 3.3, tables 1-26. None of the 91 concentration profiles for metals showed any definite trends with sediment depth when analysed using regression analysis. The results of these analyses have not, therefore, been presented.

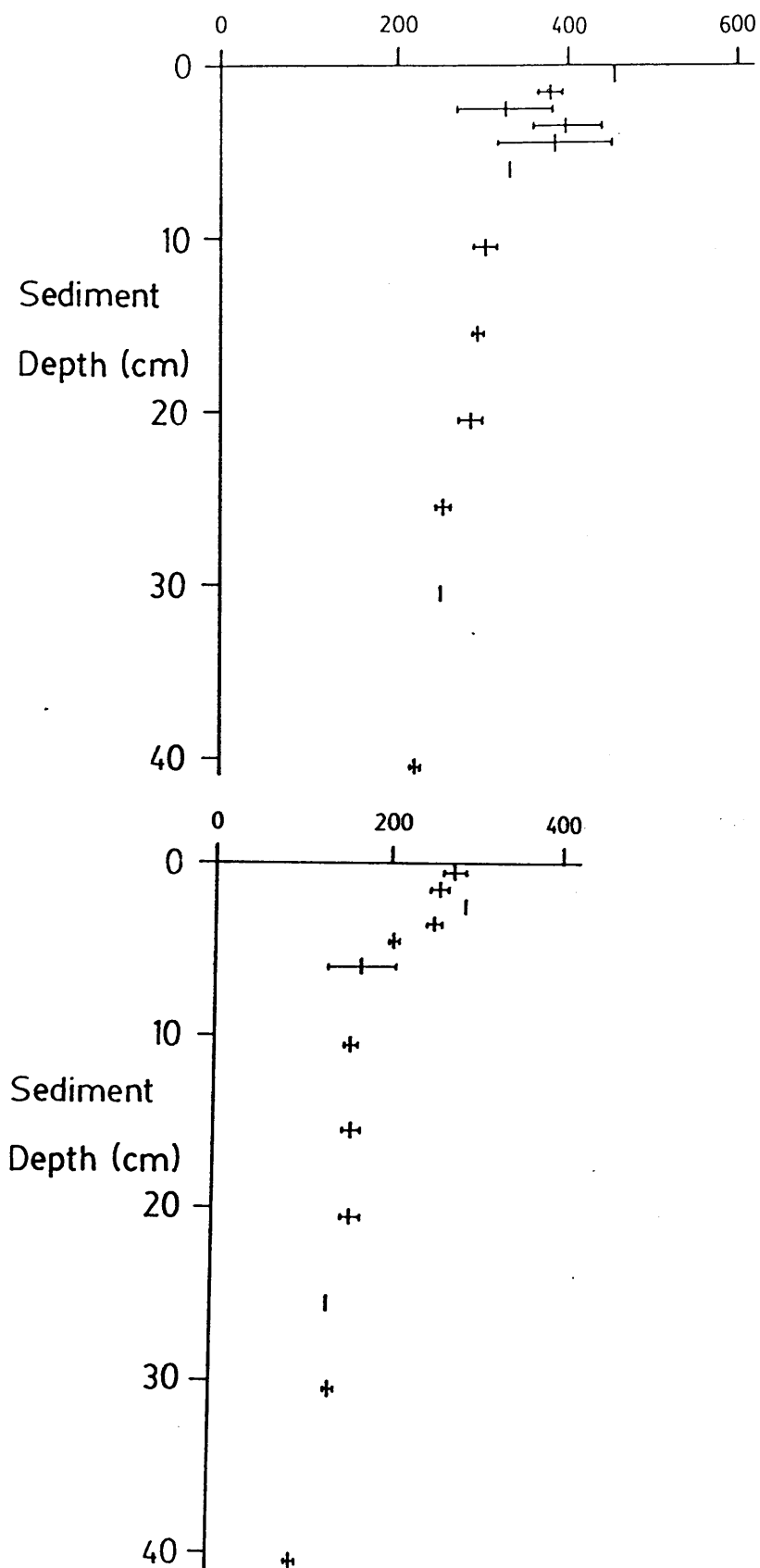


Figure 3.19. (Top) Water content (mean, sd) as % dry weight for each sediment depth at station 1.

Figure 3.20. (Bottom) Water content (mean, sd) as % dry weight for each sediment depth at station 2.

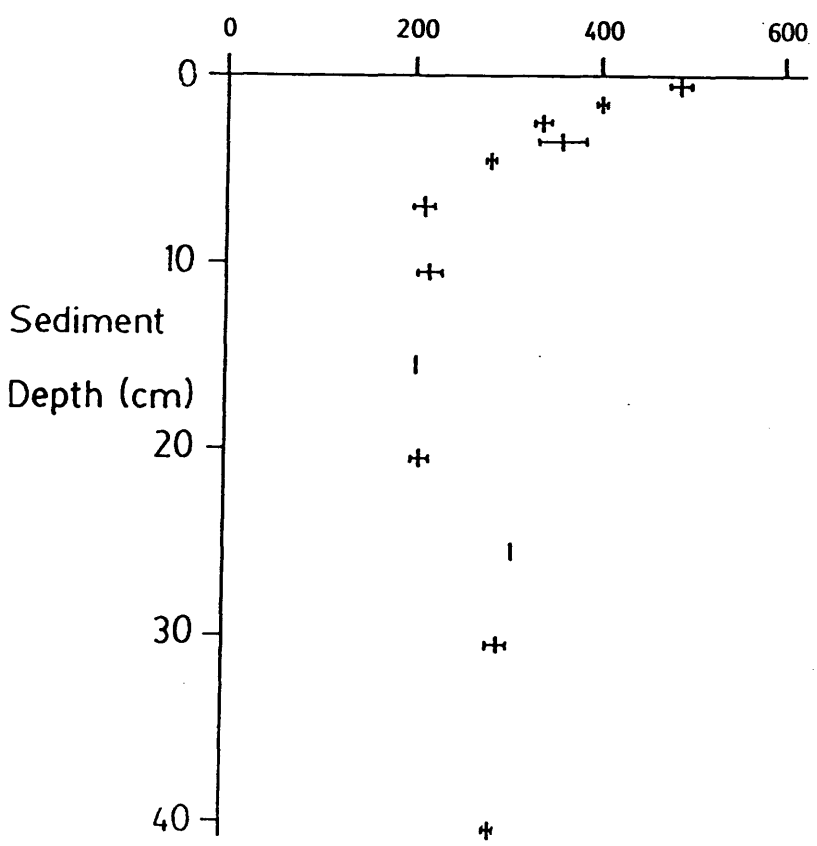
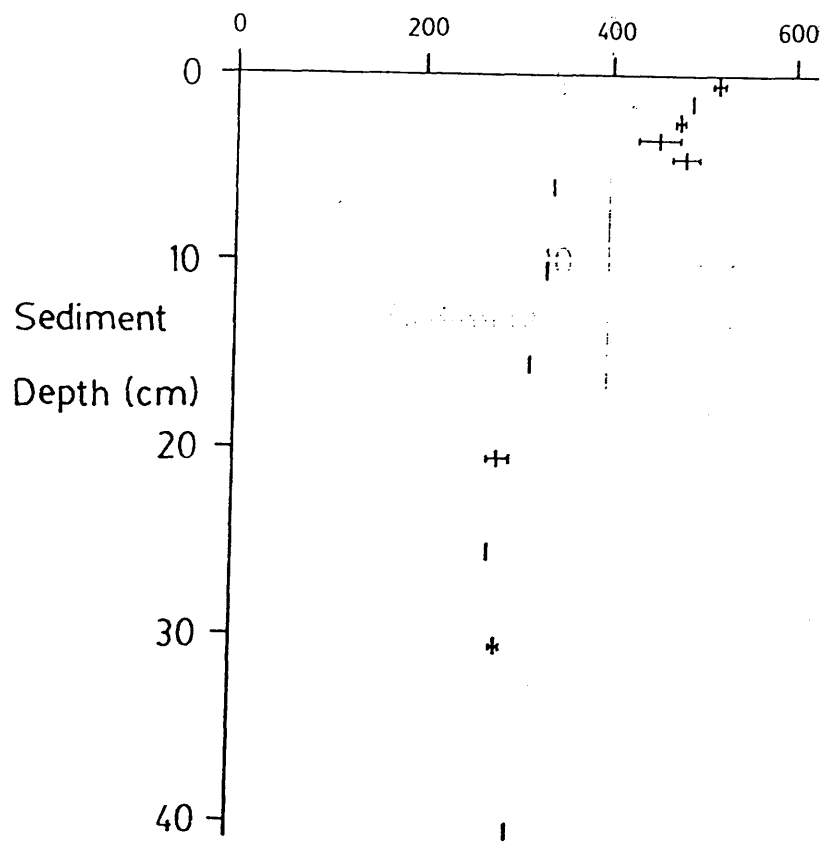


Figure 3.21. (Top) Water content (mean, sd) as % dry weight for each sediment depth at station 4.

Figure 3.22. (Bottom) Water content (mean, sd) as % dry weight for each sediment depth at station 5.

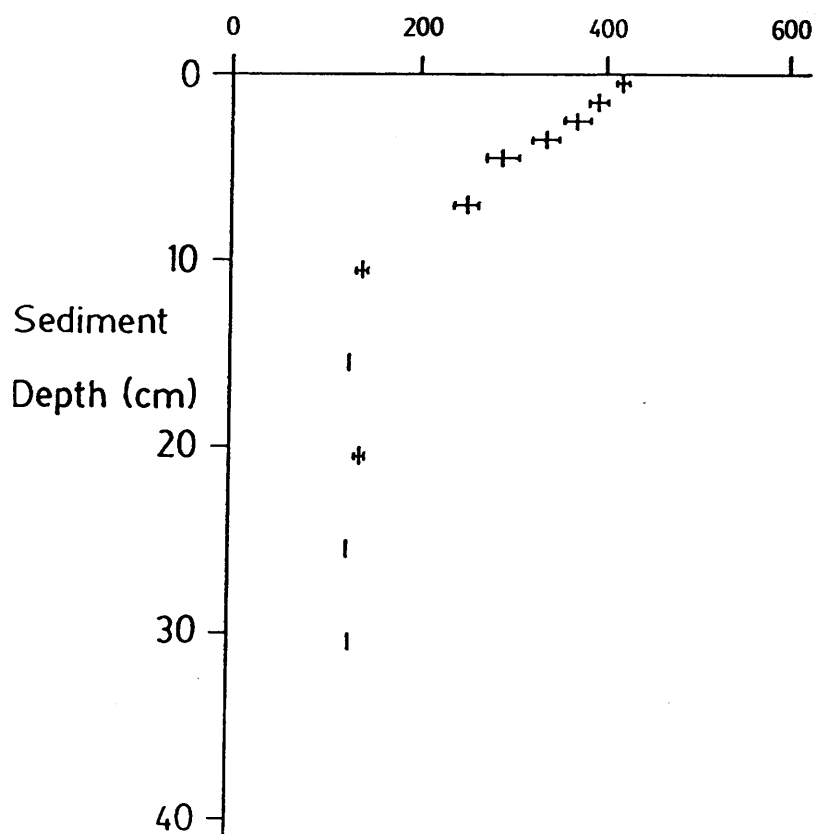
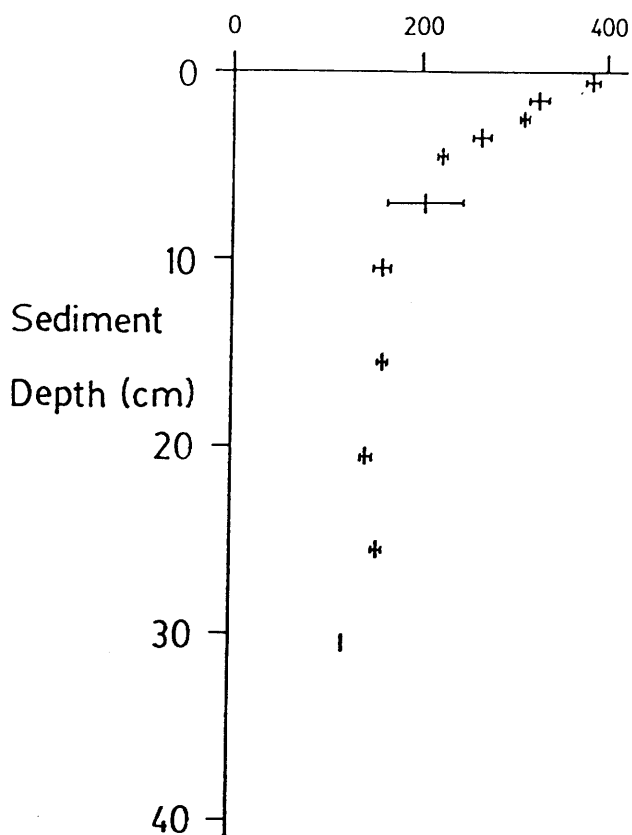
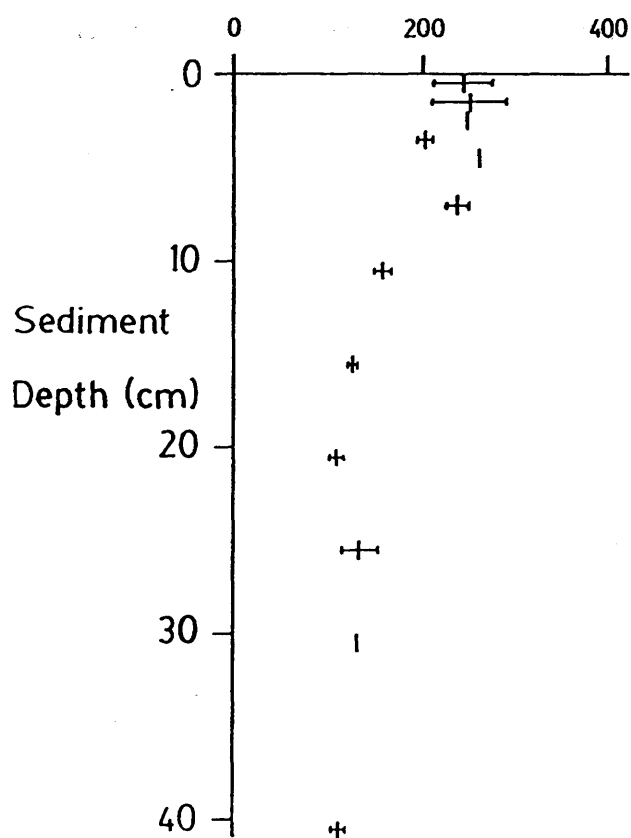


Figure 3.23. (Top) Water content (mean, sd) as % dry weight for each sediment depth at station 6.

Figure 3.24. (Bottom) Water content (mean, sd) as % dry weight for each sediment depth at station 7.



**Figure 3.25.** Water content (mean, sd) as % dry weight for each sediment depth at station 8.

### Nutrient concentrations.

The concentrations of dissolved silicate, phosphate, sulphate, nitrate and ammonium for each depth at each station (mean and sd) are given in appendix 3.2 tables 1-10. Profiles of nutrient concentration with depth into the sediment are shown in figures 3.26-3.29 for silicate, 3.30-3.33 for phosphate, 3.34-3.37 for sulphate, 3.38-3.41 for nitrate and 3.42-3.45 for ammonium. The vertical lines on these graphs represent the depth range over which the samples were collected.

In general the concentrations of silicate and sulphate increased from the surface into the sediment although this pattern was not always clearly defined, for example for silicate at station 6, figure 3.28. The concentration of phosphate generally decreased from the sediment surface into the sediment. The phosphate concentration profiles show some sub-surface increases in concentration, for example at station 8, 10-11 cm depth (figure 3.33).

The concentration-depth profiles for ammonium and nitrate show fairly consistent sub-surface peaks in concentration. These sub-surface peaks are followed by a gradual decrease in concentration with increasing sediment depth. The peak in concentration occurred at between 1 and 7.5 cm depth for both nitrate and ammonium. At station 5 the nitrate profile also shows a second sub-surface peak in concentration at 10-11 cm (figure 3.39).

Regression lines have been calculated for nutrient concentration (as the dependent variable) against sediment depth, micro-organism numbers, meiofaunal numbers (total meiofauna, total metazoa, nematodes and foraminiferans), water content and individual metal concentrations (as the independent, predictor

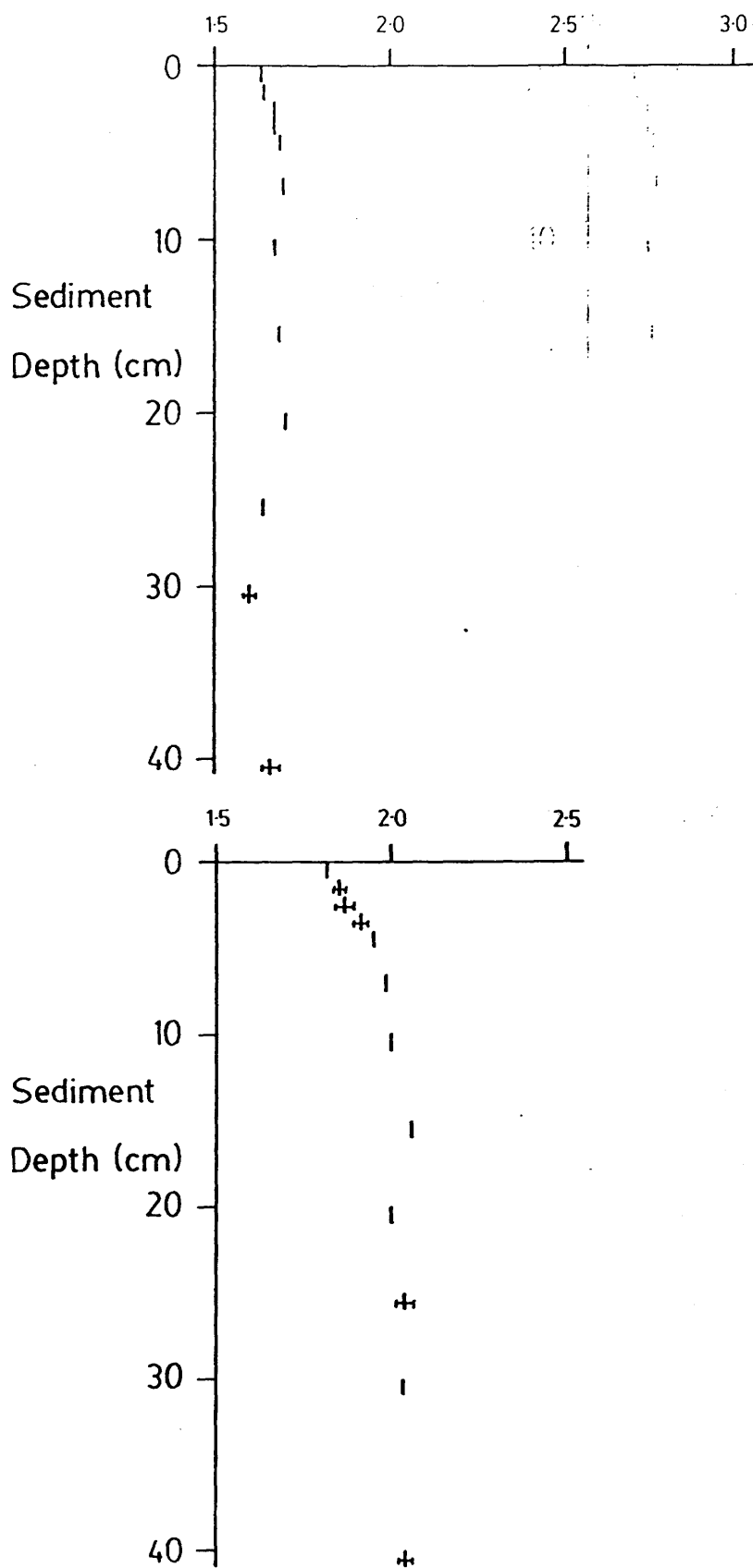


Figure 3.26. Silicate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 1 (top) and station 2 (bottom).



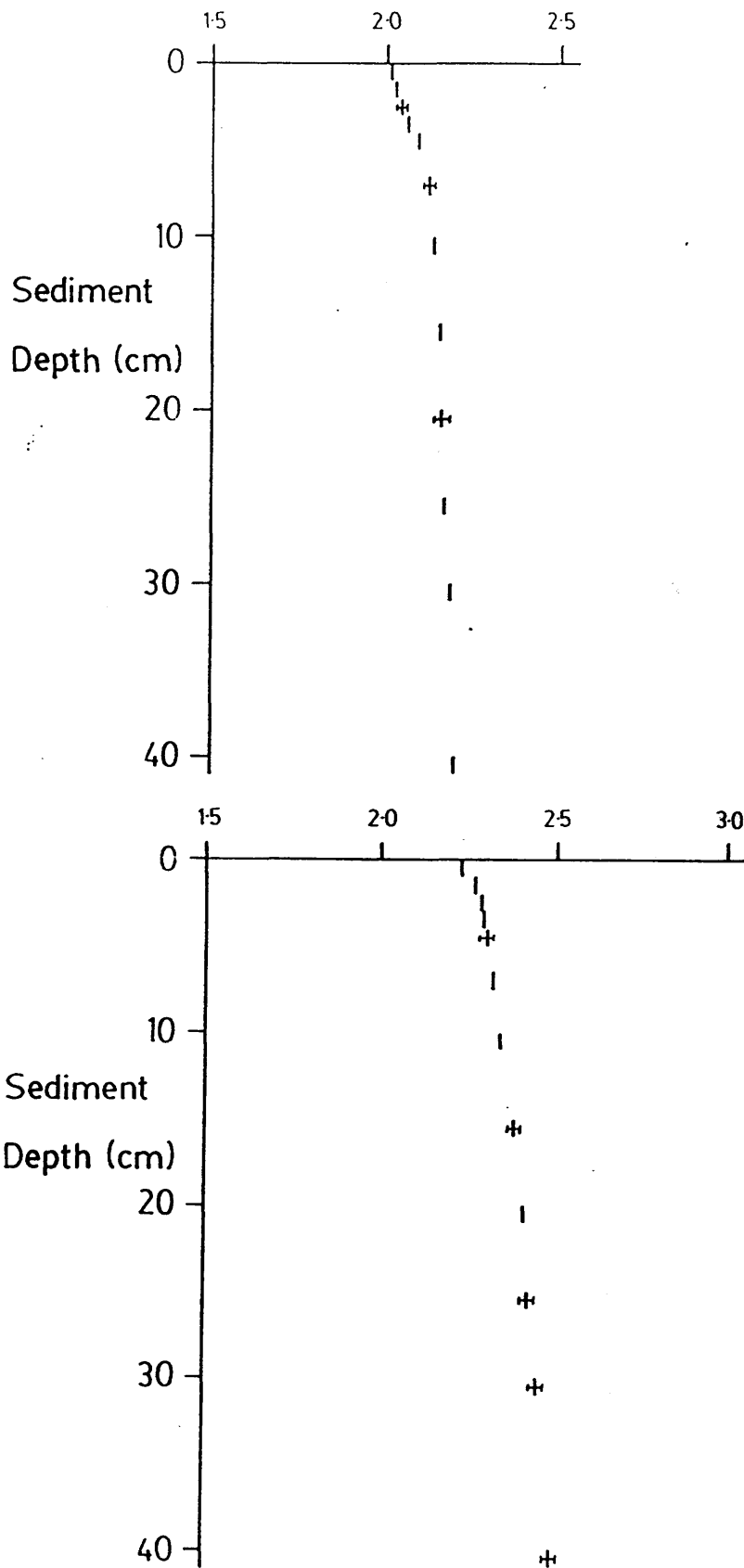


Figure 3.27. Silicate concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 4 (top) and station 5 (bottom).

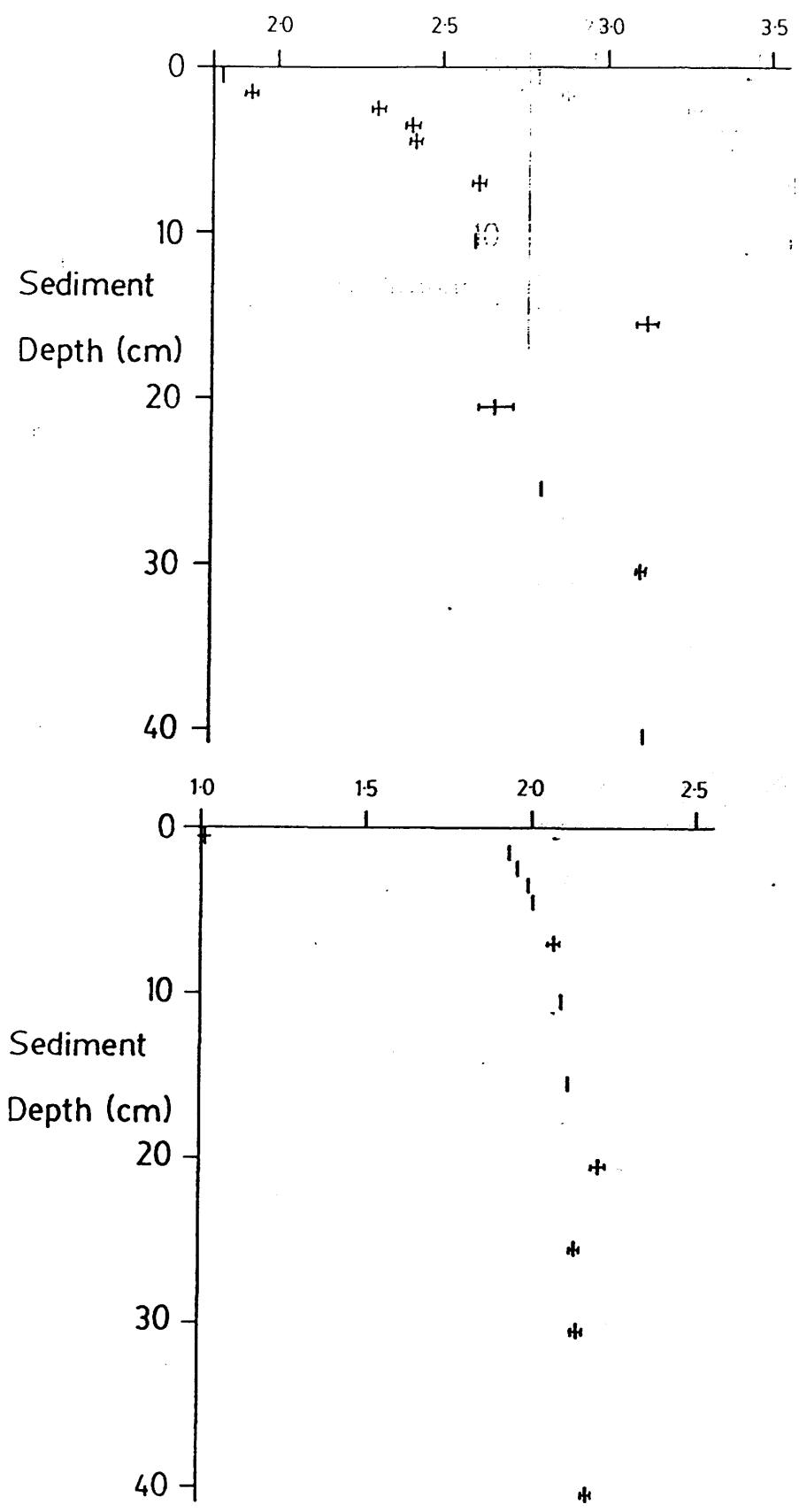


Figure 3.28. Silicate concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 6 (top) and station 7 (bottom).

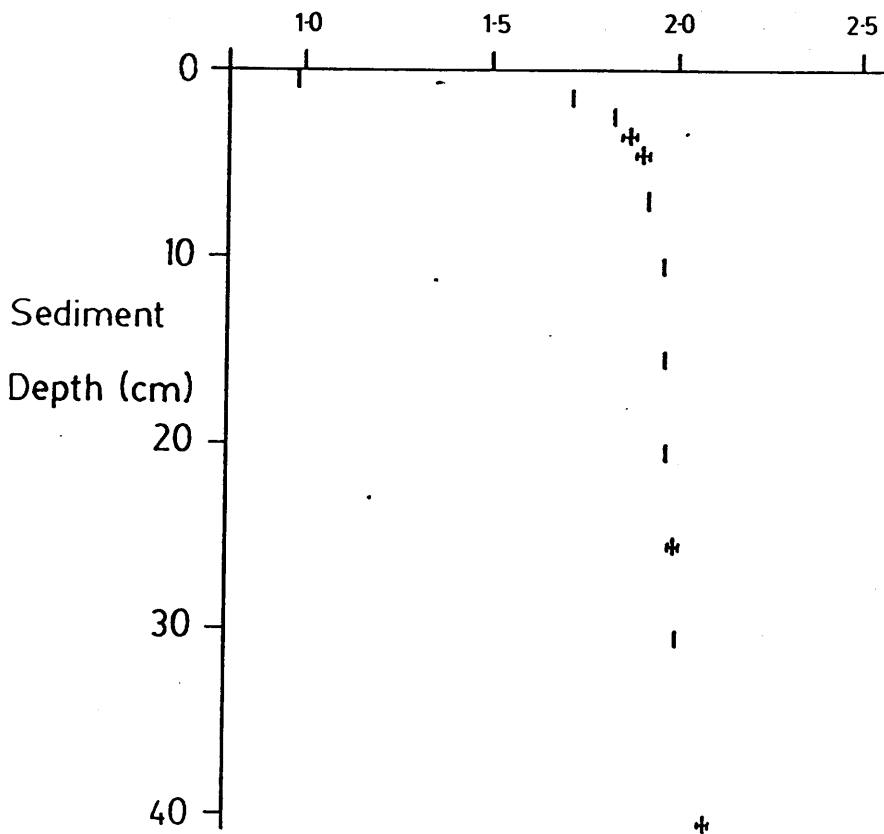


Figure 3.29. Silicate concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 8.

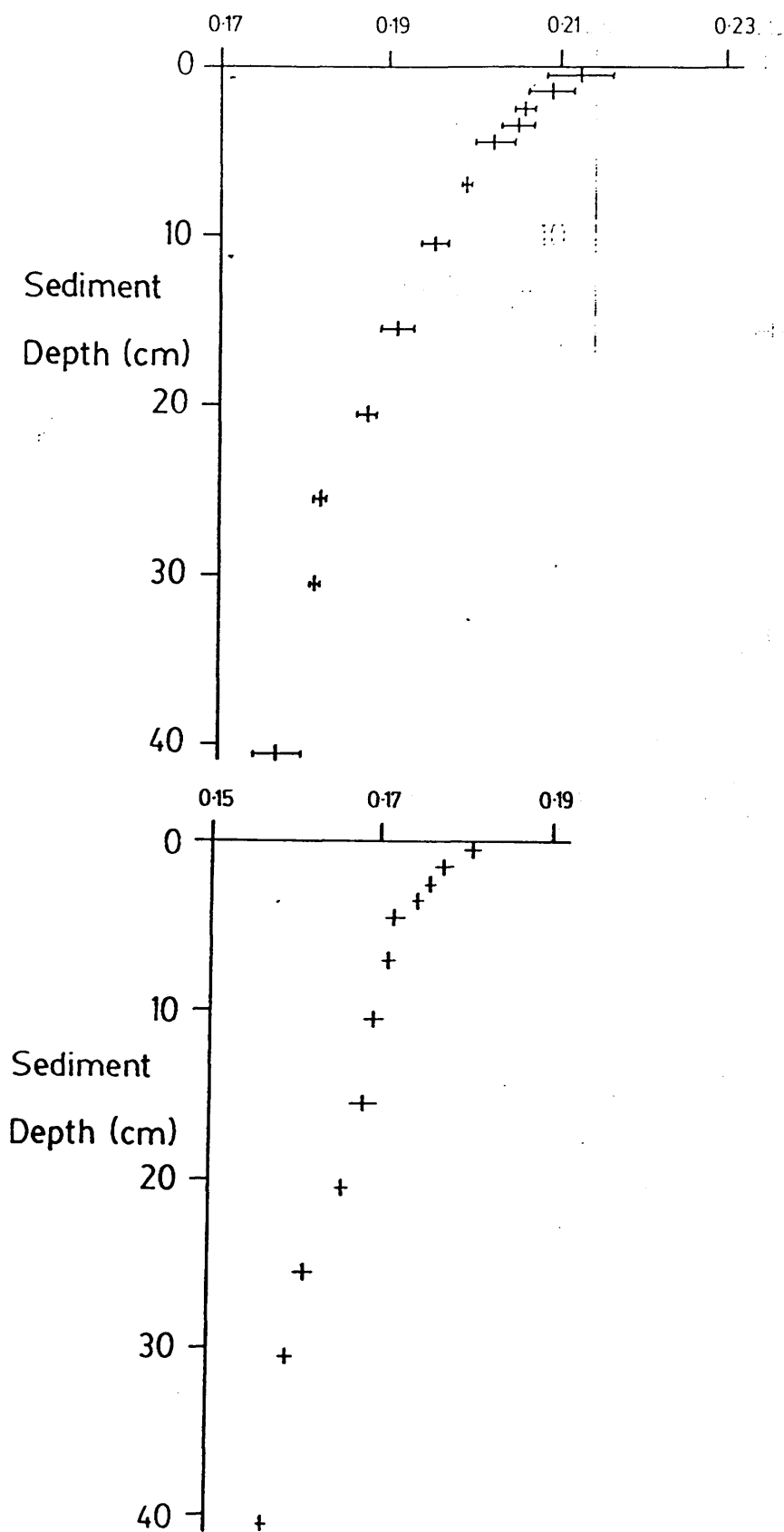
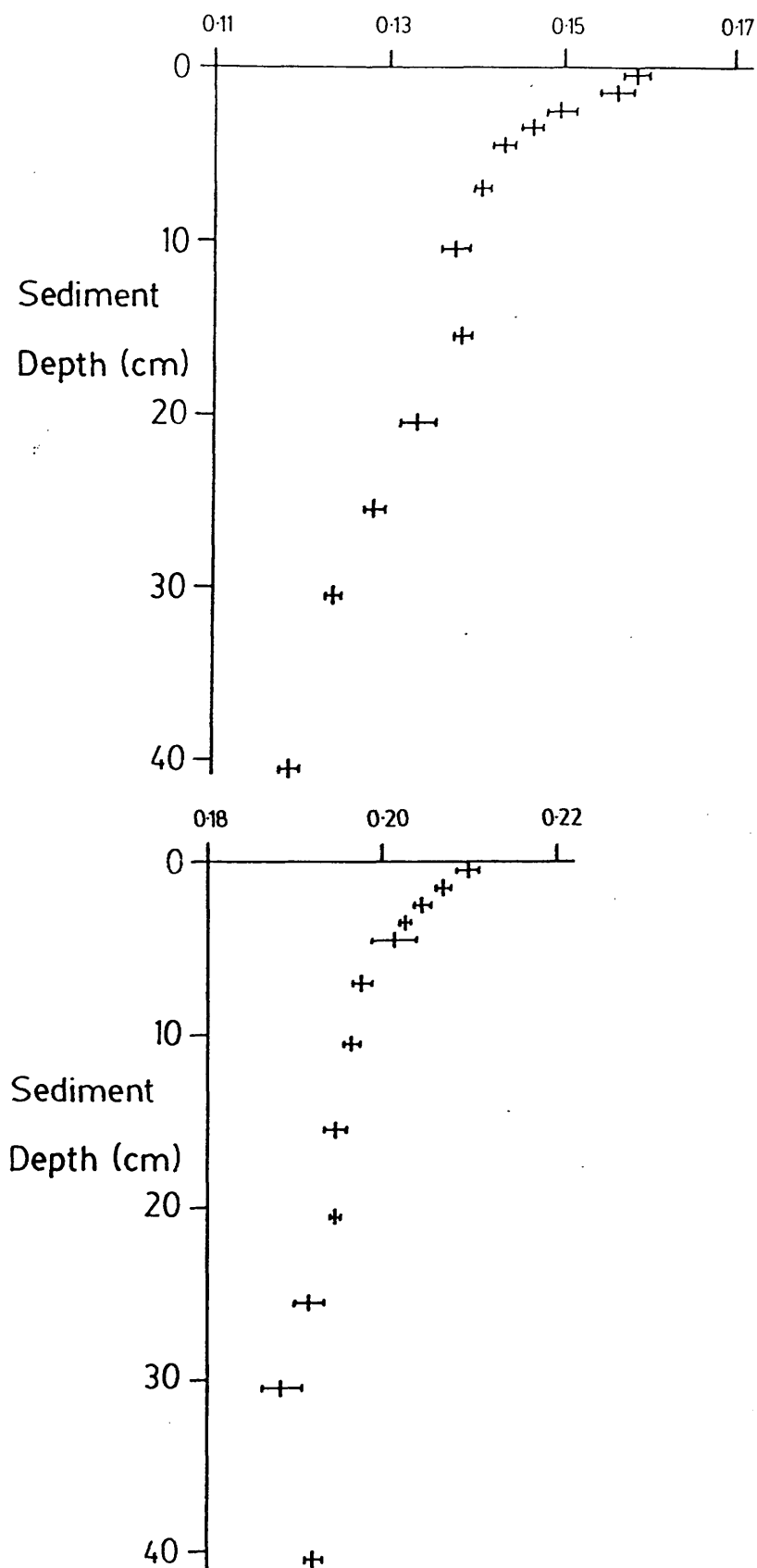
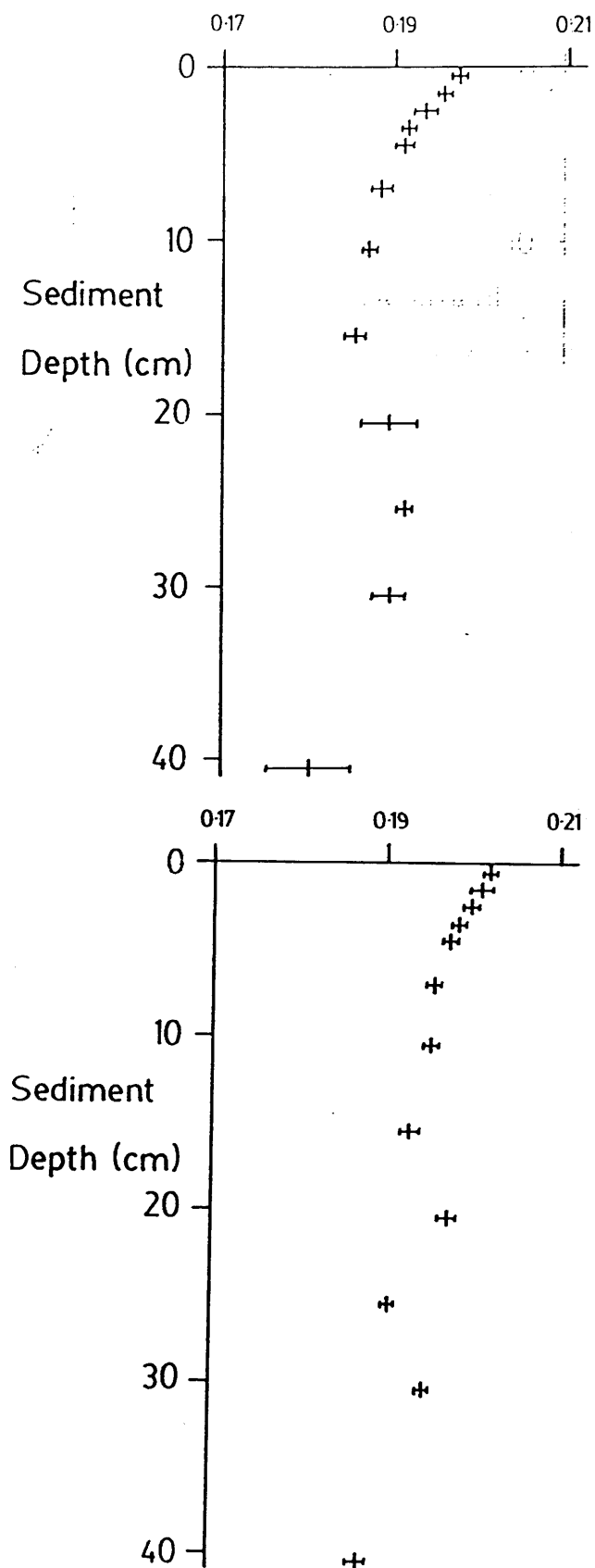


Figure 3.30. Phosphate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 1 (top) and station 2 (bottom).



**Figure 3.31.** Phosphate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 4 (top) and station 5 (bottom).



**Figure 3.32.** Phosphate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 6 (top) and station 7 (bottom).

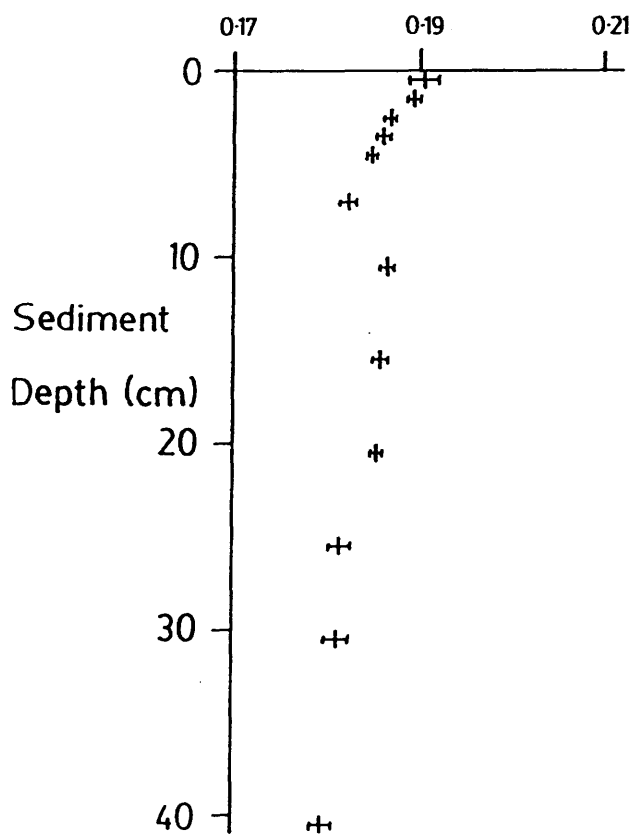


Figure 3.33. Phosphate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 8.

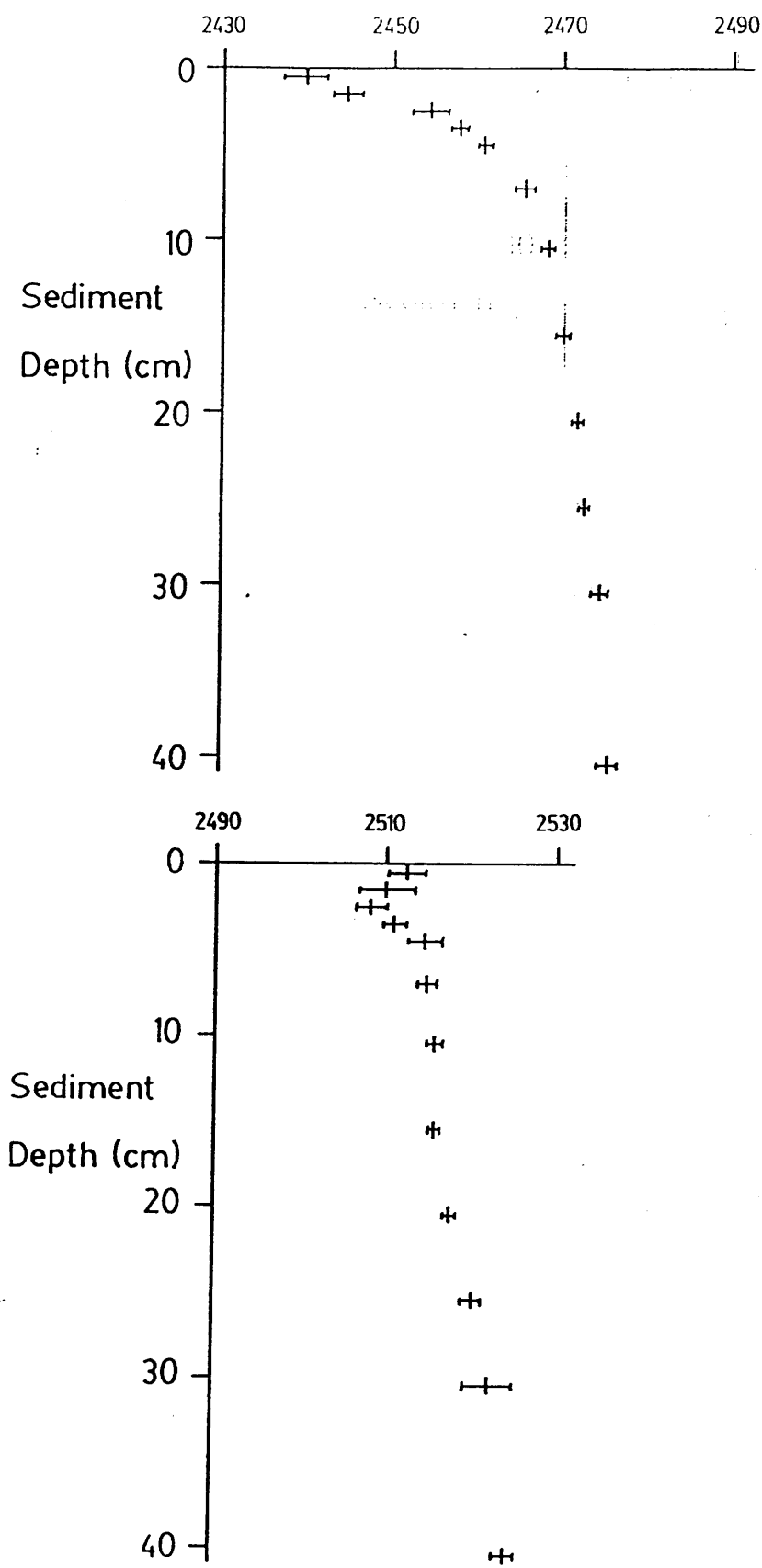


Figure 3.34. Sulphate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 1 (top) and station 2 (bottom).



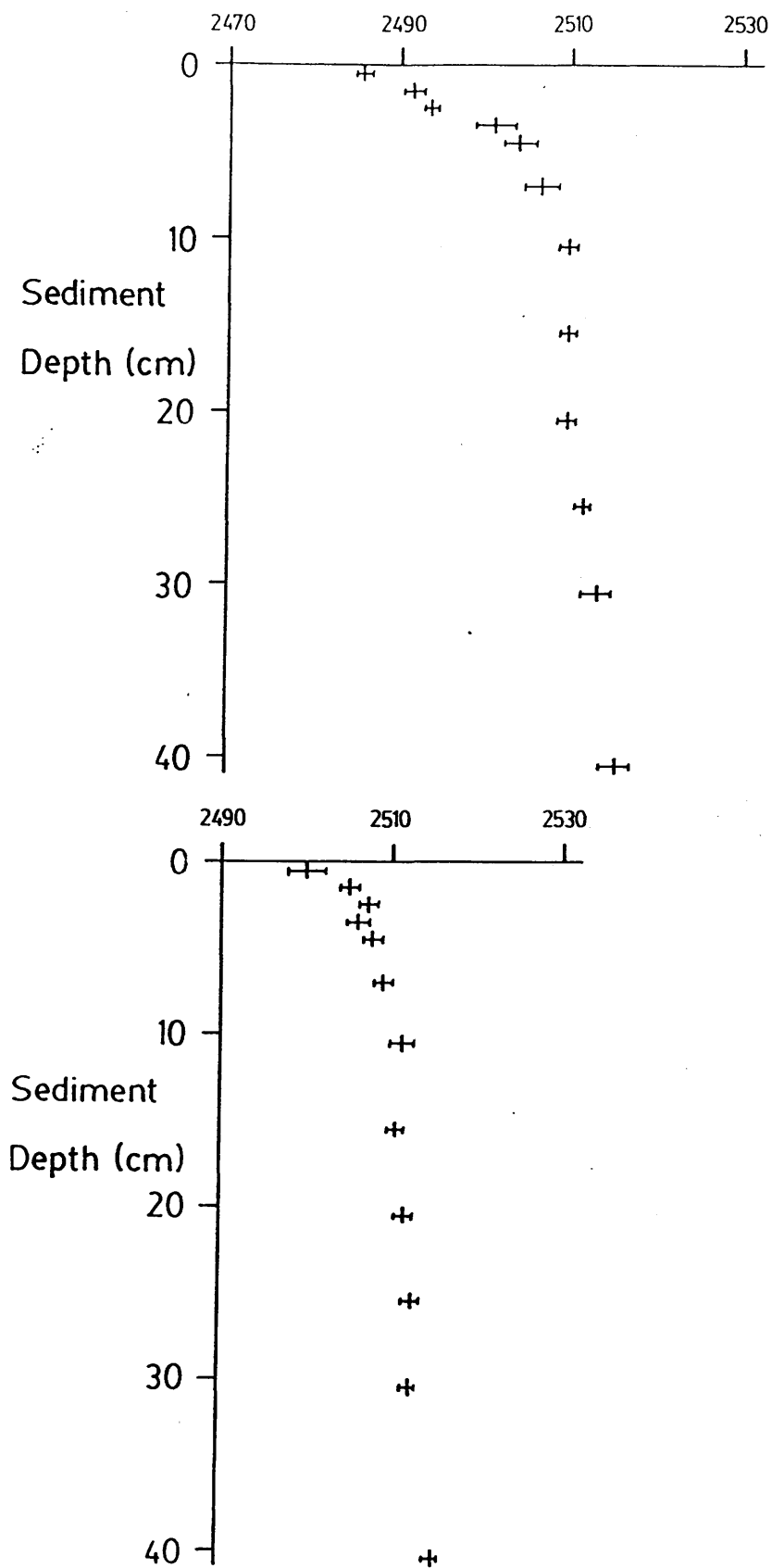


Figure 3.35. Sulphate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 4 (top) and station 5 (bottom).

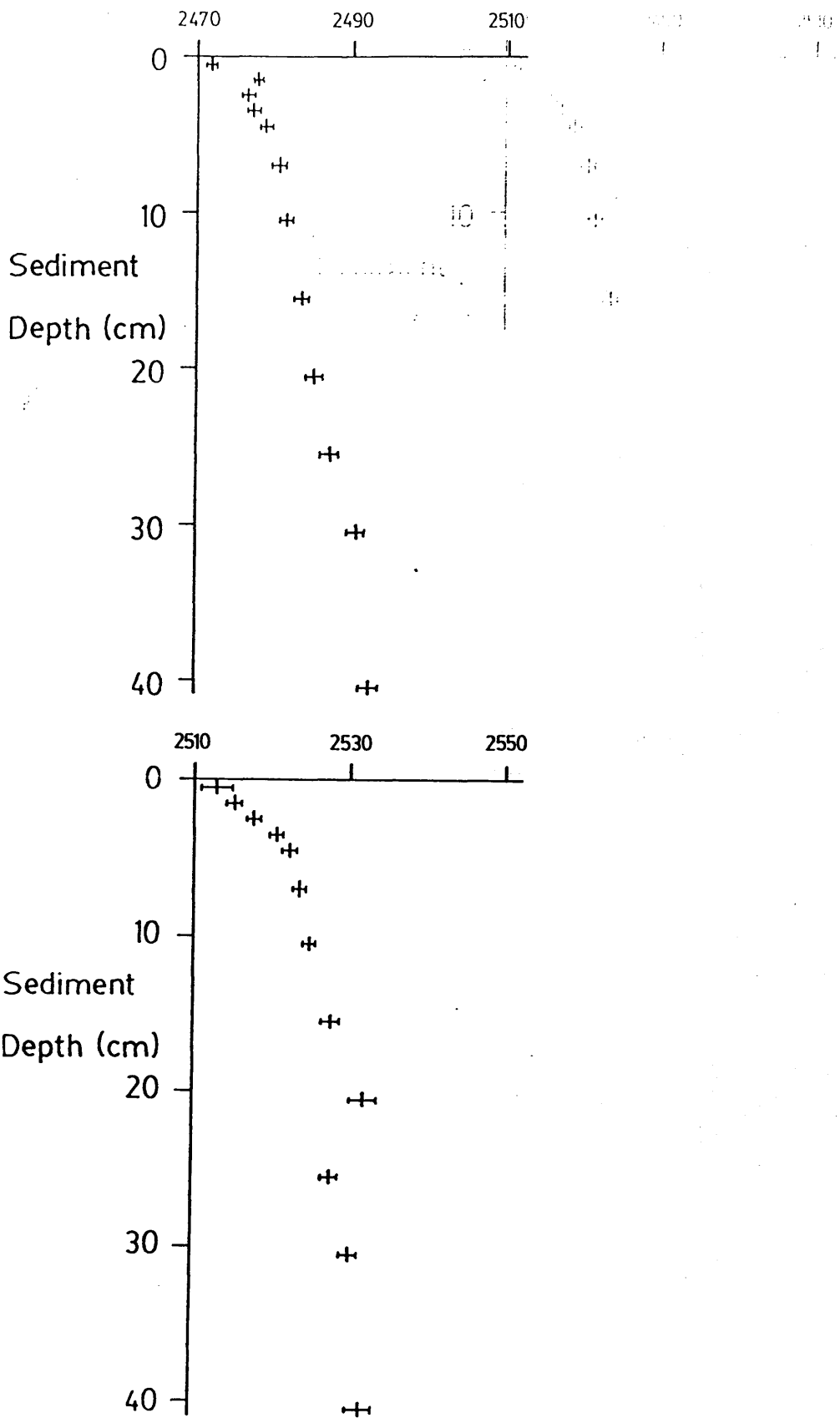


Figure 3.36. Sulphate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 6 (top) and station 7 (bottom).

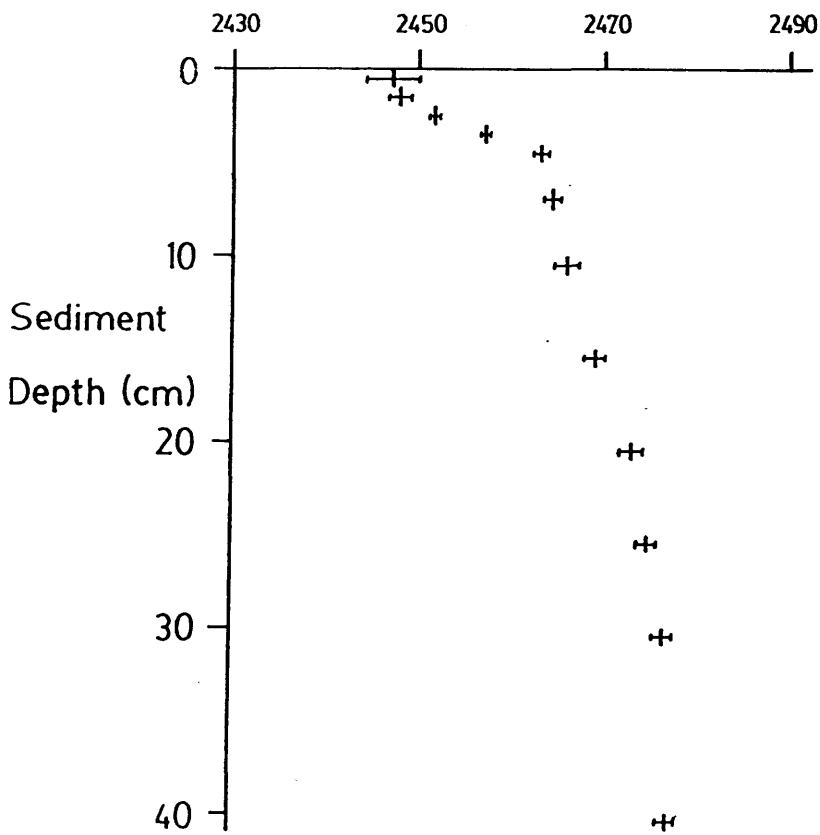


Figure 3.37. Sulphate concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 8.

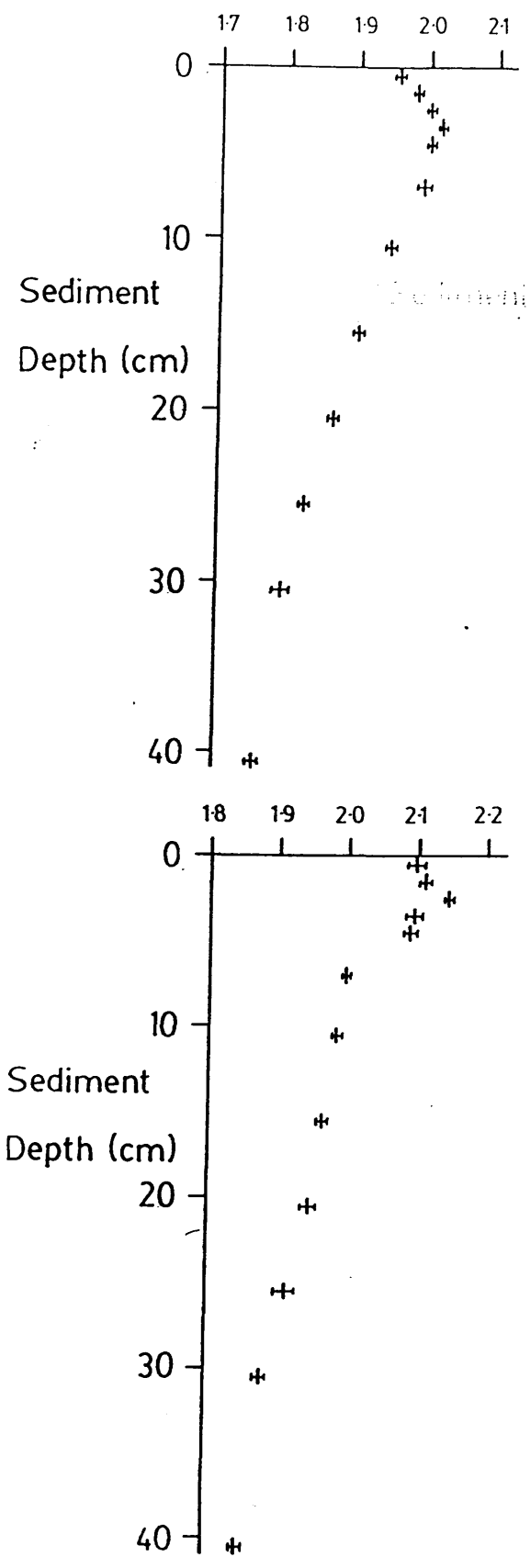


Figure 3.38. Nitrate concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 1 (top) and station 2 (bottom).

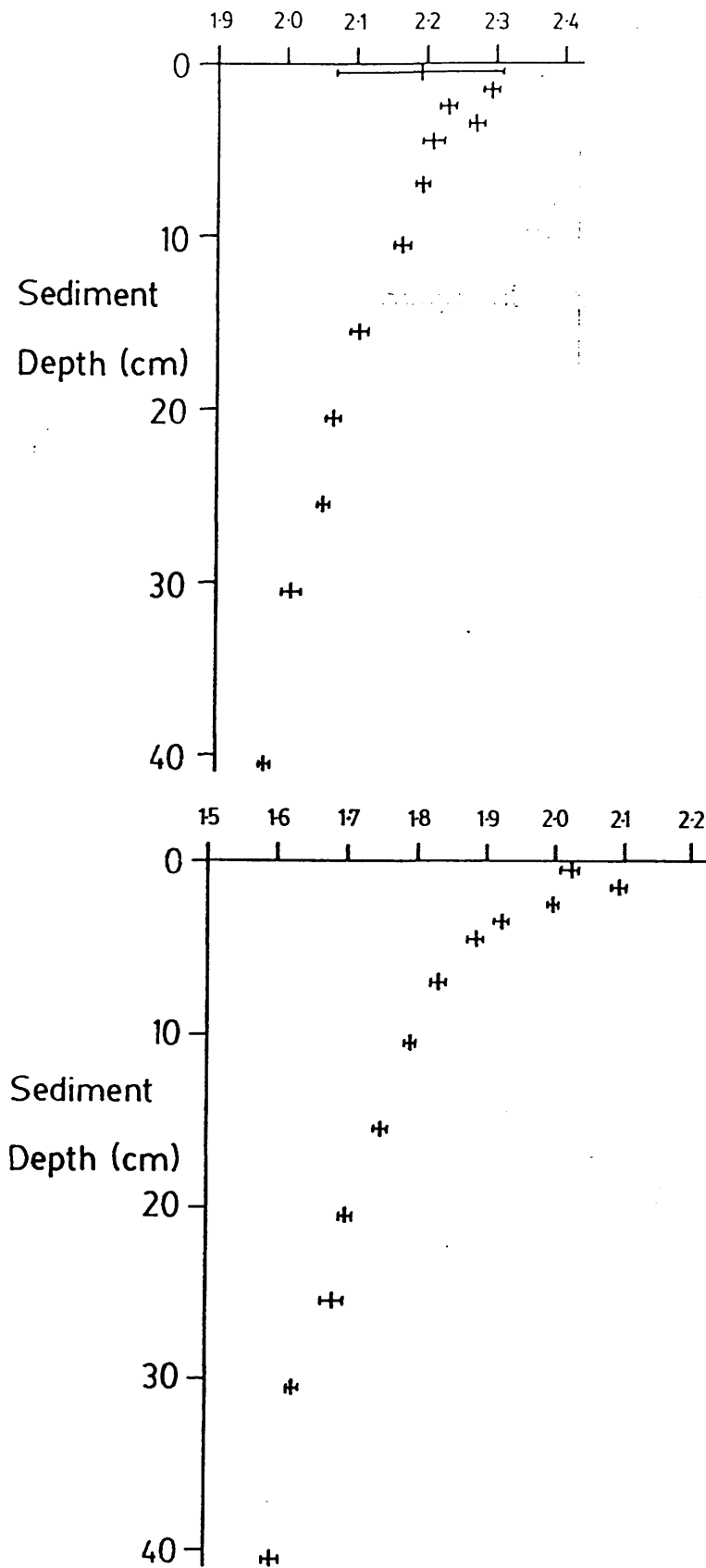


Figure 3.39. Nitrate concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 4 (top) and station 5 (bottom).

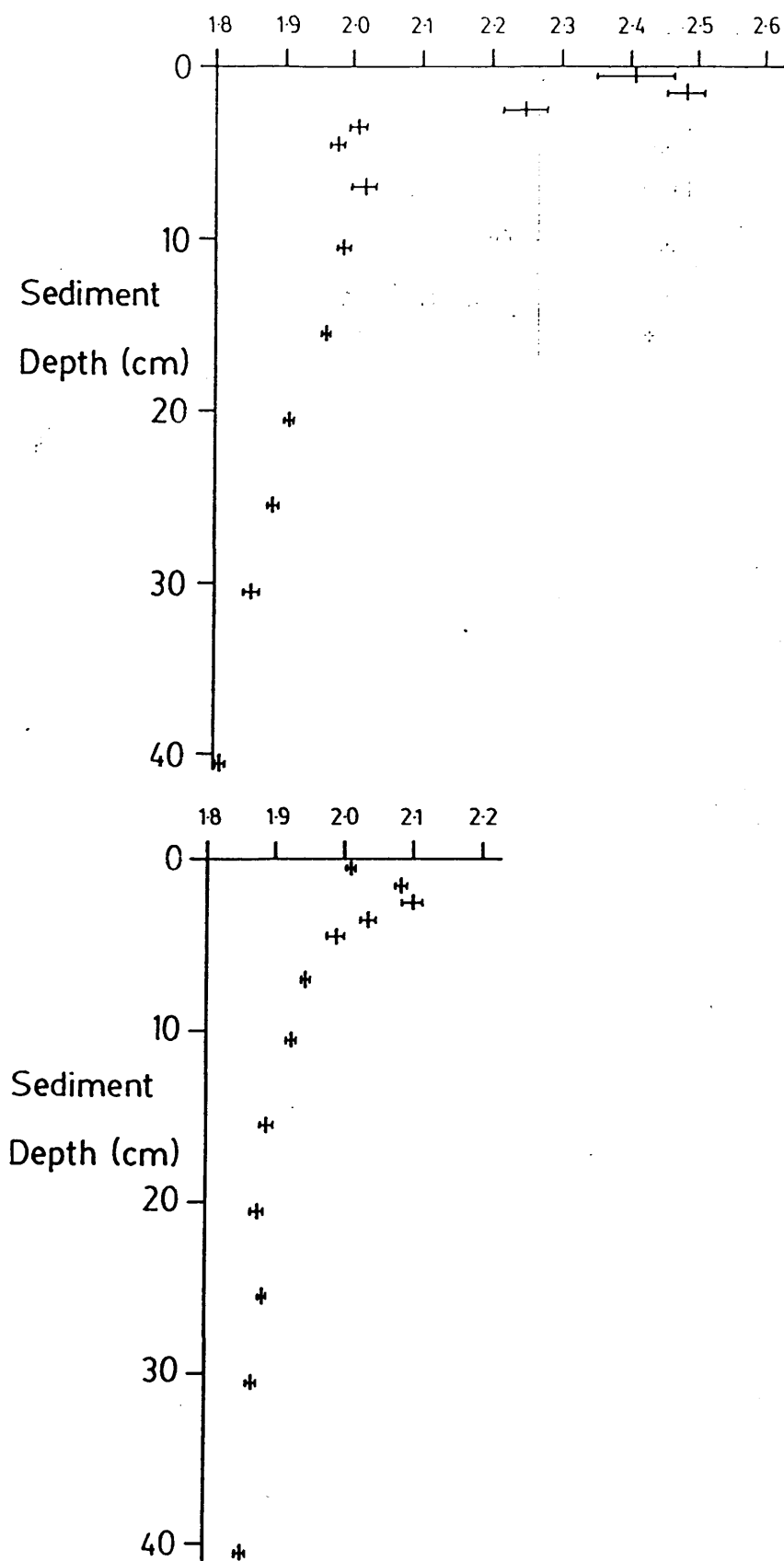


Figure 3.40. Nitrate concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 6 (top) and station 7 (bottom).

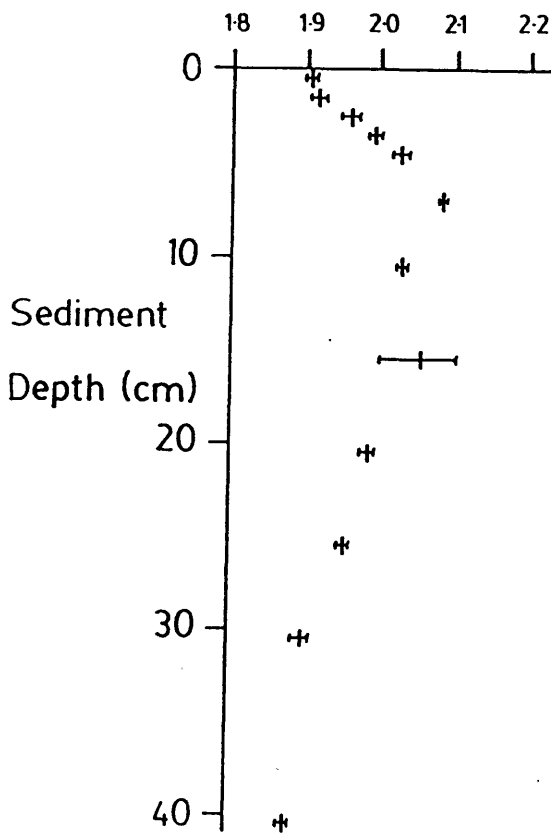


Figure 3.41. Nitrate concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 8.

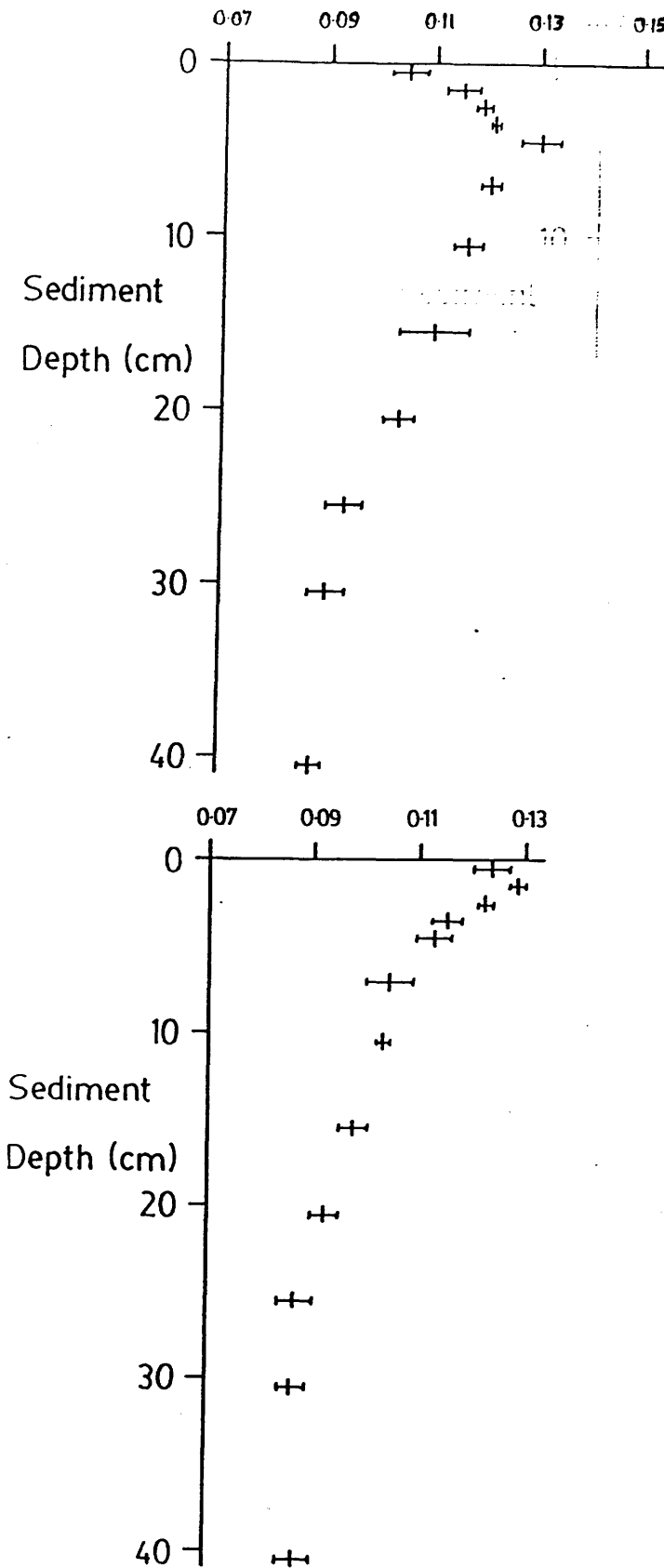


Figure 3.42. Ammonium concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 1 (top) and station 2 (bottom).



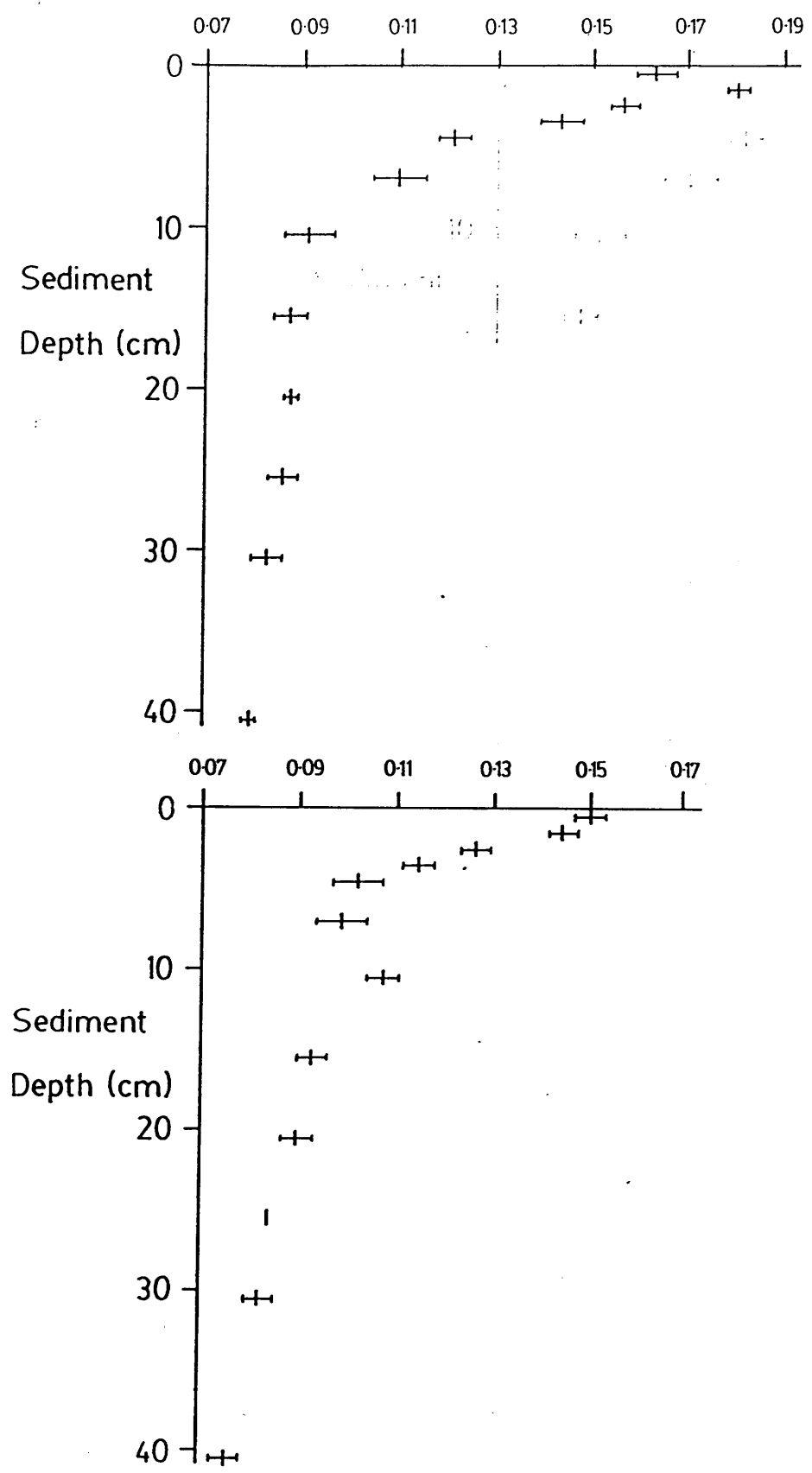


Figure 3.43. Ammonium concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 4 (top) and station 5 (bottom).

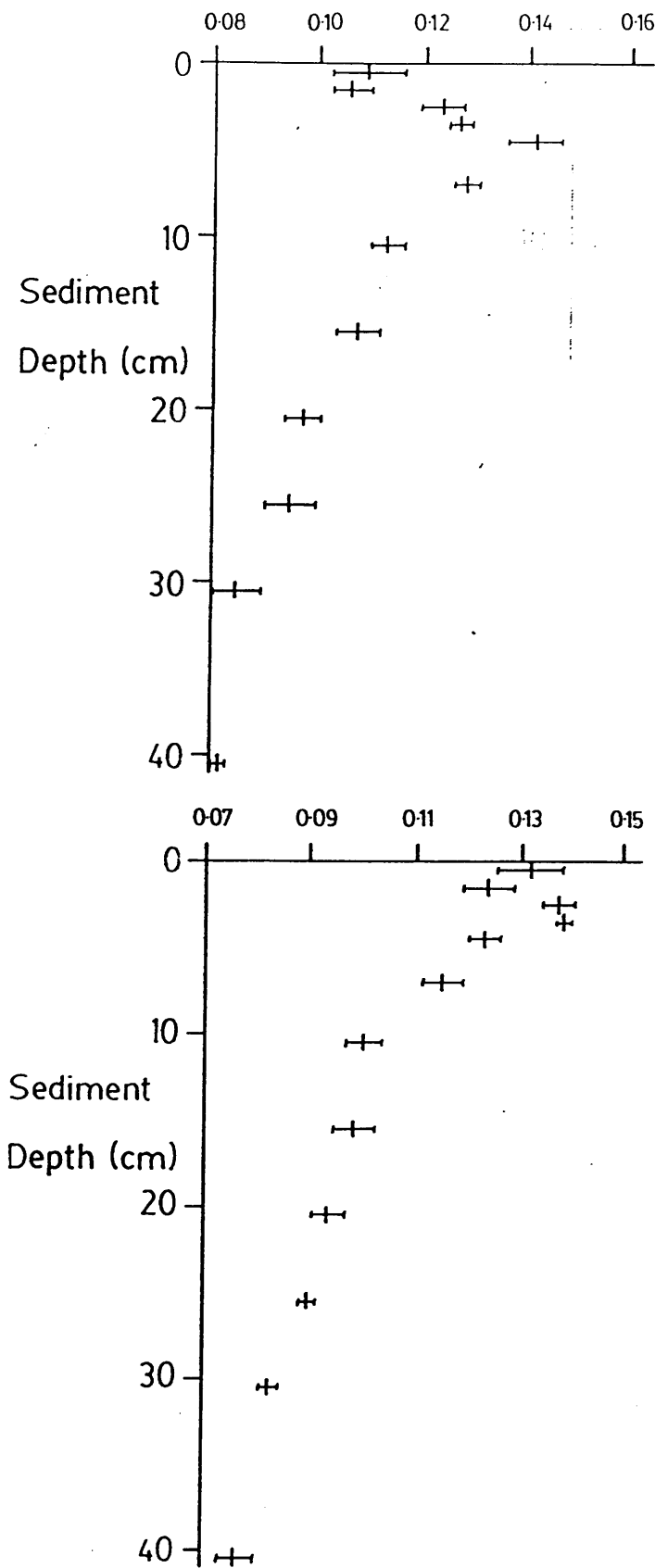
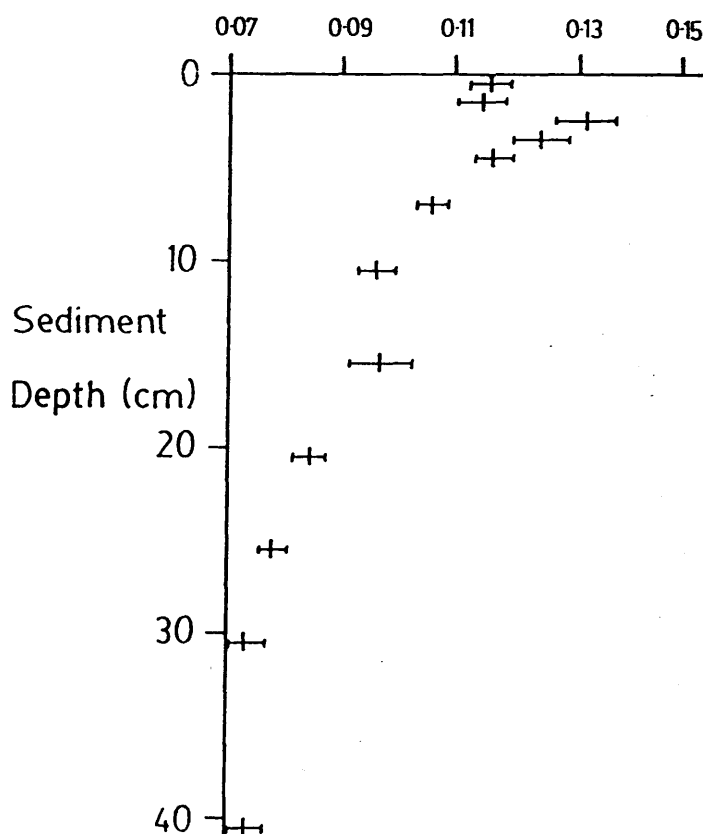


Figure 3.44. Ammonium concentration ( $\text{mg l}^{-1}$ ; mean, sd) for each sediment depth at station 6 (top) and station 7 (bottom).



**Figure 3.45.** Ammonium concentration (mg l<sup>-1</sup>; mean, sd) for each sediment depth at station 8.

variables). These regressions were calculated for the original data and after transformation of the original data. The transformations used were square root,  $\log_{10}$  and negative reciprocal. Each of these series of regression analyses produced 700 regression lines. The best-fit regression was determined as the regression which gave the largest value for the correlation coefficient. Most of the best-fit regressions were for the original data or negative reciprocal transformed data. Only 216 of the 700 best-fit regressions were significant. The coefficients for the regression lines of these significant regressions are shown in tables 3.22/23 for silicate, 3.24-26 for phosphate, 3.27/28 for sulphate, 3.29/30 for nitrate and 3.31/32 for ammonium. The coefficients of non-significant regressions have not been quoted. Summaries of which regressions are significant are given in tables 3.33-3.37 for silicate, phosphate, sulphate, nitrate and ammonium.

At most of the stations the regressions of silicate against sediment depth, micro-organism numbers, meiofaunal numbers (all sub-divisions) and water content are significant. Some of the regressions of silicate against barium and phosphorous are also significant. None of the regressions of silicate against lithium, sodium, potassium, magnesium, calcium, strontium, iron, zinc, sulphur, boron and silicon are significant.

All of the regressions of phosphate against sediment depth, micro-organism numbers, metazoan numbers and nematode numbers are significant. Most of the regressions of phosphate against total meiofaunal numbers and water content are significant. Some of the regressions of phosphate against foraminiferan numbers, barium, zinc, phosphorous and silicon are also significant. None of the regressions of phosphate against lithium, sodium, potassium, magnesium, calcium, strontium, iron, sulphur and boron are

Predictor variable	station no.	m	c	r	p	t
Sediment depth	2	4.905 $\times 10^{-5}$	1.8998	0.7609	0.001<p<0.01	-
	4	4.5392 $\times 10^{-3}$	2.0503	0.8961	p<0.001	-
	5	6.0709 $\times 10^{-3}$	2.2671	0.9731	p<0.001	-
	6	2.7346 $\times 10^{-2}$	2.2014	0.8087	0.001<p<0.01	-
Micro-organisms	2	-1.1821 $\times 10^{-2}$	-0.4861	0.9767	p<0.001	-1/x
	4	-4.0948 $\times 10^{-3}$	-0.4590	0.9581	p<0.001	-1/x
	5	-5.2470 $\times 10^{-3}$	-0.4094	0.8899	p<0.001	-1/x
	6	-3.1445 $\times 10^{-2}$	-0.3388	0.9471	p<0.001	-1/x
	7	-0.1244	2.2313	0.8764	p<0.001	-
	8	-0.1640	2.1037	0.8503	p<0.001	-
Total meiofauna	2	-4.972 $\times 10^{-3}$	-0.5013	0.7530	0.001<p<0.01	-1/x
	4	-2.5734 $\times 10^{-3}$	-0.4669	0.8037	0.001<p<0.01	-1/x
	5	-2.2256 $\times 10^{-3}$	-0.4201	0.7064	0.01<p<0.02	-1/x
	6	-1.0129 $\times 10^{-2}$	-0.3725	0.7956	0.001<p<0.01	-1/x
	7	-6.0702 $\times 10^{-2}$	2.1240	0.9545	p<0.001	-
	8	-6.3394 $\times 10^{-2}$	2.0223	0.9711	p<0.001	-
Metazoa	2	-1.0218 $\times 10^{-2}$	-0.4984	0.8349	p<0.001	-1/x
	4	-4.6474 $\times 10^{-3}$	-0.4661	0.8331	p<0.001	-1/x
	5	-5.022 $\times 10^{-3}$	-0.4174	0.8130	0.001<p<0.01	-1/x
	6	-2.4071 $\times 10^{-2}$	-0.3622	0.8860	p<0.001	-1/x
	7	-0.1192	2.1335	0.9138	p<0.001	-
	8	-0.1017	2.0393	0.8456	p<0.001	-
Nematodes	2	-1.5875 $\times 10^{-2}$	0.4977	0.8385	p<0.001	-1/x

Table 3.22. Coefficients of the significant regression lines ( $y=mx + c$ ) calculated for silicate at each station for each predictor variable.  $t$ =transformation.

Predictor variable	station no.	m	c	r	p	t
Nematodes	4	-5.556 $\times 10^{-3}$	-0.4660	0.8373	$p < 0.001$	-1/x
	5	-6.378 $\times 10^{-3}$	-0.4169	0.8276	$p < 0.001$	-1/x
	6	-3.2576 $\times 10^{-2}$	-0.3606	0.8837	$p < 0.001$	-1/x
	7	-0.1384	2.1306	0.9241	$p < 0.001$	-
	8	-0.1432	2.0328	0.8888	$p < 0.001$	-
Foraminifera	4	-5.624 $\times 10^{-3}$	-0.4680	0.7556	$0.001 < p < 0.01$	-1/x
	6	-1.7080 $\times 10^{-2}$	-0.3813	0.6921	$0.01 < p < 0.02$	-1/x
	7	-3.4237 $\times 10^{-2}$	0.3259	0.9778	$p < 0.001$	$\log_{10} x$
	8	-6.3488 $\times 10^{-2}$	-0.5070	0.9884	$p < 0.001$	-1/x
Water content	2	-3.2975 $\times 10^{-4}$	-0.4468	0.9317	$p < 0.001$	-1/x
	4	-1.4327 $\times 10^{-4}$	-0.4197	0.9397	$p < 0.001$	-1/x
	6	-7.7848 $\times 10^{-4}$	-0.2339	0.9343	$p < 0.001$	-1/x
	7	-1.8279 $\times 10^{-3}$	2.4178	0.6488	$0.02 < p < 0.05$	-
Barium	4	0.2211	-0.4988	0.7483	$0.001 < p < 0.01$	-1/x
Phosphorous	7	-7.858 $\times 10^{-2}$	-0.4698	0.8385	$p < 0.001$	-1/x

Table 3.23. Coefficients of the significant regression lines ( $y = mx + c$ ) calculated for silicate at each station for each predictor variable.  $t$  = transformation.

Predictor variable	station no.	m	c	r	p	t
Sediment depth	1	-2.3427 $\times 10^{-2}$	-4.8119	0.9752	$p < 0.001$	-1/x
	2	-1.948 $\times 10^{-2}$	-5.6536	0.9711	$p < 0.001$	-1/x
	4	-4.9900 $\times 10^{-2}$	-6.5938	0.9413	$p < 0.001$	-1/x
	5	-1.0900 $\times 10^{-2}$	-4.8969	0.8608	$p < 0.001$	-1/x
	6	-7.240 $\times 10^{-3}$	-5.1682	0.7021	$0.01 < p < 0.02$	-1/x
	7	-7.389 $\times 10^{-3}$	-5.0044	0.8450	$p < 0.001$	-1/x
	8	-6.212 $\times 10^{-3}$	-5.3241	0.8216	$0.001 < p < 0.01$	-1/x
Micro-organisms	1	4.4566 $\times 10^{-3}$	0.1864	0.8307	$p < 0.001$	-
	2	3.6782 $\times 10^{-3}$	0.1620	0.8837	$p < 0.001$	-
	4	3.4184 $\times 10^{-3}$	0.1262	0.9105	$p < 0.001$	-
	5	2.4808 $\times 10^{-3}$	0.1905	0.9607	$p < 0.001$	-
	6	1.6499 $\times 10^{-3}$	0.1868	0.7797	$0.001 < p < 0.01$	-
	7	1.4779 $\times 10^{-3}$	0.1931	0.7662	$0.001 < p < 0.01$	-
	8	1.7940 $\times 10^{-3}$	0.1822	0.8818	$p < 0.001$	-
Total meiofauna	1	2.3084 $\times 10^{-3}$	0.1918	0.6197	$0.02 < p < 0.05$	-
	2	1.4286 $\times 10^{-3}$	0.1670	0.6124	$0.02 < p < 0.05$	-
	4	2.1450 $\times 10^{-3}$	0.1328	0.7609	$0.001 < p < 0.01$	-
	5	1.1030 $\times 10^{-3}$	0.1954	0.8087	$0.001 < p < 0.01$	-
	6	5.075 $\times 10^{-4}$	0.1866	0.6116	$0.02 < p < 0.05$	-
	8	5.382 $\times 10^{-4}$	0.1835	0.6921	$0.01 < p < 0.02$	-
Metazoa	1	3.979 $\times 10^{-3}$	0.1911	0.6716	$0.02 < p < 0.05$	-
	2	3.538 $\times 10^{-3}$	0.1660	0.7043	$0.01 < p < 0.02$	-
	4	3.8599 $\times 10^{-3}$	0.1322	0.7855	$0.001 < p < 0.01$	-

Table 3.24. Coefficients of the significant regression lines ( $y=mx + c$ ) calculated for phosphate at each station for each predictor variable. t=transformation.

Predictor variable	station no.	m	c	r	p	t
Metazoa	5	2.4451 $\times 10^{-3}$	0.1942	0.9083	$p < 0.001$	-
	6	1.2085 $\times 10^{-3}$	0.1881	0.6892	$0.01 < p < 0.02$	-
	7	1.1329 $\times 10^{-3}$	0.1946	0.6116	$0.02 < p < 0.05$	-
	8	9.799 $\times 10^{-4}$	0.1832	0.6950	$0.01 < p < 0.02$	-
Nematodes	1	5.133 $\times 10^{-3}$	0.1909	0.6841	$0.01 < p < 0.02$	-
	2	4.760 $\times 10^{-3}$	0.1658	0.7232	$0.001 < p < 0.01$	-
	4	4.619 $\times 10^{-3}$	0.1321	0.7899	$0.001 < p < 0.01$	-
	5	3.0866 $\times 10^{-3}$	0.1939	0.9176	$p < 0.001$	-
	6	1.6459 $\times 10^{-3}$	0.1880	0.6928	$0.01 < p < 0.02$	-
	7	1.2675 $\times 10^{-3}$	0.1947	0.5908	$0.02 < p < 0.05$	-
	8	1.3055 $\times 10^{-3}$	0.1833	0.6856	$0.01 < p < 0.02$	-
Foraminifera	4	4.712 $\times 10^{-3}$	0.1337	0.7183	$0.001 < p < 0.01$	-
	5	1.7327 $\times 10^{-3}$	0.1967	0.6550	$0.02 < p < 0.05$	-
	8	9.206 $\times 10^{-4}$	0.1842	0.5857	$0.02 < p < 0.05$	-

Table 3.25. Coefficients of the significant regression lines ( $y = mx + c$ ) calculated for phosphate at each station for each predictor variable.  $t$ =transformation.



Predictor variable	station no.	m	c	r	p	t
Water content	1	1.5951 $\times 10^{-4}$	0.1441	0.9306	$p < 0.001$	-
	2	1.1045 $\times 10^{-4}$	0.1483	0.9149	$p < 0.001$	-
	4	1.1978 $\times 10^{-4}$	0.0933	0.8944	$p < 0.001$	-
	5	5.010 $\times 10^{-5}$	0.1840	0.6008	$0.02 < p < 0.05$	-
	6	4.4263 $\times 10^{-5}$	0.1805	0.8432	$p < 0.001$	-
	7	3.0572 $\times 10^{-5}$	0.1888	0.8473	$p < 0.001$	-
Barium	1	-3.100	-4.6951	0.5848	$0.02 < p < 0.05$	-1/x
	4	-0.1808	0.1590	0.6907	$0.01 < p < 0.02$	-
Zinc	2	-8.244 $\times 10^{-2}$	-5.6454	0.6768	$0.01 < p < 0.02$	-1/x
	4	-0.1209	-6.9007	0.6723	$0.01 < p < 0.02$	-1/x
Phosphorous	7	1.2028 $\times 10^{-2}$	0.1936	0.6977	$0.01 < p < 0.02$	-
Silicon	1	-9.221 $\times 10^{-3}$	0.2277	0.8248	$p < 0.001$	-
	2	-4.638 $\times 10^{-3}$	0.1869	0.6301	$0.02 < p < 0.05$	-

Table 3.26. Coefficients of the significant regression lines ( $y=mx + c$ ) calculated for phosphate at each station for each predictor variable. t=transformation.

Predictor variable	station no.	m	c	r	p	t
=====						
Sediment depth	1	0.7228	2453.23	0.8085	0.001<p<0.01	-
	2	0.4566	2507.92	0.8614	p<0.001	-
	4	0.5944	2496.11	0.7962	0.001<p<0.01	-
	5	0.2586	2505.81	0.8526	p<0.001	-
	6	0.4508	2475.79	0.9602	p<0.001	-
	7	0.4266	2518.02	0.8538	p<0.001	-
	8	0.7286	2454.23	0.8718	p<0.001	-
Micro-organisms	1	-8.2652 x10 <sup>-7</sup>	-4.0430 x10 <sup>-4</sup>	0.9711	p<0.001	-1/x
	2	-2.8117	2519.65	0.7092	0.001<p<0.01	-
	4	-2.6966	2514.00	0.9854	p<0.001	-
	5	-1.4674	2514.01	0.9197	p<0.001	-
	6	-3.7647 x10 <sup>-7</sup>	-4.0219 x10 <sup>-4</sup>	0.8313	p<0.001	-1/x
	7	-4.0913 x10 <sup>-7</sup>	-3.9544 x10 <sup>-4</sup>	0.9165	p<0.001	-1/x
	8	-1.1134 x10 <sup>-6</sup>	-4.0413 x10 <sup>-4</sup>	0.9555	p<0.001	-1/x
Total meiofauna	1	-4.8970 x10 <sup>-7</sup>	-4.0520 x10 <sup>-4</sup>	0.8579	p<0.001	-1/x
	4	-2.9307 x10 <sup>-7</sup>	-3.9854 x10 <sup>-4</sup>	0.9044	p<0.001	-1/x
	5	-1.1084 x10 <sup>-7</sup>	-3.9821 x10 <sup>-4</sup>	0.8532	p<0.001	-1/x
	6	-1.0776 x10 <sup>-7</sup>	-4.0263 x10 <sup>-4</sup>	0.5992	0.02<p<0.05	-1/x
	7	-1.4726 x10 <sup>-7</sup>	-3.9590 x10 <sup>-4</sup>	0.7043	0.01<p<0.02	-1/x
	8	-3.1211 x10 <sup>-7</sup>	-4.0500 x10 <sup>-4</sup>	0.7576	0.001<p<0.01	-1/x
Metazoa	1	-8.2368 x10 <sup>-7</sup>	-4.0509 x10 <sup>-4</sup>	0.8972	p<0.001	-1/x
	4	-5.2311 x10 <sup>-7</sup>	-3.9846 x10 <sup>-4</sup>	0.9236	p<0.001	-1/x
	5	-2.3376 x10 <sup>-7</sup>	-3.9811 x10 <sup>-4</sup>	0.9050	p<0.001	-1/x
=====						

Table 3.27. Coefficients of the significant regression lines (y=mx + c) calculated for sulphate at each station for each predictor variable. t=transformation

Predictor variable	station no.	m	c	r	p	t
Metazoa	6	-2.5661 $\times 10^{-7}$	-4.0252 $\times 10^{-4}$	0.6760	0.01<p<0.02	-1/x
	7	-3.2024 $\times 10^{-7}$	-3.9584 $\times 10^{-4}$	0.7583	0.001<p<0.01	-1/x
	8	-6.1396 $\times 10^{-7}$	-4.0471 $\times 10^{-4}$	0.8319	p<0.001	-1/x
Nematodes	1	-1.0549 $\times 10^{-6}$	-4.0505 $\times 10^{-4}$	0.9061	p<0.001	-1/x
	4	-6.2168 $\times 10^{-7}$	-3.9845 $\times 10^{-4}$	0.9220	p<0.001	-1/x
	5	-1.8305	2512.00	0.9006	p<0.001	-
	6	-3.5938 $\times 10^{-7}$	-4.0249 $\times 10^{-4}$	0.7021	0.01<p<0.02	-1/x
	7	-3.5919 $\times 10^{-7}$	-3.9586 $\times 10^{-4}$	0.7369	0.001<p<0.01	-1/x
	8	-7.9948 $\times 10^{-7}$	-4.0483 $\times 10^{-4}$	0.8000	0.001<p<0.01	-1/x
Foraminifera	1	-1.1450 $\times 10^{-6}$	-4.0541 $\times 10^{-4}$	0.7727	0.001<p<0.01	-1/x
	4	-6.5124 $\times 10^{-7}$	-3.9865 $\times 10^{-4}$	0.8672	p<0.001	-1/x
	5	-1.8459 $\times 10^{-7}$	-3.9833 $\times 10^{-4}$	0.7436	0.001<p<0.01	-1/x
	7	-2.6001 $\times 10^{-7}$	-3.9597 $\times 10^{-4}$	0.6356	0.02<p<0.05	-1/x
Water content	1	-0.1504	2511.62	0.8955	p<0.001	-
	2	-9.451 $\times 10^{-2}$	2532.03	0.8385	p<0.001	-
	4	-8.858 $\times 10^{-2}$	2537.70	0.9006	p<0.001	-
	5	-4.9641 $\times 10^{-9}$	-3.9709 $\times 10^{-4}$	0.6261	0.02<p<0.05	-1/x
	6	-1.0211 $\times 10^{-8}$	-4.074 $\times 10^{-4}$	0.9094	p<0.001	-1/x
	7	-5.0905 $\times 10^{-2}$	2535.73	0.9482	p<0.001	-
	8	-0.1467	2491.03	0.8325	p<0.001	-
Barium	4	1.4831	49.8746	0.7874	0.001<p<0.01	$\sqrt{y}$
Silicon	2	9.232 $\times 10^{-4}$	3.3969	0.8198	0.001<p<0.01	$\text{Log}_{10}$

Table 3.28. Coefficients of the significant regression lines ( $y=mx + c$ ) calculated for silicate at each station for each predictor variable. t=transformation.

Predictor variable	station no.	m	c	r	p	t
Sediment depth	1	-1.475 $\times 10^{-4}$	-0.5978	0.9680	$p < 0.001$	-1/x
	2	-1.8163 $\times 10^{-3}$	-0.4750	0.9518	$p < 0.001$	-1/x
	4	-1.9646 $\times 10^{-3}$	-0.4441	0.9602	$p < 0.001$	-1/x
	5	-3.4452 $\times 10^{-3}$	-0.5063	0.9365	$p < 0.001$	-1/x
	6	-2.9415 $\times 10^{-3}$	-0.4539	0.7791	$0.001 < p < 0.01$	-1/x
	7	-1.3945 $\times 10^{-3}$	-0.4905	0.8735	$p < 0.001$	-1/x
	7	-1.3945 $\times 10^{-3}$	-0.4905	0.8735	$p < 0.001$	-1/x
Micro-organisms	2	4.6915 $\times 10^{-2}$	1.9135	0.8355	$p < 0.001$	-
	4	2.2571 $\times 10^{-2}$	2.0632	0.7173	$0.001 < p < 0.01$	-
	5	5.9545 $\times 10^{-2}$	1.6311	0.9338	$p < 0.001$	-
	6	1.8369 $\times 10^{-2}$	0.2728	0.9220	$p < 0.001$	$\log_{10}$
	7	6.676 $\times 10^{-3}$	-0.5223	0.7078	$0.01 < p < 0.02$	-1/x
Total meiofauna	5	2.4692 $\times 10^{-2}$	1.7539	0.7232	$0.001 < p < 0.01$	-
	6	2.7267 $\times 10^{-2}$	1.9705	0.7148	$0.001 < p < 0.01$	-
Metazoa	5	5.741 $\times 10^{-2}$	1.7214	0.8608	$p < 0.001$	
	6	6.698 $\times 10^{-2}$	1.9394	0.8301	$p < 0.001$	-
Nematodes	5	7.408 $\times 10^{-2}$	1.7133	0.8922	$p < 0.001$	-
	6	8.957 $\times 10^{-2}$	1.9362	0.8167	$0.001 < p < 0.01$	
Foraminifera	6	4.451 $\times 10^{-2}$	1.9958	0.5941	$0.02 < p < 0.05$	-

Table 3.29. Coefficients of the significant regression lines ( $y=mx + c$ ) calculated for nitrate at each station for each predictor variable. t=transformation.

Predictor variable	station no.	m	c	r	p	t
Water content	1	$-1.2469 \times 10^{-4}$	0.0691	0.7899	$0.001 < p < 0.01$	-
	2	$1.5354 \times 10^{-3}$	1.7148	0.9529	$p < 0.001$	-
	4	$8.904 \times 10^{-4}$	1.8085	0.8198	$0.001 < p < 0.01$	-
	6	$5.0550 \times 10^{-4}$	-6.6016	0.9333	$p < 0.001$	-1/x
	7	$1.5775 \times 10^{-4}$	-0.5463	0.9132	$p < 0.001$	-1/x
Lithium	8	0.3578	-0.5530	0.7969	$0.001 < p < 0.01$	-1/x
Sodium	8	$7.016 \times 10^{-6}$	-0.5708	0.6325	$0.02 < p < 0.05$	-1/x
Potassium	8	$1.4714 \times 10^{-4}$	-0.5607	0.5908	$0.02 < p < 0.05$	-1/x
Magnesium	8	$5.125 \times 10^{-5}$	-0.5596	0.6132	$0.02 < p < 0.05$	-1/x
Calcium	8	$1.4763 \times 10^{-4}$	-0.5567	0.5874	$0.02 < p < 0.05$	-1/x
Barium	1	-0.2805	-0.4831	0.6753	$0.01 < p < 0.02$	-1/x
	4	-0.2775	-0.4359	0.5762	$0.02 < p < 0.05$	-1/x
Zinc	2	$-7.403 \times 10^{-3}$	-0.4752	0.6317	$0.02 < p < 0.05$	-1/x
	4	$-3.8833 \times 10^{-3}$	-0.4552	0.6419	$0.02 < p < 0.05$	-1/x
Phosphorous	7	0.2714	1.9120	0.8491	$p < 0.001$	-
Sulphur	7	$4.240 \times 10^{-4}$	1.6654	0.6017	$0.02 < p < 0.05$	-
Boron	8	$1.2860 \times 10^{-2}$	0.2396	0.6964	$0.01 < p < 0.02$	$\log_{10}$
Silicon	1	$-5.924 \times 10^{-2}$	2.1249	0.6708	$0.01 < p < 0.02$	-
	2	$-6.726 \times 10^{-2}$	2.2618	0.6943	$0.01 < p < 0.02$	-

Table 3.30. Coefficients of the significant regression lines ( $y=mx + c$ ) calculated for nitrate at each station for each predictor variable. t=transformation.

Predictor variable	station no.	m	c	r	p	t
Sediment depth	1	-8.067 $\times 10^{-2}$	-8.130	0.8666	$p < 0.001$	-1/x
	2	-0.1030	-8.2816	0.9252	$p < 0.001$	-1/x
	4	-0.1765	-6.9984	0.8683	$p < 0.001$	-1/x
	5	-0.1422	-8.0277	0.9110	$p < 0.001$	-1/x
	6	-0.1046	-8.0177	0.8301	$p < 0.001$	-1/x
	7	-0.1460	-7.5285	0.9695	$p < 0.001$	-1/x
	8	-0.1843	-7.9265	0.9808	$p < 0.001$	-1/x
Micro-organisms	2	8.2801 $\times 10^{-2}$	0.0892	0.9290	$p < 0.001$	-
	4	9.906 $\times 10^{-3}$	0.0795	0.9466	$p < 0.001$	-
	5	8.7369 $\times 10^{-3}$	0.0769	0.9450	$p < 0.001$	-
	7	7.054 $\times 10^{-3}$	0.0955	0.7113	$0.001 < p < 0.01$	-
	8	1.0677 $\times 10^{-2}$	0.0842	0.7280	$0.001 < p < 0.01$	-
Total Meiofauna	2	3.130 $\times 10^{-3}$	0.1004	0.6261	$0.02 < p < 0.05$	-
	4	6.369 $\times 10^{-3}$	0.0982	0.8149	$0.001 < p < 0.01$	-
	5	4.1981 $\times 10^{-3}$	0.0932	0.9689	$p < 0.001$	-
Metazoa	2	7.929 $\times 10^{-3}$	0.0982	0.7382	$0.001 < p < 0.01$	-
	4	1.1373 $\times 10^{-2}$	0.0965	0.8337	$p < 0.001$	-
	5	8.949 $\times 10^{-3}$	0.0892	0.9327	$p < 0.001$	-
Nematodes	8	6.361 $\times 10^{-3}$	0.0888	0.6892	$0.01 < p < 0.02$	-
	2	1.0554 $\times 10^{-2}$	0.0977	0.7483	$0.001 < p < 0.01$	-
	4	1.3607 $\times 10^{-2}$	0.0961	0.8385	$p < 0.001$	-
	5	1.1220 $\times 10^{-2}$	0.0884	0.9354	$p < 0.001$	-
	8	7.780 $\times 10^{-3}$	0.0907	0.6116	$0.02 < p < 0.05$	-

Table 3.31. Coefficients of the significant regression lines ( $y=mx + c$ ) calculated for ammonium at each station for each predictor variable. t=transformation.

Predictor variable	station no.	m	c	r	p	t
Foraminifera	4	1.4142 $\times 10^{-2}$	0.1006	0.7804	0.001<p<0.01	-
	5	6.908 $\times 10^{-3}$	0.0979	0.07470	0.001<p<0.01	-
Water content	1	1.1513 $\times 10^{-2}$	-12.997	0.6213	0.02<p<0.05	-1/x
	2	2.4340 $\times 10^{-4}$	0.0593	0.9386	p<0.001	-
	4	-1.4327 $\times 10^{-4}$	-0.4197	0.9455	p<0.001	-1/x
	5	1.9740 $\times 10^{-4}$	0.0479	0.06797	0.01<p<0.02	-
	7	1.6760 $\times 10^{-4}$	0.0700	0.9225	p<0.001	
	8	2.9839 $\times 10^{-4}$	0.0458	0.8462	p<0.001	-
Sodium	8	1.1308 $\times 10^{-3}$	-20.651	0.7190	0.001<p<0.01	-1/x
Potassium	8	2.4117 $\times 10^{-2}$	-19.169	0.6970	0.01<p<0.02	-1/x
Magnesium	8	8.522 $\times 10^{-3}$	-19.109	0.7246	0.001<p<0.01	-1/x
Calcium	8	2.5833 $\times 10^{-2}$	-19.051	0.7403	0.001<p<0.01	-1/x
Strontium	8	1.4759	-19.463	0.7517	0.001<p<0.01	-1/x
Barium	1	-13.472	-7.3892	0.6856	0.01<p<0.02	-1/x
	4	-36.62	-5.269	0.6921	0.01<p<0.02	-1/x
	6	-10.478	-7.8795	0.6033	0.02<p<0.05	-1/x

Table 3.32. Coefficients of the significant regression lines ( $y=mx + c$ ) calculated for ammonium at each station for each predictor variable. t=transformation.

Station number	1	2	4	5	6	7	8
Predictor variable							
Depth	N	S	S	S	S	N	N
Micro-organism numbers	N	S	S	S	S	S	S
Total meiofauna	N	S	S	S	S	S	S
Metazoa	N	S	S	S	S	S	S
Nematodes	N	S	S	S	S	S	S
Foraminifera	N	S	S	N	S	S	S
Water content	N	S	S	N	S	S	N
Li	N	N	N	N	N	N	N
Na	N	N	N	N	N	N	N
K	N	N	N	N	N	N	N
Mg	N	N	N	N	N	N	N
Ca	N	N	N	N	N	N	N
Sr	N	N	N	N	N	N	N
Ba	N	N	S	N	N	N	N
Fe	N	N	N	N	N	N	N
Zn	N	N	N	N	N	N	N
P	N	N	N	N	N	S	N
S	N	N	N	N	N	N	N
B	N	N	N	N	N	N	N
Si	N	N	N	N	N	N	N

Table 3.33. Significant/non-significant regressions for silicate against all predictor variables at all stations. S=significant, N=non-significant.



Station number	1	2	4	5	6	7	8
Predictor variable							
=====							
Depth	S	S	S	S	S	S	S
Micro-organism numbers	S	S	S	S	S	S	S
Total meiofauna	S	S	S	S	S	N	S
Metazoa	S	S	S	S	S	S	S
Nematodes	S	S	S	S	S	S	S
Foraminifera	N	N	S	S	N	N	S
Water content	S	S	S	S	S	S	N
Li	N	N	N	N	N	N	N
Na	N	N	N	N	N	N	N
K	N	N	N	N	N	N	N
Mg	N	N	N	N	N	N	N
Ca	N	N	N	N	N	N	N
Sr	N	N	N	N	N	N	N
Ba	S	N	S	N	N	N	N
Fe	N	N	N	N	N	N	N
Zn	N	S	S	N	N	N	N
P	N	N	N	N	N	S	N
S	N	N	N	N	N	N	N
B	N	N	N	N	N	N	N
Si	S	S	N	N	N	N	N
=====							

Table 3.34. Significant/non-significant regressions for phosphate against all predictor variables at all stations. S=significant, N=non-significant.

Station number	1	2	4	5	6	7	8
Predictor variable							
Depth	S	S	S	S	S	S	S
Micro-organism numbers	S	S	S	S	S	S	S
Total meiofauna	S	N	S	S	S	S	S
Metazoa	S	N	S	S	S	S	S
Nematodes	S	N	S	S	S	S	S
Foraminifera	S	N	S	S	N	S	S
Water content	S	S	S	S	S	S	S
Li	N	N	N	N	N	N	N
Na	N	N	N	N	N	N	N
K	N	N	N	N	N	N	N
Mg	N	N	N	N	N	N	N
Ca	N	N	N	N	N	N	N
Sr	N	N	N	N	N	N	N
Ba	N	N	S	N	N	N	N
Fe	N	N	N	N	N	N	N
Zn	N	N	N	N	N	N	N
P	N	N	N	N	N	N	N
S	N	N	N	N	N	N	N
B	N	N	N	N	N	N	N
Si	N	S	N	N	N	N	N

Table 3.35. Significant/non-significant regressions for sulphate against all predictor variables at all stations. S=significant, N=non-significant.

Station number	1	2	4	5	6	7	8
Predictor variable							
Depth	S	S	S	S	S	S	N
Micro-organism numbers	N	S	S	S	S	S	N
Total meiofauna	N	N	N	S	S	N	N
Metazoa	N	N	N	S	S	N	N
Nematodes	N	N	N	S	S	N	N
Foraminifera	N	N	N	N	S	N	N
Water content	S	S	S	N	S	S	N
Li	N	N	N	N	N	N	S
Na	N	N	N	N	N	N	S
K	N	N	N	N	N	N	S
Mg	N	N	N	N	N	N	S
Ca	N	N	N	N	N	N	S
Sr	N	N	N	N	N	N	N
Ba	S	N	S	N	N	N	N
Fe	N	N	N	N	N	N	N
Zn	N	S	S	N	N	N	N
P	N	N	N	N	N	S	N
S	N	N	N	N	N	S	N
B	N	N	N	N	N	N	S
Si	S	S	N	N	N	N	N

Table 3.36. Significant/non-significant regressions for nitrate against all predictor variables at all stations. S=significant, N=non-significant.

Station number	1	2	4	5	6	7	8
Predictor variable							
Depth	S	S	S	S	S	S	S
Micro-organism numbers	N	S	S	S	N	S	S
Total meiofauna	N	S	S	S	N	N	N
Metazoa	N	S	S	S	N	N	S
Nematodes	N	S	S	S	N	N	S
Foraminifera	N	N	S	S	N	N	N
Water content	S	S	S	S	N	S	S
Li	N	N	N	N	N	N	N
Na	N	N	N	N	N	N	S
K	N	N	N	N	N	N	S
Mg	N	N	N	N	N	N	S
Ca	N	N	N	N	N	N	S
Sr	N	N	N	N	N	N	S
Ba	S	N	S	N	S	N	N
Fe	N	N	N	N	N	N	N
Zn	N	S	N	N	N	N	N
P	N	N	N	N	N	S	N
S	N	N	N	N	N	N	S
B	N	N	N	N	N	N	N
Si	N	S	N	N	S	N	N

Table 3.37. Significant/non-significant regressions for ammonium against all predictor variables at all stations. S=significant, N=non-significant.

significant.

All of the regressions of sulphate against sediment depth, micro-organism numbers and water content are significant. Most of the regressions of sulphate against total meiofaunal numbers, metazoan numbers, nematode numbers and foraminiferan numbers are significant. Some of the regressions of sulphate against barium and silicon are also significant. None of the regressions of sulphate against lithium, sodium, potassium, magnesium, calcium, strontium, iron, zinc, phosphorous, sulphur and boron are significant.

Most of the regressions of nitrate against sediment depth, micro-organism numbers and water content are significant. Some of the regressions of nitrate against meiofaunal numbers (all subdivisions), lithium, sodium, potassium, magnesium, calcium, barium, zinc, phosphorous, sulphur, boron and silicon are significant. None of the regressions of nitrate against strontium and iron are significant.

All of the regressions of ammonium against sediment depth are significant. Most of the regressions of ammonium against micro-organism numbers, metazoan numbers, nematode numbers and water content are significant. Some of the regressions of ammonium against total meiofauna, foraminiferan numbers, sodium, potassium, magnesium, calcium, strontium, barium, zinc, phosphorous, sulphur and silicon are significant. None of the regressions of ammonium against lithium, iron and boron are significant.

### Discussion.

In general the numbers of micro-organisms decreased exponentially into the sediment (table 3.12, figures 3.5-3.11). This exponential decrease may be related to the supply of organic carbon to the sediments (Marshall, 1979; Lochte and Turley, 1988; Suess, 1988). The relationship I found between micro-organism numbers and sediment depth differs from that found by Meadows and Tait (1985) which followed a  $\text{Log}_{10}$  curve.

The sub-surface increases in micro-organism numbers found at some stations (e.g. at station 5, 3-4cm > 2-3cm) may be related to bioturbation of the sediment or to the presence of a localised supply of organic carbon (Marshall, 1979). In general, however, the profiles of micro-organism numbers with depth are very consistent, this may be due to the low faunal densities in these sediments, producing a very low bioturbation rate (Guinasso and Schink, 1975; Thiel, 1975).

The surface densities of micro-organisms which I found were in the range of  $4.75 - 10.9 \times 10^6 \text{ g}^{-1}$  dry weight. Other authors have reported densities ranging from  $5 \times 10^2$  to  $84 \times 10^6 \text{ g}^{-1}$  (Ehrlich et al, 1972; Thiel, 1975; Marshall, 1979; Meadows and Tait, 1985). The differences between the lower densities found by most other workers and the densities I have found may be due to the use of a direct counting method in my work, most other workers having used colony forming unit counts. Direct counting tends, in shallow-water sediment to overestimate the number of micro-organism, as some cells counted may not have been alive when collected (Jones, 1979). For these deep-sea samples, however, the use of a direct counting method may give more meaningful results as many of the micro-organisms found in the deep-sea are obligate barophiles and cannot grow under ship-board incubation conditions (Jannasch and Wirsén,

1983). The direct counting method also has the advantage that, as the samples are preserved immediately upon collection, there is little chance of contamination of cultures under ship-board conditions (Thiel, 1975).

The micro-organism densities reported here are only for the bulk sediment along with any micro-nodules present. The density of micro-organisms on larger manganese nodules may, however, be very high (Ehrlich et al, 1972). No nodules were available for the calculation of nodule densities in this study, as all of the nodules were required for metal analysis by Imperial College London.

Evidence is now appearing for the transport of living unicellular phytoplanktonic and cyanobacterial cells from the surface layers of the sea into the abyssal regions (Lochte and Turley, 1988). These living cells, reported from the Atlantic, are transported by phytodetritus sedimenting during and after the spring phytoplanktonic bloom. Some of the micro-organisms counted in the surface sediment samples I collected may have come from this source.

The redox potential of the sediments used in this study was measured by P.S. Meadows and A. Tufail. The redox potential shows a decrease from the sediment surface to between 2 and 10 cm, followed by a slow increase in redox with increasing sediment depth. This drop in redox below the sediment-water interface may be related to metabolism of organic matter by the high density of micro-organisms at the interface.

Another reason for the decrease in redox potential near the sediment-water interface may be oxygen consumption by meiofauna near the sediment surface (Smith and Hinga, 1983; Smith et al,

1983). In general the meiofauna showed an exponential decrease in numbers from the sediment surface into the sediment (table 3.21, figures 3.12-3.18), no meiofauna being found below 10cm. This maximum depth of penetration of the meiofauna agrees with the zone of biological mixing used by Guinasso and Schink (1975) for their mixing rate calculations for abyssal sediments.

The densities of foraminifera at the interface were significantly higher than those of the metazoan meiofauna. At greater sediment depths, however, the densities of metazoan meiofauna were significantly higher than those of the foraminifera (table 3.20). This decrease in meiofaunal numbers away from the sediment-water interface may be due to a number of factors. These factors include; compaction of the sediment, reducing the size of the interstices; and, the availability of organic carbon as a food source (Thiel, 1983; Woods and Tietjen, 1985).

The floc (possible phytodetritus) found in the surface sediment samples in this study may represent a significant proportion of the detrital (and thus the organic carbon) input to this deep-sea system. Gooday (1988) has noted that many foraminifera migrate from the surface sediment into the phytodetritus layer in Atlantic sediments. This migration may also occur in these deep Pacific samples. The presence of a phytodetrital floc in the surface sediment samples is also a good indicator of the relatively undisturbed nature of the sediment surface of the boxcore samples (A. Gooday, pers. comm.).

Most of the work on deep-sea meiofaunal densities has been reported in the form of total density  $10\text{cm}^{-2}$  sediment surface. The data in tables 3.13-3.19 (meiofaunal density) has been condensed into this form in table 3.38 for comparison. The densities of meiofauna I found were in the range of 39-95 individuals  $10\text{cm}^{-2}$ .



Station no.	Total meiofauna	Metazoa	Nematodes	Foraminifera
1	39.7334	27.0666	21.8666	12.6668
2	54.4760	30.6191	24.5714	24.3811
4	94.0951	57.7146	49.1426	36.3809
5	85.6668	53.8335	45.0000	31.8333
6	81.3333	46.8335	36.0003	33.0000
7	53.3340	29.0666	23.3334	24.2666
8	80.4998	55.1668	37.8333	25.3333

Table 3.38. Total densities of the four main meiofaunal sub-divisions as no.10cm<sup>-2</sup> of sediment surface.

This density is within the range of deep-sea meiofaunal densities quoted by Thistle (1979), Shirayama (1983), Thiel (1983), Woods and Tietjen (1985) and Mullineaux (1987), who found densities of 10-150 individuals  $10\text{cm}^{-2}$ .

The number of taxa I found was less than that quoted by some workers (Thiel, 1983; Mullineaux, 1987). This difference may be due to two factors. Firstly, some of the soft taxa may have been lost in the preservation and extraction processes used in my study. The preservation of bulk sediment samples in unbuffered formalin (the only preservative available aboard ship) can cause the loss of soft taxa (Thiel, 1983; Meiofaunal preservative comparison, section 1). The second reason for the lower number of taxa found in my study may be the absence of any nodule-attached meiofauna. These hard-substrate meiofauna may represent a significant proportion of the total number of meiofaunal taxa (Dugolinsky et al, 1977; Thiel, 1978, 1983; Shirayama, 1983; Mullineaux, 1987).

Despite the lower number of taxa found in my study, the relative numbers of animals in each of the major taxa (foraminifera, nematodes, harpacticoid copepods) compares favourably with that reported by other workers. The foraminifera are generally the most abundant taxon (table 3.38) followed by the nematodes and then the copepods (Marshall, 1979; Thiel, 1983; Woods and Tietjen, 1985). In my study, however, considerably more nauplii were found than has been reported by other workers (Thistle, 1979; Thiel, 1983). This may represent a seasonal breeding response to the spring phytodetrital input. Meiofaunal diversity is generally very high in the deep-sea, probably due to a combination of the stability of the environment and the miniaturization and simple anatomy of the deep-sea meiofauna (Coull, 1972; Dayton and Hessler,

1972; Heip and Decraemer, 1974; Thistle, 1979; Rex, 1981).

Most of the foraminifera found in my study were of the agglutinating type. This finding agrees with those of Marshall (1979) and Douglas and Woodruff (1981) in the Pacific and that of Gooday (1986) for the Atlantic. These agglutinating foraminifera may be partially responsible for the formation of manganese nodules. This process may take the form of binding of manganese micro-nodules onto the surface of larger nodules by agglutinating foraminifera (Dugolinsky et al, 1977; Schnier et al, 1978) or the precipitation of manganese/iron oxides into faunal structures on nodule surfaces (Thiel, 1978). Another cause of manganese nodules growth may be the precipitation of manganese/iron oxides from solution by bacteria adjacent to or on the surface of existing nodules (Ehrlich et al, 1972; Ehrlich, 1978; Schnier et al, 1978).

Despite the presence of meiofauna in only the surface 10 cm of sediment and the total absence of macrofauna, burrows were found extending over 35 cm into the sediment. Some of these burrows were infilled with more recently deposited sediment (visible due to colour differences), others were open burrows 1-3 mm in diameter often at very high densities ( $1-11 \times 10^3 \text{ m}^{-2}$ ) (P.S. Meadows and A. Tufail, pers. comm.). These open burrows, often uninhabited, have also been reported from the Atlantic by Weaver and Schultheiss (1983) and Meadows and Tait (1985). The Atlantic sediments also contained some burrows <0.5 mm in diameter, which are more likely to be meiofaunal burrows. No burrows of this, lower, size range were observed in our sediment samples.

The presence of open burrows at almost all depths in the sediment is likely to have had a major effect on the water content of the sediment (Keller, 1974; Weaver and Schultheiss, 1983). The water contents found in my study were in the range of 244.8 - 515.4

% dry weight for the surface sediment (appendix tables 3.1.1-3.1.7) and decreased to 127.9 - 291.6 at 30-31 cm (the deepest samples consistently available). This drop from the sediment surface to 31 cm is within the range quoted by Hagerty (1974) and Handa and Yamazaki (1986) for <sup>ei</sup> ~~the~~ sediment samples. The water content-depth profiles for my samples (figures 3.19-3.25) show a rapid drop in water content in the top 10cm of the sediment column. This depth is consistent with the maximum depth to which meiofauna were found, and thus the maximum depth of present day bioturbation.

Bioturbation by interstitial fauna near the sediment-water interface is also likely to have a great effect on the chemical environment of the sediment (Guinasso and Schink, 1975). Thus the greatest changes in dissolved nutrient and metal concentrations would be expected near the sediment-water interface. In general this expected pattern was found for all of the nutrients I have studied, the changes in concentration with depth being greatest near the interface.

There is very little literature on nutrient concentrations in sediments of the central Pacific region with which to compare my data. The sediments of this area of the Pacific have been drilled by the Deep Sea Drilling Project (DSDP) (Presley and Kaplan, 1971). The DSDP studies have, however, generally been concerned with sediments from over 10 metres below the sediment-water interface and thus are not, in most cases, relevant to my work.

Manheim and Sayles (1974) have reported concentration profiles for dissolved sulphate and ammonium from the porewater of Pacific sediments. Their data is broadly in agreement with mine, their sulphate concentrations ranging from 2.4 - 2.6  $\text{gl}^{-1}$ , their ammonium concentrations ranging from 0 - 0.25  $\text{mg l}^{-1}$ . These ranges are

slightly broader than those in my samples, which may indicate different levels of biological activity in their sediment samples compared with mine (Guinasso and Schink, 1975). Manheim and Sayles' (1974) data also shows sub-surface peaks in both ammonium and nitrate concentration similar to those in my data (figures 3.38-3.45).

Berner (1980) has reported nitrate concentrations in the porewater from Atlantic deep-sea sediments. These porewater from sediments contained up to  $2.48 \text{ mg l}^{-1}$  of nitrate, the concentration profiles showing very distinct sub-surface peaks in concentration. The presence of sub-surface peaks in concentration of nitrate was also reported by Goloway and Bender (1982) for all of their deep-sea samples. The concentration of nitrate in their samples ranged from  $1.24\text{--}3.1 \text{ mg l}^{-1}$ . These values for the maximum concentration are in the same range as the maximum in my samples. In Berner's samples, however, the minimum nitrate concentration was  $< 1 \text{ mg l}^{-1}$  whereas all of my concentrations were  $> 1.5 \text{ mg l}^{-1}$ .

The reasons for the presence of a peak in concentration of nitrate and ammonium below the sediment-water interface, followed by a decrease with increasing sediment depth may be related to the breakdown of organic matter in the surface sediment. The nutrients released from this breakdown tend to diffuse both into and out of the sediment. Thus the peak in concentration may be due to a balance in two, antagonistic, processes (production by breakdown of organic matter and diffusion into and out of the sediment). Nitrate in sediments has been reported to be a sensitive indicator of diagenetic processes driven by the breakdown of organic matter (Goloway and Bender, 1982). The decrease in concentration of nitrate, ammonium and phosphate with depth into the sediment is, therefore, possibly due to a combination of uptake by micro-

organisms and sorption/mineralization reactions with the clay particles of the sediment (Berner, 1980; Kastner, 1981).

The concentrations of both sulphate and silicate increase with sediment depth (figures 3.26-3.29 and 3.34-3.37). This may be due to the breakdown of relatively stable biogenic material as the sediment is buried. This biogenic material includes the tests of sedimentary foraminifera and planktonic radiolaria and the frustules of planktonic diatoms (Kastner, 1981). Much of this siliceous material is carried to the deep-sea as a continual detrital 'rain' of material. In addition, however, to this continual deposition of material there also appear to be seasonal pulsed inputs (phytodetritus) (Gooday, 1988; Lochte and Turley, 1988). The importance of surface productivity and spring phytoplankton blooms for deep-sea nutrient supply and benthic nutrient regeneration is presently being reviewed in the light of this new evidence for rapid transport of organic matter to the central oceanic abyssal plains (Rex, 1981; Lochte and Turley, 1988; Suess, 1988).

There is considerably more literature on dissolved metal concentrations in sediments from the Pacific. This is due to international interest in the suitability of manganese nodule deposits for commercial exploitation. The high variability in concentration of the dissolved metals with sediment depth (appendix tables 3.3.1-3.3.26) has been reported by other workers (Manheim and Sayles, 1974). The concentrations they reported for sodium, potassium, calcium and magnesium for the top 22 cm of their cores are very similar to those found in this study. The calcium enrichment of these sediments with respect to normal seawater is probably due to the dissolution of calcium carbonate between the

lysocline (the depth at which considerable carbonate dissolution begins) and the carbonate compensation depth (CCD, the depth at which carbonate is dissolved faster than it is buried) (Manheim and Sayles, 1974; Demars et al, 1976).

The concentrations of copper, nickel, iron and manganese found in my samples was too low for the analytical method to detect. These metals are commonly found in high concentrations in manganese nodules and tend to be depleted in the porewaters (Cronan, 1974; 1980). The samples collected by Presley and Kaplan (1971) from the same area of the Pacific as my samples showed concentrations in the same range as mine for Boron. Most of their samples were, however, collected from > 6 metres into the sedimentary column and are thus not comparable to my own.

Manheim and Sayles (1974) have reported large changes in the concentrations of some metals in porewaters due to warming from 1°C (bottom-water temperature) to 5°C (shipboard cold-room temperature). In general the magnitude of the changes were in the order magnesium > sodium > potassium > calcium > silicon > strontium > boron > lithium (change for lithium = 0) for their samples. In general they found that the concentrations of monovalent ions increased on warming, the concentrations of divalent ions decreasing. Their study showed that, although the changes in cation concentration could be up to 60 %, anion concentrations were not generally affected by warming to 5°C. The changes in cation concentration in their samples appeared to be due to changes in the cation exchange capacity of the sediments with temperature. The magnitude of any effects warming may have had on my samples cannot be assessed as no non-warmed controls are available.

The results of this survey, the Tamar estuary survey and my

laboratory experiments have been compared in my general discussion. The relative importance of the various biological and physico-chemical parameters I have measured in the field and laboratory and the implications for nutrient regeneration from sediments and oceanic productivity are discussed in full in the general discussion.



**SECTION FOUR - TAMAR ESTUARY SURVEY.**

---

## Introduction

The Tamar estuary has been widely studied by various workers from the M.B.A. and I.M.E.R.. These workers have studied many aspects of the fauna, chemistry and physical hydrography of the river and estuary from its upstream limit of tidal influence to the sandy beaches on either side of Plymouth sound.

General information on the physical and hydrographic conditions in the Tamar estuary and its tributaries, the Lynher and the Tavy are given in Hartley and Spooner (1938) and Mommaerts (1969a). Studies have also been made of the microbial production (Joint, 1978); factors affecting meiofaunal distribution and production (Harris, 1972a,b,c; Warwick and Gee, 1984); factors affecting meiofaunal and foraminiferan production (Ellison, 1984; Teare and Price, 1979; Warwick and Price, 1979); the macrofauna of the Tamar river catchment (Nutall and Purves, 1974); the macrofauna of the intertidal muds (Spooner and Moore, 1940); and factors affecting macrofaunal production and distribution (Davy and George, 1986; Price and Warwick, 1980; Warwick and Price, 1975).

A number of studies have been made on various aspects of the chemistry of both the overlying water (Butler and Tibbits, 1972; Knox et al, 1981, 1986; Mommaerts, 1969b, 1970; Morris et al, 1981, 1982, 1985) and of the interstitial waters (Watson et al 1985a, b). Studies have also been made on the salinity and temperature conditions (Milne, 1938), some aspects of faunal effects on interstitial salinity and redox state (Smith, 1956) and on fluxes of water, salt and sediment (Uncles, 1985).

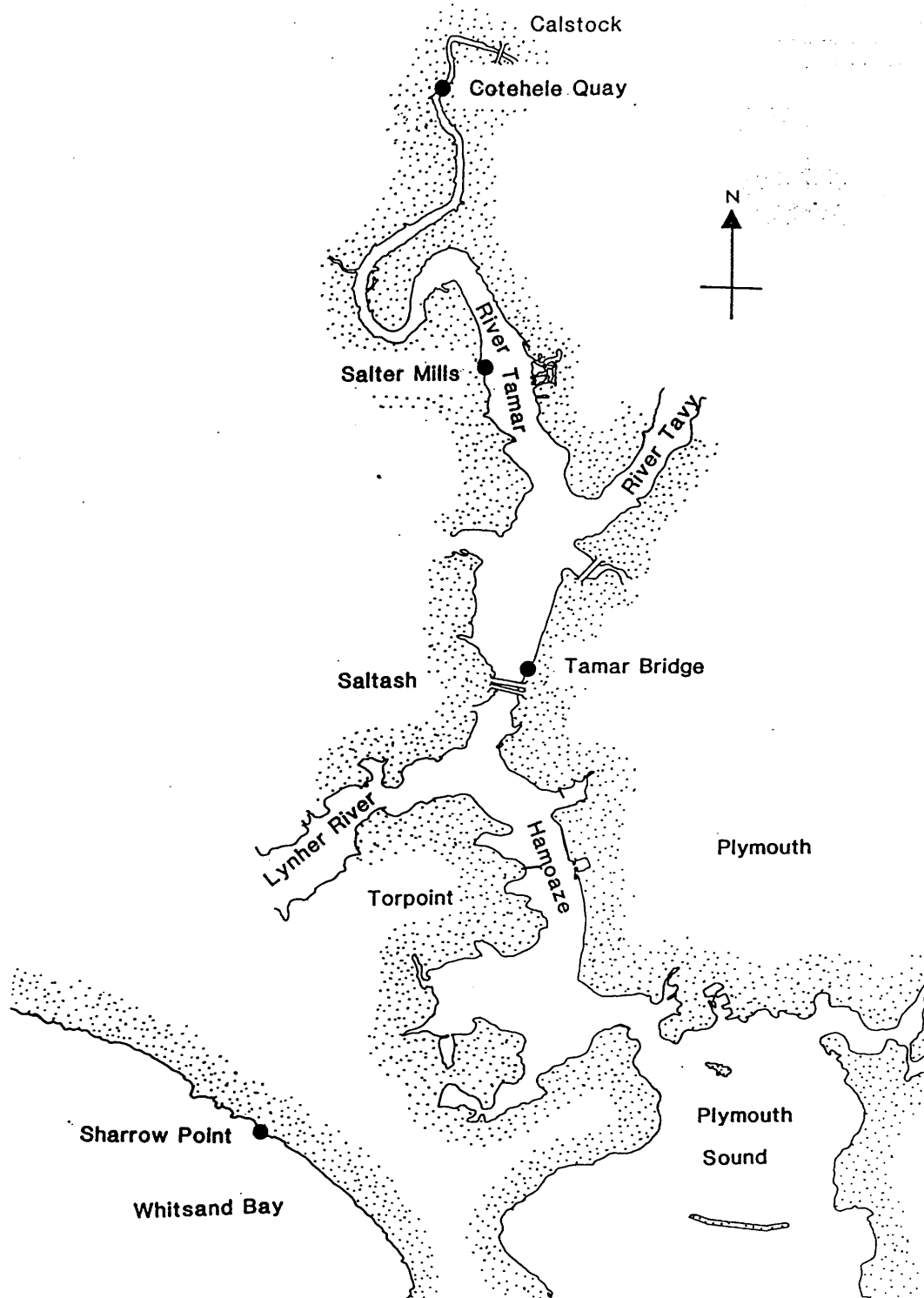
The survey work presented here was carried out in conjunction with an NERC Estuarine Processes Workshop study of the Tamar estuary, Plymouth, Devon. There were two purposes to my work on the

Tamar estuary. The first of these was to examine changes in the sediment meiofauna, microbiology and nutrient concentration with sediment depth during transition from freshwater to seawater along the length of the estuary. The second purpose was to try to relate changes in the other measured parameters quantitatively to changes in nutrient concentration.

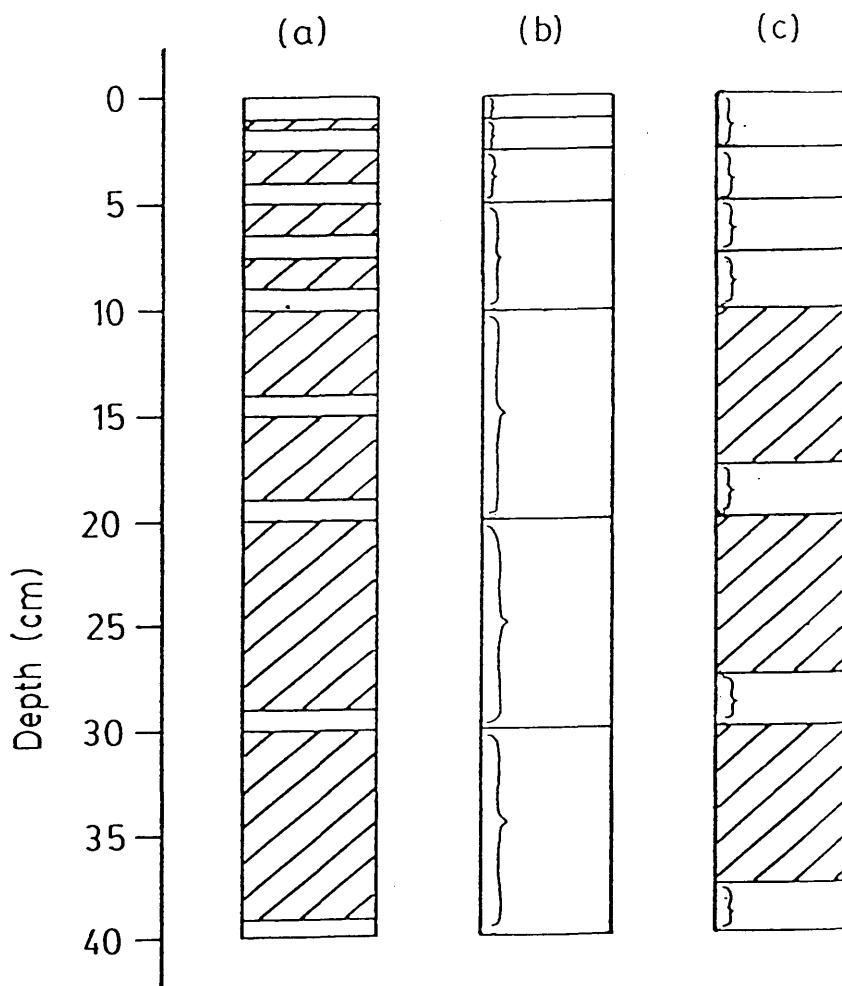
Four sites were studied (figure 4.1), these were Cotehele Quay, Salter Mills, Tamar Bridge and Sharrow point. At each site core samples for porewater nutrient concentration (1 core), micro-organism numbers (1 core), and meiofauna (2 cores) were collected. At one site (Sharrow Point ) no nutrient samples were collected. Samples were taken at mid-tide level on an ebbing tide. Other parameters including Eh, pH, water content, shear strength, macrofaunal numbers and particle size were measured by other workers. Eh and pH values were taken by A.Tufail and P.S.Meadows, water content values were taken by M.S.Hariri, and have been used here with their permission.

The depths used for sampling each of the parameters are shown in figure 4.2. These depths were chosen to give fine resolution of the measured parameters near the sediment-water interface, where the most rapid changes would be expected (Reeburgh, 1978).

The Tamar is tidal for nearly 30 km of its course and is joined 5.5 km from the sea by the river Lynher and at 9.5 km by the river Tavy. The Tamar flows over devonian and carboniferous slates, shales and grits followed by an alluvial flood plain (Hartley and Spooner, 1938). The sediments deposited in the estuary are typical of those from flood plains, being fine grained and tending to form semi-fluid deposits. Sediments of this kind are characteristic of many estuaries in the south-west of Britain. The Tamar forms a fairly typical Ria estuary towards its mouth (ie it is a drowned



**Figure 4.1** Map of the Tamar estuary, Plymouth, Devon. Showing the sampling sites used in this survey ( ● ).



**Figure 4.2.** Sampling positions for the sediment cores. Bracketed section = use of all sediment, unbracketed section = maximum range of sample, hatched area = unused sediment. core a = micro-organism samples; core b = meiofauna; core c = nutrients.

river valley) (Perkins, 1972; Strahler, 1976).

The Cotehele Quay site (nat. grid 424 683, plate 4.1) is on the west bank of the estuary and on the upstream side of the Cotehele Quay slipway. The shore is inclined at approximately 30 degrees to the horizontal. The substrate is composed of fine, slightly fluid mud containing occasional large rocks. At 20-30 cm depth there is a patchy layer of gravel. The lower shore has a fairly smooth surface with occasional water run-off channels. During emmersion a green film of motile algae appears on the sediment surface, especially around mid-tide level. The top of the shore is bordered by stone walls along part of its length. These walls have a covering of small algae. Apart from these, no macroflora are in evidence. No epifaunal macrofauna are visible on any part of the shore.

The Salter Mills site (nat. grid 432 638, plate 4.2) is on the west bank of the estuary. The site is inclined at only a few degrees to the horizontal. The sediment is a fine, fairly soft mud. Towards low tide there is a steep slope bordering the main stream channel. The surface of the mud flat is indented with what appear to be feeding marks of demersal fish. The sediment surface, especially towards the high tide mark is strewn with bivalve shells and many small Carcinus maenas. At the top of the shore the sediment contains more gravel, with occasional large rocks. On these rocks macroalgae including Ascophyllum nodosum and Fucus ceranoides are found in abundance.

The Tamar Bridge site (nat. grid 438 592, plate 4.3) is on the east bank of the estuary approximately 500 metres upstream of the Tamar bridge. At the top of the shore the substrate consists of rocks and broken concrete slabs. Towards mid-tide level the shore



Plate 4.1. Cotehele Quay site, Tamar estuary.





Plate 4.2. Slater Mills site, Tamar estuary.





Plate 4.3. Tamar Bridge site, Tamar estuary.

flattens except for a steep slope bordering the main stream channel. The sediment on the lower shore is fine mud with a smooth surface. The upper shore is marked by the presence of many macroalgae including Fucus vesiculosus, F.ceranoides, F.serratus, Ascophyllum nodosum and Pelvetia canaliculata. The presence of these species indicates that this site is almost totally marine (McLusky, 1981; Perkins, 1974). Few macrofauna are in evidence anywhere on the shore. The lower shore, however, is marked with feeding depressions similar to those at Salter Mills.

Sharrow Point (nat. grid 468 489, plate 4.4) is a clean, sandy beach inclined at approximately 10 degrees to the horizontal. The site is wholly marine, being situated on the open coast, west of Plymouth. There are rock outcrops down the beach which are profusely covered with barnacles, limpets and gastropods. Few macroalgae are in evidence on the site. The macro-algae present are mainly small species found on and around the rock outcrops. There is a small amount of freshwater run-off down the beach which starts as an upwelling approximately 50 metres from the high tide mark.



Plate 4.4. Sharrow point site, Tamar estuary.

## Materials and Methods

### Nutrient samples

A 10 cm diameter split core lined with a polythene bag was pushed into the sediment to a depth of >40 cm. This was then dug out, laid horizontally and split lengthways to expose the sediment. 2.5cm sections of the core were cut at the depths shown in figure 4.2 and placed into 1 litre plastic containers. The porewater was extracted from these sections using positive air pressure (3 atmospheres) supplied by a compressed air tank (plate 4.5). Extracted porewater was collected in sterile, acid washed 30ml plastic universal tubes. Filtration was through a Whatman no.1 prefilter to retain most of the sediment, and then a glass fibre filter (Whatman GF/F,  $0.7\mu\text{m}$ ) to retain finer particulates. This extraction was carried out within 30 minutes of sectioning the core sample. Samples were filtered in order of increasing sediment depth. A single sediment section generally yielded 10 - 15 ml of porewater.

The porewater samples were sterile filtered using 25mm diameter Millipore 0.22 $\mu\text{m}$  GSWP membrane filters in Swinnex filter holders before freezing. These nutrient samples were kept frozen prior to being analysed. All analyses were done using small scale techniques described in section 1. The extracted porewater was sufficient for 4 - 6 analyses of each of the dissolved nutrients (ammonia, phosphate, silicate, nitrate and sulphate).

Some sediment samples below 10 cm depth could not be filtered due to the cohesive nature of the sediment. Some nutrient profiles presented are therefore incomplete.

### Micro-organism counts

These were done using the Smear ratio technique described in section 1. A 10 cm diameter core was taken and split as for the





Plate 4.5. Positive pressure porewater extraction equipment used in the Tamar survey.

nutrient samples. At each of the sampling depths shown in figure 4.2 the sediment in contact with the core liner was removed and a 2 - 3 ml sample of the remaining sediment was transferred into a preweighed 7 ml glass bijou bottle containing 1 ml of 10% formalin. The bottle was then tightly sealed and shaken to mix the sediment and formalin.

At sites 1 and 2 the surface sediment (0 - 2.5cm) tended to slump when the core was laid horizontally for sectioning. At these sites the top two micro-organism samples were taken by cutting a section vertically through the sediment surface with a spade to produce an exposed sediment face. The positions of the 0-1 and 1.5-2.5 cm samples were marked on the sediment face. Sediment samples were removed from the exposed face as above. The deeper samples were then taken using a core. On return to the laboratory the bijou bottles were reweighed to determine the exact amount of sediment collected. The number of micro-organisms per gram of sediment was then determined by direct counting.

#### Meiofauna

Two replicate cores were collected as above and sectioned at, the depths shown in figure 4.2, into polythene bags. A volume of dilute Steedmans solution equivalent to that of the sediment, was added to the bags to preserve the meiofauna. Meiofauna were counted in each of ~~four~~ 10 cm<sup>3</sup> subsamples from each core. These subsamples were wet sieved (500µm) to remove macrofauna, following which the meiofauna were extracted by the decantation technique.

The numbers of each meiofaunal taxa were counted using a dissecting microscope. A compound microscope was used for identification as necessary.

## Results

### Micro-organism counts

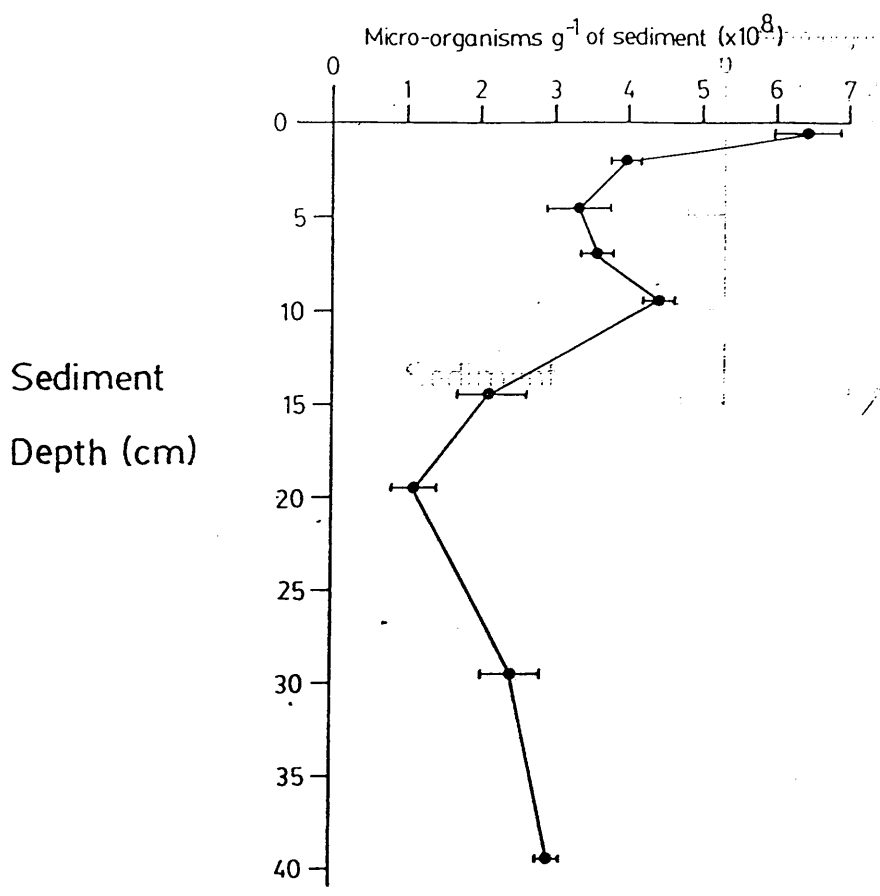
The number of micro-organisms per gram of sediment for each depth sample at Cotehele Quay, Salter Mills and Tamar Bridge are shown in appendix 4.1 tables 1, 2 and 3 respectively. The number of micro-organisms per gram of sediment for each station at Sharrow point is shown in appendix table 4.1.4. Depth profiles of micro-organism numbers are shown in figures 4.3 (Cotehele Quay), 4.4 (Salter Mills), 4.5 (Tamar Bridge), and 4.6 (Sharrow Point).

The profile in figure 4.6 (Sharrow Point) consists of surface sediment counts of micro-organisms taken from a transect down the beach on a receding tide. Two sediment samples were collected at different times from each station at this site. All other profiles consist of vertical sediment profiles for a single station.

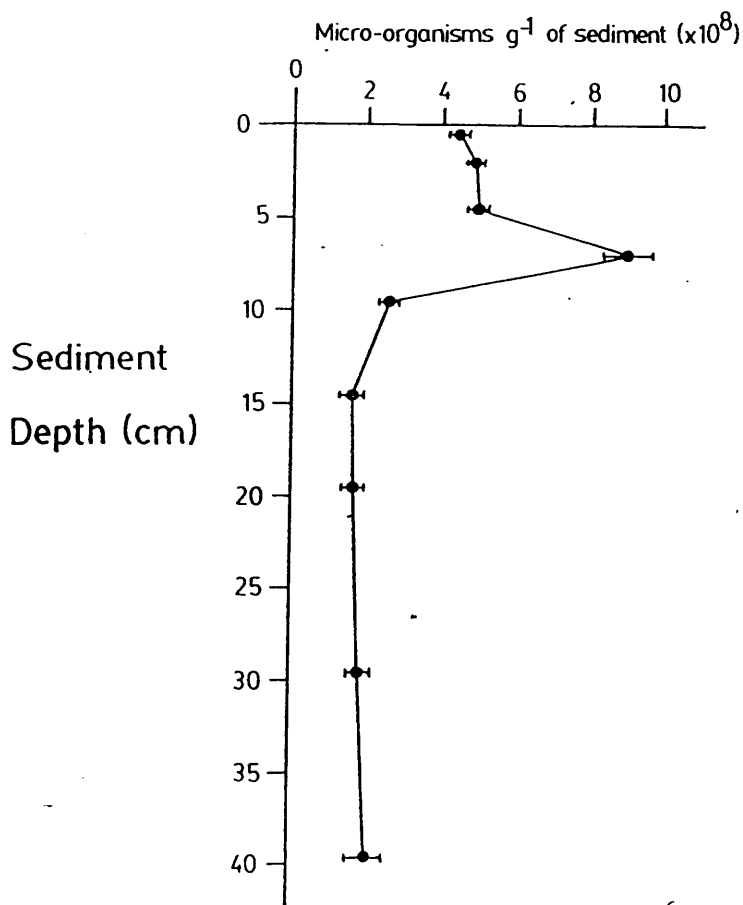
Numbers of micro-organisms per gram of sediment decreased from Cotehele Quay to Salter Mills and then increase again to Tamar bridge. This change has been tested statistically using students t-tests, the results of which are shown in tables 4.1, 4.2 and 4.3. The decreases in micro-organism numbers from Cotehele Quay to Salter Mills and subsequent increases to Tamar Bridge were significant for all depths (tables 4.1 and 4.2). The numbers of micro-organisms per gram of sediment at Tamar bridge were also significantly lower than those at Cotehele Quay at all but one depth (table 4.3).

### Nutrient analyses

The salinity and concentrations of dissolved nutrients in the interstitial water samples from Cotehele Quay, Salter Mills and Tamar Bridge are shown in appendix 4.2 tables 1-3 respectively. Depth profiles of these nutrient concentrations are shown in figures 4.7-4.9 (Cotehele Quay), 4.10-4.12 (Salter Mills) and 4.13-



**Figure 4.3.** Cotehele Quay site. Depth profile of micro-organism numbers per gram of sediment (mean and sd).



**Figure 4.4.** Salter Mills site. Depth profile of micro-organism numbers per gram of sediment (mean and sd).



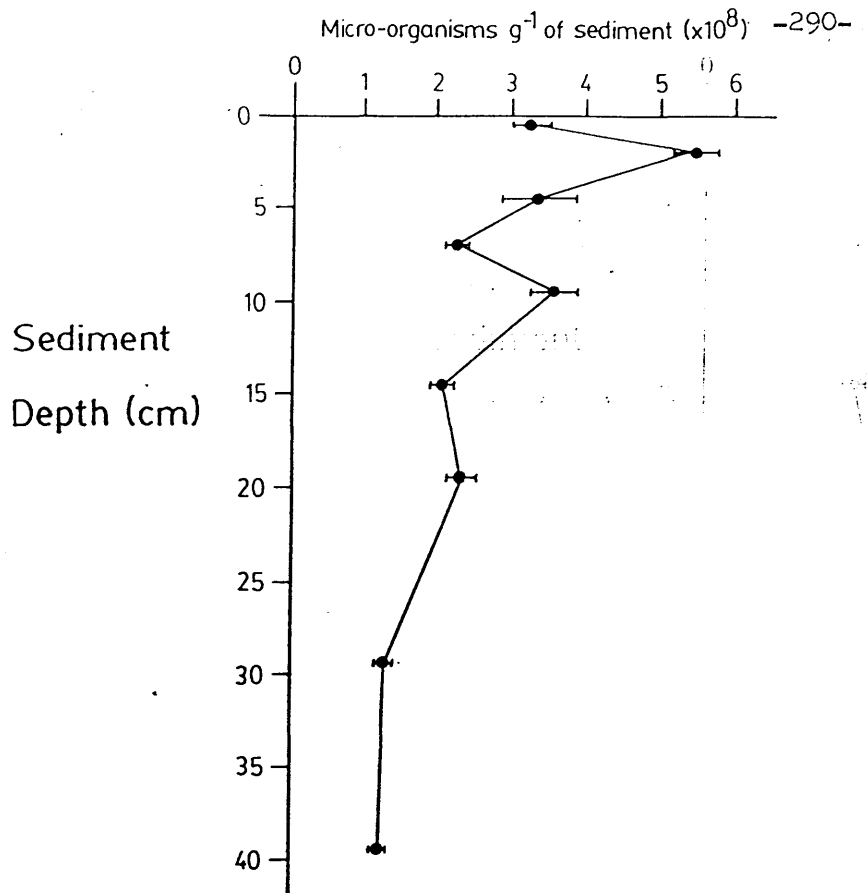


Figure 4.5. Tamar Bridge site. Depth profile of micro-organism numbers per gram of sediment (mean and sd).

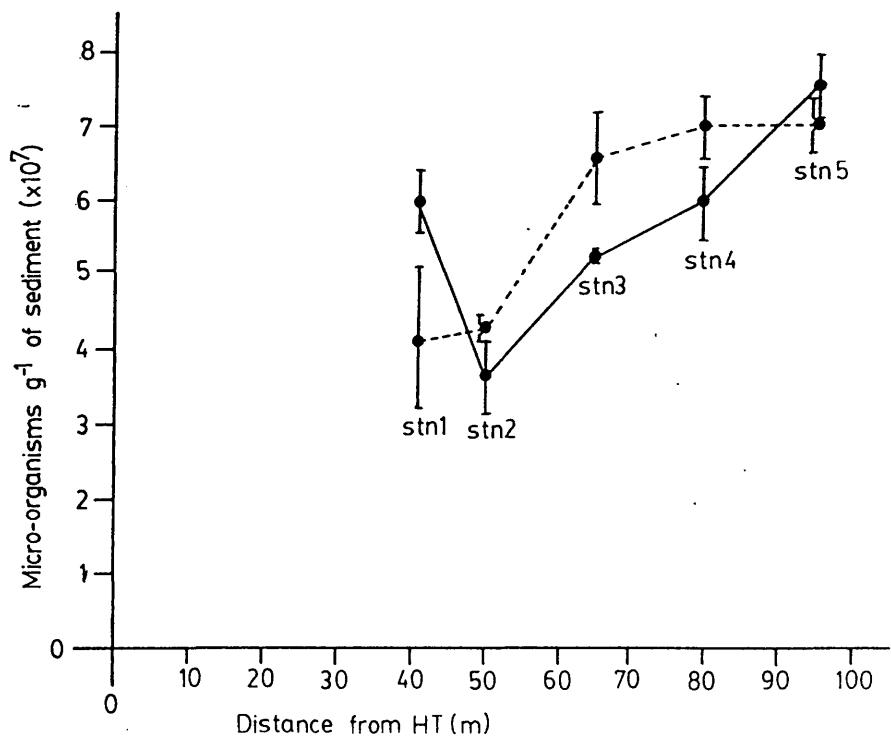


Figure 4.6. Micro-organism numbers g<sup>-1</sup> of sediment (x10<sup>7</sup>) along a transect down the beach at Sharrow point. Solid line = first sampling time, broken line = second sampling time.

Depth (cm)	students t	p
0 - 1	10.9144	p < 0.001
1.5 - 2.5	9.8044	p < 0.001
4 - 5	10.3472	p < 0.001
6.5 - 7.5	22.3147	p < 0.001
9 - 10	15.3103	p < 0.001
14 - 15	2.7608	0.02 > p > 0.01
19 - 20	4.8036	p < 0.001
29 - 30	3.4636	0.01 > p > 0.001
39 - 40	4.9731	p < 0.001

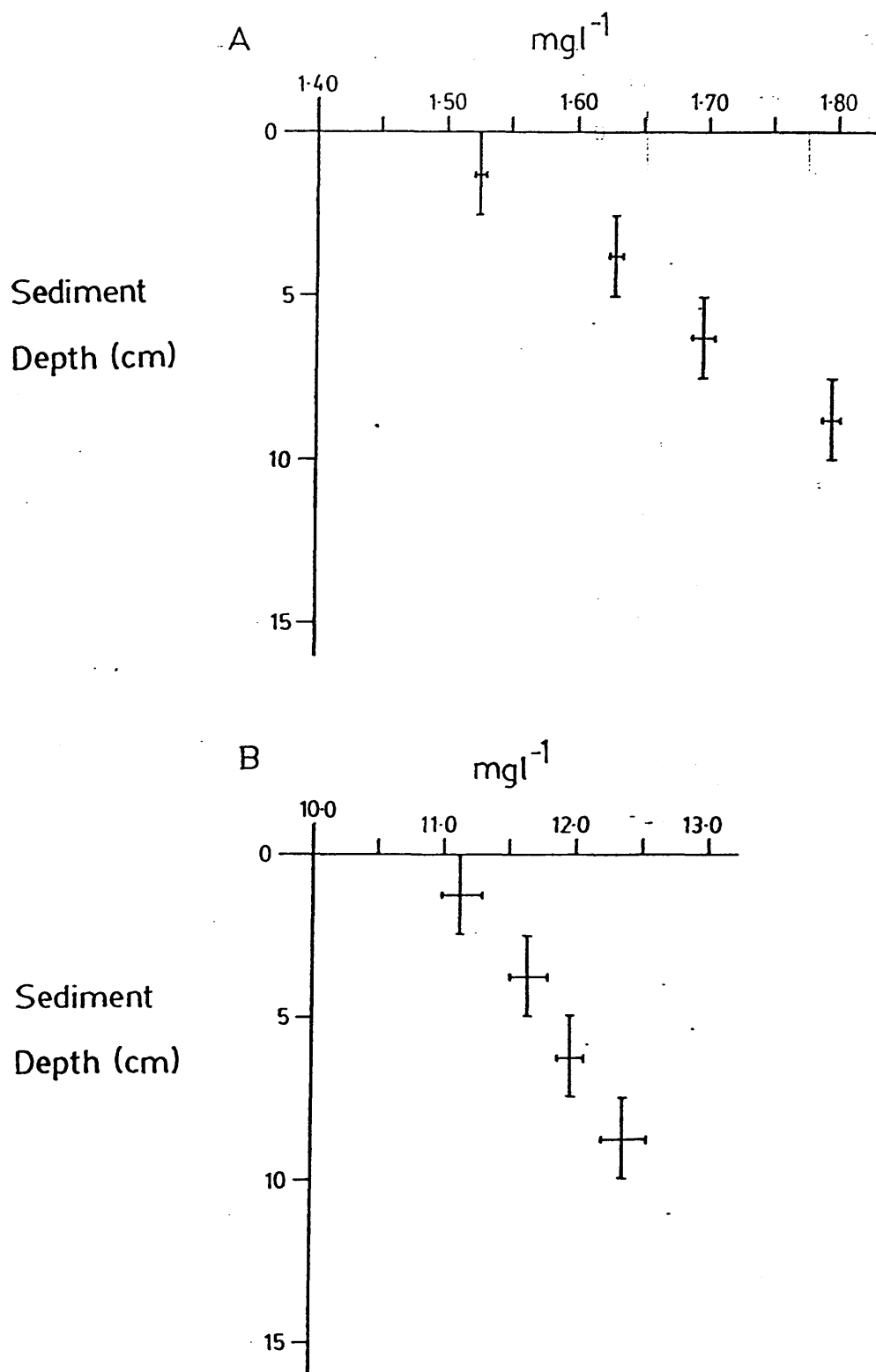
Table 4.1. Students t- test comparison of numbers of micro-organisms/g of sediment at Cotehele Quay and Salter Mills sites for each depth sample. In all cases degrees of freedom = 94.

Depth (cm)	students t	p
0 - 1	16.6508	p < 0.001
1.5 - 2.5	4.2690	p < 0.001
4 - 5	9.0094	p < 0.001
6.5 - 7.5	28.3358	p < 0.001
9 - 10	6.7249	p < 0.001
14 - 15	4.0121	p < 0.001
19 - 20	5.7887	p < 0.001
29 - 30	5.9922	p < 0.001
39 - 40	2.7067	0.02 > p > 0.01

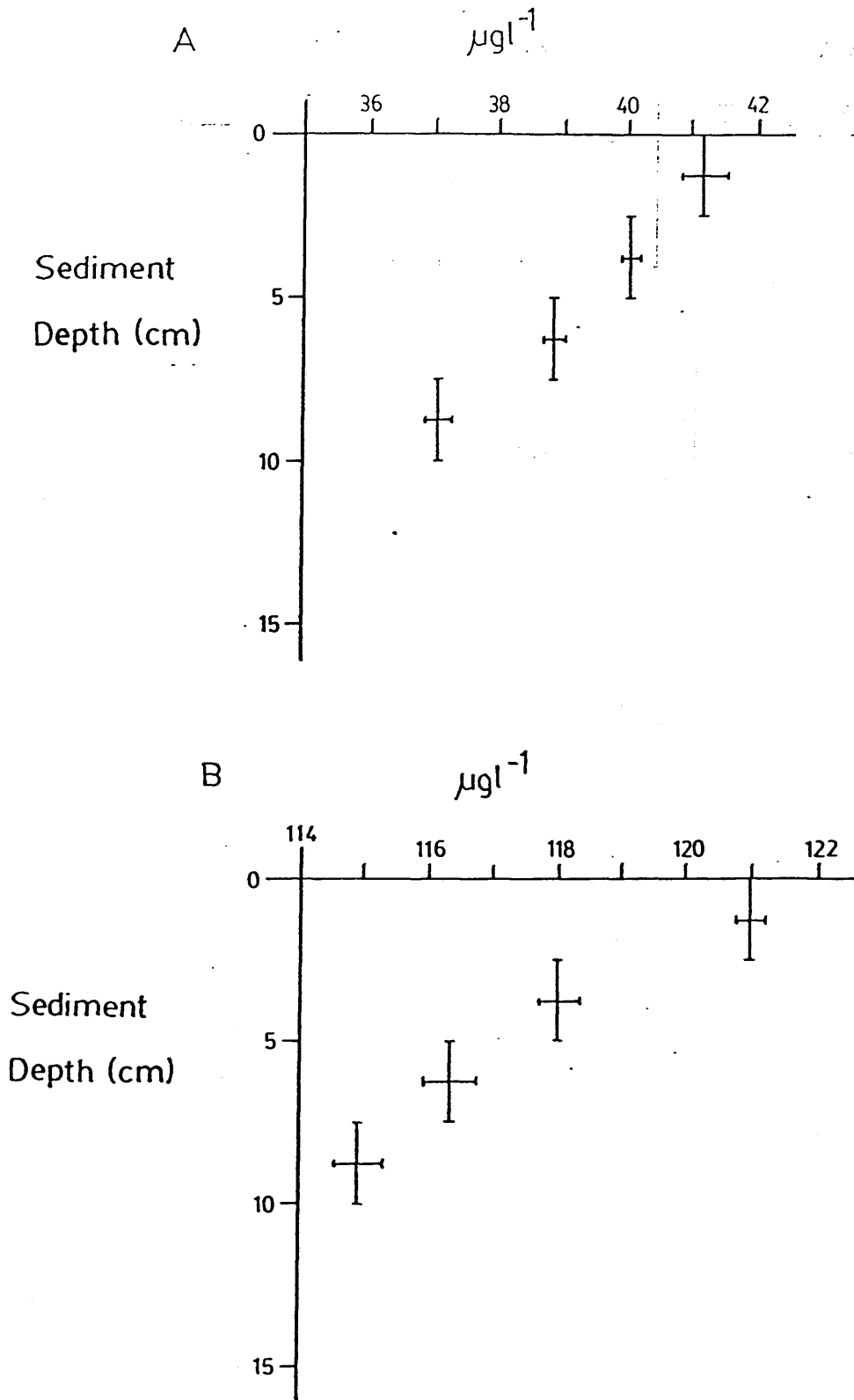
Table 4.2. Students t-test comparisons of number of micro-organism/g of sediment at Salter Mills and Tamar Bridge sites for each depth sample. In all cases degrees of freedom = 94.

Depth (cm)	students t	p
0 - 1	18.3232	$p < 0.001$
1.5 - 2.5	12.1881	$p < 0.001$
4 - 5	0.2310	$0.9 > p > 0.8$
6.5 - 7.5	16.0047	$p < 0.001$
9 - 10	7.3625	$p < 0.001$
14 - 15	4.0032	$0.01 > p > 0.001$
19 - 20	5.7887	$p < 0.001$
29 - 30	5.9922	$p < 0.001$
39 - 40	5.9195	$p < 0.001$

Table 4.3. Students t-test comparison of numbers of micro-organisms/g of sediment at Cotehele Quay and Tamar Bridge for each depth sample. In all cases degrees of freedom = 94.



**Figure 4.7.** Depth profiles of interstitial dissolved nitrate (a) and silicate (b) concentrations for the Cotehele Quay site. Vertical bar = depth range of sample; Horizontal bar = s.d.



**Figure 4.8.** Depth profiles of interstitial dissolved phosphate (a) and ammonia (b) concentrations for the Cotehele Quay site. Vertical bar = depth range of sample; Horizontal bar = s.d.

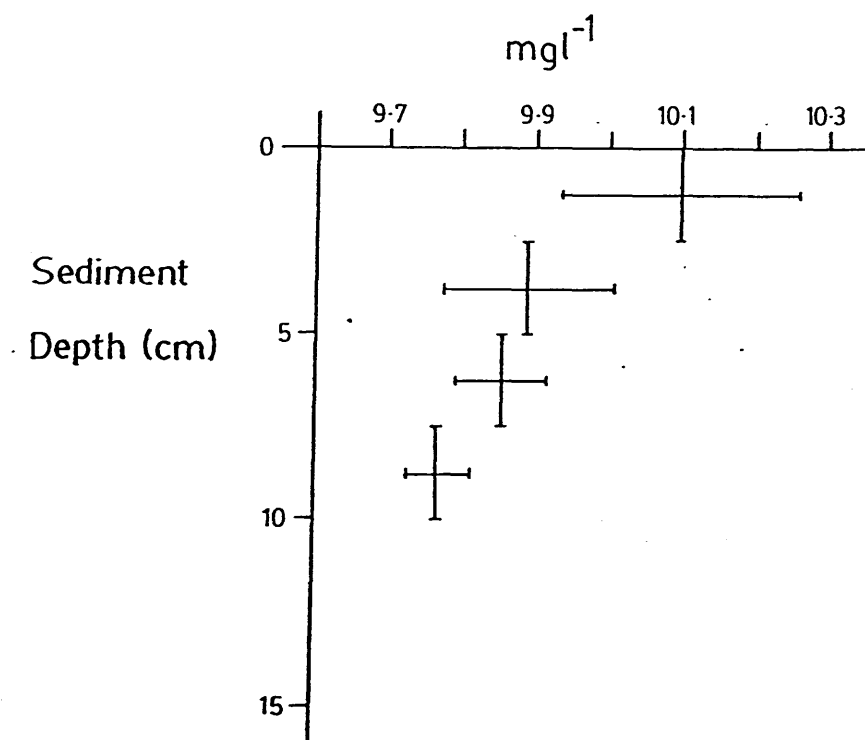


Figure 4.9. Depth profile of interstitial dissolved sulphate concentration for the Cotehele Quay site.

Vertical bar = depth range of sample; Horizontal bar = s.d.

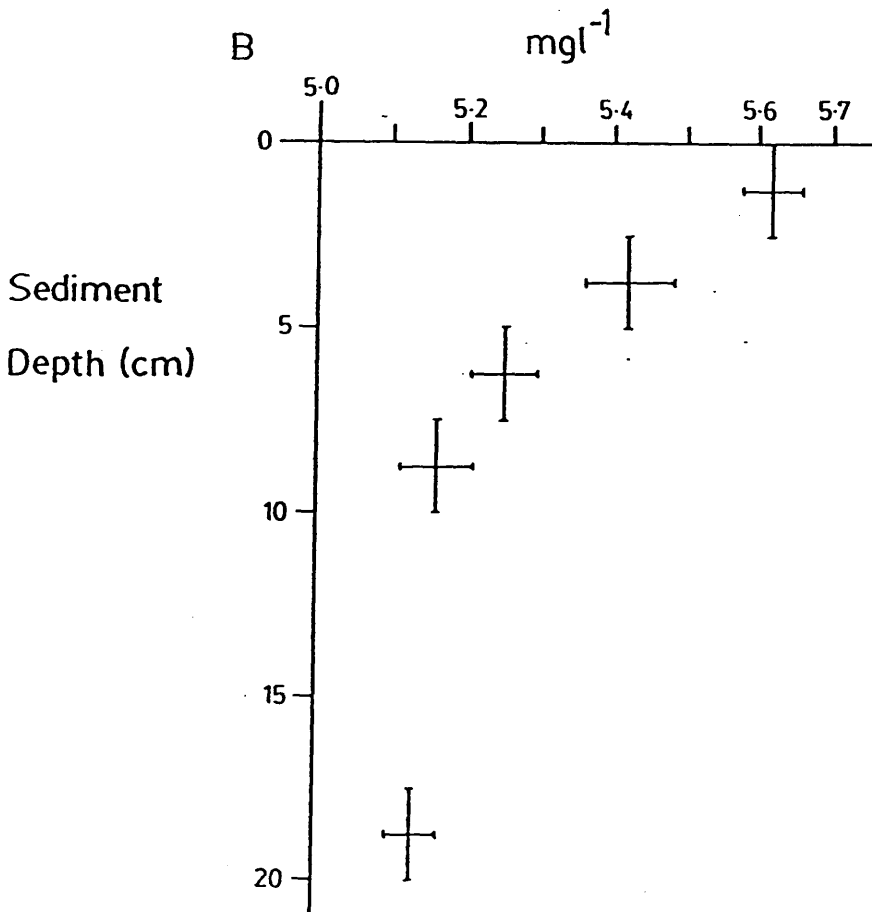
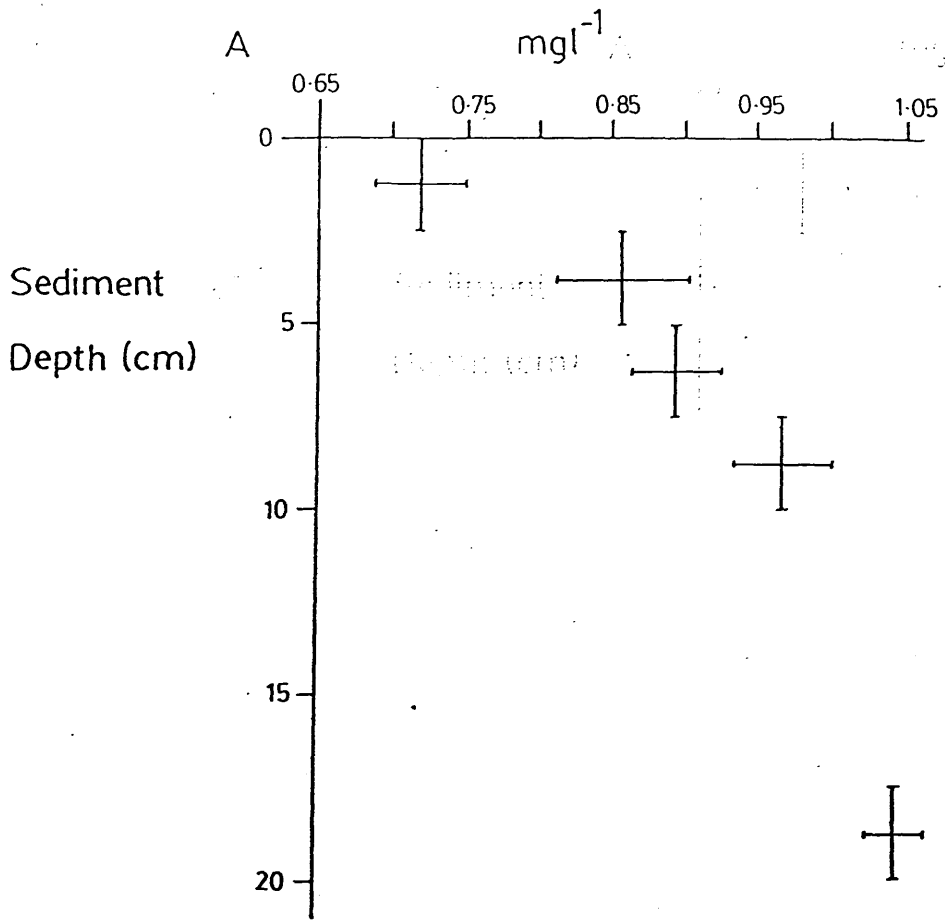


Figure 4.10. Depth profiles of interstitial dissolved nitrate (a) and silicate (b) concentrations for the Salter Mills Site.

Vertical bar = depth range of sample; Horizontal bar = s.d.



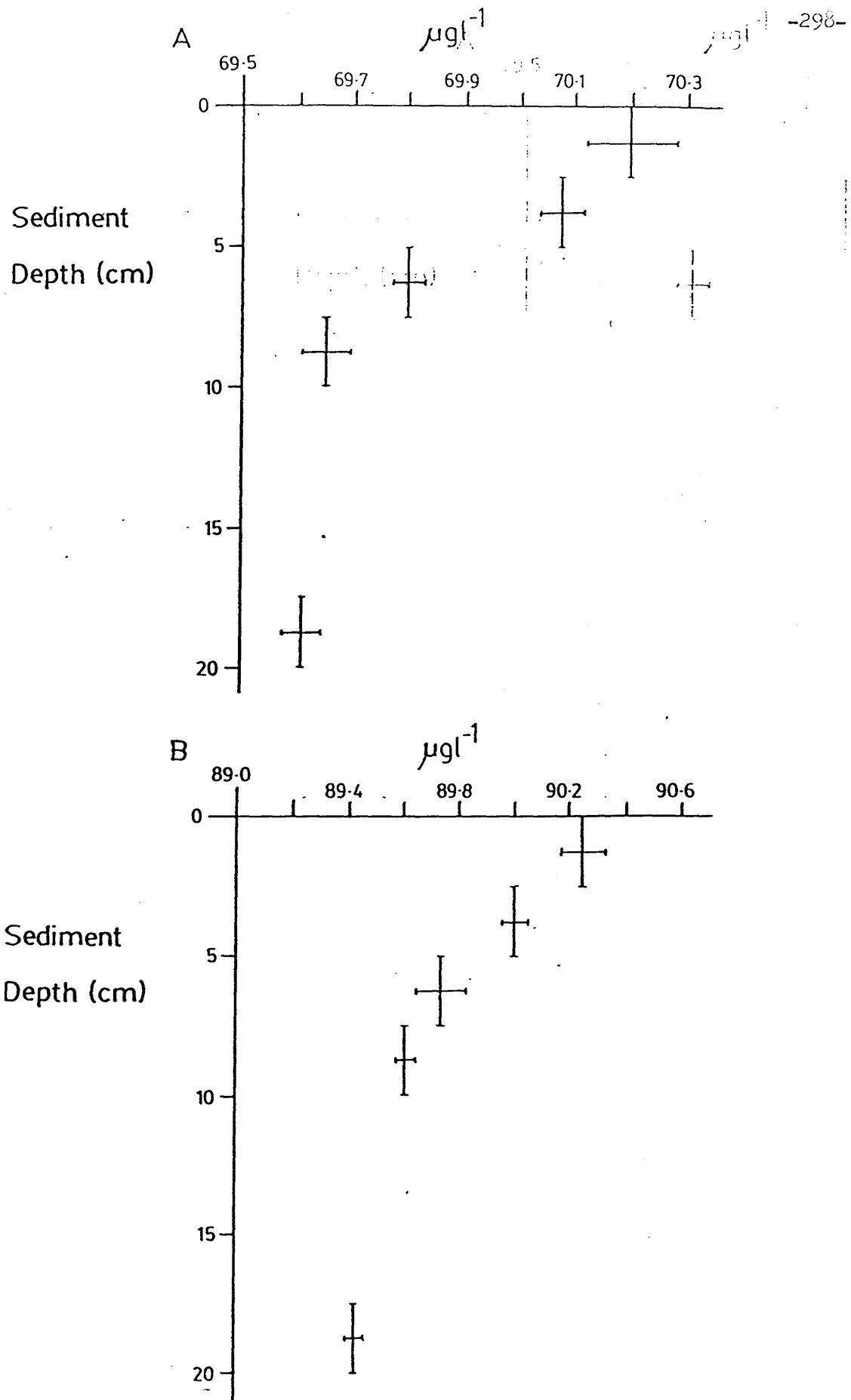


Figure 4.11. Depth profiles of interstitial dissolved phosphate (a) and ammonia (b) concentrations for the Salter Mills site.

Vertical bar = depth range of sample; Horizontal bar = s.d.

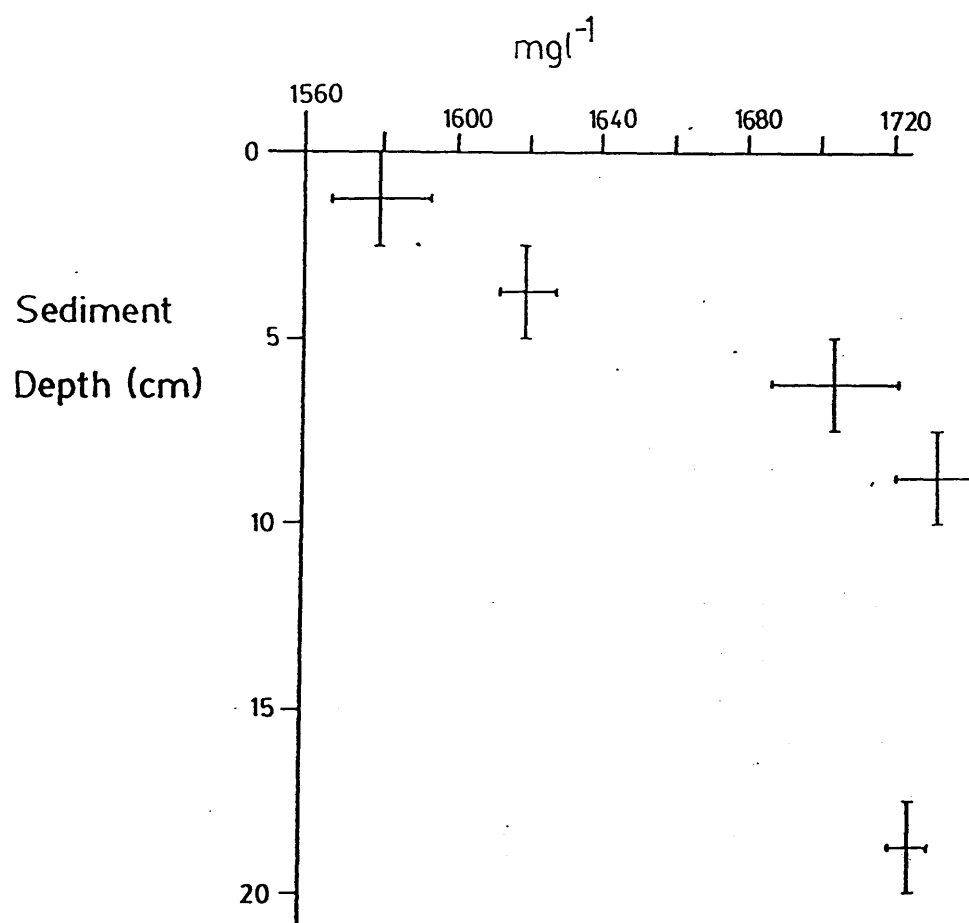
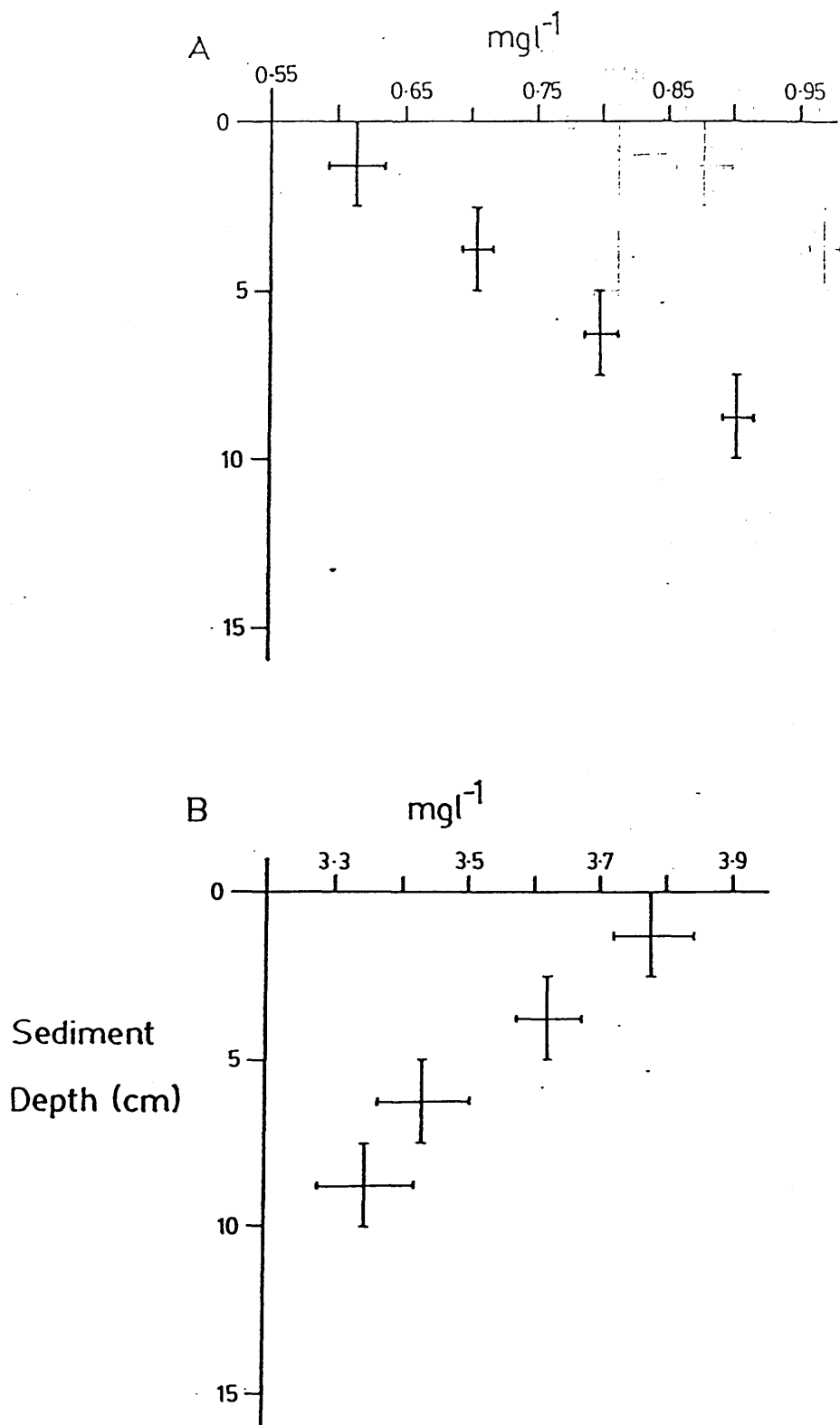
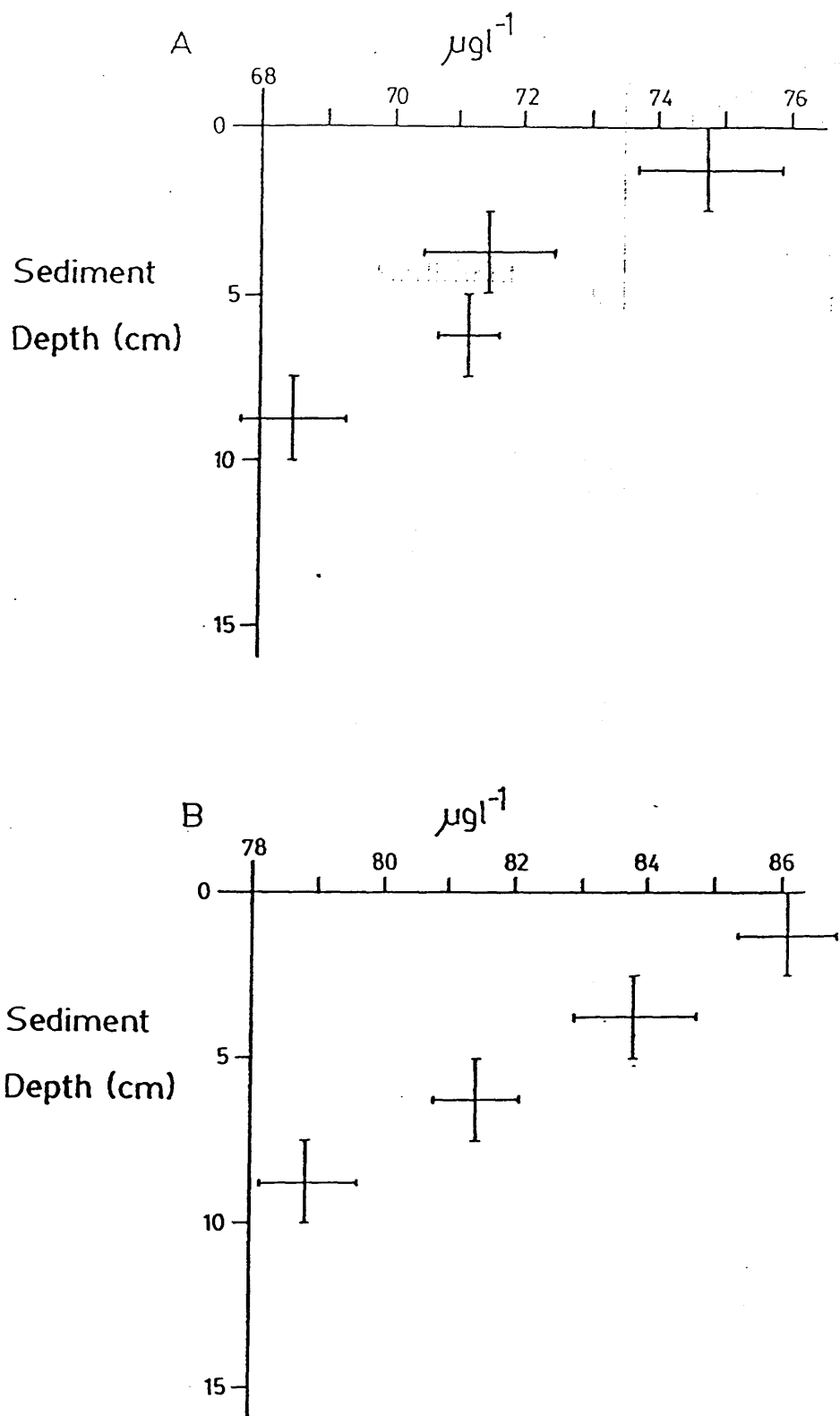


Figure 4.12. Depth profile of interstitial dissolved sulphate concentration for the Salter Mills site.

Vertical bar = depth range of sample; Horizontal bar = s.d.

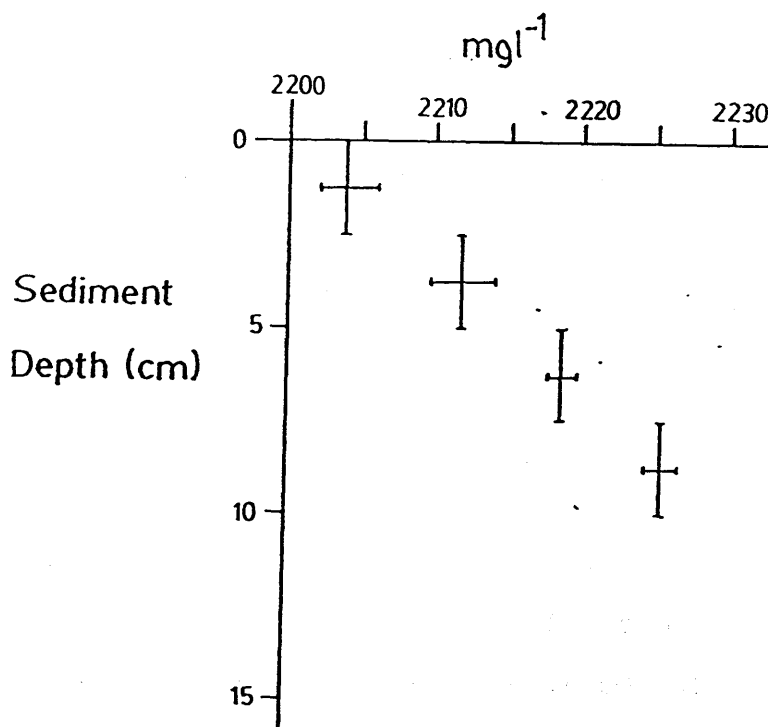


**Figure 4.13.** Depth profiles of interstitial dissolved nitrate (a) and silicate (b) concentrations for the Tamar Bridge site. Vertical bar = depth range of sample; Horizontal bar = s.d.



**Figure 4.14.** Depth profiles of interstitial dissolved phosphate (a) and ammonia (b) concentrations for the Tamar Bridge site.

Vertical bar = depth range of sample; Horizontal bar = s.d.



**Figure 4.15.** Depth profile of interstitial dissolved sulphate concentration for the Tamar Bridge site.

Vertical bar = depth range of sample; Horizontal bar = s.d.

#### 4.15 (Tamar Bridge).

In general the concentrations of dissolved silicate, phosphate and ammonia <sup>de</sup>increased with sediment depth whereas concentrations of dissolved nitrate and sulphate <sup>in</sup>decreased. This pattern was fairly constant along the length of the estuary. At the Salter Mills site, nutrient samples could be extracted from deeper sediment than at the other sites. At this site the nutrient levels appeared to stabilise below the 7.5-10 cm sample, with the exception of dissolved sulphate concentration which decreased slightly.

The change in nutrient concentration with depth has been statistically tested for each site using one way analyses of variance. In all cases the changes were significant ( $p < 0.05$ ), phosphate, silicate and ammonia concentrations decreasing with depth, sulphate and nitrate concentrations increasing with depth.

The concentrations of dissolved nutrients also change between sites along the estuary (appendix tables 4.2.1-4.2.3 and figures 4.7-4.15). Phosphate and sulphate increased in concentration during transition from freshwater to seawater; nitrate, silicate and ammonia decreasing. These concentration changes have also been tested using one way analyses of variance. At all depths in the sediment and for all nutrients the changes in concentration were significant.

#### Meiofaunal numbers

The numbers of each taxon of meiofauna found at Cotehele Quay, Salter Mills, Tamar Bridge and Sharrow point are shown in tables 4.4-4.7 respectively. These values represent mean densities for the four replicates taken at each depth.

The lowest densities of meiofauna were generally found at the Cotehele Quay site. At this site the dominant meiofaunal group were

Meiofaunal type/depth (cm)	0-1	1-2.5	2.5-5	5-10	10-20	20-30	30-40
Nematodes	14.25 (1.58)	11.25 (0.97)	13.50 (1.24)	10.25 (1.15)	8.00 (0.95)	6.25 (0.75)	2.00 (0.32)
Copepods	5.50 (0.65)	1.25 (0.21)	0.25 (0.85)	-	-	-	-
Isopods	4.25 (0.85)	-	-	-	-	-	-
Oligochaetes	11.25 (1.15)	7.25 (0.84)	3.75 (0.25)	1.25 (0.15)	-	-	-
Ciliates	8.75 (0.64)	6.50 (0.45)	5.25 (0.54)	3.25 (0.19)	1.25 (0.55)	-	-
Polychaetes	6.50 (0.45)	3.25 (0.25)	1.75 (0.75)	-	-	-	-
Nauplii	23.50 (2.85)	16.75 (1.15)	10.25 (1.10)	8.25 (0.94)	-	-	-

Table 4.4. Numbers  $\text{cm}^{-3}$  of each meiofaunal taxon found at the Cotehele site, mean (sd), for each of the depth samples. n=4 in all cases.

Meiofaunal type/depth (cm)	0-1	1-2.5	2.5-5	5-10	10-20	20-30	30-40
Nematodes	57.50 (4.54)	63.25 (5.86)	48.50 (3.15)	35.25 (2.85)	11.50 (2.15)	9.50 (1.14)	8.25 (0.92)
Copepods	6.25 (0.85)	1.15 (0.23)	0.50 (0.75)	-	-	-	-
Oligochaetes	16.25 (2.34)	9.50 (1.86)	6.25 (0.95)	3.25 (1.25)	-	-	-
Ciliates	9.25 (1.18)	7.50 (0.86)	4.75 (0.65)	2.25 (0.45)	-	-	-
Polychaetes	17.50 (2.28)	11.25 (1.85)	8.75 (0.65)	4.25 (0.85)	1.25 (0.55)	-	-
Foraminifera	6.00 (0.85)	8.25 (1.15)	6.25 (0.74)	4.00 (0.65)	2.75 (0.45)	-	-
Turbellarians	4.50 (0.86)	1.50 (0.24)	-	-	-	-	-
Ostracods	2.50 (0.45)	0.50 (0.75)	-	-	-	-	-
Bivalves/Brachiopods	0.50 (0.75)	-	-	-	-	-	-

Table 4.5. Numbers  $\text{cm}^{-3}$  of each meiofaunal taxon found at Salter Mills, mean (sd), for each of the depth samples. n=4 in all cases.



Meiofaunal type/depth (cm)	0-1	1-2.5	2.5-5	5-10	10-20	20-30	30-40
Nematodes	83.50 (5.45)	64.25 (3.86)	48.50 (4.65)	36.00 (2.28)	11.50 (1.85)	6.25 (1.15)	1.15 (0.54)
Copepods	5.25 (0.86)	3.25 (0.24)	1.50 (0.75)	-	-	-	-
Oligochaetes	8.50 (0.95)	3.25 (0.24)	-	-	-	-	-
Ciliates	11.00 (2.37)	10.50 (1.25)	14.50 (0.86)	11.25 (1.25)	8.50 (0.96)	3.25 (0.45)	-
Polychaetes	28.50 (3.55)	14.50 (2.18)	11.50 (0.94)	4.25 (0.64)	-	-	-
Foraminifera	12.25 (1.85)	11.50 (0.95)	6.50 (0.95)	1.25 (0.22)	-	-	-
Turbellarians	2.00 (1.25)	3.20 (1.45)	2.50 (0.55)	1.25 (0.83)	0.50 (0.75)	-	-
Ostracods	8.50 (2.24)	2.50 (0.14)	-	-	-	-	-
Bivalves/brachiopods	1.50 (0.75)	-	-	-	-	-	-
Archannelids	2.00 (0.85)	1.50 (0.75)	0.50 (0.75)	-	-	-	-

Table 4.6. Numbers  $\text{cm}^{-3}$  of each meiofaunal taxon found at Tamar Bridge, mean (sd), for each of the depth samples. n=4 in all cases.

Meiofaunal type/depth (cm)	0-1	1-2.5	2.5-5	5-10	10-20	20-30	30-40
Nematodes	27.50 (3.86)	21.75 (1.68)	26.50 (2.86)	11.25 (2.08)	8.50 (1.14)	6.50 (0.86)	4.00 (1.15)
Copepods	4.50 (0.65)	2.25 (1.15)	1.50 (0.75)	-	-	-	-
Oligochaetes	6.00 (0.85)	2.00 (1.24)	1.50 (0.75)	0.25 (0.75)	-	-	-
Ciliates	8.50 (0.96)	7.25 (1.24)	4.75 (0.86)	2.25 (0.85)	-	-	-
Polychaetes	11.50 (2.46)	10.75 (1.86)	11.25 (1.15)	6.25 (0.95)	1.50 (0.75)	-	-
Turbellarians	7.50 (1.24)	6.75 (0.86)	8.50 (1.85)	4.25 (0.35)	3.75 (0.86)	1.00 (0.85)	-
Ostracods	4.50 (1.45)	2.75 (0.86)	1.50 (1.15)	-	-	-	-
Archannelids	1.00 (0.75)	-	-	-	-	-	-

Table 4.7. Numbers  $\text{cm}^{-3}$  of each meiofaunal taxon found at Sharrow Point, mean (sd), for each of the depth samples. n=4 in all cases.

nauplius larvae. Nauplii and isopods were only found at this site.

The highest numbers of most meiofaunal taxa were generally found at the Tamar Bridge site. The only exceptions to this are the nauplii and isopods found at the Cotehele Quay site and the oligochaetes found at Salter Mills. The Tamar Bridge site also contained the highest numbers of meiofaunal taxa (11) found in this survey.

Large numbers of nematodes were found at all the sites. These were present at all of the depths sampled (40cm). Nematode size and shape appeared to change with depth into the sediment at the three estuarine sites, animals being shorter and thinner in the deeper samples.

Most of the meiofauna were found in the upper layers of sediment, numbers decreasing with depth. For some groups, however, peak numbers occurred below the sediment surface (for example nematodes at Salter Mills, table 4.5; ciliates at Tamar Bridge, table 4.6).

The changes in numbers of each meiofaunal taxon occurring at 3 or more sites have been statistically tested using two way analyses of variance. The results of these analyses are shown in table 4.8.

Numbers of nematodes, copepods, oligochaetes, ciliates and polychaetes all changed significantly between depths. The changes in numbers of turbellarians and ostracods between depths, however, were not significant. Numbers of nematodes, oligochaetes, ciliates and turbellarians all changed significantly between sites. The changes in numbers of copepods, polychaetes and ostracods between sites, however, were not significant. There was significant interaction between sites or depths for any of the meiofaunal taxa tested.

Taxon / source	d.f.	F value	p
=====			
Nematodes			
depths	6, 56	6.6802	0.1 > p > 0.05
sites	3, 56	7.0698	0.1 > p > 0.05
interaction	18, 56	0.7954	p > 0.1
Copepods			
depths	6, 56	56.2049	0.01 > p > 0.001
sites	3, 56	0.7986	p > 0.1
interaction	18, 56	0.9863	p > 0.1
Oligochaetes			
depths	6, 56	17.5511	0.05 > p > 0.01
sites	3, 56	5.6534	0.1 > p > 0.05
interaction	18, 56	1.1453	p > 0.1
Ciliates			
depths	6, 56	15.2157	0.05 > p > 0.01
sites	3, 56	12.4062	0.05 > p > 0.01
interaction	18, 56	0.8564	p > 0.1
Polychaetes			
depths	6, 56	10.5563	0.05 > p > 0.01
sites	3, 56	3.9155	p > 0.1
interaction	18, 56	1.4215	p > 0.1
Turbellarians			
depths	6, 56	2.9603	p > 0.1
sites	3, 56	10.8929	0.05 > p > 0.01
interaction	18, 56	0.8685	p > 0.1
Ostracods			
depths	6, 56	4.3077	p > 0.1
sites	3, 56	1.8821	p > 0.1
interaction	18, 56	1.1012	p > 0.1
=====			

Table 4.8. Two way analyses of variance on changes in numbers of selected meiofaunal taxa between sites and between depths.

Changes in numbers of each meiofaunal taxa appearing at less than 3 sites have been tested using t-tests. The results of these tests for changes between depths within a site are shown in table 4.9. The results of these tests for changes between sites at a single depth are shown in table 4.10.

The changes in numbers of nauplii, foraminiferans, and archiannelids with depth at Cotehele Quay, Salter Mills and Tamar Bridge were generally significant. The only non-significant changes with depth were for foraminiferans and archiannelids at Tamar Bridge between the 0-1 and 1-2.5 cm depths. The changes in numbers of foraminiferans, bivalves/brachiopods and archiannelids between Salter Mills, Tamar Bridge and Sharrow Point were generally significant. The only exception to this was the difference in numbers of foraminiferans between Salter Mills and Tamar Bridge at the 2.5-5 cm depth which was not significant.

Site / Taxon	Depths compared (cm)	t value	p
<u>Cotehele Quay - Nauplii</u>			
	0-1 / 1-2.5	6.5891	p < 0.001
	1-2.5 / 2.5-5	12.2535	p < 0.001
	2.5-5 / 5-10	4.1467	0.01 > p > 0.001
	5-10 / 10-20	26.3298	p < 0.001
<u>Salter Mills - Foraminiferans</u>			
	0-1 / 1-2.5	4.7202	0.01 > p > 0.001
	1-2.5 / 2.5-5	4.3875	0.01 > p > 0.001
	2.5-5 / 5-10	6.8532	p < 0.001
	5-10 / 10-20	4.7434	0.01 > p > 0.001
	10-20 / 20-30	18.3333	p < 0.001
<u>Tamar Bridge - Foraminiferans</u>			
	0-1 / 1-2.5	1.0819	0.4 > p > 0.3
	1-2.5 / 2.5-5	11.1648	p < 0.001
	2.5-5 / 5-10	16.1515	p < 0.001
	5-10 / 10-20	17.0455	p < 0.001
<u>Tamar Bridge - Archiannelids</u>			
	0-1 / 1-2.5	1.3232	0.4 > p > 0.3
	1-2.5 / 2.5-5	2.8284	0.05 > p > 0.01
	2.5-5 / 5-10	2.0000	0.1 > p > 0.05

Table 4.9. t-tests on changes in numbers of selected meiofaunal taxa with sediment depth. d.o.f. = 6 in all cases.

Taxon / sites compared	depth (cm)	t value	p
<u>Foraminiferans</u>			
Salter Mills / Tamar Bridge			
	0-1	9.2096	p < 0.001
	1-2.5	6.5364	p < 0.001
	2.5-5	0.6228	0.6 > p > 0.5
	5-10	12.0223	p < 0.001
	10-20	18.3333	p < 0.001
<u>Bivalves/Brachiopods</u>			
Salter Mills / Tamar Bridge			
	0-1	2.8284	0.05 > p > 0.01
<u>Archiannelids</u>			
Tamar Bridge / Sharrow Point			
	0-1	2.6465	0.05 > p > 0.01
	1-2.5	6.0000	p < 0.001
	2.5-5	2.0000	0.1 > p > 0.05

Table 4.10. t-test comparisons on changes in numbers of selected meiofaunal taxa between sites. In all cases d.o.f. = 6.

## Discussion

Micro-organism numbers per gram of sediment decrease at intermediate salinities in the Tamar estuary. This pattern is characteristic of flora and fauna in estuaries. In general there are fewer species which can withstand the fairly harsh environmental conditions found within estuaries (Barnes, 1974; Friedrich, 1969; Green, 1968; McLusky, 1981; Tait, 1981).

Micro-organism numbers also decrease by a factor of 5 from Tamar Bridge to Sharrow Point. The overlying water salinity only changes by  $5 \text{ gl}^{-1}$  between these sites. A change of this magnitude, whilst it would probably inhibit freshwater species, is unlikely to affect species from lower in the estuary (Cameron et al, 1984). Thus it is likely that the change in micro-organism numbers is due to the change from fine grained mud (at Tamar bridge) to clean sand (at Sharrow point) (Droop and Wood, 1968; Friedrich, 1969; Green, 1968; Jones, 1979; McLeod, 1971; Perkins, 1974; Tait, 1981).

The changes in dissolved interstitial nutrient concentrations with increasing sediment depth in the Tamar estuary are comparable with those reported by other workers (Berner, 1976; Green, 1968; Perkins, 1974; Suess, 1976; Watson et al, 1985a, b; Zeitzschel, 1980). Reasons for these changes include bioturbation, physical and chemical adsorption and desorption and degradation of organic matter. Bioturbation and biological transport and transformation of nutrients are frequently inter-related (Alexander, 1971; Aller, 1978a, 1978b, 1980, 1982; Berner, 1976, 1980; Broecker, 1971; Cullen, 1973; Droop and Wood, 1968; Hennig et al, 1983; Hines, 1982; Lee and Swartz, 1980; Lerman, 1978; Nixon et al, 1980; Ray and Aller, 1978; Rheinheimer, 1974; Yingst and Rhoads, 1980).

The numbers of meiofauna found in this study were generally highest at the most marine site within the estuary (Tamar Bridge,



table 4.6). This site also contained the highest number of meiofaunal taxa. The increase in taxa towards the mouth of the estuary is due to the presence of marine species, invading the estuary. The lowest number of taxa was found at the uppermost site (Cotehele Quay, table 4.4). This type of change in both numbers of taxa and animal numbers has also been reported by other workers (Gerlach, 1971; Wolff et al, 1980; Woods, 1985).

The densities of nematodes found in the muddy samples in my study were an order of magnitude lower than those found by Warwick and Gee (1984). This difference was also reflected in the lower percentage of nematodes in the total meiofauna. These differences may be due to spatial variations within the estuary (Warwick and Gee worked on samples from different sites) or they may reflect seasonal density changes. In the sandy samples from Sharrow point the densities of meiofauna I found were similar to those found by Harris (1979c).

The decrease in numbers of meiofaunal taxa and animals between Tamar Bridge and Sharrow point is probably due to a combination of factors. These factors include the lower bacterial numbers at Sharrow Point (appendix tables 4.1.1 - 4.1.4), the change from fine-grained mud to medium/coarse sand and the change in salinity (mean and range) between the two stations (Coull, 1973; McIntyre, 1969; Schroder and van Es, 1980).

The isopods found at Cotehele Quay are more commonly associated with freshwater muds. At this site they are probably towards the limit of their salinity tolerance.

Numbers of oligochaetes peak at the Salter Mills site (table 4.5). Oligochaetes are commonly associated with anaerobic or organically polluted areas (Gray and Ventilla, 1971; Lasserre,

1971). The Salter Mills sediment has a relatively low surface Eh (figure 4.17) indicating a low oxygen tension. The numbers of oligochaetes do not, however, appear to be directly correlated with Eh either within a site or between sites. Numbers of oligochaetes are lower at both the Cotehele Quay site - which has a higher surface Eh, and at Tamar Bridge - which has a slightly lower surface Eh than Salter Mills.

The decrease in meiofaunal numbers with depth in the sediment has been reported by many workers (Coull, 1973; Coull and Palmer, 1984; Fenchel, 1968, 1978; Gerlach, 1978; Joint et al, 1982; Malan and McLachlan, 1985; McIntyre, 1969; Reise, 1985; Woods, 1985). There is also some mention in the literature of the peaks in numbers below the sediment surface (Joint et al, 1982; Harris, 1972a; Malan and McLachlan, 1985) which were found for some taxa at some sites in this study. The decrease in numbers of meiofauna with depth in the sediment is probably due to changes in oxygen and food availability and compaction of the sediment. Compaction causes a decrease in the size of the interstices, restricting animal movement (Jensen, 1987; Reise, 1985). The changes in nematode size and shape with depth which I observed would seem to support the latter reason.

The changes in interstitial nutrient concentration along the estuary follow the same pattern as those reported by other workers in both overlying and interstitial water (Boynton and Kemp, 1985; Hines et al, 1982). These changes are related to natural and anthropogenic inputs to the estuary, flocculation, biological, physical and chemical transport between overlying and interstitial water and transformations within the estuary (Boynton and Kemp, 1985; Hines, 1982). Changes within estuaries are complicated by the presence of more than one river input (Elderfield, 1978). This

factor may have affected the results presented here, since the river Tavy joins the Tamar upstream of Tamar Bridge.

At Salter Mills the levels of dissolved nutrients stabilise at 10-20 cm depth. Stabilisation of nutrient levels appears to occur within the same zone as is occupied by the Redox Potential Discontinuity (RPD) layer (figures 4.10-4.12 and 4.17). Changes in Redox potentials can cause alterations in the surface active charge (the charge on the surface of the particle) of redox sensitive elements such as iron and sulphur (Berner, 1976; Lynch and Poole, 1979 p.105). This alteration of sediment surface active charge is also related to many other environmental parameters (Billen, 1978; Meadows and Anderson, 1979). The stabilisation of nutrient concentration in the RPD layer has also been noted by other workers (Boynton and Kemp, 1985; Broecker, 1974; Yingst and Rhoads, 1980). Reasons for this effect include the presence of adsorption equilibria and a reduction in bioturbation below the RPD layer (Aller, 1982; Lee and Swartz, 1980).

The following part of this discussion concerns the relationships between the work which I carried out and that carried out by the other people with whom I was working. Eh and pH data are used with the permission of A. Tufail and P.S.Meadows, water content data are used with the permission of M.S.Hariri.

In general the depth profiles of micro-organism numbers show a good visual correlation with Eh and pH profiles (figures 4.16, 4.17 and 4.18). Numbers of micro-organisms appear to increase with increasing Eh and increase with decreasing pH. These correlations have been tested statistically. The results are shown in table 4.11. The analyses showed no significant correlation (no correlation coefficients  $> 0.95$ ) between micro-organism numbers and

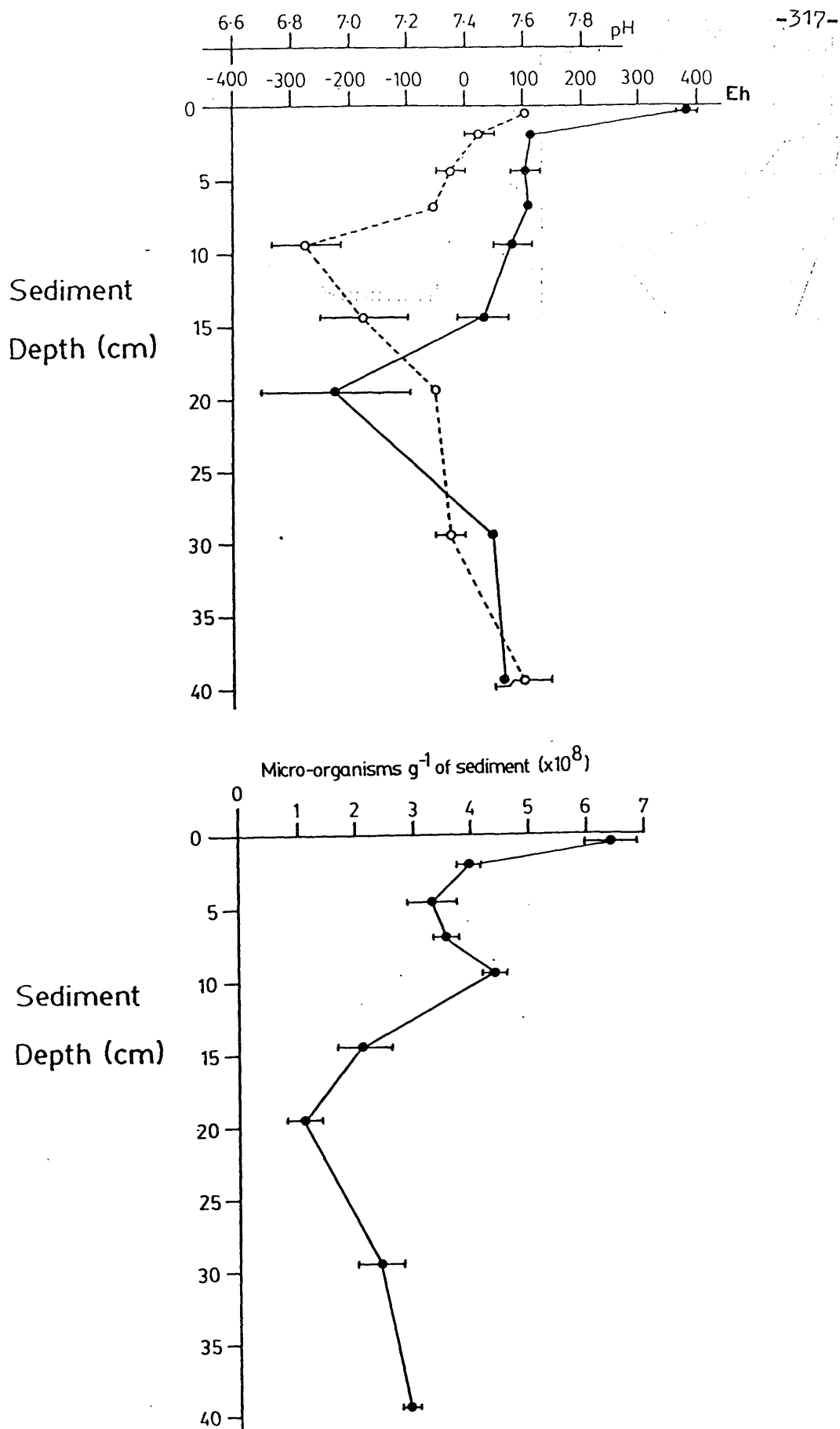


Figure 4.16. Cotehele Quay site. (a) Eh (mV) and pH depth profiles, means and sd's. Solid line = Eh, broken line = pH. Eh and pH data supplied by A.Tufail and P.S.Meadows. (b) micro-organism number profile (mean and sd).

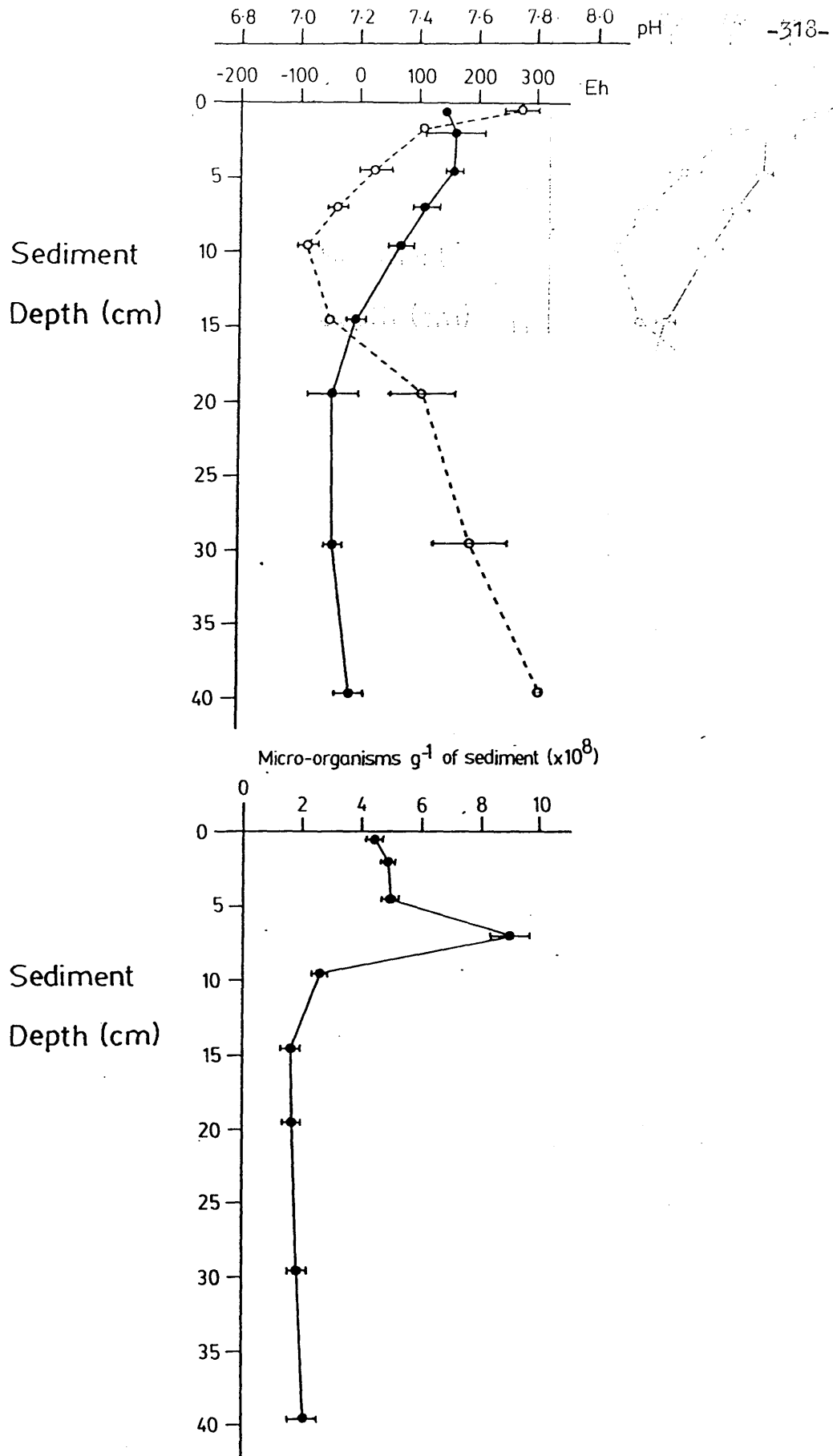


Figure 4.17. Salter Mills site. (a) Eh (mV) and pH depth profiles, means and sd's. Solid line = Eh, broken line = pH. Eh and pH data supplied by A.Tufail and P.S.Meadows. (b) micro-organism number profile (mean and sd).

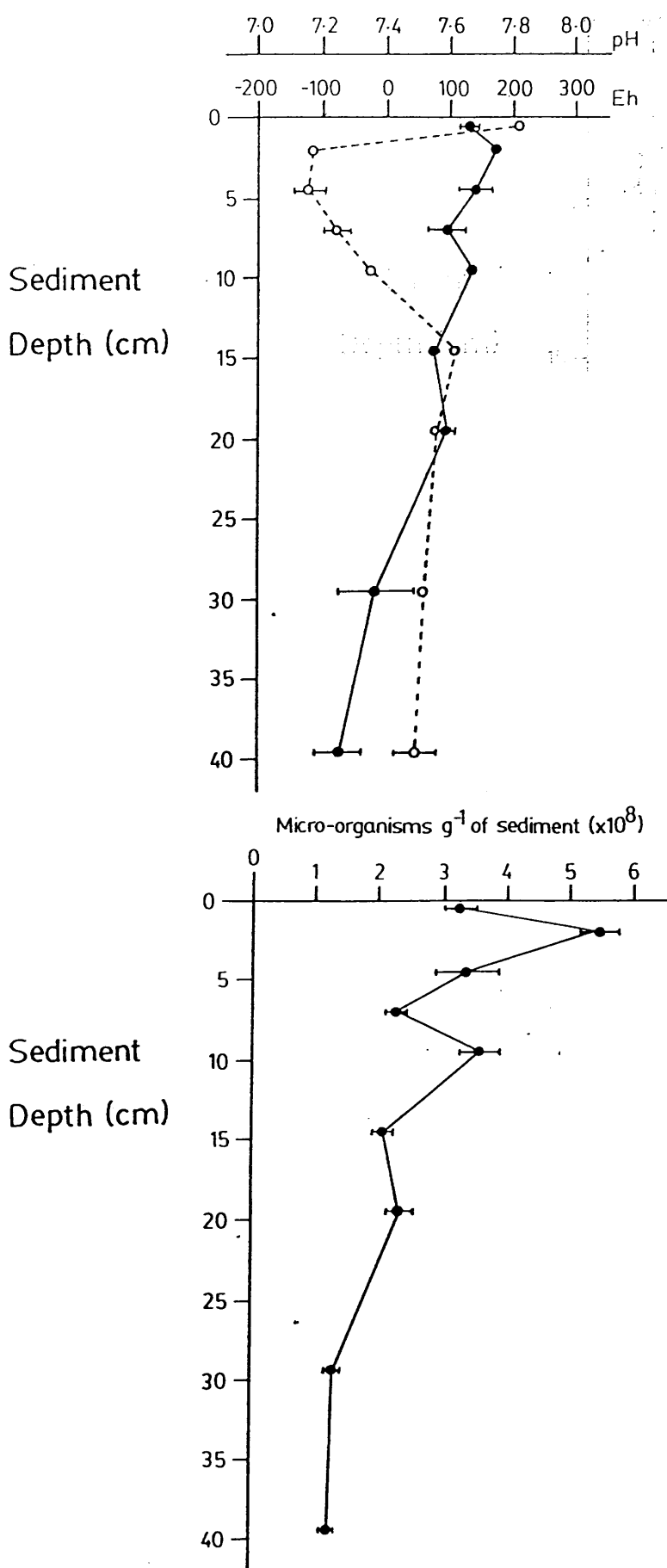


Figure 4.18. Tamar Bridge site. (a) Eh (mV) and pH depth profiles, means and sd's. Solid line = Eh, broken line = pH. Eh and pH data supplied by A.Tufail and P.S.Meadows. (b) micro-organism number profile (mean and sd).

Site	Parameters compared	correlation coefficient
=====		
Cotehele Quay	Micro-organism numbers / Eh	0.5259
	Micro-organism numbers / pH	0.2328
Salter Mills	Micro-organism numbers / Eh	0.5304
	Micro-organism numbers / pH	-0.2425
Tamar Bridge	Micro-organism numbers / Eh	0.5575
	Micro-organism numbers / pH	-0.4435
=====		

Table 4.11. Correlation coefficients for micro-organism numbers with Eh and pH for the depth samples from Cotehele Quay, Salter Mills and Tamar Bridge sites. Eh and pH data supplied by A.Tufail and P.S.Meadows. for  $p=0.05$  correlation coefficient = 0.5760.

either Eh or pH within a single core.

Other workers have found significant relationships between Eh or pH and micro-organism numbers (Droop and Wood, 1968; Friedman and Sanders, 1978; Hines, 1982; Krom and Berner, 1979; Morris, 1978; Rhoads, 1974; Wood, 1965, 1967). Most of this work was done using viable micro-organism counting methods. The use of a direct counting method in this study may, however, have obscured any relationships which existed (Alexander, 1965; Frederick, 1965; Jones, 1979; Lynch and Poole, 1979).

Possible correlations between nutrient concentration, micro-organism numbers, numbers of various individual meiofaunal taxa, salinity, Eh, pH and water content have been tested using a series of linear regression analyses. These analyses were made possible by access to the original data of P.S.Meadows, A.Tufail and M.S.Hariri, for which I thank them.

Linear regressions were performed on the data from a single site at a time. Only the Cotehele Quay, Salter Mills and Tamar Bridge sites were examined, as these were the only sites where a full range of data was available. The data for the regression analyses was divided up into depth bands of 2.5 cm in order to cross-match the different parameters. Where more than one depth sample had been taken within a single 2.5 cm band (e.g. the micro-organism number samples in the top 2.5 cm of the sediment) a mean value of the individual depth samples was used for the regressions. Only the meiofaunal taxa found at all three sites were used in these regressions. The taxa used were nematodes, copepods, polychaetes, oligochaetes and ciliates.

Each parameter (micro-organism numbers, meiofaunal numbers, salinity, Eh, pH, water content) was regressed against each nutrient four times. These four regressions were using the original



nutrient data and three transformed sets of nutrient data. The transformations used were  $\sqrt{y}$ ,  $\log_{10} y$  and  $-1/y$ . This produced a total of 200 regressions per site (ten parameters x five nutrients x four transformations). For each nutrient the best fit regression for each parameter was chosen on the basis of the correlation coefficient of the regression line. This gave a total of 50 best-fit regressions per site. The coefficients of the best fit regressions for each parameter at all three sites are given in tables 4.12 (silicate), 4.13 (phosphate), 4.14 (sulphate), 4.15 (nitrate) and 4.16 (ammonium). A summary of the number of significant regressions found for each nutrient/parameter combination is given in table 4.17. The values in this table range between zero and three. A value of zero indicates that no significant relationships were found at any of the three sites. A value of three indicates that significant relationships were found at all three sites.

Table 4.17 shows that the variable which generally had the greatest effect on nutrient concentration was the salinity of the interstitial water. The interstitial salinity is related to the salinity regime of the overlying water and to the slope of the shore (Barnes, 1974; Friedrich, 1969; Green, 1968; McLeod, 1971; McLusky, 1981; Perkins, 1974; Tait, 1981). It is possible that some of the residual variation in the nutrient concentrations, not accounted for by the calculated equations, is attributable to this source. Thus an important factor in the prediction of nutrient concentrations may be the relative immersion times of the sediment in water of different salinities.

Muddy sediments tend to be well 'damped' due to their low permeability. This means that their salinity changes are usually

Parameter	Station	t	m	c	r	p
=====						
M.O. numbers	C/Q	-1/y	-7.843	-0.625	0.3130	
	S/M	-1/y	-6.4872	-0.835	0.6438	*
	T/B	-1/y	-9.5863	-0.762	0.5826	*
Nematodes	C/Q	--	-18.361	41.633	0.7918	***
	S/M	--	-22.135	35.87	0.5987	*
	T/B	--	-21.624	39.625	0.4863	
Copepods	C/Q	-1/y	-34.299	-17.745	0.7629	***
	S/M	-1/y	-30.835	-21.6282	0.5868	*
	T/B	-1/y	-31.525	-19.4190	0.6342	*
Oligochaetes	C/Q	-1/y	-84.83	-47.715	0.8899	****
	S/M	-1/y	-75.632	-51.625	0.9214	****
	T/B	-1/y	-80.587	-54.81	0.4184	
Polychaetes	C/Q	-1/y	-45.965	-26.128	0.8289	****
	S/M	-1/y	-51.634	-24.872	0.6243	*
	T/B	-1/y	-55.226	-35.614	0.4182	
Ciliates	C/Q	-1/y	-57.280	-30.280	0.4017	
	S/M	-1/y	-63.865	-26.182	0.4318	
	T/B	-1/y	-60.554	-37.626	0.5324	
Salinity	C/Q	-1/y	19.259	12.767	0.9602	****
	S/M	-1/y	23.892	6.715	0.9823	****
	T/B	-1/y	26.264	3.684	0.8764	****
Eh	C/Q	-1/y	-1535.5	-792.6	0.6753	**
	S/M	-1/y	-1629.76	-648.7	0.5438	
	T/B	-1/y	-1938.72	-527.75	0.3872	
pH	C/Q	--	-2.2097	10.9254	0.6994	**
	S/M	--	-1.9083	11.6287	0.5872	*
	T/B	--	-2.012	9.3182	0.4136	
Water content	C/Q	--	-187.64	502.92	0.8044	***
	S/M	--	-203.54	603.87	0.6322	*
	T/B	--	-254.72	612.64	0.4196	
=====						

**Table 4.12.** Best-fit regression line coefficients for silicate against all other parameters. C/Q = Cotehele Quay, S/M = Salter Mills, T/B = Tamar Bridge. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=12 in all cases.

Parameter	Station	t	m	c	r	p
=====						
M.O. numbers	C/Q	—	0.0682	1.436	0.1095	
	S/M	—	0.1236	1.5862	0.3162	
	T/B	—	0.0942	1.9243	0.1827	
Nematodes	C/Q	-1/y	2123.6	65.290	0.8689	****
	S/M	-1/y	2001.72	72.72	0.4386	
	T/B	-1/y	1862.79	89.64	0.6324	*
Copepods	C/Q	—	0.6946	-29.29	0.6189	*
	S/M	—	0.7863	-20.342	0.5892	*
	T/B	—	0.9241	-31.682	0.6314	*
Oligochaetes	C/Q	—	2.0577	-77.25	0.5126	
	S/M	—	1.995	-89.38	0.8637	****
	T/B	—	2.1268	-80.67	0.4325	
Polychaetes	C/Q	—	1.0776	-40.66	0.7778	***
	S/M	—	1.2146	-58.724	0.6287	*
	T/B	—	0.8214	-36.21	0.5314	
Ciliates	C/Q	—	1.4861	-54.018	0.9359	****
	S/M	—	1.6962	-63.214	0.5987	*
	T/B	—	1.7384	-60.862	0.3124	
Salinity	C/Q	—	-0.4667	19.454	0.9863	****
	S/M	—	-0.5963	8.632	0.8642	****
	T/B	—	-0.7244	3.758	0.9311	****
Eh	C/Q	—	30.58	-1065.5	0.6216	*
	S/M	—	19.612	-992.12	0.5385	
	T/B	—	26.43	-870.6	0.5179	
pH	C/Q	—	0.1566	1.1057	0.5322	
	S/M	—	0.2162	0.982	0.9209	****
	T/B	—	0.3824	1.365	0.5282	
Water content	C/Q	-1/y	22650	768.88	0.8316	****
	S/M	-1/y	20126	899.64	0.9209	****
	T/B	-1/y	21263.3	812.72	0.5712	
=====						

**Table 4.13.** Best-fit regression line coefficients for phosphate against all other parameters. C/Q = Cotehele Quay, S/M = Salter Mills, T/B = Tamar Bridge. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=12 in all cases.

Parameter	Station	t	m	c	r	p
M.O. numbers	C/Q	-1/y	-100.08	-4.396	0.3550	
	S/M	-1/y	-86.79	-5.624	0.5826	*
	T/B	-1/y	-80.43	-6.197	0.4182	
Nematodes	C/Q	—	-3.720	54.95	0.7050	**
	S/M	—	-5.322	63.28	0.6351	*
	T/B	—	-5.387	69.62	0.5982	*
Copepods	C/Q	-1/y	-419.76	-34.711	0.8264	*
	S/M	-1/y	-583.61	-62.788	0.4186	
	T/B	-1/y	-396.24	-18.124	0.6271	*
Oligochaetes	C/Q	-1/y	-1020.3	-82.213	0.9471	****
	S/M	-1/y	-980.64	-97.65	0.8124	***
	T/B	-1/y	-911.58	-102.54	0.5862	*
Polychaetes	C/Q	-1/y	-555.00	-45.544	0.8854	****
	S/M	-1/y	-633.72	-55.6271	0.7961	****
	T/B	-1/y	-611.86	-60.7214	0.5626	
Ciliates	C/Q	-1/y	-709.00	-55.954	0.4182	
	S/M	-1/y	-812.721	-66.72	0.3874	
	T/B	-1/y	-855.96	-78.824	0.3186	
Salinity	C/Q	-1/y	215.45	19.448	0.8264	****
	S/M	-1/y	186.724	8.78	0.7982	***
	T/B	-1/y	211.82	3.126	0.9503	****
Eh	C/Q	-1/y	-20279	-1589.1	0.6126	*
	S/M	-1/y	-18624	-1764.9	0.7983	***
	T/B	-1/y	-11836	-1986.8	0.5632	
pH	C/Q	—	-0.4722	12.816	0.7893	***
	S/M	—	-0.3126	18.318	0.4444	
	T/B	—	-0.2626	16.624	0.5382	
Water content	C/Q	—	-43.980	709.2	0.6724	**
	S/M	—	-40.86	812.63	0.8283	***
	T/B	—	-35.241	786.12	0.5689	

Table 4.14. Best-fit regression line coefficients for sulphate against all other parameters. C/Q = Cotehele Quay, S/M = Salter Mills, T/B = Tamar Bridge. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=12 in all cases.

Parameter	Station	t	m	c	r	p
=====						
M.O. numbers	C/Q	-1/y	-7.843	-0.625	0.5862	*
	S/M	-1/y	-10.8181	-0.986	0.3130	
	T/B	-1/y	-9.624	-0.8221	0.4183	
Nematodes	C/Q	--	-18.361	41.633	0.7918	***
	S/M	--	-15.436	58.62	0.4327	
	T/B	--	-22.619	63.8624	0.6127	*
Copepods	C/Q	-1/y	-34.299	-19.745	0.5733	
	S/M	-1/y	-43.818	-22.515	0.7629	***
	T/B	-1/y	-48.624	-23.839	0.6827	**
Oligochaetes	C/Q	-1/y	-84.83	-47.715	0.9102	****
	S/M	-1/y	-96.421	-50.68	0.8899	****
	T/B	-1/y	-107.35	-62.721	0.8624	****
Polychaetes	C/Q	-1/y	-45.965	-26.128	0.8299	****
	S/M	-1/y	-55.724	-35.722	0.5417	
	T/B	-1/y	-63.821	-43.86	0.7219	***
Ciliates	C/Q	-1/y	-57.280	-30.280	0.8214	***
	S/M	-1/y	-64.172	-32.71	0.9017	****
	T/B	-1/y	-50.162	-38.2143	0.6215	*
Salinity	C/Q	-1/y	19.259	12.767	0.8779	****
	S/M	-1/y	27.624	8.125	0.9602	****
	T/B	-1/y	35.186	3.179	0.9244	****
Eh	C/Q	-1/y	-1535.5	-792.6	0.6753	**
	S/M	-1/y	-1684.82	-461.24	0.5823	*
	T/B	-1/y	-1982.12	-315.67	0.4196	
pH	C/Q	--	-2.2097	10.9254	0.8994	****
	S/M	--	-1.8973	8.612	0.6327	*
	T/B	--	-1.7822	6.1286	0.5711	
Water content	C/Q	--	-187.64	502.92	0.8044	***
	S/M	--	-202.73	418.37	0.9063	****
	T/B	--	-218.26	480.80	0.5761	*
=====						

Table 4.15. Best-fit regression line coefficients for nitrate against all other parameters. C/Q = Cotehele Quay, S/M = Salter Mills, T/B = Tamar Bridge. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=12 in all cases.

Parameter	Station	t	m	c	r	p
=====						
M.O. numbers	C/Q	—	0.1641	-15.17	0.3899	
	S/M	—	0.2438	-18.217	0.4186	
	T/B	—	0.3164	-21.17	0.5124	
Nematodes	C/Q	-1/y	10343	99.15	0.5982	*
	S/M	-1/y	18632.4	119.63	0.6885	**
	T/B	-1/y	9418.38	83.24	0.5133	
Copepods	C/Q	—	0.6092	-70.63	0.6124	*
	S/M	—	0.9866	-82.744	0.4186	
	T/B	—	0.4132	-93.187	0.8062	***
Oligochaetes	C/Q	—	1.5544	-179.17	0.9701	****
	S/M	—	1.9863	-190.87	0.3244	
	T/B	—	1.9924	-211.333	0.6177	*
Polychaetes	C/Q	—	0.8540	-98.73	0.7138	***
	S/M	—	0.9964	-136.872	0.9160	****
	T/B	—	0.7422	-143.114	0.6124	*
Ciliates	C/Q	-1/y	14561.2	128.255	0.2272	
	S/M	-1/y	15896.72	135.6225	0.1793	
	T/B	-1/y	18721.4	163.827	0.3583	
Salinity	C/Q	—	-0.3162	38.301	0.9375	****
	S/M	—	-0.4813	47.625	0.8277	****
	T/B	—	-0.5624	49.832	0.9188	****
Eh	C/Q	—	27.992	-3155.1	0.6324	*
	S/M	—	25.633	-4567.61	0.7321	***
	T/B	—	20.18	-2196.82	0.5619	
pH	C/Q	-1/y	1339.8	18.656	0.6133	*
	S/M	-1/y	1587.73	27.6321	0.5444	
	T/B	-1/y	1764.92	31.7827	0.8414	****
Water content	C/Q	-1/y	127676	1277.7	0.8444	****
	S/M	-1/y	101264	1458.63	0.5922	*
	T/B	-1/y	113272	1862.11	0.4138	
=====						

Table 4.16. Best-fit regression line coefficients for ammonium against all other parameters. C/Q = Cotehele Quay, S/M = Salter Mills, T/B = Tamar Bridge. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=12 in all cases.

Parameter	SiO <sub>4</sub>	PO <sub>4</sub>	SO <sub>4</sub>	NO <sub>3</sub>	NH <sub>4</sub>
Micro-organisms	2	0	1	1	0
Nematodes	2	2	3	2	2
Copepods	3	3	2	2	2
Oligochaetes	2	1	3	3	2
Polychaetes	2	2	2	2	3
Ciliates	0	2	0	3	0
Salinity	3	3	3	3	3
Eh	1	1	2	2	2
pH	2	1	1	2	2
Water content	2	2	2	3	2

Table 4.17. Summary of numbers of significant best-fit regressions of all parameters against each nutrient. 0 = significant at no stations, 3 = significant at all stations.

slower and of smaller magnitude than those of sandy sediments. Muddy sediments also tend to retain water of a higher salinity than that of the overlying water (Emery et al, 1957). The sediment at all the muddy sites within the Tamar estuary was relatively impermeable to water (A. Tufail pers. comm.). The permeability of the sediment will also determine the rate of exchange of interstitial with overlying water as will the level of biological activity (Aller, 1980, 1982; Martens, 1978; Stanley, 1978). The rate of change of concentration with depth found in this study indicates relatively high levels of biological activity within the top 10-20 cm of sediment (Berner, 1980).

At all the muddy sites, core samples showed that biological activity was taking place in the sediment to depths of over 40 cm. This was indicated by the presence of open burrows surrounded by aerobic (light brown) sediment within the anaerobic (black) sediment zone. It would be interesting in any future study to investigate the chemical effects of this biological activity below the RPD layer in relatively impermeable sediments and to determine what modifications would have to be made to any model of porewater nutrient concentration to allow for this activity (Aller, 1978, 1980, 1982; Lee and Swartz, 1980; Ray and Aller, 1982).

Berner (1976, 1980) and others have used diagenetic equations to predict past environmental conditions from buried sediments. This application is only valid if the buried material is below the zone of bioturbation. None of the nutrient samples collected in this study were below this zone. This was indicated by the high macrofaunal densities (Emery et al, 1957; M. Hariri pers. comm.) combined with burrows extending more than 40 cm into the sediment (Reineck and Singh, 1980). It may not be valid, therefore, to interpret the nutrient concentrations found in this study in terms



of past conditions despite their apparent stabilization at depths of 10-20 cm. This stabilization may, however, represent an area of reduced bioturbation compared with the sediment surface.

A full discussion of the significance of the correlations found by the linear regressions in this study is included in the general discussion of my thesis. In the general discussion the relationships between nutrient concentration and other parameters in the Tamar estuary are compared with those found in both my Pacific survey work and my laboratory experiments. The implications of these relationships for nutrient regeneration in estuaries and oceanic productivity are also discussed in the general discussion.

### GENERAL DISCUSSION.

My laboratory flux experiments have shown that meiofauna affect nutrient fluxes through the sediment-water interface of inshore sediments. The effects of meiofauna can increase or reduce the flux, depending on the nutrient and types and, to a lesser extent, the densities of animals present. My field surveys have shown that nutrient concentrations in sediments can be related to the densities of meiofauna as well as to levels of various physical and chemical parameters.

The factors which I have studied in my laboratory work (section two) are ranked in table b according to the extent of their effect on nutrient fluxes. Ranking was performed after converting the number of significant differences in flux between levels of a parameter to a percentage of the maximum number of differences which could have occurred. A percentage measure was used because of the different numbers of differences which could have occurred in each experiment (second experiment = 3; third experiment = 10). The results from my first laboratory experiment, comparing macrofauna, meiofauna and micro-organisms, were not used as only a single level of each parameter was used. The overlying water and underlying water data from my laboratory studies have been ranked separately.

The factors which I have studied in my Pacific survey (section three) are ranked in table c. Ranking on this data was performed using the number of stations at which significant relationships were found (maximum = 7). This method of ranking was also used for the data from my Tamar survey (section four), the results from which are given in table d.

The results from my laboratory experiments and field surveys have not been compared statistically. This is due to the low number

Nutrient		SiO <sub>4</sub>	PO <sub>4</sub>	SO <sub>4</sub>	NO <sub>3</sub>	NH <sub>4</sub>
Treatment/ Chamber						
=====						
Nematodes	O	4	1	1	1	1
	U	1	1	1	1	7
Copepods	O	1	1	1	1	1
	U	1	8	1	7	5
Nematodes plus Copepods	O	1	1	1	1	1
	U	1	1	1	7	1
Whole meiofauna	O	1	5	1	7	1
	U	8	1	1	1	5
Salinity	O	7	8	1	1	5
	U	7	4	5	3	8
Particle size range	O	5	4	1	6	7
	U	6	6	7	3	4
Compaction	O	8	6	1	8	6
	U	5	5	8	3	1
Oxygen saturation	O	6	6	8	1	7
	U	1	7	6	3	1
=====						

Table b. Factors investigated in my laboratory flux experiments, ranked according to number of significant differences between levels of each parameter. O = overlying water; U = underlying water.

	SiO <sub>4</sub>	PO <sub>4</sub>	SO <sub>4</sub>	NO <sub>3</sub>	NH <sub>4</sub>
Parameter					
Micro-organisms	16	17	18	18	18
Total meiofauna	16	15	15	12	14
Metazoa	16	17	15	12	16
Nematodes	16	17	15	12	16
Foraminifera	15	14	14	3	12
Water content	14	15	18	18	19
Lithium	1	1	1	3	1
Sodium	1	1	1	3	4
Potassium	1	1	1	3	4
Magnesium	1	1	1	3	4
Calcium	1	1	1	3	4
Strontium	1	1	1	1	4
Barium	12	11	12	12	14
Iron	1	1	1	1	1
Zinc	1	11	1	12	4
Phosphorous	12	10	1	3	4
Sulphur	1	1	1	3	4
Boron	1	1	1	3	1
Silicon	1	11	12	12	12

Table c. Factors investigated in my Pacific survey, ranked according to number of stations at which significant relationships were found.

	SiO <sub>4</sub>	PO <sub>4</sub>	SO <sub>4</sub>	NO <sub>3</sub>	NH <sub>4</sub>
Parameter					
Micro-organisms	3	1	2	1	1
Nematodes	3	5	8	2	3
Copepods	9	9	4	2	3
Oligochaetes	3	2	8	2	3
Polychaetes	3	5	4	2	9
Ciliates	1	5	1	8	1
Salinity	9	9	8	8	9
Eh	2	2	4	2	3
pH	3	2	2	2	3
Water content	3	5	4	8	3

Table d. Factors investigated in my Tamar estuary survey, ranked according to number of stations at which significant relationships were found.

of cross-matched variables (variables occurring in more than one survey).

The results of my laboratory experiments show that the major factors affecting nutrient flux from and to the overlying water were generally physical or chemical rather than biological. In the underlying water, however, the reverse was generally found, biological factors being more important. The order of ranking of variables differed greatly between nutrients (table b).

My field surveys showed that a number of biological, physical and chemical parameters are highly correlated with nutrient concentrations (tables c and d). In these surveys, however, it is impossible to separate causal from non-causal relationships. For example, if micro-organism density and nitrate concentrations show similar depth profiles in a sediment it may indicate that micro-organisms are affecting nitrate concentration, or that nitrate concentration is affecting micro-organism density, or that micro-organism density and nitrate concentration are both being affected by another factor.

The possible causes of the effects of macrofaunal, meiofaunal and microbial density and activity include bioturbation, sediment ventilation, active transport and feeding. These, and the effects of particle size range, compaction, oxygen saturation and water content, have been discussed in section two (p.151). The possible effects of salinity on nutrient fluxes have been discussed in section two (p.156) and four (p.322). The effects of Eh and pH have also been discussed in section four (p.316).

Many of the biological, physical and chemical factors which I have investigated are interrelated. Compaction, water content and particle size range are, to a large extent, interdependent. Changes

in compaction will also alter the water content through the expulsion of pore-water (section two p.158). Alterations in the particle size range will also affect the compaction and the water content. Meiofaunal population structure may be related to the microbial population as well as to the macrofaunal population (section two p.151). Separating the effects of these mutually interdependent variables is impossible in most cases.

The changes in deposited material within the benthic boundary zone, including changes during burial and regeneration of nutrients, are all classified as diagenesis (Berner, 1976, 1980; Wilson et al, 1985). Many models have been developed for the diagenesis of nutrients in sediments. The majority of these models are dependent primarily upon physical and chemical parameters (for references see p.8). Sediment diffusion coefficients are used as constants in the calculation of fluxes and concentrations in all of these models. Sediment diffusion coefficients relate to the rate of diffusion of an ion through the porewaters of a sediment and are affected by the tortuosity of the sediment (see p.158). Where biological parameters have been included in models, they have generally been in the form of a modified (biological) diffusion coefficient.

Modification of the diffusion coefficient to include biological effects on fluxes assumes that the biological effects are either homogenous or predictably inhomogenous within the sediment sample under consideration. This assumption may be approximately true if the coefficient is calculated for a large area of sediment, such that an average sedimentary environment may be used. On a small scale the application of a biological diffusion coefficient may not be valid. This is due to the problems involved in defining the effects of a mutually interacting, non-homogenous,

mobile group of organisms within the sediment.

There are also problems in relating physical parameters to fluxes in the presence of bioturbating organisms. For example, compaction of sediments during burial reduces the pore-space and increases the tortuosity (Duursma and Bosch, 1970; Lerman, 1978; Berner, 1980). Changes in tortuosity change the sediment diffusion coefficient. Bioturbating animals may modify these changes by compacting sediment during movement or burrow construction, decreasing the rate of diffusion. Alternatively burrowing animals may increase the surface area of the sediment and reduce the compaction, increasing the rate of diffusion (see table a, p.10; Coull, 1973; Aller, 1978a; Yingst and Rhoads, 1980; Matisoff et al, 1985; Ray and Aller, 1985). These effects, although described separately here, may occur in the same sediment, in close proximity, causing a large degree of spatial inhomogeneity.

The interactions between ions in solution in the sediment and between ions and the biota also present problems for modelling. For example, transport of dissolved hydrogen sulphide from anaerobic to aerobic zones in the sediment may affect sulphate and phosphate concentrations. Iron (III) ions readily adsorb phosphate ions but are easily reduced by hydrogen sulphide to produce iron (II) ions, which adsorb phosphate less readily (Svennson and Soderland, 1977). In addition to this hydrogen sulphide is unstable in aerobic environments and is readily oxidised to produce sulphate ions. Sulphate ions transported into anaerobic environments may be utilised as an energy source by sulphate-reducing bacteria, which produce hydrogen sulphide (Postgate, 1984). All of the processes described above usually take place in only part of the sediment column, and tend to produce localised high concentrations. This



will have major effects on diffusion in the sediment because the rate of diffusion between two points is proportional to the difference in concentration between the points (Berner, 1980).

A large amount of work is now being done on satellite imaging of oceanic productivity (Lintz and Simonett, 1976; Cracknell, 1982; Maul, 1985). The lack of information on processes and rates of benthic nutrient regeneration, however, presents a range of problems for marine productivity studies (Harrison, 1979; Maull, 1985). Localised benthic nutrient regeneration may be the main source of nutrients, especially in inshore areas away from terrestrial inputs. The rates of benthic regeneration of limiting nutrients, such as nitrogen in many inshore waters, are likely to control the productivity of primary producers and hence of higher trophic levels.

Only recently, with the advent of the Global Ocean Flux Study (1984), has there been a major attempt to correlate benthic regeneration of nutrients with primary productivity and to try and model the processes involved. The Global Ocean Flux Study is, however, concerned primarily with effects on scales of  $10^2$  to  $10^4$  kilometers and 1 to  $10^3$  years (GOFs, 1984). Studies on these spatial and temporal scales are likely to yield a large amount of information on the long-term effects of environmental perturbations on nutrient cycling. They will not, however, provide as much insight into the effects of localised perturbations.

Localised environmental perturbations commonly encountered in inshore areas include changes in estuaries caused by land development and changes in freshwater flow (Emery et al, 1957; Barnes, 1974; Perkins, 1974; Elliot and McLusky, 1985). Localised disturbances of the deep-sea environment would include the possible future dredging of manganese nodules and crusts (Cronan, 1980;

Osmond, 1981). The latter is likely to have major effects on deep-sea environments which are naturally very stable and slow-changing (Bruun, 1957; Marshall, 1979; Thistle, 1979; Osmond, 1981; Thiel, 1983).

Despite the large amount of work that has been done on modelling diagenetic reactions there is still a great need for detailed descriptions of the interaction of biological, physical and chemical processes during diagenesis. Aspects of diagenesis which particularly need further examination include specific activity measurements for all types of infauna and long-term experiments and monitoring of the effects of biological processes on the redistribution of nutrient elements within sediments. Ideally these studies should be a combination of in situ monitoring and laboratory experiments. This combined approach to nutrient regeneration studies could provide information on a wide range of biological parameters under controlled conditions whilst retaining a definite relationship to the natural environment (Smith, 1984). It is obvious, therefore, that a large amount of work on biological interactions with nutrient diagenesis is still needed if the effects of future changes in ocean use on oceanic productivity are to be predicted.

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**APPENDICES. - 2.1 to 2.9 (Flux experiments).**

Treatment/ Chamber	Time (days)	0	1	2	3
=====					
Micro-organisms only.	O	1.9284 (0.0068)	1.9578 (0.0286)	1.9827 (0.0610)	2.0099 (0.0472)
	U	1.9774 (0.0046)	1.9342 (0.0122)	1.8933 (0.0131)	1.8670 (0.0257)
Meiofauna	O	2.0131 (0.0305)	2.1403 (0.0260)	2.3542 (0.0511)	2.4194 (0.0466)
	U	1.9661 (0.0160)	1.8942 (0.0532)	1.7864 (0.0216)	1.6543 (0.0218)
Macrofauna plus meiofauna	O	1.9383 (0.0210)	1.9700 (0.0347)	2.0900 (0.0143)	2.2299 (0.0191)
	U	1.9616 (0.0150)	1.9235 (0.0045)	1.8610 (0.0483)	1.8283 (0.0384)
=====					

Table 2.1.1. Flux experiment 1. Concentrations of silicate (mean, (sd)  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water of each treatment at each sampling time.  $n=3$  in all cases.



Treatment/ Chamber	Time (days)	0	1	2	3
=====					
Micro-organisms only.	O	0.974 (0.144)	0.539 (0.125)	0.627 (0.037)	0.637 (0.095)
	U	1.103 (0.0.092)	1.236 (0.121)	1.424 (0.100)	1.535 (0.133)
Meiofauna	O	1.037 (0.138)	1.005 (0.074)	0.900 (0.055)	0.848 (0.069)
	U	1.170 (0.146)	1.358 (0.099)	1.595 (0.072)	1.725 (0.082)
Macrofauna plus meiofauna	O	0.822 (0.088)	0.172 (0.059)	0.148 (0.063)	0.103 (0.023)
	U	1.124 (0.082)	1.249 (0.132)	1.512 (0.023)	1.593 (0.106)
=====					

Table 2.1.2. Flux experiment 1. Concentrations of phosphate (mean, (sd)  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water of each treatment at each sampling time. n=3 in all cases.

Treatment/ Chamber	Time (days)	0	1	2	3
=====					
Micro-organisms only.	O	2221.50 (10.01)	2233.00 (4.30)	2217.00 (3.74)	2225.75 (6.87)
	U	2223.25 (5.54)	2231.50 (14.99)	2223.50 (11.06)	2233.50 (6.18)
Meiofauna	O	2217.25 (4.26)	2204.25 (5.40)	2186.00 (6.96)	2176.00 (4.95)
	U	2205.50 (5.85)	2204.75 (7.26)	2196.50 (4.03)	2191.75 (5.80)
Macrofauna plus meiofauna	O	2135.75 (6.68)	2157.00 (4.64)	2122.00 (4.30)	2102.75 (5.36)
	U	2185.00 (5.92)	2186.75 (5.12)	2163.75 (3.96)	2145.75 (7.26)
=====					

Table 2.1.3. Flux experiment 1. Concentrations of sulphate (mean (sd),  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water of each treatment at each sampling time. n=3 in all cases.

Treatment/ Chamber	Time (days)	0	1	2	3
=====					
Micro-organisms only.	O	1.8113 (0.0111)	1.6712 (0.0478)	1.2600 (0.0543)	1.1755 (0.0405)
	U	1.8129 (0.0024)	1.7134 (0.0185)	1.5443 (0.0116)	1.3171 (0.0258)
Meiofauna	O	1.7373 (0.0165)	1.5813 (0.0709)	1.2738 (0.0329)	1.1375 (0.0319)
	U	1.6923 (0.0015)	1.6459 (0.0231)	1.3157 (0.0189)	1.2354 (0.0100)
Macrofauna plus meiofauna	O	1.6753 (0.0125)	1.5565 (0.0572)	1.2390 (0.0448)	1.0588 (0.0456)
	U	1.7515 (0.0015)	1.6984 (0.0188)	1.4268 (0.0175)	1.3190 (0.0118)
=====					

**Table 2.1.4.** Flux experiment 1. Concentrations of nitrate (mean, (sd),  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water of each treatment at each sampling time.  $n=3$  in all cases.

Treatment/ Chamber	Time (days)	0	1	2	3
=====					
Micro-organisms only.	O	3.6523 (0.0199)	4.0538 (0.0547)	4.6463 (0.0817)	5.1563 (0.0635)
	U	3.8257 (0.0110)	3.9767 (0.0429)	4.1225 (0.0210)	4.5866 (0.0263)
Meiofauna	O	3.1145 (0.0132)	3.2943 (0.1076)	4.0413 (0.0784)	4.1185 (0.0758)
	U	3.3013 (0.0106)	3.4242 (0.0261)	3.6820 (0.0181)	3.9908 (0.0159)
Macrofauna plus meiofauna	O	3.3948 (0.0065)	3.6630 (0.0533)	4.1555 (0.0713)	4.3695 (0.0589)
	U	3.6217 (0.0116)	3.7617 (0.0253)	3.8463 (0.0199)	3.9172 (0.0303)
=====					

Table 2.1.5. Flux experiment 1. Concentrations of ammonium (mean, (sd),  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water of each treatment at each sampling time. n=3 in all cases.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
1 / O	-1/y	2.3526x10 <sup>-2</sup> (3.408x10 <sup>-3</sup> )	1.8925 (6.38x10 <sup>-3</sup> )	0.7071	**
1 / U	—	-9.277x10 <sup>-3</sup> (1.545x10 <sup>-3</sup> )	-0.5191 (2.891x10 <sup>-3</sup> )	0.7556	**
2 / O	—	9.3568x10 <sup>-2</sup> (6.779x10 <sup>-3</sup> )	1.9232 (1.268x10 <sup>-2</sup> )	0.9187	**
2 / U	—	-9.151x10 <sup>-2</sup> (2.643x10 <sup>-2</sup> )	1.8513 (4.945x10 <sup>-2</sup> )	0.4888	*
3 / O	-1/y	3.2303x10 <sup>-2</sup> (2.272x10 <sup>-3</sup> )	-0.4983 (4.251x10 <sup>-3</sup> )	0.9230	**
3 / U	-1/y	-2.8744x10 <sup>-2</sup> (2.019x10 <sup>-3</sup> )	-0.5172 (3.778x10 <sup>-3</sup> )	0.9230	**

**Table 2.2.1.** Flux experiment 1. Coefficients of the best-fit regressions for silicate against time. Treatment 1=micro-organisms only; 2=macrofauna plus meiofauna; 3=meiofauna only. O=overlying water chamber, U=underlying water chamber. \* = 0.05 > p > 0.02; \*\* = 0.02 > p > 0.01; \*\*\* = 0.01 > p > 0.001; \*\*\*\* = p < 0.001. n = 36 in all cases.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
1 / O	—	0.1022 (0.0217)	0.8020 (0.0405)	0.6168	*
1 / U	—	-0.0305 (0.0206)	0.9458 (0.0385)	0.1817	
2 / O	—	5.451x10 <sup>-2</sup> (1.751x10 <sup>-2</sup> )	0.9657 (3.275x10 <sup>-2</sup> )	0.4461	*
2 / U	—	-7.736x10 <sup>-2</sup> (1.565x10 <sup>-2</sup> )	1.0788 (2.927x10 <sup>-2</sup> )	0.6332	*
3 / O	—	0.1407 (3.180x10 <sup>-2</sup> )	0.9539 (5.950x10 <sup>-2</sup> )	0.5891	*
3 / U	—	-0.1083 (2.680x10 <sup>-2</sup> )	1.1516 (5.013x10 <sup>-2</sup> )	0.5523	*

Table 2.2.2. Flux experiment 1. Coefficients of the best-fit regressions for phosphate against time. Treatment 1=micro-organisms only; 2=macrofauna plus meiofauna; 3=meiofauna only. O=overlying water chamber, U=underlying water chamber. \* = 0.05 > p > 0.02; \*\* = 0.02 > p > 0.01; \*\*\* = 0.01 > p > 0.001; \*\*\*\* = p < 0.001. n = 36 in all cases.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
1 / O	—	-0.8622 (3.650)	2244.66 (6.83)	0.3406	
1 / U	-1/y	8.087x10 <sup>-7</sup> (4.133x10 <sup>-7</sup> )	-4.504x10 <sup>-4</sup> (7.731x10 <sup>-7</sup> )	0.2739	
2 / O	—	-0.4900 (3.375)	2194.99 (6.31)	0.1761	
2 / U	—	5.011 (1.973)	2208.60 (3.69)	0.3674	
3 / O	-1/y	-7.0228x10 <sup>-6</sup> (8.487x10 <sup>-7</sup> )	-4.556x10 <sup>-4</sup> (1.588x10 <sup>-6</sup> )	0.8112	*
3 / U	-1/y	3.7199x10 <sup>-6</sup> (2.736x10 <sup>-7</sup> )	-4.548x10 <sup>-4</sup> (5.119x10 <sup>-7</sup> )	0.9165	*

Table 2.2.3. Flux experiment 1. Coefficients of the best-fit regressions for sulphate against time. Treatment 1=micro-organisms only; 2=macrofauna plus meiofauna; 3=meiofauna only. O=overlying water chamber, U=underlying water chamber. \* = 0.05 > p > 0.02; \*\* = 0.02 > p > 0.01; \*\*\* = 0.01 > p > 0.001; \*\*\*\* = p < 0.001. n = 36 in all cases.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
1 / O	—	-0.2080 (0.0147)	1.7806 (0.0275)	0.9171	**
1 / U	—	0.1543 (0.0065)	1.8250 (0.0122)	0.9701	**
2 / O	—	-0.2372 (7.890x10 <sup>-3</sup> )	1.7749 (1.476x10 <sup>-2</sup> )	0.9813	**
2 / U	-1/y	6.827x10 <sup>-2</sup> (3.428x10 <sup>-3</sup> )	-0.5494 (6.414x10 <sup>-3</sup> )	0.9586	**
3 / O	Log <sub>10</sub> Y	-6.579x10 <sup>-2</sup> (2.670x10 <sup>-3</sup> )	0.2497 (4.995x10 <sup>-3</sup> )	0.9721	**
3 / U	-1/y	8.0958x10 <sup>-2</sup> (7.943x10 <sup>-3</sup> )	-0.5592 (1.486x10 <sup>-2</sup> )	0.8637	**

Table 2.2.4. Flux experiment 1. Coefficients of the best-fit regressions for nitrate against time. Treatment 1=micro-organisms only; 2=macrofauna plus meiofauna; 3=meiofauna only. O=overlying water chamber, U=underlying water chamber. \* = 0.05 > p > 0.02; \*\* = 0.02 > p > 0.01; \*\*\* = 0.01 > p > 0.001; \*\*\*\* = p < 0.001. n = 36 in all cases.



Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
1 / O	—	0.5868 (0.0171)	3.4363 (0.0319)	0.9854	**
1 / U	-1/y	-1.6792x10 <sup>-2</sup> (7.621x10 <sup>-4</sup> )	-0.2707 (1.426x10 <sup>-3</sup> )	0.9659	**
2 / O	—	0.3254 (2.475x10 <sup>-2</sup> )	3.4205 (4.361x10 <sup>-2</sup> )	0.9116	**
2 / U	—	-9.697x10 <sup>-2</sup> (1.874x10 <sup>-2</sup> )	3.6383 (3.506x10 <sup>-2</sup> )	0.6512	*
3 / O	-1/y	3.8001x10 <sup>-2</sup> (2.449x10 <sup>-3</sup> )	-0.3179 (4.581x10 <sup>-3</sup> )	0.9343	**
3 / U	—	-0.1671 (1.750x10 <sup>-2</sup> )	3.3807 (3.274x10 <sup>-2</sup> )	0.8485	**

Table 2.2.5. Flux experiment 1. Coefficients of the best-fit regressions for ammonia against time. Treatment 1=micro-organisms only; 2=macrofauna plus meiofauna; 3=meiofauna only. O=overlying water chamber, U=underlying water chamber. \* = 0.05 > p > 0.02; \*\* = 0.02 > p > 0.01; \*\*\* = 0.01 > p > 0.001; \*\*\*\* = p < 0.001. n = 36 in all cases.

Treatment	1	2	3
1	X X	34.3955 ****	90.0386 ****
2	80.5824 ****	X X	15.3063 ***
3	115.3713 ****	14.2765 ***	X X

Table 2.3.1. Flux experiment 1. t-tests comparing initial silicate flux in each treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	1	2	3
1	X X	5.1310 *	3.0001
2	5.4340 *	X X	7.1227 **
3	6.9048 *	2.9908	X X

Table 2.3.2. Flux experiment 1. t-tests comparing initial phosphate flux in each treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	1	2	3
1	X X	2.2460	4.2385
2	1.5576	X X	7.9407 **
3	13.2427 ***	19.7265 ***	X X

Table 2.3.3. Flux experiment 1. t-tests comparing initial sulphate flux in each treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	1	2	3
1	X X	5.2507 *	42.4490 ****
2	23.0841 ***	X X	90.1912 ****
3	25.1937 ***	10.6182 ***	X X

Table 2.3.4. Flux experiment 1. t-tests comparing initial nitrate flux in each treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	1	2	3
=====			
1	X X	26.0678 ***	36.5713 ****
2	21.1503 ***	X X	56.6001 ****
3	10.6352 ***	8.1980 **	X X
=====			

Table 2.3.5. Flux experiment 1. t-tests comparing initial ammonia flux in each treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Table 2.4.1. Flux experiment 2. Concentrations (mean, (sd);  $\text{mg l}^{-1}$ ) of silicate in the overlying (O) and underlying (U) water of each treatment. W = whole meiofauna; N=nematodes; Cp=copepods; NCp=nematodes plus copepods; C=control (no meiofauna). L=low density; M=medium density; H=high density. n=9 in all cases.

Treatment /chamber	Time 0 (days)	7	14	28
WL / O	1.917 (0.047)	2.102 (0.013)	2.148 (0.065)	2.219 (0.089)
WL / U	1.898 (0.035)	2.014 (0.030)	2.089 (0.007)	2.147 (0.102)
WM / O	1.831 (0.054)	2.145 (0.072)	2.318 (0.200)	2.206 (0.286)
WM / U	1.823 (0.083)	2.088 (0.053)	2.174 (0.072)	2.117 (0.063)
WH / O	1.903 (0.025)	2.237 (0.054)	2.378 (0.161)	2.294 (0.289)
WH / U	1.874 (0.079)	2.112 (0.090)	2.175 (0.115)	2.178 (0.082)
NL / O	1.915 (0.069)	2.031 (0.022)	2.031 (0.042)	2.113 (0.023)
NL / U	1.933 (0.060)	1.999 (0.034)	2.027 (0.038)	2.037 (0.040)
NM / O	1.949 (0.121)	2.011 (0.015)	2.082 (0.004)	2.150 (0.064)
NM / U	1.973 (0.090)	1.972 (0.019)	2.052 (0.009)	2.097 (0.016)
NH / O	1.951 (0.027)	2.025 (0.051)	2.174 (0.019)	2.298 (0.074)
NH / U	1.909 (0.070)	2.045 (0.046)	2.087 (0.048)	2.099 (0.059)
CpL / O	1.851 (0.008)	1.964 (0.020)	1.974 (0.018)	2.043 (0.021)

Table 2.4.1. continued.

Treatment /chamber	Time (days)	0	7	14	28
CpL / U		1.862 (0.076)	1.959 (0.016)	1.935 (0.022)	1.913 (0.027)
CpM / O		1.910 (0.115)	1.983 (0.015)	2.033 (0.038)	2.031 (0.007)
CpM / U		1.838 (0.142)	1.938 (0.024)	1.954 (0.058)	1.908 (0.017)
CpH / O		1.895 (0.144)	2.048 (0.016)	2.095 (0.055)	2.159 (0.029)
CpH / U		1.881 (0.053)	1.949 (0.013)	1.912 (0.029)	1.879 (0.039)
NCpL / O		1.817 (0.110)	2.040 (0.029)	2.077 (0.079)	2.108 (0.067)
NCpL / U		1.875 (0.066)	2.017 (0.017)	2.111 (0.060)	2.129 (0.029)
NCpM / O		1.899 (0.086)	2.063 (0.066)	2.149 (0.053)	2.176 (0.074)
NCpM / U		1.901 (0.103)	2.046 (0.009)	2.106 (0.052)	2.121 (0.039)
NCpH / O		1.870 (0.032)	2.103 (0.021)	2.155 (0.078)	2.130 (0.084)
NCpH / U		1.923 (0.015)	2.138 (0.023)	2.238 (0.034)	2.106 (0.053)
C / O		1.939 (0.119)	2.007 (0.040)	2.023 (0.026)	2.036 (0.012)
C / U		1.813 (0.031)	1.979 (0.035)	1.937 (0.027)	1.995 (0.045)

Table 2.4.2. Flux experiment 2. Concentrations (mean, (sd);  $\text{mg l}^{-1}$ ) of phosphate in the overlying (O) and underlying (U) water of each treatment. W = whole meiofauna; N=nematodes; Cp=copepods; NCp=nematodes plus copepods; C=control (no meiofauna). L=low density; M=medium density; H=high density. n=9 in all cases.

Treatment /chamber	Time 0 (days)	7	14	28
WL / O	1.127 (0.014)	1.092 (0.021)	1.064 (0.007)	1.045 (0.012)
WL / U	1.061 (0.084)	1.079 (0.017)	1.074 (0.017)	1.071 (0.011)
WM / O	1.097 (0.028)	1.085 (0.029)	1.050 (0.039)	1.038 (0.023)
WM / U	1.151 (0.054)	1.100 (0.024)	1.061 (0.033)	1.068 (0.002)
WH / O	1.042 (0.048)	1.063 (0.020)	1.049 (0.018)	1.040 (0.010)
WH / U	1.099 (0.048)	1.071 (0.018)	1.041 (0.021)	1.050 (0.019)
NL / O	1.081 (0.041)	1.108 (0.008)	1.112 (0.006)	1.099 (0.007)
NL / U	1.063 (0.024)	1.124 (0.013)	1.109 (0.011)	1.086 (0.005)
NM / O	1.102 (0.027)	1.102 (0.008)	1.096 (0.012)	1.086 (0.009)
NM / U	1.101 (0.017)	1.082 (0.026)	1.077 (0.022)	1.082 (0.006)
NH / O	1.049 (0.041)	1.100 (0.006)	1.088 (0.011)	1.085 (0.012)
NH / U	1.109 (0.049)	1.108 (0.032)	1.064 (0.013)	1.069 (0.009)
CpL / O	1.027 (0.046)	1.096 (0.016)	1.074 (0.019)	1.090 (0.009)

Table 2.4.2. continued.

Treatment /chamber	Time (days)	0	7	14	28
CpL / U		1.117 (0.002)	1.109 (0.016)	1.100 (0.007)	1.078 (0.018)
CpM / O		1.082 (0.017)	1.074 (0.031)	1.086 (0.017)	1.065 (0.002)
CpM / U		1.041 (0.024)	1.089 (0.024)	1.100 (0.015)	1.092 (0.016)
CpH / O		1.080 (0.051)	1.088 (0.013)	1.080 (0.013)	1.080 (0.017)
CpH / U		1.083 (0.018)	1.086 (0.013)	1.101 (0.012)	1.100 (0.005)
NCpL / O		1.107 (0.039)	1.090 (0.023)	1.097 (0.009)	1.081 (0.001)
NCpL / U		1.098 (0.052)	1.105 (0.028)	1.086 (0.008)	1.074 (0.008)
NCpM / O		1.099 (0.019)	1.100 (0.009)	1.080 (0.027)	1.066 (0.010)
NCpM / U		1.095 (0.048)	1.104 (0.021)	1.079 (0.017)	1.096 (0.021)
NCpH / O		1.108 (0.022)	1.093 (0.016)	1.074 (0.008)	1.058 (0.026)
NCpH / U		1.055 (0.050)	1.092 (0.019)	1.088 (0.001)	1.063 (0.027)
C / O		1.094 (0.020)	1.112 (0.026)	1.116 (0.024)	1.104 (0.014)
C / U		1.076 (0.007)	1.088 (0.022)	1.111 (0.005)	1.103 (0.006)



Table 2.4.3. Flux experiment 2. Concentrations (mean, (sd);  $\text{mg l}^{-1}$ ) of sulphate in the overlying (O) and underlying (U) water of each treatment. W = whole meiofauna; N=nematodes; Cp=copepods; NCp=nematodes plus copepods; C=control (no meiofauna). L=low density; M=medium density; H=high density. n=9 in all cases.

Treatment /chamber	Time (days)	0	7	14	28
WL / O		2279.08 (39.6299)	2246.56 (66.4381)	2231.69 (33.9707)	2318.49 (32.7103)
WL / U		2147.66 (21.7854)	2209.10 (98.6928)	2238.01 (42.5479)	2207.12 (30.3455)
WM / O		2276.98 (52.4273)	2240.34 (46.8787)	2306.53 (56.3703)	2313.70 (35.3213)
WM / U		2208.40 (72.5736)	2198.57 (60.8761)	2196.21 (52.6171)	2254.38 (38.9902)
WH / O		2186.95 (78.2751)	2253.84 (48.5285)	2291.52 (12.8570)	2365.96 (24.1293)
WH / U		2262.40 (54.5180)	2215.40 (42.4137)	2202.10 (14.3912)	2303.47 (30.4871)
NL / O		2236.09 (122.5497)	2201.19 (16.7495)	2239.97 (19.5413)	2198.94 (53.0937)
NL / U		2228.13 (24.7180)	2200.70 (69.6022)	2165.87 (35.4355)	2195.83 (33.4341)
NM / O		2227.17 (19.8115)	2245.56 (21.6702)	2288.58 (3.8878)	2296.47 (32.3888)
NM / U		2292.67 (38.4397)	2173.86 (51.4573)	2197.54 (38.9701)	2190.75 (39.1772)
NH / O		2216.53 (131.8818)	2253.19 (41.8875)	2264.37 (63.2843)	2308.69 (23.0371)
NH / U		2260.85 (43.9289)	2247.33 (36.9536)	2173.45 (51.7585)	2162.02 (42.1284)
CpL / O		2392.25 (16.3926)	2201.03 (36.0245)	2220.32 (21.2645)	2250.74 (33.5043)

Table 2.4.3. continued.

Treatment /chamber	Time (days)	0	7	14	28
CpL / U		2225.70 (133.2194)	2219.47 (63.3471)	2279.03 (24.0721)	2263.44 (46.2648)
CpM / O		2222.89 (136.8692)	2210.52 (38.9795)	2204.00 (13.0639)	2181.63 (52.2307)
CpM / U		2201.90 (103.3447)	2218.56 (56.3811)	2271.13 (80.8728)	2279.17 (22.0166)
CpH / O		2225.59 (100.3200)	2241.18 (51.9870)	2218.89 (36.0323)	2160.72 (20.9015)
CpH / U		2257.56 (89.4444)	2240.56 (19.7022)	2288.05 (16.4748)	2261.53 (15.4163)
NCpL / O		2237.94 (81.6853)	2211.86 (12.5822)	2209.40 (39.0062)	2252.30 (52.2518)
NCpL / U		2172.76 (39.2690)	2207.69 (53.1521)	2243.25 (23.7499)	2213.95 (16.9844)
NCpM / O		2186.82 (60.5473)	2195.90 (61.0394)	2230.62 (9.7698)	2314.28 (51.3973)
NCpM / U		2281.29 (111.2110)	2222.47 (67.0324)	2207.84 (19.6952)	2255.73 (15.7992)
NCpH / O		2221.93 (59.3755)	2208.82 (51.8092)	2343.98 (9.9629)	2358.54 (18.8616)
NCpH / U		2198.71 (79.3486)	2254.92 (33.3318)	2230.64 (30.0936)	2258.70 (9.0924)
C / O		2285.76 (101.1070)	2196.34 (88.1617)	2248.21 (49.3972)	2291.07 (48.7117)
C / U		2279.80 (66.6653)	2198.36 (8.9146)	2268.96 (43.4991)	2228.04 (53.6928)

Table 2.4.4. Flux experiment 2. Concentrations (mean, (sd);  $\text{mg l}^{-1}$ ) of nitrate in the overlying (O) and underlying (U) water of each treatment. W = whole meiofauna; N=nematodes; Cp=copepods; NCp=nematodes plus copepods; C=control (no meiofauna). L=low density; M=medium density; H=high density. n=9 in all cases.

Treatment /chamber	Time 0 (days)	7	14	28
WL / O	1.7550 (0.0547)	1.6524 (0.0215)	1.6146 (0.0320)	1.5937 (0.0234)
WL / U	1.8222 (0.0671)	1.8961 (0.0217)	1.9546 (0.0374)	1.9615 (0.0536)
WM / O	1.8790 (0.0113)	1.5932 (0.0271)	1.5796 (0.0760)	1.4997 (0.0604)
WM / U	1.7730 (0.0233)	1.9272 (0.0226)	1.9391 (0.0442)	1.9220 (0.0120)
WH / O	1.8596 (0.0893)	1.5092 (0.0254)	1.4498 (0.1600)	1.4239 (0.2164)
WH / U	1.8058 (0.0467)	1.9888 (0.0247)	1.9637 (0.0151)	2.1068 (0.1384)
NL / O	1.7158 (0.2513)	1.7089 (0.0111)	1.6813 (0.0176)	1.6839 (0.0515)
NL / U	1.8256 (0.0551)	1.7882 (0.0145)	1.8294 (0.0079)	1.9024 (0.0615)
NM / O	1.8568 (0.0246)	1.6825 (0.0088)	1.6552 (0.0255)	1.6042 (0.0232)
NM / U	1.8145 (0.1238)	1.8568 (0.0131)	1.8632 (0.0404)	1.9186 (0.0789)
NH / O	1.7608 (0.0388)	1.6601 (0.0109)	1.5812 (0.0164)	1.5152 (0.0430)
NH / U	1.8821 (0.0326)	1.8757 (0.0288)	1.8455 (0.0382)	1.9886 (0.0852)
CpL / O	1.7113 (0.0322)	1.7136 (0.0086)	1.6582 (0.0904)	1.6811 (0.0404)

Table 2.4.4. continued.

Treatment /chamber	Time (days)	0	7	14	28
CpL / U		1.7988 (0.0274)	1.7875 (0.0153)	1.8498 (0.0439)	1.8374 (0.0260)
CpM / O		1.8459 (0.0521)	1.7758 (0.1056)	1.7707 (0.1811)	1.6728 (0.0461)
CpM / U		1.7913 (0.1056)	1.8047 (0.0041)	1.8458 (0.0590)	1.8936 (0.0495)
CpH / O		1.8085 (0.1371)	1.6851 (0.0195)	1.8456 (0.1472)	1.6535 (0.0207)
CpH / U		1.7888 (0.0843)	1.8412 (0.0113)	1.8894 (0.0747)	1.9459 (0.0274)
NCpL / O		1.8386 (0.0752)	1.6681 (0.0178)	1.6367 (0.0155)	1.5993 (0.0142)
NCpL / U		1.7941 (0.0680)	1.8228 (0.0159)	1.8287 (0.0287)	1.8992 (0.0464)
NCpM / O		1.6805 (0.0839)	1.6466 (0.0169)	1.6291 (0.0739)	1.5508 (0.0204)
NCpM / U		1.7161 (0.0677)	1.8694 (0.0262)	1.8806 (0.0265)	1.9730 (0.0809)
NCpH / O		1.7871 (0.0889)	1.6114 (0.0235)	1.5315 (0.0565)	1.4982 (0.1019)
NCpH / U		1.7801 (0.1319)	1.9121 (0.0243)	2.0158 (0.0646)	1.9940 (0.0946)
C / O		1.7861 (0.1005)	1.7177 (0.0051)	1.6562 (0.0691)	1.6657 (0.0019)
C / U		1.8321 (0.1357)	1.7731 (0.0122)	1.7834 (0.0254)	1.8320 (0.0372)

Table 2.4.5. Flux experiment 2. Concentrations (mean, (sd);  $\text{mg l}^{-1}$ ) of ammonia in the overlying (O) and underlying (U) water of each treatment. W = whole meiofauna; N=nematodes; Cp=copepods; NCp=nematodes plus copepods; C=control (no meiofauna). L=low density; M=medium density; H=high density. n=9 in all cases.

Treatment /chamber	Time 0 (days)	7	14	28
WL / O	3.6461 (0.1283)	3.7828 (0.0407)	3.8052 (0.0144)	3.8672 (0.1375)
WL / U	3.6551 (0.0589)	3.4360 (0.0327)	3.5560 (0.0337)	3.5011 (0.0177)
WM / O	3.7484 (0.0888)	3.7266 (0.0478)	3.9255 (0.0523)	3.9408 (0.1558)
WM / U	3.6289 (0.1173)	3.5208 (0.0304)	3.4503 (0.0442)	3.4031 (0.0864)
WH / O	3.8978 (0.1816)	3.7975 (0.0463)	3.9934 (0.1373)	3.8269 (0.1901)
WH / U	3.9363 (0.1131)	3.3666 (0.0274)	3.3619 (0.0831)	3.3720 (0.0863)
NL / O	3.6705 (0.2126)	3.7058 (0.0325)	3.7911 (0.0102)	3.6995 (0.0322)
NL / U	3.7855 (0.0826)	3.6407 (0.0160)	3.6373 (0.0560)	3.5826 (0.0578)
NM / O	3.9091 (0.1822)	3.7726 (0.0231)	3.8720 (0.0528)	3.7813 (0.0595)
NM / U	3.6176 (0.1238)	3.5637 (0.0585)	3.5685 (0.0464)	3.5234 (0.0310)
NH / O	3.6910 (0.0388)	3.7591 (0.0614)	3.8699 (0.0866)	3.9448 (0.0803)
NH / U	3.8612 (0.0326)	3.5162 (0.0825)	3.5068 (0.0407)	3.4240 (0.0511)
CpL / O	3.7373 (0.0322)	3.7588 (0.0579)	3.7310 (0.0557)	3.7476 (0.0225)

Table 2.4.5. continued.

Treatment /chamber	Time (days)	0	7	14	28
CpL / U		3.8307 (0.0274)	3.5917 (0.0340)	3.5152 (0.0159)	3.4447 (0.0305)
CpM / O		3.6823 (0.0521)	3.7882 (0.0358)	3.7948 (0.0734)	3.7930 (0.0380)
CpM / U		3.7890 (0.1056)	3.4785 (0.0268)	3.3666 (0.0274)	3.4559 (0.0633)
CpH / O		3.8816 (0.1371)	3.7962 (0.0235)	3.8688 (0.0693)	3.8492 (0.0794)
CpH / U		3.7781 (0.0843)	3.4886 (0.1102)	3.4018 (0.0242)	3.3991 (0.0182)
NCpL / O		3.6798 (0.0752)	3.7421 (0.0522)	3.8737 (0.0473)	3.8095 (0.0180)
NCpL / U		3.8208 (0.0680)	3.5249 (0.0785)	3.4817 (0.0288)	3.3679 (0.0607)
NCpM / O		3.7560 (0.0839)	3.8009 (0.0629)	3.6938 (0.0609)	3.9739 (0.0682)
NCpM / U		3.8398 (0.0677)	3.4479 (0.1237)	3.4346 (0.0290)	3.3223 (0.0358)
NCpH / O		3.9197 (0.0889)	3.6902 (0.1917)	3.9021 (0.0704)	4.1211 (0.0958)
NCpH / U		3.7717 (0.1319)	3.4929 (0.0742)	3.4505 (0.0539)	3.1797 (0.2149)
C / O		3.6489 (0.1005)	3.7404 (0.0361)	3.6940 (0.0119)	3.7355 (0.0191)
C / U		3.7573 (0.1357)	3.5277 (0.0524)	3.6993 (0.0493)	3.6297 (0.0399)

Table 2.5.1. Flux experiment 2. Coefficients for the best-fit regressions of silicate against time. O = overlying water chamber; U = underlying water chamber. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; C = control. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n = 36 in all cases.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
WL / O	—	$9.765 \times 10^{-3}$ ( $1.918 \times 10^{-3}$ )	1.9768 ( $3.076 \times 10^{-2}$ )	0.8331	****
WL / U	—	$-8.527 \times 10^{-3}$ ( $1.671 \times 10^{-3}$ )	1.9325 ( $2.680 \times 10^{-2}$ )	0.8337	****
WM / O	—	$1.1905 \times 10^{-2}$ ( $6.039 \times 10^{-3}$ )	1.9790 ( $9.687 \times 10^{-2}$ )	0.4827	***
WM / U	$\log_{10} y$	$-1.9826 \times 10^{-3}$ ( $7.539 \times 10^{-4}$ )	0.2864 ( $1.209 \times 10^{-2}$ )	0.5916	****
WH / O	$-1/y$	$2.597 \times 10^{-3}$ ( $1.171 \times 10^{-3}$ )	$-0.4905$ ( $1.878 \times 10^{-2}$ )	0.5128	***
WH / U	$-1/y$	$-2.3127 \times 10^{-3}$ ( $7.865 \times 10^{-4}$ )	$-0.5105$ ( $1.261 \times 10^{-2}$ )	0.6403	****
NL / O	—	$6.318 \times 10^{-3}$ ( $1.346 \times 10^{-3}$ )	1.9449 ( $2.159 \times 10^{-2}$ )	0.8106	****
NL / U	—	$-3.386 \times 10^{-3}$ ( $1.261 \times 10^{-3}$ )	1.9573 ( $2.023 \times 10^{-2}$ )	0.6008	****
NM / O	—	$7.173 \times 10^{-3}$ ( $1.765 \times 10^{-3}$ )	1.9608 ( $2.831 \times 10^{-2}$ )	0.7649	****
NM / U	—	$-4.888 \times 10^{-3}$ ( $1.276 \times 10^{-3}$ )	1.9635 ( $2.047 \times 10^{-2}$ )	0.7443	****
NH / O	—	$1.2732 \times 10^{-2}$ ( $1.391 \times 10^{-3}$ )	1.9559 ( $2.231 \times 10^{-2}$ )	0.9397	****
NH / U	—	$-6.026 \times 10^{-3}$ ( $1.913 \times 10^{-3}$ )	1.9613 ( $3.068 \times 10^{-2}$ )	0.6693	****
CpL / O	—	$6.1687 \times 10^{-3}$ ( $8.959 \times 10^{-4}$ )	1.8826 ( $1.437 \times 10^{-2}$ )	0.8989	****

Table 2.5.1. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
CpL / U	--	-1.003x10 <sup>-3</sup> (1.495x10 <sup>-3</sup> )	1.9051 (2.399x10 <sup>-2</sup> )	0.2302	
CpM / O	--	4.079x10 <sup>-3</sup> (1.752x10 <sup>-3</sup> )	1.9392 (2.810x10 <sup>-2</sup> )	0.5357	****
CpM / U	--	-1.818x10 <sup>-3</sup> (2.291x10 <sup>-3</sup> )	1.8871 (3.674x10 <sup>-2</sup> )	0.1871	
CpH / O	--	8.649x10 <sup>-3</sup> (2.288x10 <sup>-3</sup> )	1.9435 (3.669x10 <sup>-2</sup> )	0.7396	****
CpH / U	-1/y	-2.170x10 <sup>-4</sup> (3.442x10 <sup>-4</sup> )	-0.5225 (5.521x10 <sup>-3</sup> )	0.2408	
NCpL / O	--	8.997x10 <sup>-3</sup> (2.778x10 <sup>-3</sup> )	1.9002 (4.456x10 <sup>-2</sup> )	0.6804	****
NCpL / U	--	-8.578x10 <sup>-3</sup> (1.874x10 <sup>-3</sup> )	1.9280 (3.005x10 <sup>-2</sup> )	0.8031	****
NCpM / O	--	9.185x10 <sup>-3</sup> (2.363x10 <sup>-3</sup> )	1.9594 (3.790x10 <sup>-2</sup> )	0.7497	****
NCpM / U	--	-7.124x10 <sup>-3</sup> (2.064x10 <sup>-3</sup> )	1.9561 (3.311x10 <sup>-2</sup> )	0.7057	****
NCpH / O	-1/y	1.9417x10 <sup>-3</sup> (6.968x10 <sup>-4</sup> )	-0.5099 (1.118x10 <sup>-2</sup> )	0.6173	****
NCpH / U	-1/y	-1.3090x10 <sup>-3</sup> (7.262x10 <sup>-4</sup> )	-0.4935 (1.165x10 <sup>-2</sup> )	0.4123	**
C / O	--	5.939x10 <sup>-3</sup> (2.245x10 <sup>-3</sup> )	1.9037 (3.600x10 <sup>-2</sup> )	0.5941	****
C / U	--	-5.785x10 <sup>-3</sup> (1.567x10 <sup>-3</sup> )	1.8641 (2.513x10 <sup>-2</sup> )	0.7308	****



Table 2.5.2. Flux experiment 2. Coefficients for the best-fit regressions of phosphate against time. O = overlying water chamber; U = underlying water chamber. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; C = control. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n = 36 in all cases.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
WL / O	-1/y	$-2.4253 \times 10^{-3}$ ( $3.772 \times 10^{-4}$ )	$-0.8953$ ( $6.050 \times 10^{-3}$ )	0.8866	****
WL / U	—	$2.20 \times 10^{-4}$ ( $1.111 \times 10^{-3}$ )	$1.0685$ ( $1.782 \times 10^{-2}$ )	0.3098	
WM / O	—	$-2.2027 \times 10^{-3}$ ( $7.936 \times 10^{-4}$ )	$1.0944$ ( $1.273 \times 10^{-2}$ )	0.6156	****
WM / U	—	$-2.799 \times 10^{-3}$ ( $1.059 \times 10^{-3}$ )	$1.1289$ ( $1.699 \times 10^{-2}$ )	0.5933	****
WH / O	-1/y	$-2.291 \times 10^{-4}$ ( $6.931 \times 10^{-4}$ )	$-0.9515$ ( $1.112 \times 10^{-2}$ )	0.2966	
WH / U	—	$-1.7048 \times 10^{-3}$ ( $8.479 \times 10^{-4}$ )	$1.0861$ ( $1.360 \times 10^{-2}$ )	0.4658	***
NL / O	—	$4.707 \times 10^{-4}$ ( $6.340 \times 10^{-4}$ )	$1.0941$ ( $1.017 \times 10^{-2}$ )	0.2074	
NL / U	—	$2.966 \times 10^{-4}$ ( $7.897 \times 10^{-4}$ )	$1.0919$ ( $1.267 \times 10^{-2}$ )	0.2915	
NM / O	—	$6.245 \times 10^{-4}$ ( $3.995 \times 10^{-4}$ )	$1.1041$ ( $6.41 \times 10^{-3}$ )	0.3406	*
NM / U	—	$-5.728 \times 10^{-4}$ ( $5.219 \times 10^{-4}$ )	$1.0926$ ( $8.37 \times 10^{-3}$ )	0.1342	
NH / O	-1/y	$7.772 \times 10^{-4}$ ( $6.809 \times 10^{-4}$ )	$-0.9355$ ( $1.092 \times 10^{-2}$ )	0.1643	
NH / U	-1/y	$-1.338 \times 10^{-3}$ ( $6.927 \times 10^{-4}$ )	$-0.9042$ ( $1.111 \times 10^{-2}$ )	0.4461	***
CpL / O	—	$1.7224 \times 10^{-3}$ ( $9.566 \times 10^{-4}$ )	$1.0561$ ( $1.534 \times 10^{-2}$ )	0.4111	**

Table 2.5.2. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
CpL / U	--	-1.4095x10 <sup>-3</sup> (3.192x10 <sup>-4</sup> )	1.1183 (5.12x10 <sup>-3</sup> )	0.7918	****
CpM / O	-1/y	-4.183x10 <sup>-4</sup> (4.467x10 <sup>-4</sup> )	-0.9238 (7.164x10 <sup>-3</sup> )	0.1049	
CpM / U	-1/y	1.3408x10 <sup>-3</sup> (6.264x10 <sup>-4</sup> )	-0.9428 (1.005x10 <sup>-2</sup> )	0.4960	***
CpH / O	$-\sqrt{y}$	-3.90x10 <sup>-5</sup> (3.441x10 <sup>-4</sup> )	1.0407 (5.52x10 <sup>-3</sup> )	0.3146	
CpH / U	-1/y	5.732x10 <sup>-4</sup> (2.842x10 <sup>-4</sup> )	-0.9225 (4.559x10 <sup>-3</sup> )	0.4669	***
NCpL / O	--	-8.041x10 <sup>-4</sup> (5.969x10 <sup>-4</sup> )	1.1036 (9.57x10 <sup>-3</sup> )	0.2627	
NCpL / U	--	-1.0109x10 <sup>-3</sup> (7.636x10 <sup>-4</sup> )	1.1031 (1.225x10 <sup>-2</sup> )	0.2530	
NCpM / O	-1/y	-1.1300x10 <sup>-3</sup> (4.005x10 <sup>-4</sup> )	-0.9070 (6.424x10 <sup>-3</sup> )	0.6229	****
NCpM / U	-1/y	-8.31x10 <sup>-5</sup> (6.619x10 <sup>-4</sup> )	-0.9140 (1.062x10 <sup>-2</sup> )	0.3130	
NCpH / O	-1/y	-1.5459x10 <sup>-3</sup> (4.180x10 <sup>-4</sup> )	-0.9049 (6.704x10 <sup>-3</sup> )	0.7314	****
NCpH / U	--	-3.81x10 <sup>-5</sup> (8.820x10 <sup>-4</sup> )	1.0748 (1.415x10 <sup>-2</sup> )	0.3162	
C / O	--	2.286x10 <sup>-4</sup> (5.911x10 <sup>-4</sup> )	1.1035 (9.48x10 <sup>-3</sup> )	0.2898	
C / U	-1/y	8.240x10 <sup>-4</sup> (3.450x10 <sup>-4</sup> )	-0.9042 (5.534x10 <sup>-3</sup> )	0.5477	****

Table 2.5.3. Flux experiment 2. Coefficients for the best-fit regressions of sulphate against time. O = overlying water chamber; U = underlying water chamber. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; C = control. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n = 36 in all cases.

Treatment /chamber	transf-ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
WL / O	—	1.653 (1.428)	2248.71 (22.91)	0.1732	
WL / U	-1/y	-3.849x10 <sup>-7</sup> (3.390x10 <sup>-7</sup> )	-4.5947x10 <sup>-4</sup> (4.5947x10 <sup>-4</sup> )	0.1612	
WM / O	—	1.918 (1.367)	2260.89 (21.93)	0.2846	
WM / U	-1/y	-3.698x10 <sup>-7</sup> (2.636x10 <sup>-7</sup> )	-4.4249x10 <sup>-6</sup> (4.228x10 <sup>-6</sup> )	0.1871	
WH / O	—	6.181 (1.231)	2198.82 (19.75)	0.8295	
WH / U	—	-1.838 (1.443)	2223.33 (23.14)	0.2324	****
NL / O	-1/y	-1.6737x10 <sup>-7</sup> (3.642x10 <sup>-7</sup> )	-4.4891x10 <sup>-6</sup> (5.481x10 <sup>-6</sup> )	0.2775	
NL / U	-1/y	-2.2483x10 <sup>-7</sup> (2.607x10 <sup>-7</sup> )	-4.5245x10 <sup>-6</sup> (4.182x10 <sup>-6</sup> )	0.1549	
NM / O	—	2.5712 (0.6487)	2232.95 (10.40)	0.7563	****
NM / U	—	-2.677 (1.552)	2246.50 (24.89)	0.3899	**
NH / O	-1/y	6.400x10 <sup>-7</sup> (3.847x10 <sup>-7</sup> )	-4.5063x10 <sup>-4</sup> (6.170x10 <sup>-6</sup> )	0.3715	*
NH / U	—	-3.822 (1.233)	2257.73 (19.78)	0.6626	****
CpL / O	—	-3.559 (2.113)	2309.68 (33.89)	0.3782	*

Table 2.5.3. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c <sup>r</sup> (sd <sub>c</sub> )	r	p
CpL / U	—	1.680 (2.027)	2226.33 (32.51)	0.1703	
CpM / O	-1/y	-2.6927x10 <sup>-7</sup> (3.947x10 <sup>-7</sup> )	-4.5065x10 <sup>-4</sup> (6.331x10 <sup>-6</sup> )	0.2258	
CpM / U	-1/y	5.998x10 <sup>-7</sup> (3.757x10 <sup>-7</sup> )	-4.5366x10 <sup>-4</sup> (6.026x10 <sup>-6</sup> )	0.3507	*
CpH / O	—	-2.601 (1.563)	2243.46 (25.07)	0.3728	*
CpH / U	—	0.478 (1.277)	2256.06 (20.48)	0.2915	
NCpL / O	—	0.730 (1.404)	2218.93 (22.52)	0.2665	
NCpL / U	-1/y	2.887x10 <sup>-7</sup> (2.267x10 <sup>-7</sup> )	-4.5629x10 <sup>-4</sup> (3.635x10 <sup>-6</sup> )	0.2324	
NCpM / O	—	4.750 (1.295)	2173.72 (20.78)	0.7287	****
NCpM / U	-1/y	-7.6863x10 <sup>-8</sup> (3.680x10 <sup>-7</sup> )	-4.4545x10 <sup>-4</sup> (5.903x10 <sup>-6</sup> )	0.3082	
NCpH / O	—	5.677 (1.471)	2213.78 (23.60)	0.7470	****
NCpH / U	-1/y	3.430x10 <sup>-7</sup> (2.555x10 <sup>-7</sup> )	-4.517x10 <sup>-4</sup> (4.097x10 <sup>-6</sup> )	0.2608	
C / O	—	1.137 (2.180)	2241.42 (34.97)	0.2665	
C / U	—	-0.948 (1.289)	2255.41 (20.67)	0.2074	

Table 2.5.4. Flux experiment 2. Coefficients for the best-fit regressions of nitrate against time. O = overlying water chamber; U = underlying water chamber. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; C = control. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n = 36 in all cases.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
WL / O	-1/y	$-1.8806 \times 10^{-3}$ ( $4.387 \times 10^{-4}$ )	$-0.5826$ ( $7.037 \times 10^{-3}$ )	0.7823	****
WL / U	—	$4.754 \times 10^{-3}$ ( $1.450 \times 10^{-3}$ )	$1.8504$ ( $2.326 \times 10^{-2}$ )	0.6856	****
WM / O	-1/y	$-4.2172 \times 10^{-3}$ ( $9.275 \times 10^{-4}$ )	$-0.5637$ ( $1.488 \times 10^{-2}$ )	0.8006	****
WM / U	-1/y	$1.2513 \times 10^{-3}$ ( $4.984 \times 10^{-4}$ )	$-0.5451$ ( $7.993 \times 10^{-3}$ )	0.5701	***
WH / O	—	$-1.3394 \times 10^{-2}$ ( $4.847 \times 10^{-3}$ )	$1.7244$ ( $7.774 \times 10^{-2}$ )	0.6132	****
WH / U	-1/y	$2.4239 \times 10^{-3}$ ( $5.720 \times 10^{-4}$ )	$-0.5402$ ( $9.175 \times 10^{-3}$ )	0.7791	****
NL / O	-1/y	$-1.95 \times 10^{-4}$ ( $1.120 \times 10^{-3}$ )	$-0.5890$ ( $1.796 \times 10^{-2}$ )	0.3114	
NL / U	—	$3.295 \times 10^{-3}$ ( $1.270 \times 10^{-3}$ )	$1.7690$ ( $2.037 \times 10^{-2}$ )	0.5848	****
NM / O	-1/y	$-2.7164 \times 10^{-3}$ ( $4.881 \times 10^{-4}$ )	$-0.5568$ ( $7.829 \times 10^{-3}$ )	0.8550	****
NM / U	-1/y	$9.934 \times 10^{-4}$ ( $5.571 \times 10^{-4}$ )	$-0.5494$ ( $8.935 \times 10^{-3}$ )	0.4062	**
NH / O	-1/y	$-3.2304 \times 10^{-3}$ ( $3.824 \times 10^{-4}$ )	$-0.5763$ ( $6.133 \times 10^{-3}$ )	0.9301	****
NH / U	—	$3.841 \times 10^{-3}$ ( $1.704 \times 10^{-3}$ )	$1.8509$ ( $2.734 \times 10^{-2}$ )	0.5206	****
CpL / O	-1/y	$-4.806 \times 10^{-4}$ ( $5.240 \times 10^{-4}$ )	$-0.5860$ ( $8.405 \times 10^{-3}$ )	0.1225	

Table 2.5.4. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
CpL / U	-1/y	5.341x10 <sup>-4</sup> (2.797x10 <sup>-4</sup> )	-0.5567 (4.486x10 <sup>-3</sup> )	0.4405	***
CpM / O	-1/y	-1.8942x10 <sup>-3</sup> (8.526x10 <sup>-4</sup> )	-0.5451 (1.368x10 <sup>-2</sup> )	0.5128	****
CpM / U	-1/y	1.1535x10 <sup>-3</sup> (4.912x10 <sup>-4</sup> )	-0.5601 (7.878x10 <sup>-3</sup> )	0.5394	****
CpH / O	-1/y	-1.5312x10 <sup>-3</sup> (6.345x10 <sup>-4</sup> )	-0.5689 (1.018x10 <sup>-2</sup> )	0.5523	****
CpH / U	—	5.415x10 <sup>-3</sup> (1.497x10 <sup>-3</sup> )	1.7992 (2.402x10 <sup>-2</sup> )	0.7232	****
NCpL / O	-1/y	-2.4814x10 <sup>-3</sup> (5.317x10 <sup>-4</sup> )	-0.5654 (8.258x10 <sup>-3</sup> )	0.8087	****
NCpL / U	—	3.651x10 <sup>-3</sup> (1.133x10 <sup>-3</sup> )	1.7915 (1.816x10 <sup>-2</sup> )	0.6790	****
NCpM / O	—	-3.335x10 <sup>-3</sup> (1.499x10 <sup>-3</sup> )	1.6759 (2.404x10 <sup>-2</sup> )	0.5138	***
NCpM / U	—	8.230x10 <sup>-3</sup> (1.760x10 <sup>-3</sup> )	1.7590 (2.823x10 <sup>-2</sup> )	0.8093	****
NCpH / O	-1/y	-3.6498x10 <sup>-3</sup> (9.272x10 <sup>-4</sup> )	-0.5814 (1.487x10 <sup>-2</sup> )	0.7543	****
NCpH / U	—	7.210x10 <sup>-3</sup> (2.755x10 <sup>-3</sup> )	1.8376 (4.418x10 <sup>-2</sup> )	0.5891	****
C / O	—	-4.115x10 <sup>-3</sup> (1.763x10 <sup>-3</sup> )	1.7568 (2.827x10 <sup>-2</sup> )	0.5367	****
C / U	—	5.19x10 <sup>-4</sup> (1.965x10 <sup>-3</sup> )	1.7988 (3.151x10 <sup>-2</sup> )	0.3033	

Table 2.5.5. Flux experiment 2. Coefficients for the best-fit regressions of ammonia against time. O = overlying water chamber; U = underlying water chamber. W = whole meiofauna; N = nematodes; Cp = copepods; NCp = nematodes plus copepods; C = control. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n = 36 in all cases.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
WL / O	--	$7.099 \times 10^{-3}$ ( $2.615 \times 10^{-3}$ )	3.6884 ( $4.194 \times 10^{-2}$ )	0.6058	****
WL / U	--	$-3.377 \times 10^{-3}$ ( $2.410 \times 10^{-3}$ )	3.5784 ( $3.865 \times 10^{-2}$ )	0.2846	
WM / O	-1/y	$1.774 \times 10^{-3}$ ( $2.550 \times 10^{-3}$ )	-0.3079 ( $4.090 \times 10^{-2}$ )	0.2214	
WM / U	-1/y	$-6.256 \times 10^{-4}$ ( $1.676 \times 10^{-4}$ )	-0.2782 ( $2.688 \times 10^{-3}$ )	0.7348	****
WH / O	--	$-9.48 \times 10^{-4}$ ( $4.381 \times 10^{-3}$ )	3.8902 ( $7.027 \times 10^{-2}$ )	0.3082	
WH / U	--	$-1.610 \times 10^{-2}$ ( $5.930 \times 10^{-3}$ )	3.7064 ( $9.511 \times 10^{-2}$ )	0.6058	****
NL / O	--	$1.126 \times 10^{-3}$ ( $3.021 \times 10^{-3}$ )	3.7029 ( $4.846 \times 10^{-2}$ )	0.2915	
NL / U	-1/y	$-3.835 \times 10^{-4}$ ( $1.215 \times 10^{-4}$ )	-0.2693 ( $1.948 \times 10^{-3}$ )	0.6701	****
NM / O	--	$3.174 \times 10^{-3}$ ( $2.898 \times 10^{-3}$ )	3.8726 ( $4.648 \times 10^{-2}$ )	0.1342	
NM / U	-1/y	$-2.107 \times 10^{-4}$ ( $2.467 \times 10^{-4}$ )	-0.2779 ( $3.956 \times 10^{-3}$ )	0.1581	
NH / O	--	$9.125 \times 10^{-3}$ ( $2.423 \times 10^{-3}$ )	3.7053 ( $3.887 \times 10^{-2}$ )	0.7382	****
NH / U	-1/y	$-1.0052 \times 10^{-3}$ ( $2.620 \times 10^{-4}$ )	-0.2679 ( $4.202 \times 10^{-3}$ )	0.7450	****
CpL / O	--	$9.00 \times 10^{-5}$ ( $2.911 \times 10^{-3}$ )	3.7426 ( $4.669 \times 10^{-2}$ )	0.3162	

Table 2.5.5. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
CpL / U	-1/y	-9.502x10 <sup>-4</sup> (1.949x10 <sup>-4</sup> )	-0.2670 (3.126x10 <sup>-3</sup> )	0.8210	****
CpM / O	-√y	8.434x10 <sup>-4</sup> (6.697x10 <sup>-4</sup> )	1.9298 (1.074x10 <sup>-2</sup> )	0.2258	
CpM / U	--	-1.0161x10 <sup>-2</sup> (4.028x10 <sup>-3</sup> )	3.6470 (6.460x10 <sup>-2</sup> )	0.5727	****
CpH / O	--	-2.11x10 <sup>-4</sup> (3.779x10 <sup>-3</sup> )	3.8507 (6.061x10 <sup>-2</sup> )	0.3162	
CpH / U	-1/y	-9.247x10 <sup>-4</sup> (2.724x10 <sup>-4</sup> )	-0.2737 (4.639x10 <sup>-3</sup> )	0.6993	****
NCpL / O	--	4.795x10 <sup>-3</sup> (7.378x10 <sup>-3</sup> )	3.7175 (0.1183)	0.2345	
NCpL / U	-1/y	-1.1118x10 <sup>-3</sup> (2.718x10 <sup>-4</sup> )	-0.2690 (4.360x10 <sup>-3</sup> )	0.7668	****
NCpM / O	--	8.301x10 <sup>-3</sup> (2.665x10 <sup>-3</sup> )	3.7720 (4.274x10 <sup>-2</sup> )	0.6648	****
NCpM / U	-1/y	-1.2342x10 <sup>-3</sup> (3.381x10 <sup>-4</sup> )	-0.2708 (5.422x10 <sup>-3</sup> )	0.7266	****
NCpH / O	--	1.0136x10 <sup>-2</sup> (4.539x10 <sup>-3</sup> )	3.7841 (7.280x10 <sup>-2</sup> )	0.5158	***
NCpH / U	-1/y	-1.6486x10 <sup>-3</sup> (4.278x10 <sup>-4</sup> )	-0.2694 (6.862x10 <sup>-3</sup> )	0.7463	****
C / O	-1/y	1.956x10 <sup>-4</sup> (1.930x10 <sup>-4</sup> )	-0.2712 (3.095x10 <sup>-3</sup> )	0.0548	
C / U	-1/y	-1.476x10 <sup>-4</sup> (2.148x10 <sup>-4</sup> )	-0.2721 (3.445x10 <sup>-3</sup> )	0.2236	



Treatment	WL	WM	WH
WL	X X	0.9815	0.5659
WM	10.8978 ***	X X	0.5015
WH	0.2912	8.7750 **	X X

Table 2.6.1. Flux experiment 2. t-tests comparing initial silicate flux in each density of the whole meiofauna treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NL	NM	NH
NL	X X	5.6588 *	13.1712 ***
NM	1.8733	X X	6.3559 *
NH	2.8327	1.2172	X X

Table 2.6.2. Flux experiment 2. t-tests comparing initial silicate flux in each density of the nematode treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases

Treatment	CpL	CpM	CpH
CpL	X X	2.5542	2.6001
CpM	0.7662	X X	4.1313
CpH	0.2033	0.8964	X X

Table 2.6.3. Flux experiment 2. t-tests comparing initial silicate flux in each density of the copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NCpL	NCpM	NCpH
NCpL	X X	0.0019	0.0015
NCpM	1.3499	X X	1.3014
NCpH	2.4464	1.3006	X X

Table 2.6.4. Flux experiment 2. t-tests comparing initial silicate flux in each density of the nematode plus copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	WL	WM	WH
WL	X X	11.6096 ***	65.0558 ****
WM	4.0895	X X	2.9137
WH	2.7211	1.5787	X X

Table 2.6.5. Flux experiment 2. t-tests comparing initial phosphate flux in each density of the whole meiofauna treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NL	NM	NH
NL	X X	0.3032	0.7533
NM	1.5155	X X	0.5640
NH	3.1415	2.0198	X X

Table 2.6.6. Flux experiment 2. t-tests comparing initial phosphate flux in each density of the nematode treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	CpL	CpM	CpH
CpL	X X	3.5320	2.8012
CpM	6.8302 *	X X	0.8166
CpH	5.7080 *	1.5387	X X

Table 2.6.7. Flux experiment 2. t-tests comparing initial phosphate flux in each density of the copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NCpL	NCpM	NCpH
NCpL	X X	1.1344	2.1471
NCpM	1.5221	X X	1.1135
NCpH	1.7125	0.0988	X X

Table 2.6.8. Flux experiment 2. t-tests comparing initial phosphate flux in each density of the nematode plus copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	WL	WM	WH
WL	X X	0.5808	11.0174 ***
WM	0.1457	X X	10.3734 ***
WH	0.0307	0.1053	X X

Table 2.6.9. Flux experiment 2. t-tests comparing initial sulphate flux in each density of the whole meiofauna treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* = 0.05 > p > 0.02; \*\* = 0.02 > p > 0.01; \*\*\* = 0.01 > p > 0.001; \*\*\*\* = p < 0.001. n=3 in all cases.

Treatment	NL	NM	NH
NL	X X	7.9913 **	3.6708
NM	3.0502	X X	0.9185
NH	6.6174 *	2.7792	X X

Table 2.6.10. Flux experiment 2. t-tests comparing initial sulphate flux in each density of the nematode treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* = 0.05 > p > 0.02; \*\* = 0.02 > p > 0.01; \*\*\* = 0.01 > p > 0.001; \*\*\*\* = p < 0.001. n=3 in all cases.

Treatment	CpL	CpM	CpH
CpL	X X	3.4417	1.8362
CpM	2.0256	X X	2.4441
CpH	2.8178	5.7127 *	X X

Table 2.6.11. Flux experiment 2. t-tests comparing initial sulphate flux in each density of the copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NCpL	NCpM	NCpH
NCpL	X X	9.2993 **	10.0778 ***
NCpM	1.6153	X X	1.8886
NCpH	0.7046	3.0926	X X

Table 2.6.12. Flux experiment 2. t-tests comparing initial sulphate flux in each density of the nematode plus copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	WL	WM	WH
WL	X X	6.7897 *	4.5877 *
WM	0.6623	X X	0.0667
WH	3.9983	4.4520	X X

Table 2.6.13. Flux experiment 2. t-tests comparing initial nitrate flux in each density of the whole meiofauna treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NL	NM	NH
NL	X X	7.9047 **	9.4180 **
NM	0.0043	X X	1.3121
NH	0.6845	0.5910	X X

Table 2.6.14. Flux experiment 2. t-tests comparing initial nitrate flux in each density of the nematode treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	CpL	CpM	CpH
CpL	X X	4.3680 *	3.7120
CpM	2.7740	X X	1.5400
CpH	5.3738 *	2.1794	X X

Table 2.6.15. Flux experiment 2. t-tests comparing initial nitrate flux in each density of the copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NCpL	NCpM	NCpH
NCpL	X X	2.7522	2.6976
NCpM	5.7967 *	X X	0.7188
NCpH	3.3583	0.9021	X X

Table 2.6.16. Flux experiment 2. t-tests comparing initial nitrate flux in each density of the nematode plus copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.



Treatment	WL	WM	WH
WL	X X	0.9891	3.9421
WM	6.0885 *	X X	8.2328 **
WH	6.2987 *	7.7208 **	X X

Table 2.6.17. Flux experiment 2. t-tests comparing initial ammonia flux in each density of the whole meiofauna treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NL	NM	NH
NL	X X	1.9102	8.5813 **
NM	2.2855	X X	6.4169 *
NH	6.2989 *	7.7208 **	X X

Table 2.6.18. Flux experiment 2. t-tests comparing initial ammonia flux in each density of the nematode treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	CpL	CpM	CpH
CpL	X X	1.7755	0.0903
CpM	2.2405	X X	2.1759
CpH	5.2486 *	1.6425	X X

Table 2.6.19. Flux experiment 2. t-tests comparing initial ammonia flux in each density of the copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	NCpL	NCpM	NCpH
NCpL	X X	3.0538	3.1816
NCpM	0.8987	X X	1.1652
NCpH	3.5842	2.8489	X X

Table 2.6.20. Flux experiment 2. t-tests comparing initial ammonia flux in each density of the nemtode plus copepod treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	2.7264	4.0410	0.6149
N	5.7881 *	X X	8.1089 **	2.8914
Cp	8.1103 **	2.8271	X X	2.5971
NCp	5.1051 *	5.6242 *	7.8211 **	X X

Table 2.6.21. Flux experiment 2. t-tests comparing initial flux of silicate in each treatment at low animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	2.9583	4.8972 *	1.6159
N	11.4937 ***	X X	3.1130	1.7876
Cp	2.3807	2.9953	X X	4.5445 *
NCp	10.3550 ***	2.3054	4.6313 *	X X

Table 2.6.22. Flux experiment 2. t-tests comparing initial flux of silicate in each treatment at medium animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	6.7332 *	1.3977	2.0474
N	2.3299	X X	7.0607 **	5.4188 *
Cp	6.4747 *	4.8710 *	X X	0.8946
NCp	2.4061	0.4798	3.4891	X X

Table 2.6.23. Flux experiment 2. t-tests comparing initial flux of silicate in each treatment at high animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	6.3079 *	2.7722	9.6040 **
N	0.1095	X X	2.1418	2.4109
Cp	2.4799	3.0636	X X	3.9870
NCp	1.7673	2.1687	0.9250	X X

Table 2.6.24. Flux experiment 2. t-tests comparing initial flux of phosphate in each treatment at low animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	4.7018 *	2.6727	1.1433
N	3.3913	X X	2.6156	4.7432 *
Cp	6.3345 *	4.0876	X X	1.8655
NCp	10.4217 ***	0.9155	2.7111	X X

Table 2.6.25. Flux experiment 2. t-tests comparing initial flux of phosphate in each treatment at medium animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	1.8803	0.2892	2.8453
N	0.1076	X X	1.6454	4.8814 *
Cp	4.1200	4.0020	X X	3.3586
NCp	2.6649	2.5048	1.3775	X X

Table 2.6.26. Flux experiment 2. t-tests comparing initial flux of phosphate in each treatment at high animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	4.1196	3.0563	1.4410
N	6.8700 *	X X	6.2279 *	3.3291
Cp	0.2118	4.1097	X X	6.0338 *
NCp	1.2001	6.8334 *	0.8059	X X

Table 2.6.27. Flux experiment 2. t-tests comparing initial flux of sulphate in each treatment at low animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	20.6458 ***	0.9128	6.5515 *
N	8.8143 **	X X	6.0101 *	16.8129 ***
Cp	1.6837	9.1786 **	X X	7.9165 **
NCp	2.3205	4.9538 *	4.0835	X X

Table 2.6.28. Flux experiment 2. t-tests comparing initial flux of sulphate in each treatment at medium animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	14.7632 ***	6.8657 *	1.0271
N	13.7488 ***	X X	11.0271 ***	17.9784 ***
Cp	3.1902	10.0886 ***	X X	11.5143 ***
NCp	0.3753	13.1642 ***	2.8779	X X

Table 2.6.29. Flux experiment 2. t-tests comparing initial flux of sulphate in each treatment at high animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	4.0948	5.4428 *	2.7982
N	1.9904	X X	0.8151	6.8414 *
Cp	4.5248	2.4722	X X	7.6747 **
NCp	1.5587	0.5271	3.1884	X X

Table 2.6.30. Flux experiment 2. t-tests comparing initial flux of nitrate in each treatment at low animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	4.4858 *	5.3650 *	3.3002
N	0.9427	X X	2.0840	1.5494
Cp	0.6445	0.4270	X X	3.7011
NCp	4.6129 *	5.2422 *	5.3245 *	X X

Table 2.6.31. Flux experiment 2. t-tests comparing initial flux of nitrate in each treatment at medium animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	3.1603	6.8953 *	1.8139
N	4.9640 *	X X	5.9069 *	1.0026
Cp	3.3715	1.9231	X X	5.2442 *
NCp	0.9506	2.9965	1.6300	X X

Table 2.6.32. Flux experiment 2. t-tests comparing initial flux of nitrate in each treatment at high animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.



Treatment	W	N	Cp	NCp
W	X X	5.4491 *	6.5964 *	0.9226
N	2.7442	X X	0.9627	1.4659
Cp	9.9090 **	8.2236 **	X X	1.8809
NCp	9.0511 **	7.7249 **	1.5268	X X

Table 2.6.33. Flux experiment 2. t-tests comparing initial flux of ammonia in each treatment at low animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	8.3577 **	6.5953 *	5.7206 *
N	1.7907	X X	0.0456	5.1350 *
Cp	6.9359 *	5.2144 *	X X	4.6854 *
NCp	7.8396 **	6.3257 *	4.0773	X X

Table 2.6.34. Flux experiment 2. t-tests comparing initial flux of ammonia in each treatment at medium animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Treatment	W	N	Cp	NCp
W	X X	8.3180 **	0.5346	5.6946 ** *
N	1.5125	X X	6.7183 *	0.6442
Cp	2.7228	1.2598	X X	6.2032 *
NCp	3.1681	4.2509	5.0628 *	X X

Table 2.6.35. Flux experiment 2. t-tests comparing initial flux of ammonia in each treatment at high animal density. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Table 2.7.1. Flux experiment 3. Concentrations of silicate (mean, (sd);  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water chambers of each treatment. S = salinity ( $^{\circ}/_{\infty}$ ); P = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $\text{O}_2$  = partial pressure of oxygen (%); A = animals (as for table 2.4.1). n=9 in all cases.

Treatment /chamber	Time (days)	0	7	14	28
S/5/O		1.872 (0.144)	1.958 (0.121)	2.076 (0.048)	2.324 (0.035)
S/5/U		1.897 (0.187)	1.643 (0.081)	1.476 (0.085)	1.384 (0.142)
S/15/O		1.897 (0.224)	2.132 (0.144)	2.389 (0.163)	2.695 (0.076)
S/15/U		1.932 (0.087)	1.795 (0.104)	1.554 (0.075)	1.234 (0.230)
S/25/O		1.915 (0.241)	2.248 (0.099)	2.548 (0.260)	3.124 (0.163)
S/25/U		1.972 (0.077)	1.358 (0.096)	1.106 (0.067)	0.865 (0.061)
S/35/O		1.863 (0.141)	2.153 (0.081)	2.372 (0.119)	2.853 (0.252)
S/35/U		1.905 (0.118)	1.421 (0.050)	1.154 (0.094)	0.986 (0.177)
S/45/O		1.965 (0.172)	2.021 (0.261)	2.074 (0.043)	2.124 (0.160)
S/45/U		1.950 (0.089)	1.806 (0.098)	1.725 (0.039)	1.655 (0.148)
PS/N/O		1.933 (0.177)	2.158 (0.043)	2.432 (0.103)	2.968 (0.138)
PS/N/U		1.979 (0.149)	1.487 (0.109)	1.262 (0.088)	1.013 (0.091)

Table 2.7.1. continued.

Treatment /chamber	Time (days)	0	7	14	28
PS/Si/O		1.865 (0.099)	2.032 (0.045)	2.159 (0.122)	2.425 (0.086)
PS/Si/U		1.829 (0.106)	1.528 (0.113)	1.379 (0.076)	1.187 (0.159)
PS/VFS/O		1.859 (0.068)	2.086 (0.090)	2.209 (0.047)	2.543 (0.066)
PS/VFS/U		1.950 (0.120)	1.632 (0.036)	1.458 (0.117)	1.283 (0.078)
PS/FS/O		1.769 (0.188)	1.916 (0.140)	2.054 (0.106)	2.355 (0.061)
PS/FS/U		1.956 (0.139)	1.698 (0.088)	1.558 (0.116)	1.472 (0.164)
PS/MS/O		1.728 (0.066)	1.958 (0.136)	2.103 (0.049)	2.465 (0.065)
PS/MS/U		1.925 (0.247)	1.556 (0.188)	1.394 (0.117)	1.214 (0.179)
C/VL/O		1.859 (0.209)	2.065 (0.140)	2.136 (0.047)	2.318 (0.120)
C/VL/U		1.942 (0.106)	1.726 (0.127)	1.628 (0.170)	1.532 (0.093)
C/L/O		1.882 (0.089)	1.974 (0.135)	2.086 (0.035)	2.166 (0.023)
C/L/U		1.853 (0.155)	1.718 (0.122)	1.659 (0.154)	1.586 (0.117)
C/N/O		1.924 (0.136)	2.057 (0.142)	2.214 (0.054)	2.569 (0.171)
C/N/U		1.927 (0.229)	1.814 (0.250)	1.687 (0.060)	1.587 (0.162)
C/H/O		1.946 (0.035)	1.973 (0.132)	2.006 (0.083)	2.056 (0.150)
C/H/U		1.843 (0.149)	1.813 (0.058)	1.797 (0.033)	1.762 (0.117)

Table 2.7.1. continued.

Treatment /chamber	Time (days)	0	7	14	28
C/VH/O		1.876 (0.165)	1.912 (0.190)	1.953 (0.025)	1.998 (0.074)
C/VH/U		1.880 (0.171)	1.838 (0.132)	1.818 (0.050)	1.793 (0.139)
O <sub>2</sub> /0/O		1.886 (0.222)	1.823 (0.077)	1.724 (0.079)	1.654 (0.110)
O <sub>2</sub> /0/U		1.858 (0.084)	1.772 (0.108)	1.685 (0.170)	1.613 (0.068)
O <sub>2</sub> /5/O		1.909 (0.158)	1.954 (0.166)	1.923 (0.069)	1.891 (0.142)
O <sub>2</sub> /5/U		1.778 (0.040)	1.796 (0.162)	1.774 (0.075)	1.784 (0.115)
O <sub>2</sub> /10/O		1.789 (0.198)	1.812 (0.132)	1.853 (0.060)	1.924 (0.050)
O <sub>2</sub> /10/U		1.809 (0.085)	1.724 (0.145)	1.685 (0.090)	1.631 (0.082)
O <sub>2</sub> /15/O		1.992 (0.111)	2.003 (0.166)	2.012 (0.121)	2.074 (0.087)
O <sub>2</sub> /15/U		1.944 (0.098)	1.736 (0.074)	1.783 (0.039)	1.821 (0.126)
O <sub>2</sub> /21/O		1.872 (0.078)	1.983 (0.197)	2.086 (0.090)	2.213 (0.060)
O <sub>2</sub> /21/U		1.855 (0.104)	1.715 (0.060)	1.672 (0.050)	1.625 (0.133)
A/N/O		1.893 (0.129)	1.946 (0.032)	1.993 (0.027)	2.062 (0.068)
A/N/U		1.778 (0.126)	1.712 (0.048)	1.698 (0.038)	1.685 (0.103)
A/Cp/O		1.935 (0.234)	1.987 (0.032)	2.013 (0.070)	2.083 (0.045)
A/Cp/U		1.935 (0.091)	1.897 (0.063)	1.855 (0.035)	1.815 (0.093)

Table 2.7.1. continued.

Treatment /chamber	Time (days)	0	7	14	28
A/NCp/O		1.859 (0.066)	1.973 (0.046)	2.101 (0.108)	2.214 (0.043)
A/NCp/U		1.892 (0.125)	1.827 (0.060)	1.812 (0.076)	1.794 (0.116)
A/W/O		1.992 (0.096)	2.124 (0.162)	2.176 (0.076)	2.312 (0.045)
A/W/U		1.942 (0.122)	1.763 (0.109)	1.654 (0.063)	1.524 (0.058)
A/Co/O		1.811 (0.098)	1.895 (0.072)	1.965 (0.115)	2.113 (0.090)
A/Co/U		1.874 (0.121)	1.792 (0.143)	1.672 (0.152)	1.587 (0.124)

Table 2.7.2. Flux experiment 3. Concentrations of phosphate (mean, (sd);  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water chambers of each treatment. S = salinity ( $^{\circ}/_{\infty}$ ); P = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $\text{O}_2$  = partial pressure of oxygen (%); A = animals (as for table 2.4.1). n=9 in all cases.

Treatment /chamber	Time (days)	0	7	14	28
S/5/O		1.132 (0.062)	1.458 (0.072)	1.675 (0.071)	1.891 (0.110)
S/5/U		1.072 (0.104)	0.832 (0.052)	0.683 (0.051)	0.314 (0.129)
S/15/O		1.154 (0.077)	1.543 (0.068)	1.734 (0.058)	1.964 (0.087)
S/15/U		1.100 (0.063)	0.926 (0.054)	0.712 (0.037)	0.298 (0.107)
S/25/O		1.138 (0.121)	1.672 (0.086)	1.932 (0.098)	2.184 (0.120)
S/25/U		1.110 (0.039)	0.836 (0.031)	0.654 (0.047)	0.203 (0.026)
S/35/O		1.036 (0.069)	1.785 (0.069)	2.314 (0.094)	2.743 (0.018)
S/35/U		1.085 (0.118)	0.794 (0.025)	0.583 (0.040)	0.186 (0.070)
S/45/O		1.111 (0.052)	1.773 (0.111)	1.958 (0.067)	2.521 (0.011)
S/45/U		1.124 (0.121)	0.936 (0.046)	0.727 (0.074)	0.315 (0.117)
PS/N/O		0.992 (0.070)	1.326 (0.072)	1.413 (0.073)	1.624 (0.018)
PS/N/U		1.119 (0.103)	0.853 (0.046)	0.786 (0.061)	0.435 (0.086)

Table 2.7.2. continued.

Treatment /chamber	Time (days)	0	7	14	28
PS/Si/O		1.107 (0.123)	1.412 (0.051)	1.532 (0.119)	1.786 (0.105)
PS/Si/U		1.082 (0.081)	0.843 (0.021)	0.694 (0.071)	0.318 (0.124)
PS/VFS/O		1.091 (0.107)	1.416 (0.099)	1.614 (0.093)	1.836 (0.107)
PS/VFS/U		1.091 (0.073)	0.826 (0.033)	0.678 (0.092)	0.265 (0.033)
PS/FS/O		1.118 (0.119)	1.316 (0.058)	1.418 (0.094)	1.528 (0.116)
PS/FS/U		1.003 (0.035)	0.823 (0.037)	0.674 (0.070)	0.385 (0.098)
PS/MS/O		1.194 (0.052)	1.387 (0.059)	1.507 (0.058)	1.624 (0.078)
PS/MS/U		1.071 (0.111)	0.875 (0.098)	0.724 (0.044)	0.412 (0.084)
C/VL/O		1.065 (0.142)	1.394 (0.082)	1.613 (0.041)	1.784 (0.065)
C/VL/U		1.063 (0.119)	0.854 (0.110)	0.693 (0.062)	0.325 (0.035)
C/L/O		1.169 (0.052)	1.452 (0.090)	1.632 (0.044)	1.862 (0.061)
C/L/U		1.164 (0.075)	0.765 (0.081)	0.572 (0.073)	0.285 (0.108)
C/N/O		0.989 (0.030)	1.436 (0.079)	1.687 (0.074)	1.958 (0.073)
C/N/U		0.976 (0.013)	0.795 (0.033)	0.602 (0.035)	0.175 (0.114)
C/H/O		1.045 (0.061)	1.412 (0.070)	1.594 (0.064)	1.725 (0.058)
C/H/U		1.117 (0.065)	0.832 (0.099)	0.687 (0.090)	0.233 (0.072)



Table 2.7.2. continued.

Treatment /chamber	Time (days)	0	7	14	28
C/VH/O		1.053 (0.049)	1.258 (0.081)	1.397 (0.069)	1.506 (0.136)
C/VH/U		1.065 (0.089)	0.865 (0.078)	0.665 (0.055)	0.297 (0.116)
O <sub>2</sub> /0/O		1.137 (0.064)	1.198 (0.069)	1.233 (0.062)	1.354 (0.128)
O <sub>2</sub> /0/U		1.119 (0.075)	1.091 (0.058)	1.086 (0.089)	0.987 (0.074)
O <sub>2</sub> /5/O		1.083 (0.110)	1.247 (0.087)	1.408 (0.047)	1.562 (0.047)
O <sub>2</sub> /5/U		1.041 (0.111)	1.002 (0.075)	0.943 (0.049)	0.854 (0.021)
O <sub>2</sub> /10/O		1.116 (0.118)	1.352 (0.090)	1.479 (0.046)	1.624 (0.074)
O <sub>2</sub> /10/U		1.115 (0.035)	0.996 (0.065)	0.935 (0.076)	0.801 (0.101)
O <sub>2</sub> /15/O		1.107 (0.121)	1.487 (0.050)	1.586 (0.075)	1.731 (0.108)
O <sub>2</sub> /15/U		1.071 (0.113)	0.935 (0.056)	0.886 (0.054)	0.733 (0.034)
O <sub>2</sub> /21/O		1.058 (0.057)	1.501 (0.079)	1.734 (0.032)	1.986 (0.093)
O <sub>2</sub> /21/U		1.030 (0.078)	0.941 (0.031)	0.804 (0.032)	0.685 (0.053)
A/N/O		1.102 (0.086)	1.413 (0.033)	1.572 (0.044)	1.798 (0.097)
A/N/U		1.102 (0.111)	0.963 (0.067)	0.758 (0.080)	0.526 (0.070)
A/Cp/O		1.042 (0.089)	1.472 (0.132)	1.654 (0.034)	1.859 (0.096)
A/Cp/U		1.068 (0.145)	0.887 (0.042)	0.794 (0.110)	0.438 (0.082)

Table 2.7.2. continued.

Treatment /chamber	Time (days)	0	7	14	28
A/NCp/O		1.033 (0.088)	1.538 (0.089)	1.783 (0.047)	2.013 (0.081)
A/NCp/U		1.073 (0.114)	0.843 (0.049)	0.684 (0.074)	0.249 (0.074)
A/W/O		1.089 (0.134)	1.634 (0.069)	1.824 (0.077)	2.191 (0.034)
A/W/U		1.024 (0.097)	0.832 (0.065)	0.593 (0.018)	0.124 (0.073)
A/Co/O		1.098 (0.096)	1.384 (0.053)	1.559 (0.078)	1.787 (0.102)
A/Co/U		1.049 (0.099)	0.943 (0.081)	0.782 (0.049)	0.432 (0.064)

Table 2.7.3. Flux experiment 3. Concentrations of sulphate (mean, (sd);  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water chambers of each treatment. S = salinity ( $^{\circ}/_{\infty}$ ); P = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $\text{O}_2$  = partial pressure of oxygen (%); A = animals (as for table 2.4.1). n=9 in all cases.

Treatment /chamber	Time (days)	0	7	14	28
S/5/O		2243.22 (143.72)	2194.38 (82.84)	2126.43 (113.16)	2087.43 (59.42)
S/5/U		2336.20 (82.24)	2463.24 (68.41)	2498.42 (90.12)	2548.36 (62.82)
S/15/O		2171.63 (113.71)	2164.35 (117.50)	2158.42 (131.10)	2123.62 (90.69)
S/15/U		2205.90 (95.77)	2228.72 (127.33)	2239.64 (152.41)	2256.43 (117.13)
S/25/O		2321.63 (144.07)	2304.38 (63.16)	2265.73 (85.15)	2214.58 (100.63)
S/25/U		2263.40 (92.09)	2213.58 (152.06)	2194.63 (90.10)	2184.76 (48.67)
S/35/O		2142.47 (142.40)	2110.17 (112.06)	2086.42 (62.79)	2034.64 (77.83)
S/35/U		2235.50 (42.03)	2376.52 (93.00)	2485.42 (139.47)	2565.72 (94.70)
S/45/O		2272.40 (188.69)	2187.94 (140.28)	2136.58 (72.67)	2085.19 (21.45)
S/45/U		2278.40 (118.40)	2369.86 (88.38)	2412.36 (52.78)	2487.32 (120.86)
PS/N/O		2121.07 (105.22)	2106.42 (48.83)	2083.27 (117.93)	2042.53 (72.35)
PS/N/U		2096.60 (50.58)	2112.64 (79.14)	2128.62 (108.45)	2132.46 (71.83)

Table 2.7.3. continued.

Treatment /chamber	Time (days)	0	7	14	28
PS/Si/O		2234.03 (142.86)	2201.67 (82.61)	2187.36 (96.05)	2132.46 (74.12)
PS/Si/U		2259.57 (153.38)	2398.62 (78.76)	2425.67 (127.77)	2585.46 (94.53)
PS/VFS/O		2166.20 (171.78)	2145.37 (39.14)	2124.35 (42.02)	2085.75 (59.20)
PS/VFS/U		2195.23 (87.59)	2286.43 (121.66)	2301.43 (75.13)	2358.59 (56.37)
PS/FS/O		2335.40 (141.22)	2285.77 (66.69)	2216.72 (7.83)	2110.25 (49.10)
PS/FS/U		2305.40 (60.20)	2359.46 (109.18)	2398.98 (102.06)	2463.28 (74.50)
PS/MS/O		2166.80 (128.20)	2124.36 (138.36)	2094.37 (134.71)	2032.24 (67.48)
PS/MS/U		2357.77 (54.93)	2301.52 (49.16)	2275.64 (125.04)	2246.17 (86.45)
C/VL/O		2261.50 (72.53)	2185.42 (138.32)	2132.16 (32.28)	2096.43 (75.30)
C/VL/U		2217.57 (110.42)	2376.24 (119.97)	2418.63 (59.07)	2586.42 (127.03)
C/L/O		2292.20 (129.63)	2215.36 (41.78)	2146.52 (99.59)	2058.58 (145.97)
C/L/U		2405.13 (103.56)	2358.26 (58.19)	2356.26 (122.70)	2352.43 (41.17)
C/N/O		2164.07 (110.17)	2125.62 (40.28)	2110.53 (30.96)	2063.42 (119.89)
C/N/U		2125.17 (33.04)	2276.24 (92.13)	2317.62 (128.69)	2451.62 (65.09)
C/H/O		2324.17 (90.62)	2228.36 (146.11)	2154.72 (122.07)	2085.75 (63.18)
C/H/U		2373.80 (85.04)	2489.62 (55.13)	2501.10 (147.75)	2514.38 (66.22)

Table 2.7.3. continued.

Treatment /chamber	Time (days)	0	7	14	28
C/VH/O		2122.70 (139.34)	2119.64 (116.44)	2115.43 (89.02)	2101.20 (101.59)
C/VH/U		2175.13 (113.91)	2365.24 (73.12)	2485.17 (62.40)	2614.73 (33.82)
O <sub>2</sub> /0/O		2242.03 (104.38)	2228.63 (31.64)	2213.72 (54.34)	2182.62 (84.35)
O <sub>2</sub> /0/U		2397.83 (127.29)	2317.62 (44.38)	2298.64 (142.70)	2246.73 (56.39)
O <sub>2</sub> /5/O		2274.07 (110.53)	2223.33 (23.65)	2198.63 (73.25)	2164.73 (28.01)
O <sub>2</sub> /5/U		2376.80 (31.80)	2362.42 (108.00)	2360.10 (105.93)	2358.24 (110.41)
O <sub>2</sub> /10/O		2221.00 (145.13)	2199.64 (74.29)	2178.78 (109.11)	2124.86 (32.69)
O <sub>2</sub> /10/U		2070.00 (148.23)	2186.73 (77.21)	2217.64 (46.88)	2297.64 (59.15)
O <sub>2</sub> /15/O		2304.87 (144.03)	2253.54 (76.72)	2209.64 (45.97)	2099.73 (110.64)
O <sub>2</sub> /15/U		2247.70 (120.50)	2316.24 (124.99)	2368.42 (142.26)	2427.72 (83.09)
O <sub>2</sub> /21/O		2255.30 (128.30)	2196.54 (86.85)	2124.36 (140.53)	2053.42 (95.68)
O <sub>2</sub> /21/U		2264.67 (89.14)	2376.76 (127.77)	2419.62 (35.11)	2517.64 (40.97)
A/N/O		2308.80 (149.24)	2278.63 (105.05)	2234.72 (109.26)	2126.32 (111.71)
A/N/U		2083.57 (116.59)	2196.24 (92.11)	2219.86 (18.63)	2385.72 (106.85)
A/Cp/O		2206.97 (99.29)	2179.23 (56.18)	2157.72 (95.62)	2104.62 (134.45)
A/Cp/U		2334.00 (77.13)	2389.43 (25.90)	2401.26 (69.57)	2417.26 (69.51)

Table 2.7.3. continued.

Treatment /chamber	Time (days)	0	7	14	28
A/NCp/O		2094.60 (92.82)	2068.27 (72.25)	2043.62 (104.52)	1998.16 (74.15)
A/NCp/U		2274.43 (127.82)	2376.65 (129.17)	2483.32 (62.19)	2502.53 (53.58)
A/W/O		2222.13 (140.01)	2177.63 (119.98)	2132.58 (121.76)	2083.24 (123.79)
A/W/U		2128.17 (157.50)	2312.96 (69.57)	2427.76 (137.49)	2543.62 (78.00)
A/Co/O		2245.10 (108.43)	2209.45 (88.98)	2187.65 (110.71)	2110.76 (93.17)
A/Co/U		2350.80 (90.44)	2320.43 (118.79)	2305.46 (110.55)	2296.42 (97.91)

Table 2.7.4. Flux experiment 3. Concentrations of nitrate (mean, (sd);  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water chambers of each treatment. S = salinity ( $^{\circ}/_{\infty}$ ); P = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $\text{O}_2$  = partial pressure of oxygen (%); A = animals (as for table 2.4.1).  $n=9$  in all cases.

Treatment /chamber	Time (days)	0	7	14	28
S/5/O		1.7610 (0.0580)	1.7214 (0.1501)	1.6986 (0.0918)	1.6324 (0.0680)
S/5/U		1.7768 (0.0442)	1.8234 (0.1094)	1.8538 (0.0597)	1.8824 (0.0239)
S/15/O		1.8127 (0.1743)	1.7968 (0.0596)	1.7543 (0.0401)	1.7154 (0.0526)
S/15/U		1.8866 (0.0749)	1.8818 (0.0520)	1.8801 (0.0558)	1.8794 (0.0452)
S/25/O		1.6976 (0.1055)	1.6823 (0.1064)	1.6786 (0.0258)	1.6536 (0.0566)
S/25/U		1.7209 (0.0222)	1.7864 (0.0950)	1.8042 (0.0616)	1.8418 (0.0624)
S/35/O		1.7603 (0.0854)	1.7134 (0.0966)	1.6142 (0.0123)	1.5125 (0.0650)
S/35/U		1.8487 (0.861)	1.9126 (0.0243)	1.9362 (0.0201)	1.9543 (0.0161)
S/45/O		1.8065 (0.1014)	1.7653 (0.0525)	1.7186 (0.0246)	1.6245 (0.0529)
S/45/U		1.9577 (0.0206)	1.9123 (0.0702)	1.8863 (0.0756)	1.8624 (0.0178)
PS/N/O		1.8935 (0.0689)	1.7962 (0.0651)	1.7358 (0.1139)	1.5186 (0.1050)
PS/N/U		1.7917 (0.0743)	1.8487 (0.0887)	1.8754 (0.0389)	1.9082 (0.0292)

Table 2.7.4. continued.

Treatment /chamber	Time (days)	0	7	14	28
PS/Si/O		1.8670 (0.1832)	1.7986 (0.1029)	1.7286 (0.0438)	1.6943 (0.1090)
PS/Si/U		1.9120 (0.0327)	1.9186 (0.0570)	1.9218 (0.0632)	1.9263 (0.0709)
PS/VFS/O		1.7489 (0.0167)	1.7104 (0.0868)	1.6747 (0.0124)	1.6016 (0.0825)
PS/VFS/U		1.7173 (0.0352)	1.7896 (0.0680)	1.8263 (0.0468)	1.8644 (0.0163)
PS/FS/O		1.8894 (0.0714)	1.8136 (0.1347)	1.7214 (0.0250)	1.5124 (0.0410)
PS/FS/U		1.8474 (0.1000)	1.8726 (0.0646)	1.8847 (0.0299)	1.8926 (0.0114)
PS/MS/O		1.7749 (0.0645)	1.7446 (0.0360)	1.7101 (0.0279)	1.6243 (0.0303)
PS/MS/U		1.7734 (0.0694)	1.8543 (0.0720)	1.8987 (0.1241)	1.9436 (0.0218)
C/VL/O		1.8807 (0.0746)	1.7133 (0.0604)	1.6823 (0.0775)	1.5187 (0.1159)
C/VL/U		1.8868 (0.0115)	1.8764 (0.0421)	1.8748 (0.0300)	1.8724 (0.0157)
C/L/O		1.7953 (0.0896)	1.7355 (0.1140)	1.6987 (0.0253)	1.6243 (0.0415)
C/L/U		1.7316 (0.1070)	1.7853 (0.0605)	1.8138 (0.0440)	1.8463 (0.0285)
C/N/O		1.9486 (0.0778)	1.8124 (0.0752)	1.7543 (0.0180)	1.5267 (0.0842)
C/N/U		1.7997 (0.1083)	1.8546 (0.0384)	1.8756 (0.0437)	1.9186 (0.0236)
C/H/O		1.7958 (0.0605)	1.7783 (0.0541)	1.7112 (0.0258)	1.6483 (0.1360)
C/H/U		1.7281 (0.0582)	1.8237 (0.1201)	1.8698 (0.0394)	1.9246 (0.0257)



Table 2.7.4. continued.

Treatment /chamber	Time (days)	0	7	14	28
C/VH/O		1.8603 (0.0887)	1.8243 (0.0219)	1.7862 (0.0131)	1.7216 (0.1359)
C/VH/U		1.8257 (0.0265)	1.8358 (0.0393)	1.8392 (0.0643)	1.8432 (0.1098)
O <sub>2</sub> /0/O		1.7649 (0.0690)	1.7712 (0.0971)	1.7743 (0.1111)	1.7862 (0.1078)
O <sub>2</sub> /0/U		1.6741 (0.3888)	1.7214 (0.1019)	1.7843 (0.0609)	1.8642 (0.0231)
O <sub>2</sub> /5/O		1.7700 (0.0655)	1.7562 (0.0943)	1.7358 (0.0381)	1.7146 (0.0701)
O <sub>2</sub> /5/U		1.7710 (0.0747)	1.8136 (0.0519)	1.8542 (0.1128)	1.8987 (0.1081)
O <sub>2</sub> /10/O		1.8566 (0.1182)	1.8124 (0.1117)	1.7624 (0.0647)	1.6243 (0.0768)
O <sub>2</sub> /10/U		1.8970 (0.0923)	1.9091 (0.0569)	1.9063 (0.1027)	1.9102 (0.0174)
O <sub>2</sub> /15/O		1.7122 (0.1250)	1.6868 (0.1246)	1.6514 (0.1296)	1.5164 (0.0787)
O <sub>2</sub> /15/U		1.7043 (0.10598)	1.8146 (0.0693)	1.8724 (0.0561)	1.9240 (0.0714)
O <sub>2</sub> /21/O		1.8724 (0.0899)	1.8102 (0.0689)	1.7109 (0.1139)	1.5068 (0.0619)
O <sub>2</sub> /21/U		1.8478 (0.0813)	1.8738 (0.0562)	1.8858 (0.0419)	1.9036 (0.0374)
A/N/O		1.4663 (0.0434)	1.5236 (0.1049)	1.5863 (0.0261)	1.6428 (0.0323)
A/N/U		1.9088 (0.0191)	1.9126 (0.0437)	1.9158 (0.0542)	1.9197 (0.1096)
A/Cp/O		1.8395 (0.0477)	1.7864 (0.1001)	1.7124 (0.1055)	1.5963 (0.0782)
A/Cp/U		1.7929 (0.0496)	1.8543 (0.0194)	1.8787 (0.0409)	1.9068 (0.0251)

Table 2.7.4. continued.

Treatment /chamber	Time (days)	0	7	14	28
<hr/>					
A/NCp/O		1.9688 (0.0926)	1.8126 (0.1034)	1.7438 (0.1090)	1.5492 (0.0298)
A/NCp/U		1.7609 (0.0245)	1.8437 (0.0147)	1.8768 (0.1068)	1.9124 (0.1071)
A/W/O		1.7649 (0.0555)	1.6909 (0.0786)	1.6402 (0.0675)	1.5362 (0.0713)
A/W/U		1.7802 (0.0347)	1.8762 (0.0615)	1.9342 (0.0399)	1.9863 (0.1037)
A/Co/O		1.8404 (0.0212)	1.7864 (0.1022)	1.7132 (0.0805)	1.6872 (0.0850)
A/Co/U		1.7744 (0.0247)	1.8096 (0.0249)	1.8263 (0.0482)	1.8423 (0.0938)
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Table 2.7.5. Flux experiment 3. Concentrations of ammonia (mean, (sd);  $\text{mg l}^{-1}$ ) in the overlying (O) and underlying (U) water chambers of each treatment. S = salinity ( $^{\circ}/_{\infty}$ ); P = particle size range (N = natural; Si = silt; VFS = very fine sand; FS = fine sand; MS = medium sand); C = compaction (VL = very low; L = low; N = natural; H = high; VH = very high);  $\text{O}_2$  = partial pressure of oxygen (%); A = animals (as for table 2.4.1).  $n=9$  in all cases.

Treatment /chamber	Time (days)	0	7	14	28
S/5/O		3.7123 (0.1963)	3.7827 (0.0754)	2.8514 (0.1071)	4.0012 (0.0638)
S/5/U		3.8852 (0.0987)	3.8126 (0.0605)	3.7528 (0.1039)	3.5724 (0.0906)
S/15/O		3.7160 (0.1114)	3.7564 (0.1193)	3.8487 (0.1028)	4.0572 (0.0988)
S/15/U		4.0899 (0.1442)	3.9124 (0.0795)	3.7624 (0.0249)	3.4263 (0.0894)
S/25/O		3.6982 (0.0697)	3.7717 (0.1113)	3.8862 (0.1105)	4.2161 (0.0541)
S/25/U		3.8751 (0.0373)	3.7657 (0.1264)	3.6518 (0.1086)	3.2126 (0.0652)
S/35/O		3.5985 (0.1355)	3.7123 (0.0849)	3.8243 (0.1239)	4.1183 (0.1185)
S/35/U		3.9117 (0.1611)	3.7572 (0.0561)	3.6187 (0.0399)	3.3187 (0.0489)
S/45/O		3.7277 (0.0271)	3.8124 (0.0802)	3.8564 (0.0243)	4.0264 (0.0583)
S/45/U		3.7925 (0.1537)	3.7124 (0.1101)	3.5545 (0.0541)	3.4572 (0.0507)
PS/N/O		3.6508 (0.1418)	3.7133 (0.0837)	3.8252 (0.1023)	4.1096 (0.0365)
PS/N/U		3.8108 (0.1163)	3.7564 (0.0330)	3.5264 (0.1434)	3.3072 (0.1259)

Table 2.7.5. continued.

Treatment /chamber	Time (days)	0	7	14	28
PS/Si/O		3.7999 (0.0390)	3.8564 (0.0807)	3.9543 (0.0931)	4.1182 (0.1241)
PS/Si/U		3.7264 (0.1043)	3.6826 (0.1014)	3.4863 (0.0473)	3.2186 (0.0340)
PS/VFS/O		3.5670 (0.1729)	3.7127 (0.0596)	3.8264 (0.0636)	4.0963 (0.0887)
PS/VFS/U		3.8459 (0.1264)	3.7394 (0.0618)	3.6924 (0.1160)	3.4192 (0.1004)
PS/FS/O		3.6459 (0.1419)	3.7136 (0.0438)	3.7863 (0.0718)	3.9824 (0.1074)
PS/FS/U		3.8737 (0.1085)	3.8137 (0.0874)	3.7185 (0.0720)	3.6524 (0.1080)
PS/MS/O		3.5555 (0.1629)	3.6107 (0.0572)	3.6995 (0.1129)	3.9256 (0.0477)
PS/MS/U		3.8257 (0.0970)	3.7624 (0.0595)	3.7011 (0.0516)	3.5874 (0.0960)
C/VL/O		3.7994 (0.1104)	3.8257 (0.0315)	3.8564 (0.0446)	4.1982 (0.1402)
C/VL/U		3.9263 (0.1035)	3.7128 (0.0538)	3.6587 (0.0781)	3.4824 (0.1099)
C/L/O		3.7642 (0.1981)	3.8714 (0.0328)	3.9624 (0.0755)	4.1386 (0.0260)
C/L/U		3.9835 (0.0640)	3.8543 (0.0386)	3.7575 (0.0616)	3.5476 (0.0636)
C/N/O		3.9394 (0.1697)	3.9779 (0.0359)	4.0562 (0.0519)	4.1123 (0.0821)
C/N/U		3.7169 (0.1435)	3.6767 (0.1032)	3.6589 (0.0359)	3.6263 (0.1179)
C/H/O		3.8061 (0.1544)	3.8514 (0.0906)	3.9143 (0.1048)	4.0987 (0.0867)
C/H/U		3.7900 (0.1504)	3.7124 (0.0865)	3.6217 (0.0509)	3.5464 (0.1184)

Table 2.7.5. continued.

Treatment /chamber	Time (days)	0	7	14	28
C/VH/O		4.0550 (0.0492)	4.0386 (0.0850)	4.0286 (0.0589)	4.0013 (0.1043)
C/VH/U		3.5318 (0.0465)	3.5684 (0.0408)	3.5987 (0.1235)	3.6519 (0.0585)
O <sub>2</sub> /0/O		4.0100 (0.0875)	4.0796 (0.0650)	4.1543 (0.0121)	4.3016 (0.0527)
O <sub>2</sub> /0/U		3.7037 (0.0975)	3.4263 (0.1063)	3.3124 (0.1260)	2.8764 (0.0765)
O <sub>2</sub> /5/O		3.6991 (0.1275)	3.9918 (0.0632)	4.4526 (0.0722)	4.3527 (0.0180)
O <sub>2</sub> /5/U		3.9633 (0.1126)	3.6486 (0.1504)	3.4586 (0.1084)	3.0012 (0.0829)
O <sub>2</sub> /10/O		3.9929 (0.0928)	4.0126 (0.0699)	4.1526 (0.0309)	4.2364 (0.0651)
O <sub>2</sub> /10/U		3.9985 (0.0702)	3.6254 (0.1212)	3.4758 (0.0929)	3.0108 (0.0614)
O <sub>2</sub> /15/O		3.6892 (0.1636)	3.7217 (0.1215)	3.8272 (0.1095)	4.1124 (0.0938)
O <sub>2</sub> /15/U		3.9919 (0.0474)	3.7864 (0.1037)	3.6242 (0.0906)	3.2874 (0.1081)
O <sub>2</sub> /21/O		3.8168 (0.0319)	3.9016 (0.1008)	3.9826 (0.1293)	4.0986 (0.1026)
O <sub>2</sub> /21/U		3.9120 (0.0853)	3.8216 (0.0503)	3.6517 (0.0638)	3.4196 (0.0641)
A/N/O		3.8732 (0.0415)	3.8943 (0.1261)	3.9127 (0.0889)	3.9576 (0.1028)
A/N/U		3.7876 (0.1019)	3.7214 (0.0487)	3.6572 (0.0650)	3.5926 (0.0312)
A/Cp/O		3.7646 (0.0782)	3.8143 (0.0140)	3.8564 (0.0365)	3.9487 (0.0845)
A/Cp/U		3.7639 (0.0427)	3.7358 (0.0512)	3.7126 (0.1095)	3.6344 (0.1155)

Table 2.7.5. continued.

Treatment /chamber	Time (days)	0 (minutes)	7 (days)	14 (days)	28 (days)
A/NCp/O		3.9492 (0.1134)	3.9617 (0.0943)	3.9827 (0.0854)	4.0858 (0.0493)
A/NCp/U		3.7675 (0.0706)	3.6917 (0.0979)	3.6235 (0.0699)	3.4253 (0.0546)
A/W/O		3.7550 (0.1425)	3.8551 (0.0380)	3.9551 (0.1023)	4.1263 (0.0244)
A/W/U		3.6912 (0.1915)	3.6011 (0.0141)	3.5124 (0.1025)	3.3862 (0.1086)
A/Co/O		3.7256 (0.0989)	3.7573 (0.1076)	3.7862 (0.1027)	3.8424 (0.0397)
A/Co/U		3.9310 (0.1185)	3.8264 (0.0769)	3.7251 (0.0571)	3.6724 (0.1012)

Table 2.8.1. Flux experiment 3. Coefficients of the best-fit regressions of silicate against time. Treatment details as for table 2.7.1. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ .  $n=36$  in all cases.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
S/5/O	—	$1.6384 \times 10^{-2}$ ( $2.487 \times 10^{-3}$ )	$1.8568$ ( $3.989 \times 10^{-2}$ )	0.9017	****
S/5/U	-1/y	$-6.877 \times 10^{-3}$ ( $1.449 \times 10^{-3}$ )	$-0.5525$ ( $2.324 \times 10^{-2}$ )	0.8325	****
S/15/O	—	$2.8445 \times 10^{-2}$ ( $4.172 \times 10^{-3}$ )	$1.9298$ ( $6.691 \times 10^{-2}$ )	0.9072	****
S/15/U	—	$-2.5506 \times 10^{-2}$ ( $1.770 \times 10^{-3}$ )	$5.658 \times 10^{-2}$ ( $2.389 \times 10^{-2}$ )	0.9160	****
S/25/O	—	$3.0673 \times 10^{-2}$ ( $7.615 \times 10^{-3}$ )	$1.9997$ (0.1221)	0.7868	****
S/25/U	-1/y	$-2.2759 \times 10^{-2}$ ( $1.770 \times 10^{-3}$ )	$-0.5494$ ( $2.839 \times 10^{-2}$ )	0.9711	****
S/35/O	$-\sqrt{y}$	$1.1346 \times 10^{-2}$ ( $1.459 \times 10^{-2}$ )	$1.3757$ ( $2.339 \times 10^{-2}$ )	0.9263	****
S/35/U	$\log_{10} y$	$-9.997 \times 10^{-3}$ ( $1.512 \times 10^{-3}$ )	$0.2430$ ( $2.425 \times 10^{-2}$ )	0.9022	****
S/45/O	-1/y	$1.413 \times 10^{-3}$ ( $1.097 \times 10^{-3}$ )	$-0.5090$ ( $1.760 \times 10^{-2}$ )	0.3768	*
S/45/U	$-\sqrt{y}$	$-3.755 \times 10^{-3}$ ( $1.036 \times 10^{-3}$ )	$1.3807$ ( $1.611 \times 10^{-2}$ )	0.7537	****
PS/N/O	—	$3.7302 \times 10^{-2}$ ( $3.153 \times 10^{-3}$ )	$1.9158$ ( $5.058 \times 10^{-2}$ )	0.9659	****
PS/N/U	-1/y	$-1.6948 \times 10^{-2}$ ( $1.676 \times 10^{-3}$ )	$-0.5348$ ( $2.689 \times 10^{-2}$ )	0.9545	****
PS/Si/O	—	$1.9727 \times 10^{-2}$ ( $2.327 \times 10^{-3}$ )	$1.8786$ ( $3.732 \times 10^{-2}$ )	0.9370	****
PS/Si/U	$\log_{10} y$	$-6.516 \times 10^{-3}$ ( $1.038 \times 10^{-3}$ )	$0.2438$ ( $1.664 \times 10^{-2}$ )	0.8933	****

Table 2.8.1. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
PS/VFS/O	—	2.3776x10 <sup>-2</sup> (1.861x10 <sup>-3</sup> )	1.8830 (2.985x10 <sup>-2</sup> )	0.9706 <sup>3</sup>	****
PS/VFS/U	-1/y	-9.320x10 <sup>-3</sup> (1.154x10 <sup>-3</sup> )	-0.5352 (1.851x10 <sup>-2</sup> )	0.9311	****
PS/FS/O	—	2.0890x10 <sup>-2</sup> (3.299x10 <sup>-2</sup> )	1.7676 (5.291x10 <sup>-2</sup> )	0.8944	****
PS/FS/U	Log <sub>10</sub> Y	-4.230x10 <sup>-3</sup> (1.008x10 <sup>-3</sup> )	0.2713 (1.618x10 <sup>-2</sup> )	0.7987	****
PS/MS/O	—	2.5788x10 <sup>-2</sup> (2.212x10 <sup>-3</sup> )	1.7476 (3.548x10 <sup>-2</sup> )	0.9649	****
PS/MS/U	-1/y	-1.0694x10 <sup>-2</sup> (2.258x10 <sup>-3</sup> )	-0.5517 (3.612x10 <sup>-2</sup> )	0.8319	****
C/VL/O	—	1.5469x10 <sup>-2</sup> (4.086x10 <sup>-3</sup> )	1.9050 (6.554x10 <sup>-2</sup> )	0.7675	****
C/VL/U	—	-1.3698x10 <sup>-2</sup> (3.591x10 <sup>-3</sup> )	1.8748 (5.759x10 <sup>-2</sup> )	0.7701	****
C/L/O	—	1.0139x10 <sup>-2</sup> (2.222x10 <sup>-3</sup> )	1.9028 (3.563x10 <sup>-2</sup> )	0.8222	****
C/L/U	-√Y <sup>1</sup>	-3.418x10 <sup>-3</sup> (1.365x10 <sup>-3</sup> )	1.3460 (2.189x10 <sup>-2</sup> )	0.6213	****
C/N/O	—	2.3249x10 <sup>-2</sup> (3.350x10 <sup>-3</sup> )	1.9062 (5.375x10 <sup>-2</sup> )	0.9099	****
C/N/U	-1/y	-3.982x10 <sup>-3</sup> (1.304x10 <sup>-3</sup> )	-0.5276 (2.091x10 <sup>-2</sup> )	0.6950	****
C/H/O	—	3.955x10 <sup>-3</sup> (2.734x10 <sup>-3</sup> )	1.9468 (4.385x10 <sup>-2</sup> )	0.4159	**
C/H/U	—	-2.796x10 <sup>-3</sup> (2.508x10 <sup>-3</sup> )	1.8380 (4.022x10 <sup>-2</sup> )	0.3332	*
C/VH/O	-1/y	1.2632x10 <sup>-3</sup> (9.191x10 <sup>-4</sup> )	-0.5343 (1.474x10 <sup>-2</sup> )	0.3987	**
C/VH/U	—	-2.935x10 <sup>-3</sup> (3.276x10 <sup>-3</sup> )	1.8682 (5.255x10 <sup>-2</sup> )	0.2720	



Table 2.8.1. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
O <sub>2</sub> /0/O	-1/y	-2.630x10 <sup>-3</sup> (1.048x10 <sup>-3</sup> )	-0.5357 (1.681x10 <sup>-2</sup> )	0.6221	****
O <sub>2</sub> /0/U	—	-8.653x10 <sup>-3</sup> (2.921x10 <sup>-3</sup> )	1.8380 (4.684x10 <sup>-2</sup> )	0.6834	****
O <sub>2</sub> /5/O	—	-1.55x10 <sup>-3</sup> (3.522x10 <sup>-3</sup> )	1.9334 (5.469x10 <sup>-2</sup> )	0.1049	
O <sub>2</sub> /5/U	—	-1.6x10 <sup>-5</sup> (2.706x10 <sup>-3</sup> )	1.7832 (4.341x10 <sup>-2</sup> )	0.0000	
O <sub>2</sub> /10/O	-1/y	1.5786x10 <sup>-3</sup> (9.715x10 <sup>-4</sup> )	-0.5637 (1.558x10 <sup>-2</sup> )	0.4572	***
O <sub>2</sub> /10/U	—	-6.004x10 <sup>-3</sup> (2.650x10 <sup>-3</sup> )	1.7858 (4.250x10 <sup>-2</sup> )	0.5822	****
O <sub>2</sub> /15/O	-1/y	7.480x10 <sup>-4</sup> (7.759x10 <sup>-4</sup> )	-0.5056 (1.244x10 <sup>-2</sup> )	0.2915	
O <sub>2</sub> /15/U	—	-2.629x10 <sup>-3</sup> (3.148x10 <sup>-3</sup> )	1.8532 (5.049x10 <sup>-2</sup> )	0.2550	
O <sub>2</sub> /21/O	—	1.2114x10 <sup>-2</sup> (3.109x10 <sup>-3</sup> )	1.8886 (4.987x10 <sup>-2</sup> )	0.7765	****
O <sub>2</sub> /21/U	—	-7.482x10 <sup>-3</sup> (7.880x10 <sup>-3</sup> )	1.8084 (0.1264)	0.2881	
A/N/O	—	5.697x10 <sup>-3</sup> (1.903x10 <sup>-3</sup> )	1.9004 (3.052x10 <sup>-2</sup> )	0.7043	****
A/N/U	-1/y	-9.805x10 <sup>-4</sup> (7.436x10 <sup>-4</sup> )	-0.5712 (1.193x10 <sup>-2</sup> )	0.3847	**
A/Cp/O	-1/y	1.4050x10 <sup>-3</sup> (8.437x10 <sup>-4</sup> )	-0.5179 (1.353x10 <sup>-2</sup> )	0.4658	***
A/Cp/U	-1/y	-1.2288x10 <sup>-3</sup> (5.329x10 <sup>-4</sup> )	-0.5190 (8.547x10 <sup>-3</sup> )	0.5891	****
A/NCp/O	—	1.2633x10 <sup>-2</sup> (1.938x10 <sup>-3</sup> )	1.8820 (3.109x10 <sup>-2</sup> )	0.8994	****
A/NCp/U	-1/y	-9.366x10 <sup>-4</sup> (7.410x10 <sup>-4</sup> )	-0.5359 (1.189x10 <sup>-2</sup> )	0.3715	*

Table 2.8.1. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
A/W/O	—	1.089x10 <sup>-2</sup> (2.699x10 <sup>-3</sup> )	2.0176 (4.282x10 <sup>-2</sup> )	0.7874	****
A/W/U	-1/y	-4.8831x10 <sup>-3</sup> (7.814x10 <sup>-4</sup> )	-0.5269 (1.253x10 <sup>-2</sup> )	0.8922	****
A/Co/O	—	1.0694x10 <sup>-2</sup> (2.372x10 <sup>-2</sup> )	1.8150 (3.804x10 <sup>-2</sup> )	0.8185	****
A/Co/U	Log <sub>10</sub> Y	-2.6251x10 <sup>-3</sup> (8.749x10 <sup>-4</sup> )	0.2687 (1.403x10 <sup>-2</sup> )	0.6885	****

Table 2.8.2. Flux experiment 3. Coefficients of the best-fit regressions of phosphate against time. Treatment details as for table 2.7.1. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=36 in all cases.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
S/5/O	—	$2.6106 \times 10^{-2}$ ( $3.049 \times 10^{-3}$ )	1,2192 ( $4.890 \times 10^{-2}$ )	0.9381	****
S/5/U	—	$-2.6494 \times 10^{-2}$ ( $2.338 \times 10^{-3}$ )	1.0498 ( $3.750 \times 10^{-2}$ )	0.9633	****
S/15/O	—	$2.7359 \times 10^{-2}$ ( $3.276 \times 10^{-3}$ )	1.2636 ( $5.254 \times 10^{-2}$ )	0.9354	****
S/15/U	—	$-2.8914 \times 10^{-2}$ ( $1.780 \times 10^{-3}$ )	1.1132 ( $2.855 \times 10^{-2}$ )	0.9813	****
S/25/O	—	$3.5127 \times 10^{-2}$ ( $4.887 \times 10^{-3}$ )	1.3012 ( $7.839 \times 10^{-2}$ )	0.9154	****
S/25/U	—	$-3.1824 \times 10^{-2}$ ( $1.086 \times 10^{-3}$ )	1.0906 ( $1.742 \times 10^{-2}$ )	0.9940	****
S/35/O	—	$5.8751 \times 10^{-2}$ ( $1.459 \times 10^{-2}$ )	1.2498 ( $2.339 \times 10^{-2}$ )	0.9513	****
S/35/U	$\sqrt{y}$	$-2.1879 \times 10^{-2}$ ( $1.512 \times 10^{-3}$ )	1.0482 ( $2.425 \times 10^{-2}$ )	0.9813	****
S/45/O	—	$4.7147 \times 10^{-3}$ ( $1.097 \times 10^{-3}$ )	1.2632 ( $1.760 \times 10^{-2}$ )	0.9633	****
S/45/U	—	$-2.9037 \times 10^{-2}$ ( $2.370 \times 10^{-3}$ )	1.1312 ( $3.801 \times 10^{-2}$ )	0.9685	****
PS/N/O	—	$2.0845 \times 10^{-2}$ ( $2.709 \times 10^{-3}$ )	1.0834 ( $4.346 \times 10^{-2}$ )	0.9247	****
PS/N/U	$\sqrt{y}$	$-1.3744 \times 10^{-2}$ ( $1.323 \times 10^{-3}$ )	1.0493 ( $2.122 \times 10^{-2}$ )	0.9566	****
PS/Si/O	—	$2.2943 \times 10^{-2}$ ( $3.104 \times 10^{-3}$ )	1.1782 ( $4.978 \times 10^{-2}$ )	0.9192	****
PS/Si/U	—	$-2.6722 \times 10^{-2}$ ( $2.146 \times 10^{-3}$ )	1.0616 ( $3.443 \times 10^{-2}$ )	0.9690	****

Table 2.8.2. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
PS/VFS/O	—	2.5522x10 <sup>-2</sup> (1.861x10 <sup>-3</sup> )	1.1766 (2.985x10 <sup>-2</sup> )	0.9236	****
PS/VFS/U	$-\sqrt{Y}$	-1.8718x10 <sup>-2</sup> (1.107x10 <sup>-3</sup> )	1.0516 (1.775x10 <sup>-2</sup> )	0.9829	****
PS/FS/O	—	1.3861x10 <sup>-2</sup> (2.872x10 <sup>-3</sup> )	1.1752 (4.606x10 <sup>-2</sup> )	0.8367	****
PS/FS/U	—	-2.1841x10 <sup>-2</sup> (1.667x10 <sup>-3</sup> )	0.9880 (2.673x10 <sup>-2</sup> )	0.9721	****
PS/MS/O	—	1.4710x10 <sup>-2</sup> (2.091x10 <sup>-3</sup> )	1.2478 (3.353x10 <sup>-2</sup> )	0.9121	****
PS/MS/U	$-\sqrt{Y}$	-1.4016x10 <sup>-2</sup> (1.300x10 <sup>-3</sup> )	1.0364 (2.084x10 <sup>-2</sup> )	0.9597	****
C/VL/O	—	2.4620x10 <sup>-2</sup> (3.438x10 <sup>-3</sup> )	1.1624 (5.514x10 <sup>-2</sup> )	0.9149	****
C/VL/U	$-\sqrt{Y}$	-1.6410x10 <sup>-2</sup> (1.264x10 <sup>-3</sup> )	1.0396 (2.028x10 <sup>-2</sup> )	0.9716	****
C/L/O	—	2.3882x10 <sup>-2</sup> (2.340x10 <sup>-3</sup> )	1.2632 (3.753x10 <sup>-2</sup> )	0.9550	****
C/L/U	$-\sqrt{Y}$	-1.9067x10 <sup>-2</sup> (1.820x10 <sup>-3</sup> )	1.0423 (2.919x10 <sup>-2</sup> )	0.9576	****
C/N/O	—	2.2604x10 <sup>-2</sup> (3.673x10 <sup>-3</sup> )	1.1156 (5.891x10 <sup>-2</sup> )	0.9418	****
C/N/U	-1/Y	-2.8735x10 <sup>-2</sup> (1.592x10 <sup>-3</sup> )	0.9890 (2.553x10 <sup>-2</sup> )	0.9849	****
C/H/O	—	2.2727x10 <sup>-2</sup> (3.448x10 <sup>-3</sup> )	1.1656 (5.530x10 <sup>-2</sup> )	0.9017	****
C/H/U	—	-3.0739x10 <sup>-2</sup> (2.238x10 <sup>-3</sup> )	1.0938 (3.589x10 <sup>-2</sup> )	0.9747	****
C/VH/O	—	1.5535x10 <sup>-2</sup> (2.757x10 <sup>-3</sup> )	1.1132 (4.421x10 <sup>-2</sup> )	0.8724	****
C/VH/U	—	-2.7396x10 <sup>-2</sup> (2.187x10 <sup>-3</sup> )	1.0586 (3.507x10 <sup>-2</sup> )	0.9695	****

Table 2.8.2. continued.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
O <sub>2</sub> /0/O	-1/y	4.816x10 <sup>-3</sup> (1.341x10 <sup>-3</sup> )	-0.8773 (2.150x10 <sup>-2</sup> )	0.7503	****
O <sub>2</sub> /0/U	-1/y	-2.2701x10 <sup>-3</sup> (9.263x10 <sup>-4</sup> )	1.0619 (1.486x10 <sup>-2</sup> )	0.6221	****
O <sub>2</sub> /5/O	—	1.6914x10 <sup>-3</sup> (2.218x10 <sup>-3</sup> )	1.1178 (3.558x10 <sup>-2</sup> )	0.9236	****
O <sub>2</sub> /5/U	-1/y	-3.4666x10 <sup>-3</sup> (8.965x10 <sup>-4</sup> )	1.0212 (1.438x10 <sup>-2</sup> )	0.7962	****
O <sub>2</sub> /10/O	—	1.7253x10 <sup>-2</sup> (2.701x10 <sup>-3</sup> )	1.1814 (4.333x10 <sup>-2</sup> )	0.8961	****
O <sub>2</sub> /10/U	—	-1.0812x10 <sup>-2</sup> (1.894x10 <sup>-3</sup> )	1.0942 (3.037x10 <sup>-2</sup> )	0.8746	****
O <sub>2</sub> /15/O	—	2.0224x10 <sup>-2</sup> (3.771x10 <sup>-3</sup> )	1.2300 (6.049x10 <sup>-2</sup> )	0.8614	****
O <sub>2</sub> /15/U	-1/y	-6.0918x10 <sup>-3</sup> (9.728x10 <sup>-4</sup> )	1.0240 (1.488x10 <sup>-2</sup> )	0.9230	****
O <sub>2</sub> /21/O	—	3.1424x10 <sup>-2</sup> (3.622x10 <sup>-3</sup> )	1.1848 (5.809x10 <sup>-2</sup> )	0.9397	****
O <sub>2</sub> /21/U	-1/y	-6.8125x10 <sup>-3</sup> (7.668x10 <sup>-4</sup> )	1.0105 (1.230x10 <sup>-2</sup> )	0.9460	****
A/N/O	—	2.3678x10 <sup>-2</sup> (2.623x10 <sup>-3</sup> )	1.1812 (4.208x10 <sup>-2</sup> )	0.9439	****
A/N/U	Log <sub>10</sub>	-1.1796x10 <sup>-2</sup> (1.177x10 <sup>-3</sup> )	4.952x10 <sup>-2</sup> (1.888x10 <sup>-2</sup> )	0.9534	****
A/Cp/O	—	2.7245x10 <sup>-2</sup> (3.998x10 <sup>-3</sup> )	1.1730 (6.412x10 <sup>-2</sup> )	0.9072	****
A/Cp/U	$-\sqrt{y}$	-1.3140x10 <sup>-2</sup> (1.538x10 <sup>-3</sup> )	1.0417 (2.466x10 <sup>-2</sup> )	0.9381	****
A/NCp/O	—	3.2878x10 <sup>-2</sup> (4.372x10 <sup>-3</sup> )	1.1890 (7.012x10 <sup>-2</sup> )	0.9220	****
A/NCp/U	—	-2.9041x10 <sup>-2</sup> (2.083x10 <sup>-3</sup> )	1.0680 (3.341x10 <sup>-2</sup> )	0.9752	****

Table 2.8.2. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
A/W/O	—	3.6808x10 <sup>-2</sup> (4.102x10 <sup>-3</sup> )	1.2336 (6.580x10 <sup>-2</sup> )	0.9434	****
A/W/U	—	-3.2469x10 <sup>-2</sup> (1.780x10 <sup>-3</sup> )	1.0410 (2.855x10 <sup>-2</sup> )	0.9854	****
A/Co/O	—	2.3690x10 <sup>-2</sup> (2.728x10 <sup>-3</sup> )	1.1668 (4.375x10 <sup>-2</sup> )	0.9397	****
A/Co/U	—	-2.2457x10 <sup>-2</sup> (2.003x10 <sup>-3</sup> )	1.0766 (3.212x10 <sup>-2</sup> )	0.9623	****

Table 2.8.3. Flux experiment 3. Coefficients of the best-fit regressions of sulphate against time. Treatment details as for table 2.7.1. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ .  $n=36$  in all cases.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
S/5/O	—	-5.602 (3.617)	2231.48 (58.01)	0.4393	***
S/5/U	—	6.900 (2.156)	2377.03 (34.59)	0.7113	****
S/15/O	—	-1.728 (2.851)	2175.68 (45.72)	0.1871	
S/15/U	—	1.714 (3.117)	2211.67 (49.99)	0.1703	
S/25/O	—	-3.949 (3.563)	2324.96 (41.10)	0.4382	***
S/25/U	—	2.559 (2.597)	2245.45 (41.66)	0.2983	
S/35/O	—	-3.796 (2.581)	2140.01 (41.40)	0.4219	***
S/35/U	-1/y	$1.9653 \times 10^{-6}$ ( $4.586 \times 10^{-7}$ )	$-4.3956 \times 10^{-4}$ ( $7.536 \times 10^{-6}$ )	0.8044	****
S/45/O	—	-6.397 (3.139)	2248.89 (50.35)	0.5413	****
S/45/U	—	7.101 (2.522)	2299.99 (40.44)	0.6648	****
PS/N/O	—	-2.860 (3.146)	2123.36 (50.46)	0.2757	
PS/N/U	—	1.252 (2.009)	2102.25 (32.22)	0.1924	
PS/Si/O	—	-3.525 (2.557)	2232.07 (41.01)	0.4000	**
PS/Si/U	—	10.947 (3.010)	2283.23 (48.29)	0.7543	****

Table 2.8.3. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
PS/VFS/O	—	-2.871 (2.376)	2165.59 (38.11)	0.3564	*
PS/VFS/U	-1/y	1.0391x10 <sup>-6</sup> (4.455x10 <sup>-7</sup> )	-4.5102x10 <sup>-4</sup> (7.146x10 <sup>-6</sup> )	0.5933	****
PS/FS/O	-1/y	-1.6313x10 <sup>-6</sup> (3.885x10 <sup>-7</sup> )	-4.2805x10 <sup>-4</sup> (6.231x10 <sup>-6</sup> )	0.7987	****
PS/FS/U	—	5.520 (2.224)	2314.16 (35.68)	0.6173	****
PS/MS/O	—	7.526 (7.430)	2095.60 (119.20)	0.3050	
PS/MS/U	-√y	-3.925x10 <sup>-2</sup> (2.249x10 <sup>-2</sup> )	48.3825 (0.3607)	0.4837	***
C/VL/O	—	-5.660 (2.288)	2238.21 (36.70)	0.6164	****
C/VL/U	—	12.427 (2.797)	2247.48 (44.86)	0.8149	****
C/L/O	-√y	-8.879x10 <sup>-2</sup> (3.020x10 <sup>-2</sup> )	47.7389 (0.4844)	0.6812	****
C/L/U	—	-1.560 (2.233)	2387.14 (35.82)	0.2168	
C/N/O	-1/y	-7.8972x10 <sup>-7</sup> (4.811x10 <sup>-7</sup> )	-4.6359x10 <sup>-4</sup> (7.716x10 <sup>-6</sup> )	0.4604	***
C/N/U	—	10.928 (2.329)	2158.80 (37.36)	0.8295	****
C/H/O	—	-8.277 (2.826)	2299.64 (45.33)	0.6797	****
C/H/U	-1/y	7.141x10 <sup>-7</sup> (4.289x10 <sup>-7</sup> )	-4.1427x10 <sup>-4</sup> (6.879x10 <sup>-6</sup> )	0.4658	***
C/VH/O	—	-0.782 (2.822)	2124.32 (45.27)	0.0894	
C/VH/U	—	15.086 (2.302)	2225.26 (36.93)	0.9006	****



Table 2.8.3. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
O <sub>2</sub> /0/O	—	-2.134 (1.848)	2242.89 (29.64)	0.3435	*
O <sub>2</sub> /0/U	—	-4.973 (2.601)	2376.13 (41.71)	0.5177	***
O <sub>2</sub> /5/O	-1/y	-7.3764x10 <sup>-7</sup> (3.463x10 <sup>-7</sup> )	-4.4282x10 <sup>-4</sup> (5.554x10 <sup>-6</sup> )	0.5586	****
O <sub>2</sub> /5/U	-1/y	-1.1890x10 <sup>-7</sup> (4.270x10 <sup>-7</sup> )	-4.2195x10 <sup>-4</sup> (6.849x10 <sup>-6</sup> )	0.0894	
O <sub>2</sub> /10/O	—	-3.442 (2.481)	2223.24 (39.79)	0.4012	**
O <sub>2</sub> /10/U	—	7.536 (2.405)	2100.69 (38.57)	0.7036	****
O <sub>2</sub> /15/O	-1/y	-1.5088x10 <sup>-6</sup> (5.148x10 <sup>-7</sup> )	-4.3375x10 <sup>-4</sup> (8.258x10 <sup>-6</sup> )	0.6797	****
O <sub>2</sub> /15/U	—	6.266 (3.014)	2263.26 (48.34)	0.5495	****
O <sub>2</sub> /21/O	—	-7.231 (3.781)	2245.98 (60.65)	0.5177	***
O <sub>2</sub> /21/U	—	8.553 (2.145)	2289.90 (34.40)	0.7836	****
A/N/O	-1/y	-1.3464x10 <sup>-6</sup> (6.014x10 <sup>-7</sup> )	-4.3180x10 <sup>-4</sup> (9.646x10 <sup>-6</sup> )	0.5779	****
A/N/U	—	10.276 (2.362)	2095.47 (37.88)	0.8087	****
A/Cp/O	-1/y	-8.1121x10 <sup>-7</sup> (5.453x10 <sup>-7</sup> )	-4.3389x10 <sup>-4</sup> (8.747x10 <sup>-6</sup> )	0.4254	***
A/Cp/U	—	2.654 (1.657)	2352.97 (26.57)	0.4517	***
A/NCp/O	-1/y	-8.1675x10 <sup>-7</sup> (5.165x10 <sup>-7</sup> )	-4.7827x10 <sup>-4</sup> (8.285x10 <sup>-6</sup> )	0.4472	***
A/NCp/U	—	7.943 (2.761)	2311.68 (44.29)	0.6731	****

Table 2.8.3. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
A/W/O	—	-4.923 (3.168)	2214.20 (50.82)	0.4416	***
A/W/U	—	14.222 (3.193)	2178.91 (51.22)	0.8155	****
A/Co/O	-1/y	-1.011x10 <sup>-6</sup> (5.265x10 <sup>-7</sup> )	-4.4561x10 <sup>-4</sup> (8.444x10 <sup>-6</sup> )	0.5158	****
A/Co/U	—	-1.811 (2.632)	2340.46 (42.21)	0.2121	

Table 2.8.4. Flux experiment 3. Coefficients of the best-fit regressions of nitrate against time. Treatment details as for table 2.7.1. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ .  $n=36$  in all cases.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
S/5/O	—	$-4.494 \times 10^{-3}$ ( $2.463 \times 10^{-3}$ )	1.7584 ( $3.950 \times 10^{-2}$ )	0.5000	****
S/5/U	-1/y	$1.0983 \times 10^{-3}$ ( $5.140 \times 10^{-4}$ )	-0.5594 ( $8.244 \times 10^{-3}$ )	0.5595	****
S/15/O	—	$-3.860 \times 10^{-3}$ ( $2.404 \times 10^{-3}$ )	1.8220 ( $3.856 \times 10^{-2}$ )	0.4528	***
S/15/U	—	$-2.32 \times 10^{-4}$ ( $1.448 \times 10^{-3}$ )	1.8848 ( $2.322 \times 10^{-2}$ )	0.0548	
S/25/O	—	$-1.507 \times 10^{-3}$ ( $2.024 \times 10^{-3}$ )	1.6965 ( $3.247 \times 10^{-2}$ )	0.2280	
S/25/U	-1/y	$1.2476 \times 10^{-3}$ ( $5.254 \times 10^{-4}$ )	-0.5753 ( $8.427 \times 10^{-3}$ )	0.6008	****
S/35/O	$\sqrt{y}$	$-1.4278 \times 10^{-3}$ ( $6.577 \times 10^{-4}$ )	-0.5669 ( $1.055 \times 10^{-2}$ )	0.8550	****
S/35/U	—	$3.454 \times 10^{-3}$ ( $1.282 \times 10^{-3}$ )	1.8706 ( $2.056 \times 10^{-2}$ )	0.6488	****
S/45/O	-1/y	$-2.2145 \times 10^{-3}$ ( $5.210 \times 10^{-4}$ )	-0.5527 ( $8.356 \times 10^{-3}$ )	0.8025	****
S/45/U	—	$-3.236 \times 10^{-3}$ ( $1.374 \times 10^{-3}$ )	1.9443 ( $2.204 \times 10^{-2}$ )	0.5975	****
PS/N/O	—	$-1.3224 \times 10^{-2}$ ( $2.301 \times 10^{-3}$ )	1.8980 ( $3.691 \times 10^{-2}$ )	0.8764	****
PS/N/U	-1/y	$1.2795 \times 10^{-3}$ ( $5.548 \times 10^{-4}$ )	-0.5516 ( $8.899 \times 10^{-3}$ )	0.5891	****
PS/Si/O	-1/y	$-1.8759 \times 10^{-3}$ ( $9.408 \times 10^{-4}$ )	-0.5438 ( $1.509 \times 10^{-2}$ )	0.5329	****
PS/Si/U	-1/y	$-2.022 \times 10^{-4}$ ( $5.039 \times 10^{-4}$ )	-0.5270 ( $8.082 \times 10^{-3}$ )	0.1265	

Table 2.8.4. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
PS/VFS/O	—	-5.242x10 <sup>-3</sup> (1.516x10 <sup>-3</sup> )	1.7481 (2.431x10 <sup>-2</sup> )	0.7382	****
PS/VFS/U	—	5.547x10 <sup>-7</sup> (1.540x10 <sup>-3</sup> )	1.7484 (2.470x10 <sup>-2</sup> )	0.7517	****
PS/FS/O	-1/y	-4.7593x10 <sup>-3</sup> (6.513x10 <sup>-4</sup> )	-0.5231 (1.045x10 <sup>-2</sup> )	0.9176	****
PS/FS/U	—	7.100x10 <sup>-4</sup> (6.375x10 <sup>-4</sup> )	-0.5422 (1.023x10 <sup>-2</sup> )	0.3317	*
PS/MS/O	-1/y	-1.8757x10 <sup>-3</sup> (3.553x10 <sup>-4</sup> )	-0.5615 (5.699x10 <sup>-3</sup> )	0.8579	****
PS/MS/U	-1/y	8.868x10 <sup>-4</sup> (5.425x10 <sup>-4</sup> )	-0.5500 (8.701x10 <sup>-3</sup> )	0.4593	***
C/VL/O	$-\sqrt{y}$	-4.6621x10 <sup>-3</sup> (8.902x10 <sup>-4</sup> )	1.3593 (1.428x10 <sup>-2</sup> )	0.8562	****
C/VL/U	—	-5.376x10 <sup>-4</sup> (6.825x10 <sup>-4</sup> )	1.8836 (1.095x10 <sup>-2</sup> )	0.7616	****
C/L/O	-1/y	-2.0113x10 <sup>-3</sup> (6.326x10 <sup>-4</sup> )	-0.5605 (1.015x10 <sup>-2</sup> )	0.7092	****
C/L/U	—	3.891x10 <sup>-3</sup> (1.708x10 <sup>-3</sup> )	1.7466 (2.740x10 <sup>-2</sup> )	0.5848	****
C/N/O	—	-1.4624x10 <sup>-2</sup> (1.796x10 <sup>-3</sup> )	1.9396 (2.881x10 <sup>-2</sup> )	0.9322	****
C/N/U	—	4.005x10 <sup>-3</sup> (1.594x10 <sup>-3</sup> )	1.8131 (2.557x10 <sup>-2</sup> )	0.6221	****
C/H/O	—	-5.715x10 <sup>-3</sup> (2.025x10 <sup>-3</sup> )	1.8023 (3.249x10 <sup>-2</sup> )	0.6656	****
C/H/U	—	6.626x10 <sup>-3</sup> (1.890x10 <sup>-3</sup> )	1.7554 (3.031x10 <sup>-2</sup> )	0.7423	****
C/VH/O	-1/y	-1.6152x10 <sup>-3</sup> (6.652x10 <sup>-4</sup> )	-0.5377 (1.067x10 <sup>-2</sup> )	0.6091	****
C/VH/U	—	5.74x10 <sup>-4</sup> (1.695x10 <sup>-3</sup> )	1.8289 (2.719x10 <sup>-2</sup> )	0.1049	

Table 2.8.4. continued.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
O <sub>2</sub> /0/O	—	7.420x10 <sup>-4</sup> (2.439x10 <sup>-3</sup> )	1.7650 (3.912x10 <sup>-2</sup> )	0.0949	
O <sub>2</sub> /0/U	—	6.854x10 <sup>-3</sup> (1.585x10 <sup>-3</sup> )	1.6770 (2.543x10 <sup>-2</sup> )	0.8068	****
O <sub>2</sub> /5/O	—	-2.100x10 <sup>-3</sup> (2.062x10 <sup>-3</sup> )	1.7626 (3.308x10 <sup>-2</sup> )	0.3066	
O <sub>2</sub> /5/U	—	4.362x10 <sup>-3</sup> (2.271x10 <sup>-3</sup> )	1.7799 (3.642x10 <sup>-2</sup> )	0.5196	****
O <sub>2</sub> /10/O	-1/y	-2.7519x10 <sup>-3</sup> (7.691x10 <sup>-4</sup> )	-0.5358 (1.234x10 <sup>-2</sup> )	0.7490	****
O <sub>2</sub> /10/U	-1/y	1.228x10 <sup>-4</sup> (5.200x10 <sup>-4</sup> )	-0.5268 (8.340x10 <sup>-3</sup> )	0.0775	
O <sub>2</sub> /15/O	-1/y	-2.718x10 <sup>-3</sup> (1.081x10 <sup>-3</sup> )	-0.5792 (1.733x10 <sup>-2</sup> )	0.6221	****
O <sub>2</sub> /15/U	—	7.402x10 <sup>-3</sup> (1.825x10 <sup>-3</sup> )	1.7379 (2.927x10 <sup>-2</sup> )	0.7887	****
O <sub>2</sub> /21/O	-1/y	-4.7503x10 <sup>-3</sup> (7.536x10 <sup>-4</sup> )	-0.5265 (1.209x10 <sup>-2</sup> )	0.8939	****
O <sub>2</sub> /21/U	-1/y	5.535x10 <sup>-4</sup> (4.116x10 <sup>-4</sup> )	-0.5397 (6.602x10 <sup>-3</sup> )	0.3912	**
A/N/O	—	6.267x10 <sup>-3</sup> (1.559x10 <sup>-3</sup> )	1.4779 (2.500x10 <sup>-2</sup> )	0.7861	****
A/N/U	—	3.82x10 <sup>-4</sup> (1.637x10 <sup>-3</sup> )	1.9095 (2.625x10 <sup>-2</sup> )	0.0707	
A/Cp/O	-1/y	-3.0309x10 <sup>-3</sup> (7.332x10 <sup>-4</sup> )	-0.5423 (1.176x10 <sup>-2</sup> )	0.7944	****
A/Cp/U	—	3.757x10 <sup>-3</sup> (1.014x10 <sup>-3</sup> )	1.8124 (1.627x10 <sup>-2</sup> )	0.7603	****
A/NCp/O	-1/y	-4.7610x10 <sup>-3</sup> (6.994x10 <sup>-4</sup> )	-0.5122 (1.122x10 <sup>-2</sup> )	0.9072	****
A/NCp/U	-1/y	1.4430x10 <sup>-3</sup> (5.762x10 <sup>-4</sup> )	-0.5569 (9.242x10 <sup>-3</sup> )	0.6205	****

Table 2.8.4. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
A/W/O	-1/y	-2.9869x10 <sup>-3</sup> (6.410x10 <sup>-4</sup> )	-0.5688 (1.028x10 <sup>-2</sup> )	0.8276	****
A/W/U	-1/y	1.9462x10 <sup>-3</sup> (4.940x10 <sup>-3</sup> )	-0.5530 (7.924x10 <sup>-3</sup> )	0.7797	****
A/Co/O	—	-5.486x10 <sup>-3</sup> (2.055x10 <sup>-3</sup> )	1.8240 (3.296x10 <sup>-2</sup> )	0.6450	****
A/Co/U	—	2.275x10 <sup>-3</sup> (1.412x10 <sup>-3</sup> )	1.7853 (2.265x10 <sup>-2</sup> )	0.4539	***

Table 2.8.5. Flux experiment 3. Coefficients of the best-fit regressions of ammonia against time. Treatment details as for table 2.7.1. \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ .  $n=36$  in all cases.

Treatment /chamber	transf- ormation	m ( $sd_m$ )	c ( $sd_c$ )	r	p
S/5/O	—	$1.4400 \times 10^{-2}$ ( $8.883 \times 10^{-3}$ )	3.7552 (0.1425)	0.4561	***
S/5/U	-1/y	$-8.062 \times 10^{-4}$ ( $1.625 \times 10^{-4}$ )	-0.2567 ( $2.607 \times 10^{-3}$ )	0.8432	****
S/15/O	—	$1.2581 \times 10^{-2}$ ( $2.774 \times 10^{-3}$ )	3.6905 ( $4.449 \times 10^{-2}$ )	0.8204	****
S/15/U	—	$-1.9492 \times 10^{-2}$ ( $7.949 \times 10^{-3}$ )	3.9539 (0.1275)	0.6132	****
S/25/O	—	$2.2974 \times 10^{-2}$ ( $8.890 \times 10^{-3}$ )	3.5283 (0.1426)	0.6325	****
S/25/U	-1/y	$-2.977 \times 10^{-3}$ ( $2.247 \times 10^{-3}$ )	-0.2194 ( $3.604 \times 10^{-2}$ )	0.3860	**
S/35/O	—	$1.8623 \times 10^{-2}$ ( $2.955 \times 10^{-3}$ )	3.5852 ( $4.739 \times 10^{-2}$ )	0.8939	****
S/35/U	-1/y	$-1.6484 \times 10^{-3}$ ( $1.747 \times 10^{-4}$ )	-0.2543 ( $2.802 \times 10^{-3}$ )	0.9482	****
S/45/O	—	$1.0461 \times 10^{-2}$ ( $1.359 \times 10^{-3}$ )	3.7276 ( $2.180 \times 10^{-2}$ )	0.9252	****
S/45/U	$-\sqrt{y}$	$-9.380 \times 10^{-4}$ ( $1.461 \times 10^{-4}$ )	-0.2645 ( $2.343 \times 10^{-3}$ )	0.8972	****
PS/N/O	—	$1.6800 \times 10^{-2}$ ( $2.589 \times 10^{-3}$ )	3.6198 ( $4.153 \times 10^{-2}$ )	0.8989	****
PS/N/U	-1/y	$-1.5035 \times 10^{-3}$ ( $1.447 \times 10^{-4}$ )	-0.2603 ( $2.321 \times 10^{-3}$ )	0.9566	****
PS/Si/O	-1/y	$7.376 \times 10^{-4}$ ( $1.409 \times 10^{-4}$ )	-0.2637 ( $2.260 \times 10^{-3}$ )	0.8562	****
PS/Si/U	-1/y	$-1.5869 \times 10^{-3}$ ( $1.713 \times 10^{-4}$ )	-0.2650 ( $2.748 \times 10^{-3}$ )	0.9466	****

Table 2.8.5. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c <sub>f</sub> (sd <sub>c</sub> )	r	p
PS/VFS/O	—	1.8718x10 <sup>-2</sup> (2.663x10 <sup>-3</sup> )	3.5713 (4.272x10 <sup>-2</sup> )	0.9121	****
PS/VFS/U	—	-1.4997x10 <sup>-2</sup> (2.232x10 <sup>-3</sup> )	3.8579 (3.580x10 <sup>-2</sup> )	0.9050	****
PS/FS/O	—	1.2105x10 <sup>-2</sup> (2.481x10 <sup>-3</sup> )	3.6338 (3.979x10 <sup>-2</sup> )	0.8390	****
PS/FS/U	-1/y	-5.729x10 <sup>-4</sup> (1.711x10 <sup>-4</sup> )	-0.2593 (2.745x10 <sup>-3</sup> )	0.7266	****
PS/MS/O	—	1.3510x10 <sup>-2</sup> (2.711x10 <sup>-3</sup> )	3.5325 (4.348x10 <sup>-2</sup> )	0.8444	****
PS/MS/U	—	-5.736x10 <sup>-3</sup> (6.669x10 <sup>-3</sup> )	3.7215 (0.1070)	0.2470	
C/VL/O	—	1.4560x10 <sup>-2</sup> (2.423x10 <sup>-3</sup> )	3.7416 (3.886x10 <sup>-2</sup> )	0.8849	****
C/VL/U	—	-7.729x10 <sup>-4</sup> (2.826x10 <sup>-4</sup> )	-0.2596 (4.516x10 <sup>-3</sup> )	0.6557	****
C/L/O	—	1.3250x10 <sup>-2</sup> (1.640x10 <sup>-3</sup> )	3.7718 (2.630x10 <sup>-2</sup> )	0.9311	****
C/L/U	-1/y	-1.0926x10 <sup>-3</sup> (1.031x10 <sup>-4</sup> )	-0.2513 (1.654x10 <sup>-3</sup> )	0.9581	****
C/N/O	—	6.357x10 <sup>-3</sup> (1.613x10 <sup>-3</sup> )	3.9436 (2.587x10 <sup>-2</sup> )	0.7797	****
C/N/U	—	-3.073x10 <sup>-3</sup> (2.697x10 <sup>-3</sup> )	3.7073 (4.326x10 <sup>-2</sup> )	0.3391	*
C/H/O	—	1.0635x10 <sup>-2</sup> (2.472x10 <sup>-3</sup> )	3.7873 (3.965x10 <sup>-2</sup> )	0.8056	****
C/H/U	-1/y	-6.395x10 <sup>-4</sup> (1.656x10 <sup>-4</sup> )	-0.2651 (2.655x10 <sup>-3</sup> )	0.7740	****
C/VH/O	-1/y	-1.186x10 <sup>-4</sup> (1.195x10 <sup>-4</sup> )	-0.2467 (1.917x10 <sup>-3</sup> )	0.3000	
C/VH/U	—	-4.237x10 <sup>-3</sup> (1.873x10 <sup>-3</sup> )	3.5358 (3.004x10 <sup>-2</sup> )	0.5814	****



Table 2.8.5. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
O <sub>2</sub> /0/O	—	1.0449x10 <sup>-2</sup> (1.518x10 <sup>-3</sup> )	4.0084 (2.434x10 <sup>-2</sup> )	0.9088 <sup>7</sup>	****
O <sub>2</sub> /0/U	-1/y	-2.7166x10 <sup>-3</sup> (2.556x10 <sup>-4</sup> )	-0.2698 (4.099x10 <sup>-3</sup> )	0.9586	****
O <sub>2</sub> /5/O	-1/y	1.4462x10 <sup>-3</sup> (3.453x10 <sup>-4</sup> )	-0.2616 (5.537x10 <sup>-3</sup> )	0.7981	****
O <sub>2</sub> /5/U	-1/y	-2.8578x10 <sup>-3</sup> (1.983x10 <sup>-4</sup> )	-0.2523 (3.181x10 <sup>-3</sup> )	0.9767	****
O <sub>2</sub> /10/O	—	9.355x10 <sup>-3</sup> (1.896x10 <sup>-3</sup> )	3.9840 (3.040x10 <sup>-2</sup> )	0.8420	****
O <sub>2</sub> /10/U	-1/y	-2.6783x10 <sup>-3</sup> (6.154x10 <sup>-4</sup> )	-0.2553 (9.871x10 <sup>-3</sup> )	0.8087	****
O <sub>2</sub> /15/O	—	1.5711x10 <sup>-2</sup> (2.717x10 <sup>-3</sup> )	3.6452 (4.357x10 <sup>-2</sup> )	0.8775	****
O <sub>2</sub> /15/U	—	-2.4850x10 <sup>-3</sup> (2.321x10 <sup>-3</sup> )	3.9777 (3.722x10 <sup>-2</sup> )	0.9592	****
O <sub>2</sub> /21/O	-1/y	6.338x10 <sup>-4</sup> (1.558x10 <sup>-4</sup> )	-0.2612 (2.499x10 <sup>-3</sup> )	0.7893	****
O <sub>2</sub> /21/U	-1/y	-1.3525x10 <sup>-3</sup> (1.284x10 <sup>-4</sup> )	-0.2544 (2.060x10 <sup>-3</sup> )	0.9576	****
A/N/O	—	2.930x10 <sup>-3</sup> (2.299x10 <sup>-3</sup> )	3.8751 (3.687x10 <sup>-2</sup> )	0.3742	*
A/N/U	-1/y	-5.041x10 <sup>-4</sup> (1.231x10 <sup>-4</sup> )	-0.2650 (1.975x10 <sup>-3</sup> )	0.7912	****
A/Cp/O	—	6.570x10 <sup>-3</sup> (1.511x10 <sup>-3</sup> )	3.7647 (2.423x10 <sup>-2</sup> )	0.8087	****
A/Cp/U	-1/y	-3.447x10 <sup>-4</sup> (1.594x10 <sup>-4</sup> )	-0.2653 (2.557x10 <sup>-3</sup> )	0.5648	****
A/NCp/O	—	5.002x10 <sup>-3</sup> (2.258x10 <sup>-3</sup> )	3.9336 (3.622x10 <sup>-2</sup> )	0.5736	****
A/NCp/U	—	-1.8107x10 <sup>-2</sup> (3.628x10 <sup>-3</sup> )	3.8088 (5.820x10 <sup>-2</sup> )	0.8444	****

Table 2.8.5. continued.

Treatment /chamber	transf- ormation	m (sd <sub>m</sub> )	c (sd <sub>c</sub> )	r	p
A/W/O	—	1.3231x10 <sup>-2</sup> (2.266x10 <sup>-3</sup> )	3.7608 (3.635x10 <sup>-2</sup> )	0.8792	****
A/W/U	$-\sqrt{y}$	0.8221 (0.5061)	-2.573 (8.117)	0.4583	***
A/Co/O	—	4.150x10 <sup>-3</sup> (2.282x10 <sup>-3</sup> )	3.7270 (3.660x10 <sup>-2</sup> )	0.4990	***
A/Co/U	-1/y	-8.891x10 <sup>-4</sup> (1.546x10 <sup>-4</sup> )	-0.2551 (2.480x10 <sup>-3</sup> )	0.9627	****

Level	5	15	25	35	45
5	X X	7.4127 **	5.3291 *	5.2318 *	6.7036 *
15	9.2301 **	X X	0.7699	0.9130	11.5913 ***
25	4.1991	1.8601	X X	0.1408	8.6793 **
35	4.1827	21.7133 ***	7.4892 **	X X	8.4540 **
45	1.3153	6.3374 *	2.8611	4.9748 *	X X

Table 2.9.1. Flux experiment 3. t-tests comparing initial silicate flux in each level of the salinity treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Si	VFS	FS	MS
N	X X	13.4548 ***	11.0836 ***	1.4857	8.9686 **
Si	7.0446 **	X X	4.0768	0.1055	5.6633 *
VFS	2.8104	17.5661 ***	X X	0.2620	2.0880
FS	7.0446 **	0.1000	17.5661 ***	X X	0.4444
MS	1.7289	3.9591	0.2515	3.9591	X X

Table 2.9.2. Flux experiment 3. t-tests comparing initial silicate flux in each level of the particle size treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	VL	L	N	H	VH
VL	X X	3.4378	4.4173 *	7.0258 **	6.3656 *
L	2.3557	X X	9.7838 **	5.2659 *	4.3780 *
N	4.8931 *	2.4022	X X	13.3859 ***	12.1460 ***
H	7.4666 **	3.7549	0.6620	X X	0.3335
VH	6.6428 *	3.3969	0.5441	0.1009	X X

Table 2.9.3. Flux experiment 3. t-tests comparing initial silicate flux in each level of the compaction treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	0	5	10	15	21
0	X X	4.7188 *	8.8576 **	7.6049 **	13.2556 ***
5	6.5073 *	X X	3.9353	2.6328	8.4737 **
10	2.0150	4.7430 *	X X	1.4201	4.9118 *
15	4.2083	1.8883	2.4607	X X	6.3425 *
21	0.4180	2.6883	0.5333	1.7158	X X

Table 2.9.4. Flux experiment 3. t-tests comparing initial silicate flux in each level of the oxygen treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Cp	NCp	W	Co
N	X X	0.3738	7.6611 **	4.7526 *	4.9298 *
Cp	0.3077	X X	5.9963 *	4.1055	4.1496
NCp	0.0382	0.3260	X X	1.5854	1.8991
W	3.1895	3.1040	3.0630	X X	0.1645
Co	1.2894	1.9834	1.0880	5.0933 *	X X

Table 2.9.5. Flux experiment 3. t-tests comparing initial silicate flux in each level of the animal treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	5	15	25	35	45
5	X X	0.8400	4.6982 *	14.5287 ***	12.2673 ***
15	2.4708	X X	3.9608	13.7553 ***	11.2359 ***
25	6.2029 *	4.1872	X X	9.1476 **	5.6272 *
35	14.2404 ***	13.4218 ***	11.9783 ***	X X	4.7672 *
45	1.8865	0.0984	2.4071	10.7455 ***	X X

Table 2.9.6. Flux experiment 3. t-tests comparing initial phosphate flux in each level of the salinity treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Si	VFS	FS	MS
N	X X	1.5275	3.2576	5.3069 *	5.3780 *
Si	2.6321	X X	1.6945	6.4427 *	6.5991 *
VFS	15.0049 ***	13.5914 ***	X X	7.9307 **	8.2170 **
FS	10.4778 ***	5.3889 *	21.5296 ***	X X	0.7168
MS	0.2612	2.3137	11.1430 ***	8.0046 **	X X

Table 2.9.7. Flux experiment 3. t-tests comparing initial phosphate flux in each level of the particle size treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	VL	L	N	H	VH
VL	X X	0.5326	4.7610 *	1.1665	6.1849 *
L	8.1670 **	X X	6.0084 *	0.8315	6.9247 *
N	6.7785 *	17.2630 ***	X X	5.8818 *	11.1503 ***
H	3.5519	10.9095 ***	2.1890	X X	4.8872 *
VH	7.1634 **	15.2394 ***	1.4849	3.2049	X X

Table 2.9.8. Flux experiment 3. t-tests comparing initial phosphate flux in each level of the compaction treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	0	5	10	15	21
0	X X	12.8297 ***	11.5821 ***	11.1127 ***	19.8312 ***
5	3.0120	X X	0.2911	2.2699	10.2489 ***
10	12.4108 ***	10.5897 ***	X X	1.9216	9.4091 **
15	9.4451 **	6.3457 *	6.7630 *	X X	6.4261 *
21	12.1714 ***	8.7351 **	5.8801 *	1.8439	X X

Table 2.9.9. Flux experiment 3. t-tests comparing initial phosphate flux in each level of the oxygen treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Cp	NCp	W	Co
N	X X	4.0361	0.4707	1.9286	7.9179 **
Cp	47.1156 ****	X X	2.8526	5.00863 *	2.2035
NCp	41.8269 ****	1.8392	X X	1.9666	5.3491 *
W5	54.7266 ****	6.1332 *	3.7535	X X	7.9889 **
Co	33.6360 ****	5.5579 *	6.8356 *	11.2098 ***	X X

Table 2.9.10. Flux experiment 3. t-tests comparing initial phosphate flux in each level of the animal treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	5	15	25	35	45
5	X X	7.6165 *	1.1187	1.2193	0.4979
15	4.1050	X X	10.4508 ***	10.5373 ***	7.7107 **
25	3.8583	0.6248	X X	0.1260	1.8122
35	4.6032 *	0.1920	0.5050	X X	1.9199
45	0.1817	4.0306	3.7640	4.4374 *	X X

Table 2.9.11. Flux experiment 3. t-tests comparing initial sulphate flux in each level of the salinity treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Si	VFS	FS	MS
N	X X	0.4921	0.0084	0.9702	1.7349
Si	8.0227 **	X X	0.5621	1.7074	1.5275
VFS	9.2011 **	0.4479	X X	1.1657	1.7902
FS	4.2551	4.3502 *	4.6784 *	X X	2.2880
MS	2.6365	5.8802 *	6.5739 *	1.7044	X X

Table 2.9.12. Flux experiment 3. t-tests comparing initial sulphate flux in each level of the particle size treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.



Level	VL	L	N	H	VH
VL	X X	2.9697	2.0958 X	2.1591	4.0282
L	11.7241 ***	X X	0.6199	0.1824	7.0158 **
N	1.2355	11.6113 ***	X X	0.3160	5.9243 *
H	4.2265	7.7853 **	3.3245	X X	5.6301 *
VH	2.2020	15.5712 ***	3.8091	7.0122 **	X X

Table 2.9.13. Flux experiment 3. t-tests comparing initial sulphate flux in each level of the compaction treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	0	5	10	15	21
0	X X	6.1507 *	1.2685	0.5668	3.6334
5	3.2085	X X	3.8749	5.3922 *	0.1046
10	10.5932 ***	7.7063 **	X X	1.5676	2.5135
15	8.4716 **	5.8089 *	0.9855	X X	3.6742
21	12.0360 ***	9.0830 **	0.9469	1.8521	X X

Table 2.9.14. Flux experiment 3. t-tests comparing initial sulphate flux in each level of the oxygen treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Cp	NCp	W	Co
N	X X	6.9502 *	8.9479 **	3.3663	9.8165 **
Cp	11.8602 ***	X X	0.0452	2.2279	1.5246
NCp	2.3874	4.9275 *	X X	2.5014	1.6714
W	3.5427	9.6472 **	4.4626 *	X X	3.7647
Co	12.9020 ***	4.3068 *	7.6712 **	11.6239 ***	X X

Table 2.9.15. Flux experiment 3. t-tests comparing initial sulphate flux in each level of the animal treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	5	15	25	35	45
5	X X	0.5526	2.8109	1.1920	2.2796
15	1.8214	X X	2.2461	0.4931	1.6723
25	0.1959	2.0645	X X	2.5191	0.8006
35	3.3894	5.7174 *	3.2414	X X	1.8044
45	6.0679 *	4.5144 *	6.4020 *	10.6794 ***	X X

Table 2.9.16. Flux experiment 3. t-tests comparing initial nitrate flux in each level of the salinity treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Si	VFS	FS	MS
N	X X	8.5827 **	8.6900 **	7.5875 **	13.2801 ***
Si	3.8437	X X	2.8295	2.1396	0.0002
VFS	5.3643 *	9.5415 **	X X	0.5058	5.3406 *
FS	0.5986	2.8982	5.4541 *	X X	3.2276
MS	0.4560	3.4196	5.9120 *	0.1883	X X

Table 2.9.17. Flux experiment 3. t-tests comparing initial nitrate flux in each level of the particle size treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	VL	L	N	H	VH
VL	X X	11.8903 ***	2.2987	7.2463 **	11.3199 ***
L	7.2231 **	X X	14.1088 ***	4.3345 *	0.3899
N	7.8591 **	0.1464	X X	9.4310 **	13.3514 ***
H	10.6945 ***	3.2208	3.1801	X X	4.3986 *
VH	1.8251	4.1354	4.4237 *	7.1516 **	X X

Table 2.9.18. Flux experiment 3. t-tests comparing initial nitrate flux in each level of the compaction treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	0	5	10	15	21
0	X X	1.2756	1.6581	1.4615	3.2547
5	2.6996	X X	0.5759	0.4825	2.2996
10	6.8770 *	3.1932	X X	0.0242	1.5491
15	3.4988	5.4690 *	9.6858 **	X X	1.4291
21	8.8999 **	4.2711	0.8620	11.8516 ***	X X

Table 2.9.19. Flux experiment 3. t-tests comparing initial nitrate flux in each level of the oxygen treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Cp	NCp	W	Co
N	X X	3.2881	1.4440	0.6643	0.9142
Cp	5.2582 *	X X	1.4005	2.5061	2.2690
NCp	1.2911	3.3000	X X	0.8441	0.6373
W	2.0374	2.8417	0.6153	X X	0.2360
Co	2.6269	2.5576	1.0750	0.4587	X X

Table 2.9.20. Flux experiment 3. t-tests comparing initial nitrate flux in each level of the animal treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	5	15	25	35	45
5	X X	0.5864	2.0467	0.9398	1.3150
15	11.3229 ***	X X	3.3480	3.5171	2.0589
25	11.9004 ***	5.9476 *	X X	1.8065	4.1741
35	1.2201	11.1154 ***	11.5139 ***	X X	6.3381 *
45	6.3798 *	4.8192 *	8.2582 **	4.6560 *	X X

Table 2.9.21. Flux experiment 3. t-tests comparing initial ammonia flux in each level of the salinity treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Si	VFS	FS	MS
N	X X	8.5930 **	1.5492	3.9280	2.6433
Si	2.6529	X X	10.1610 ***	4.4253 *	5.4217 *
VFS	0.7872	3.7187	X X	5.4508 *	4.1216
FS	5.9026 *	8.6981 **	5.4343 *	X X	1.1365
MS	4.4282 *	5.7289 *	4.1042	1.0745	X X

Table 2.9.22. Flux experiment 3. t-tests comparing initial ammonia flux in each level of the particle size treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	VL	L	N	H	VH
VL	X X	1.3432	8.4543 **	3.4017	15.1463 ***
L	0.7500	X X	8.9896 **	2.6445	16.9277 ***
N	2.0056	0.7032	X X	4.3479 *	8.9049 **
H	2.9407	1.1395	0.5142	X X	11.2330 ***
VH	1.3454	0.0195	1.1577	2.1301	X X

Table 2.9.23. Flux experiment 3. t-tests comparing initial ammonia flux in each level of the compaction treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	0	5	10	15	21
0	X X	2.2685	1.3512	5.0721 *	4.4928 *
5	1.7528	X X	2.8230	0.6499	4.3709 *
10	2.7389	0.5767	X X	5.7552 *	3.0466
15	3.4193	1.1006	0.6584	X X	7.9175 **
21	3.3903	1.7879	1.5345	1.1627	X X

Table 2.9.24. Flux experiment 3. t-tests comparing initial ammonia flux in each level of the oxygen treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

Level	N	Cp	NCp	W	Co
N	X X	3.9693	1.9290	9.5733 **	1.1299
Cp	1.4962	X X	1.7313	7.33703 **	2.6526
NCp	4.6958 *	5.7681 *	X X	7.7172 **	0.7961
W	0.2219	1.4145	3.4596	X X	8.4711 **
Co	1.9965	0.6440	5.7518 *	1.8692	X X

Table 2.9.25. Flux experiment 3. t-tests comparing initial ammonia flux in each level of the animal treatment. Upper half of table = overlying water; lower half = underlying water. Numbers = t values; \* =  $0.05 > p > 0.02$ ; \*\* =  $0.02 > p > 0.01$ ; \*\*\* =  $0.01 > p > 0.001$ ; \*\*\*\* =  $p < 0.001$ . n=3 in all cases.

**Appendices 3.1 - 3.3. (Pacific survey).**



Depth (cm)	Water content ( % dry weight)	
	mean	sd
00 - 01	455.3425	2.2237
01 - 02	378.5981	12.7831
02 - 03	327.0098	55.8876
03 - 04	397.3958	39.5331
04 - 05	383.2764	66.9506
6.5 - 7.5	329.0111	2.8858
10 - 11	302.0709	12.6846
15 - 16	293.2830	3.2924
20 - 21	286.3314	11.4203
25 - 26	253.0353	6.1687
30 - 31	251.6640	2.7798
40 - 41	221.8162	3.1944

Table 3.1.1. Water content (% dry weight), mean and sd, for each sediment depth at station 1. n=3 for all depth samples.

Depth (cm)	Water content ( % dry weight)	
	mean	sd
00 - 01	272.3453	13.0004
01 - 02	255.5004	9.0500
02 - 03	285.1363	7.2737
03 - 04	250.3974	3.9537
04 - 05	203.5175	38.1483
6.5 - 7.5	167.1280	5.7723
10 - 11	156.9781	9.3836
15 - 16	158.3762	9.9157
20 - 21	157.5370	1.8140
25 - 26	134.9971	3.1382
30 - 31	136.9485	3.1911
40 - 41	98.2789	1.7125

Table 3.1.2. Water content (% dry weight), mean and sd, for each sediment depth at station 2. n=3 for all depth samples.

Depth (cm)	Water content ( % dry weight)	
	mean	sd
00 - 01	515.392	3.1920
01 - 02	507.1052	0.6654
02 - 03	473.9158	3.9128
03 - 04	451.9509	22.6700
04 - 05	480.9234	14.2459
6.5 - 7.5	335.8566	0.8687
10 - 11	331.7471	2.4254
15 - 16	314.4945	2.8682
20 - 21	279.7391	9.7282
25 - 26	272.1941	1.7005
30 - 31	282.4865	4.8125
40 - 41	297.4175	1.1367

Table 3.1.3. Water content (% dry weight), mean and sd, for each sediment depth at station 4. n=3 for all depth samples.

Depth (cm)	Water content ( % dry weight)	
	mean	sd
00 - 01	485.3621	10.9859
01 - 02	399.5883	4.3753
02 - 03	335.7245	7.7583
03 - 04	356.3086	25.0763
04 - 05	280.2443	4.3722
6.5 - 7.5	210.9092	9.7150
10 - 11	216.4611	11.5053
15 - 16	204.5528	1.2810
20 - 21	207.9116	3.5162
25 - 26	306.8896	0.9933
30 - 31	291.5575	8.4064
40 - 41	285.0185	2.9097

Table 3.1.4. Water content (% dry weight), mean and sd, for each sediment depth at station 5. n=3 for all depth samples.

Depth (cm)	Water content ( % dry weight)	
	mean	sd
00 - 01	384.0241	6.6599
01 - 02	325.0719	10.3291
02 - 03	310.7176	5.5408
03 - 04	264.6323	8.5849
04 - 05	222.5138	3.4104
6.5 - 7.5	202.6127	9.2270
10 - 11	161.6885	8.5921
15 - 16	159.1578	3.1975
20 - 21	144.6268	2.7408
25 - 26	157.3724	2.8950
30 - 31	127.9179	1.6841
40 - 41	n/t	n/t

Table 3.1.5. Water content (% dry weight), mean and sd, for each sediment depth at station 6. n/t=sample not taken. n=3 for all depth samples.

Depth (cm)	Water content ( % dry weight)	
	mean	sd
00 - 01	417.7797	4.9983
01 - 02	391.9737	8.3385
02 - 03	367.3609	13.2280
03 - 04	334.3454	11.6839
04 - 05	288.0587	15.6507
6.5 - 7.5	250.2314	12.0047
10 - 11	141.3418	5.2679
15 - 16	128.6404	2.2378
20 - 21	138.1709	4.8012
25 - 26	126.5127	1.2413
30 - 31	129.5078	1.5447
40 - 41	n/t	n/t

Table 3.1.6. Water content (% dry weight), mean and sd, for each sediment depth at station 7. n/t=sample not taken. n=3 for all depth samples.

Depth (cm)	Water content ( % dry weight)	
	mean	sd
00 - 01	244.8461	30.5056
01 - 02	250.7054	39.7351
02 - 03	247.3605	1.2027
03 - 04	202.9323	10.4165
04 - 05	261.0034	0.9868
6.5 - 7.5	237.7202	10.6820
10 - 11	158.0374	8.8066
15 - 16	125.4653	4.6797
20 - 21	110.6824	6.9168
25 - 26	117.0967	18.7674
30 - 31	133.2155	2.1790
40 - 41	113.6276	6.6563

Table 3.1.7. Water content (% dry weight), mean and sd, for each sediment depth at station 8. n=3 for all depth samples.

Station	1	2	4	5
Depth (cm)				
00 - 01	1.6337 (0.0055)	1.8200 (0.0075)	2.0130 (0.0056)	2.2250 (0.0082)
01 - 02	1.6403 (0.0021)	1.8550 (0.0108)	2.0237 (0.0050)	2.2640 (0.0070)
02 - 03	1.6693 (0.0047)	1.8717 (0.0191)	2.0400 (0.0111)	2.2840 (0.0092)
03 - 04	1.6767 (0.0067)	1.9183 (0.0142)	2.0563 (0.0086)	2.2907 (0.0075)
04 - 05	1.6887 (0.0049)	1.9547 (0.0080)	2.0197 (0.0090)	2.2983 (0.0147)
6.5 - 7.5	1.7040 (0.0060)	1.9887 (0.0095)	2.1167 (0.0100)	2.3160 (0.0082)
10 - 11	1.6777 (0.0029)	2.0037 (0.0057)	2.1333 (0.0068)	2.3400 (0.0181)
15 - 16	1.6923 (0.0025)	2.0597 (0.0176)	2.1540 (0.0082)	2.3803 (0.0120)
20 - 21	1.7130 (0.0092)	2.0057 (0.0071)	2.1577 (0.0045)	2.4053 (0.0095)
25 - 26	1.6430 (0.0090)	2.0360 (0.0203)	2.1667 (0.0068)	2.4217 (0.0152)
30 - 31	1.6097 (0.0125)	2.0363 (0.0083)	2.1853 (0.0081)	2.4517 (0.0138)
40 - 41	1.6663 (0.0199)	2.0453 (0.0146)	2.2027 (0.0057)	2.4957 (0.0110)

Table 3.2.1. Concentrations of silicate ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5. Mean and (sd).  $n=3$  for all depth samples.

Station	6	7	8
Depth (cm)			
00 - 01	1.8240 (0.0080)	1.0130 (0.0177)	0.9832 (0.0095)
01 - 02	1.9170 (0.0115)	1.9360 (0.0082)	1.7140 (0.0066)
02 - 03	2.2963 (0.0159)	1.9610 (0.0036)	1.8290 (0.0066)
03 - 04	2.4060 (0.0187)	1.9963 (0.0068)	1.8643 (0.0137)
04 - 05	2.4173 (0.0191)	2.0045 (0.0049)	1.9053 (0.0100)
6.5 - 7.5	2.6097 (0.0132)	2.0740 (0.0105)	1.9243 (0.0093)
10 - 11	2.5947 (0.0080)	2.0963 (0.0087)	1.9643 (0.0087)
15 - 16	3.1193 (0.0273)	2.1163 (0.0059)	1.9727 (0.0085)
20 - 21	2.6573 (0.0506)	2.2097 (0.0189)	1.9767 (0.0500)
25 - 26	2.8033 (0.0085)	2.1367 (0.0106)	1.9960 (0.0101)
30 - 31	3.1043 (0.0100)	2.1497 (0.0140)	2.0043 (0.0060)
40 - 41	3.1117 (0.0055)	2.1760 (0.0105)	2.0927 (0.0100)

Table 3.2.2. Concentrations of silicate ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8. Mean and (sd). n=3 for all depth samples.

Station	1	2	3	4
Depth (cm)				
00 - 01	0.2124 (0.0042)	0.1806 (0.0007)	0.1584 (0.0014)	0.2099 (0.0011)
01 - 02	0.2091 (0.0026)	0.1773 (0.0010)	0.1561 (0.0019)	0.2070 (0.0006)
02 - 03	0.2057 (0.0013)	0.1758 (0.0005)	0.1495 (0.0017)	0.2046 (0.0009)
03 - 04	0.2049 (0.0019)	0.1743 (0.0006)	0.1462 (0.0011)	0.2027 (0.0003)
04 - 05	0.2021 (0.0024)	0.1716 (0.0011)	0.1431 (0.0011)	0.2015 (0.0025)
6.5 - 7.5	0.1989 (0.0003)	0.1711 (0.0006)	0.1405 (0.0008)	0.1978 (0.0011)
10 - 11	0.1953 (0.0015)	0.1693 (0.0010)	0.1376 (0.0014)	0.1965 (0.0007)
15 - 16	0.1912 (0.0020)	0.1682 (0.0015)	0.1383 (0.0009)	0.1948 (0.0011)
20 - 21	0.1877 (0.0011)	0.1658 (0.0005)	0.1335 (0.0019)	0.1949 (0.0003)
25 - 26	0.1820 (0.0007)	0.1614 (0.0010)	0.1285 (0.0012)	0.1918 (0.0017)
30 - 31	0.1813 (0.0004)	0.1593 (0.0007)	0.1239 (0.0008)	0.1887 (0.0023)
40 - 41	0.1769 (0.0029)	0.1568 (0.0004)	0.1186 (0.0010)	0.1923 (0.0009)

Table 3.2.3. Concentrations of phosphate (mg/l) at stations 1, 2, 4 and 5. Mean and (sd). n=3 for all depth samples.

Station	6	7	8
Depth (cm)			
00 - 01	0.1974 (0.0009)	0.2019 (0.0006)	0.1905 (0.0014)
01 - 02	0.1956 (0.0008)	0.2011 (0.0012)	0.1893 (0.0010)
02 - 03	0.1935 (0.0012)	0.1998 (0.0009)	0.1869 (0.0005)
03 - 04	0.1914 (0.0006)	0.1984 (0.0007)	0.1862 (0.0006)
04 - 05	0.1910 (0.0009)	0.1973 (0.0006)	0.1849 (0.0003)
6.5 - 7.5	0.1884 (0.0011)	0.1955 (0.0008)	0.1824 (0.0008)
10 - 11	0.1871 (0.0006)	0.1952 (0.0009)	0.1865 (0.0007)
15 - 16	0.1855 (0.0011)	0.1928 (0.0010)	0.1858 (0.0005)
20 - 21	0.1894 (0.0018)	0.1973 (0.0010)	0.1848 (0.0005)
25 - 26	0.1911 (0.0007)	0.1905 (0.0006)	0.1814 (0.0010)
30 - 31	0.1894 (0.0019)	0.1946 (0.0007)	0.1813 (0.0011)
40 - 41	0.1801 (0.0047)	0.1875 (0.0010)	0.1795 (0.0009)

Table 3.2.4. Concentrations of phosphate ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8. Mean and (sd). n=3 for all depth samples.



Station	1	2	4	5
Depth (cm)				
00 - 01	2439.7 (2.3245)	2512.3 (2.0009)	2485.5 (0.7029)	2500.8 (1.9698)
01 - 02	2446.6 (1.5632)	2499.8 (3.1953)	2491.3 (1.0536)	2505.4 (1.0017)
02 - 03	2454.2 (2.0518)	2508.0 (1.7157)	2493.3 (0.6245)	2507.5 (1.0067)
03 - 04	2457.7 (0.7000)	2508.5 (1.3206)	2501.1 (2.1284)	2506.1 (1.2221)
04 - 05	2460.6 (0.8331)	2510.9 (1.9860)	2503.6 (1.7898)	2507.7 (1.0789)
6.5 - 7.5	2465.3 (1.0020)	2514.5 (1.0149)	2506.2 (1.9503)	2509.3 (0.9539)
10 - 11	2468.1 (0.6033)	2514.8 (0.6512)	2509.6 (0.9612)	2511.4 (1.2017)
15 - 16	2469.9 (0.6512)	2515.8 (0.4000)	2509.4 (0.9295)	2510.7 (0.8185)
20 - 21	2471.7 (0.4044)	2517.7 (0.6116)	2509.7 (1.0409)	2511.6 (0.9000)
25 - 26	2472.5 (0.4583)	2520.3 (1.0266)	2511.6 (0.9077)	2512.6 (0.8738)
30 - 31	2474.5 (0.9292)	2522.4 (2.9023)	2513.2 (1.7349)	2512.5 (0.8084)
40 - 41	2475.4 (1.0017)	2524.2 (1.0017)	2515.4 (1.4844)	2515.4 (0.7507)

Table 3.2.5. Concentrations of sulphate (mg/l) at stations 1, 2, 4 and 5. Mean and (sd). n=3 for all depth samples.

Station	6	7	8	9
Depth (cm)				
00 - 01	2471.8 (0.5035)	2512.7 (1.0536)	2447.4 (2.8538)	2471.4 (1.0148)
01 - 02	2477.8 (0.4517)	2515.1 (0.8185)	2448.2 (1.0505)	
02 - 03	2476.3 (0.5568)	2517.6 (0.9295)	2451.7 (0.5133)	
03 - 04	2477.1 (0.8623)	2520.5 (0.6430)	2457.3 (0.5509)	
04 - 05	2478.8 (0.6812)	2522.1 (0.5865)	2463.3 (0.9019)	
6.5 - 7.5	2480.5 (0.8331)	2523.5 (0.4000)	2464.7 (0.8185)	
10 - 11	2481.5 (0.4935)	2524.8 (0.6245)	2466.0 (1.1722)	
15 - 16	2483.5 (0.6033)	2527.5 (0.9849)	2469.2 (1.0505)	
20 - 21	2485.2 (1.0017)	2531.9 (1.7012)	2473.9 (1.1136)	
25 - 26	2487.3 (0.9505)	2527.5 (0.8022)	2474.8 (0.9508)	
30 - 31	2490.6 (0.9295)	2530.5 (1.0264)	2476.5 (1.0817)	
40 - 41	2492.3 (0.9165)	2531.8 (1.5875)	2477.0 (0.8509)	

Table 3.2.6. Concentrations of sulphate (mg/l) at stations 6, 7 and 8. Mean and (sd). n=3 for all depth samples.

Station	1	2	4	5
Depth (cm)				
00 - 01	1.9545 (0.0050)	2.0972 (0.0107)	2.1920 (0.1179)	2.0235 (0.0118)
01 - 02	1.9814 (0.0025)	2.1103 (0.0050)	2.2923 (0.0083)	2.0931 (0.0070)
02 - 03	1.9997 (0.0045)	2.1444 (0.0053)	2.2287 (0.0103)	1.9959 (0.0049)
03 - 04	2.0182 (0.0032)	2.0961 (0.0106)	2.2705 (0.0105)	1.9220 (0.0105)
04 - 05	2.0013 (0.0037)	2.0876 0.0085	2.2074 0.0159	1.8847 0.0087
6.5 - 7.5	1.9888 (0.0070)	1.9975 (0.0046)	2.1920 (0.0065)	1.8314 (0.0016)
10 - 11	1.9435 (0.0061)	1.9851 (0.0057)	2.1636 (0.0108)	1.7905 (0.0082)
15 - 16	1.9006 (0.0071)	1.9646 (0.0073)	2.1034 (0.0094)	1.7493 (0.0062)
20 - 21	1.8643 (0.0069)	1.9480 (0.0114)	2.0674 (0.0080)	1.6985 (0.0090)
25 - 26	1.8240 (0.0051)	1.9149 (0.0133)	2.0518 (0.0055)	1.6815 (0.0071)
30 - 31	1.7924 (0.0081)	1.8800 (0.0055)	2.0077 (0.0129)	1.6261 (0.0169)
40 - 41	1.7539 (0.0054)	1.8483 (0.0083)	1.9703 (0.0050)	1.5963 (0.0056)

Table 3.2.7. Concentrations of nitrate ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5. Mean and (sd). n=3 for all depth samples.

Station	6	7	8
Depth (cm)			
00 - 01	2.4074 (0.0566)	2.0119 (0.0044)	1.9045 (0.0061)
01 - 02	2.4834 (0.0239)	2.0828 (0.0076)	1.9146 (0.0107)
02 - 03	2.2475 (0.0290)	2.0994 (0.0132)	1.9569 0.0106)
03 - 04	2.0067 (0.0099)	2.0359 (0.0107)	1.9901 (0.0065)
04 - 05	1.9770 (0.0105)	1.9885 (0.0115)	2.0263 (0.0113)
6.5 - 7.5	2.0176 (0.0158)	1.9851 (0.0054)	2.0825 (0.0031)
10 - 11	1.9856 (0.0079)	1.9464 (0.0054)	2.0295 (0.0068)
15 - 16	1.9604 (0.0035)	1.9240 (0.0072)	2.0554 (0.0505)
20 - 21	1.9062 (0.0040)	1.8873 (0.0107)	1.9851 (0.0077)
25 - 26	1.8848 (0.0075)	1.8791 (0.0039)	1.9503 (0.0056)
30 - 31	1.8527 (0.0107)	1.8859 (0.0059)	1.9008 (0.0095)
40 - 41	1.8072 (0.0053)	1.8691 (0.0060)	1.8801 (0.0051)

Table 3.2.8. Concentrations of nitrate ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8. Mean and (sd).  $n=3$  for all depth samples.

Station	1	2	4	5
Depth (cm)				
00 - 01	0.1047 (0.0033)	0.1238 (0.0033)	0.1632 (0.0041)	0.1501 (0.0034)
01 - 02	0.1152 (0.0031)	0.1286 (0.0012)	0.1804 (0.0020)	0.1402 (0.0028)
02 - 03	0.1187 (0.0013)	0.1225 (0.0011)	0.1564 (0.0035)	0.1260 (0.0028)
03 - 04	0.1212 (0.0008)	0.1155 (0.0029)	0.1433 (0.0045)	0.1145 (0.0037)
04 - 05	0.1298 (0.0037)	0.1129 (0.0032)	0.1210 (0.0031)	0.1020 (0.0050)
6.5 - 7.5	0.1208 (0.0016)	0.1043 (0.0043)	0.1098 (0.0055)	0.0988 (0.0048)
10 - 11	0.2262 (0.0026)	0.1033 (0.0011)	0.0910 (0.0050)	0.1073 (0.0037)
15 - 16	0.1103 (0.0066)	0.0979 (0.0025)	0.0874 (0.0035)	0.0926 (0.0028)
20 - 21	0.1036 (0.0023)	0.0923 (0.0028)	0.0874 (0.0010)	0.0897 (0.0029)
25 - 26	0.0941 (0.0032)	0.0870 (0.0034)	0.0859 (0.0028)	0.0838 (0.0044)
30 - 31	0.0902 (0.0034)	0.0862 (0.0024)	0.0827 (0.0027)	0.0821 (0.0035)
40 - 41	0.0879 (0.0021)	0.0873 (0.0030)	0.0791 (0.0014)	0.0755 (0.0027)

Table 3.2.9. Concentrations of ammonium ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5. Mean and (sd). n=3 for all depth samples.

Station	6	7	8
Depth (cm)			
00 - 01	0.1025 (0.0066)	0.1321 (0.0058)	0.1164 (0.0035)
01 - 02	0.1061 (0.0038)	0.1237 (0.0046)	0.1148 (0.0042)
02 - 03	0.1232 (0.0041)	0.1373 (0.0029)	0.1328 (0.0051)
03 - 04	0.1265 (0.0020)	0.1383 (0.0013)	0.1250 (0.0046)
04 - 05	0.1411 (0.0051)	0.1230 (0.0031)	0.1166 (0.0030)
6.5 - 7.5	0.1281 (0.0025)	0.1150 (0.0038)	0.1058 (0.0026)
10 - 11	0.1130 (0.0032)	0.1004 (0.0035)	0.0964 (0.0033)
15 - 16	0.1076 (0.0041)	0.0984 (0.0036)	0.0971 (0.0055)
20 - 21	0.0975 (0.0035)	0.0937 (0.0028)	0.0845 (0.0027)
25 - 26	0.0947 (0.0047)	0.0899 (0.0013)	0.0780 (0.0024)
30 - 31	0.0845 (0.0047)	0.0828 (0.0016)	0.0733 (0.0032)
40 - 41	0.0812 (0.0020)	0.0765 (0.0032)	0.0656 (0.0037)

Table 3.2.10. Concentrations of ammonium ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8. Mean and (sd). n=3 for all depth samples.

Station	1	2	4	5
Depth.(cm)				
00 - 01	0.14	0.15	0.05	0.17
01 - 02	0.15	0.09	0.14	0.12
02 - 03	0.11	0.11	0.08	0.18
03 - 04	0.12	0.06	0.14	0.08
04 - 05	0.15	0.11	0.05	0.17
6.5 - 7.5	0.12	0.09	0.12	0.08
10 - 11	0.11	0.15	0.17	0.11
15 - 16	0.14	0.06	0.20	0.08
20 - 21	0.17	0.11	0.03	0.14
25 - 26	0.14	0.12	0.12	0.09
30 - 31	0.15	0.17	0.14	0.06
40 - 41	0.15	0.14	0.11	0.17

Table 3.3.1. Concentrations of Lithium ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station	6	7	8
Depth.(cm)			
00 - 01	0.17	0.05	0.09
01 - 02	0.11	0.09	0.09
02 - 03	0.08	0.17	0.18
03 - 04	0.15	0.11	0.15
04 - 05	0.12	0.06	0.14
6.5 - 7.5	0.14	0.09	0.17
10 - 11	0.15	0.09	0.14
15 - 16	0.12	0.12	0.17
20 - 21	0.08	0.06	0.15
25 - 26	0.15	0.06	0.09
30 - 31	0.21	0.00	0.08
40 - 41	0.15	0.12	0.08

Table 3.3.2. Concentrations of Lithium ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station	1	2	4	5
Depth. (cm)				
00 - 01	10400	10780	6720	11160
01 - 02	10700	7620	10500	9990
02 - 03	7730	9120	7730	11050
03 - 04	9590	6210	9340	6650
04 - 05	10160	9150	6560	10470
6.5 - 7.5	9340	7910	8660	6190
10 - 11	8060	9870	10280	10300
15 - 16	8320	6170	9260	7390
20 - 21	10580	7600	5440	9060
25 - 26	9300	8720	8810	7360
30 - 31	10930	10320	9850	5280
40 - 41	9370	9040	7850	11870

Table 3.3.3. Concentrations of Sodium ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station	6	7	8
Depth. (cm)			
00 - 01	11320	6580	8910
01 - 02	9450	6890	7620
02 - 03	7580	11000	11350
03 - 04	10510	8460	10900
04 - 05	9620	7830	9570
6.5 - 7.5	10750	7700	10550
10 - 11	10460	7500	8500
15 - 16	9390	8600	10520
20 - 21	7510	6360	9540
25 - 26	10790	6360	7370
30 - 31	11150	4393	7410
40 - 41	10660	9910	6300

Table 3.3.4. Concentrations of Sodium ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.



Station Depth. (cm)	1	2	4	5
00 - 01	378	421	234	434
01 - 02	389	302	423	405
02 - 03	296	369	276	430
03 - 04	347	237	383	235
04 - 05	405	363	226	424
6.5 - 7.5	345	284	360	258
10 - 11	324	383	437	359
15 - 16	306	245	407	290
20 - 21	374	299	188	354
25 - 26	382	360	355	289
30 - 31	437	405	417	231
40 - 41	378	372	318	476

Table 3.3.5. Concentrations of Potassium ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station Depth. (cm)	6	7	8
00 - 01	451	213	372
01 - 02	396	247	292
02 - 03	299	436	462
03 - 04	401	335	459
04 - 05	397	298	360
6.5 - 7.5	413	289	442
10 - 11	425	307	343
15 - 16	388	333	437
20 - 21	307	250	358
25 - 26	442	259	282
30 - 31	452	169	277
40 - 41	434	415	268

Table 3.3.6. Concentrations of Potassium ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station	1	2	4	5
Depth.(cm)				
00 - 01	1260	1279	725	1315
01 - 02	1289	937	1230	1206
02 - 03	1005	1101	843	1336
03 - 04	1158	721	1140	743
04 - 05	1248	1073	691	1252
6.5 - 7.5	1081	861	1053	775
10 - 11	976	1121	1210	1030
15 - 16	992	709	1128	837
20 - 21	1207	878	546	1015
25 - 26	1127	1041	1049	847
30 - 31	1285	1156	1147	682
40 - 41	1135	1052	919	1382

Table 3.3.7. Concentrations of Magnesium ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station	6	7	8
Depth.(cm)			
00 - 01	1339	661	1046
01 - 02	1174	765	821
02 - 03	906	1321	1337
03 - 04	1217	1021	1271
04 - 05	1171	896	1029
6.5 - 7.5	1284	870	1232
10 - 11	1243	910	983
15 - 16	1143	997	1232
20 - 21	891	765	1026
25 - 26	1294	792	812
30 - 31	1343	511	752
40 - 41	1275	1193	691

Table 3.3.8. Concentrations of Magnesium ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station	1	2	4	5
Depth. (cm)				
00 - 01	400	417	236	432
01 - 02	409	293	404	389
02 - 03	322	358	277	450
03 - 04	378	230	381	244
04 - 05	405	349	230	415
6.5 - 7.5	353	273	321	255
10 - 11	317	365	407	335
15 - 16	325	230	375	272
20 - 21	393	285	162	330
25 - 26	357	338	339	270
30 - 31	417	370	384	207
40 - 41	366	340	297	446

Table 3.3.9. Concentrations of Calcium ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station	6	7	8
Depth. (cm)			
00 - 01	443	216	345
01 - 02	387	252	276
02 - 03	279	451	440
03 - 04	401	328	421
04 - 05	386	298	337
6.5 - 7.5	423	290	401
10 - 11	402	297	316
15 - 16	373	327	409
20 - 21	289	230	336
25 - 26	426	260	257
30 - 31	420	167	244
40 - 41	406	373	226

Table 3.3.10. Concentrations of Calcium ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station Depth.(cm)	1	2	4	5
00 - 01	6.9	7.5	4.3	7.9
01 - 02	7.0	5.4	7.5	7.2
02 - 03	5.6	6.5	5.0	7.9
03 - 04	6.6	4.2	6.9	4.4
04 - 05	7.2	6.3	4.2	7.6
6.5 - 7.5	6.2	5.0	6.2	4.7
10 - 11	5.7	6.6	7.5	6.2
15 - 16	5.5	4.2	6.8	5.0
20 - 21	6.7	5.1	3.2	6.1
25 - 26	6.5	6.1	6.2	5.0
30 - 31	7.4	6.7	7.0	4.0
40 - 41	6.4	6.1	5.6	8.2

Table 3.3.11. Concentrations of Strontium ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station Depth.(cm)	6	7	8
00 - 01	8.1	4.0	6.4
01 - 02	7.1	4.6	5.1
02 - 03	5.4	8.0	8.0
03 - 04	7.4	6.1	7.7
04 - 05	7.1	5.5	6.2
6.5 - 7.5	7.9	5.2	7.5
10 - 11	7.5	5.4	5.7
15 - 16	6.9	6.0	7.3
20 - 21	5.4	4.4	6.0
25 - 26	7.7	4.8	4.8
30 - 31	7.9	3.0	4.6
40 - 41	7.5	7.0	4.2

Table 3.3.12. Concentrations of Strontium ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station Depth. (cm)	1	2	4	5
00 - 01	0.18	0.15	0.00	0.20
01 - 02	0.00	0.13	0.08	0.20
02 - 03	0.13	0.15	0.10	0.20
03 - 04	0.13	0.10	0.10	0.13
04 - 05	0.13	0.18	0.10	0.13
6.5 - 7.5	0.10	0.10	0.10	0.18
10 - 11	0.10	0.18	0.13	0.13
15 - 16	0.13	0.13	0.13	0.13
20 - 21	0.15	0.15	0.08	0.15
25 - 26	0.15	0.18	0.18	0.13
30 - 31	0.23	0.23	0.20	0.08
40 - 41	0.25	0.18	0.15	0.20

Table 3.3.13. Concentrations of Barium ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station Depth. (cm)	6	7	8
00 - 01	0.10	0.15	0.13
01 - 02	0.13	0.13	0.13
02 - 03	0.08	0.20	0.18
03 - 04	0.13	0.10	0.13
04 - 05	0.13	0.15	0.18
6.5 - 7.5	0.00	0.15	0.10
10 - 11	0.15	0.13	0.15
15 - 16	0.15	0.15	0.18
20 - 21	0.15	0.10	0.15
25 - 26	0.15	0.13	0.15
30 - 31	0.23	0.10	0.15
40 - 41	0.18	0.15	0.10

Table 3.3.14. Concentrations of Barium ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station	1	2	4	5
Depth.(cm)				
00 - 01	0.0	0.0	0.0	0.0
01 - 02	0.0	0.0	0.0	0.0
02 - 03	0.0	1.8	3.8	0.0
03 - 04	0.0	0.0	0.0	0.0
04 - 05	0.0	0.0	0.0	0.0
6.5 - 7.5	0.0	0.0	0.0	0.0
10 - 11	0.0	0.0	0.0	0.0
15 - 16	0.0	0.0	1.0	0.0
20 - 21	9.2	0.0	0.0	0.0
25 - 26	0.0	0.0	0.0	0.0
30 - 31	0.0	0.0	1.6	0.0
40 - 41	0.0	0.0	0.0	0.0

Table 3.3.15. Concentrations of Iron ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station	6	7	8
Depth.(cm)			
00 - 01	0.0	0.0	0.0
01 - 02	0.0	0.0	0.0
02 - 03	0.0	0.0	0.0
03 - 04	0.0	0.0	0.0
04 - 05	0.0	0.0	0.0
6.5 - 7.5	0.0	0.0	0.0
10 - 11	0.0	0.0	0.0
15 - 16	0.0	0.0	0.0
20 - 21	0.0	0.0	0.0
25 - 26	0.0	0.0	0.0
30 - 31	0.0	0.0	0.0
40 - 41	0.0	0.0	0.0

Table 3.3.16. Concentrations of Iron ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station	1	2	4	5
Depth. (cm)				
00 - 01	1.6	0.3	0.2	0.3
01 - 02	0.0	2.4	0.7	1.8
02 - 03	0.4	3.0	0.3	0.7
03 - 04	4.5	2.0	1.9	0.7
04 - 05	6.6	1.7	2.7	0.5
6.5 - 7.5	0.0	4.3	0.6	0.2
10 - 11	2.1	1.7	0.8	0.2
15 - 16	0.1	1.4	2.6	0.4
20 - 21	0.3	7.2	5.4	0.3
25 - 26	2.4	2.9	7.4	3.2
30 - 31	1.0	5.7	0.3	0.8
40 - 41	1.1	7.0	7.7	6.8

Table 3.3.17. Concentrations of Zinc ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station	6	7	8
Depth. (cm)			
00 - 01	0.3	3.1	2.6
01 - 02	0.2	0.3	0.2
02 - 03	0.9	0.2	3.6
03 - 04	0.2	1.9	0.3
04 - 05	0.2	7.9	6.2
6.5 - 7.5	1.4	4.7	1.4
10 - 11	0.2	0.9	3.6
15 - 16	0.5	3.4	1.8
20 - 21	0.7	1.1	3.3
25 - 26	0.4	2.0	0.9
30 - 31	0.2	0.5	0.9
40 - 41	0.8	0.8	6.7

Table 3.3.18. Concentrations of Zinc ( $\text{mg l}^{-1}$ ) at stations 6, 7, and 8 and for each sediment depth.

Station Depth. (cm)	1	2	4	5
00 - 01	0.0	0.0	0.0	0.0
01 - 02	0.0	0.0	0.0	0.0
02 - 03	0.0	0.0	0.0	0.0
03 - 04	0.6	0.0	0.6	0.0
04 - 05	0.0	0.0	0.0	0.0
6.5 - 7.5	0.4	0.0	0.0	0.0
10 - 11	0.0	0.0	0.0	0.0
15 - 16	0.0	0.0	0.0	0.0
20 - 21	0.0	0.0	0.0	0.0
25 - 26	0.0	0.0	0.0	0.0
30 - 31	0.0	0.6	0.0	0.0
40 - 41	0.0	0.0	0.6	0.6

Table 3.3.19. Concentrations of Phosphorous ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station Depth. (cm)	6	7	8
00 - 01	0.0	0.4	0.0
01 - 02	0.0	0.4	0.6
02 - 03	0.0	0.6	0.4
03 - 04	0.0	0.6	0.0
04 - 05	0.6	0.4	0.0
6.5 - 7.5	0.0	0.0	0.0
10 - 11	0.0	0.0	0.0
15 - 16	0.0	0.0	0.4
20 - 21	0.0	0.0	0.0
25 - 26	0.6	0.0	0.0
30 - 31	0.0	0.0	0.0
40 - 41	0.0	0.0	0.0

Table 3.3.20. Concentrations of Phosphorous ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.



Station	1	2	4	5
Depth. (cm)				
00 - 01	809	897	912	919
01 - 02	811	575	895	784
02 - 03	893	681	914	927
03 - 04	729	528	656	800
04 - 05	753	705	556	869
6.5 - 7.5	898	754	682	526
10 - 11	681	789	853	876
15 - 16	853	695	644	865
20 - 21	909	686	643	773
25 - 26	675	695	718	630
30 - 31	894	828	831	429
40 - 41	790	704	566	1025

Table 3.3.21. Concentrations of Sulphur ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station	6	7	8
Depth. (cm)			
00 - 01	957	751	681
01 - 02	774	891	717
02 - 03	641	922	970
03 - 04	889	682	894
04 - 05	799	658	805
6.5 - 7.5	971	702	894
10 - 11	875	621	689
15 - 16	717	730	857
20 - 21	720	588	774
25 - 26	904	547	635
30 - 31	900	583	635
40 - 41	842	840	609

Table 3.3.22. Concentrations of Sulphur ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station Depth. (cm)	1	2	4	5
00 - 01	4.1	4.6	2.6	4.6
01 - 02	4.1	3.3	4.4	4.2
02 - 03	3.3	3.9	2.9	4.6
03 - 04	3.9	2.6	3.9	2.5
04 - 05	4.7	4.1	2.4	4.6
6.5 - 7.5	4.0	3.4	3.9	2.8
10 - 11	3.8	4.6	4.7	3.9
15 - 16	3.7	3.0	4.4	3.2
20 - 21	4.4	3.6	2.1	3.9
25 - 26	4.6	4.5	4.2	3.1
30 - 31	5.2	4.9	4.9	2.5
40 - 41	4.4	4.4	3.6	5.1

Table 3.3.23. Concentrations of Boron ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station Depth. (cm)	6	7	8
00 - 01	5.0	2.3	4.1
01 - 02	4.2	2.9	3.3
02 - 03	3.2	4.7	5.2
03 - 04	4.4	3.5	5.0
04 - 05	4.2	3.1	4.1
6.5 - 7.5	4.1	3.0	5.4
10 - 11	4.6	3.3	4.1
15 - 16	4.2	1.5	5.5
20 - 21	3.3	2.8	4.5
25 - 26	4.9	2.9	3.5
30 - 31	4.8	1.9	3.8
40 - 41	4.6	4.8	3.1

Table 3.3.24. Concentrations of Boron ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

Station Depth. (cm)	1	2	4	5
00 - 01	2.0	3.3	4.0	4.8
01 - 02	2.3	1.5	4.3	4.0
02 - 03	2.3	3.3	5.3	6.0
03 - 04	2.3	2.8	4.0	5.0
04 - 05	3.0	3.3	5.3	6.5
6.5 - 7.5	4.0	5.0	4.5	6.8
10 - 11	3.8	4.8	7.3	8.0
15 - 16	4.5	3.5	5.0	8.5
20 - 21	4.8	4.0	4.5	7.8
25 - 26	3.5	4.5	5.3	5.3
30 - 31	5.0	5.3	6.8	4.8
40 - 41	4.3	4.3	4.3	7.0

Table 3.3.25. Concentrations of Silicon ( $\text{mg l}^{-1}$ ) at stations 1, 2, 4 and 5 for each sediment depth.

Station Depth. (cm)	6	7	8
00 - 01	6.0	5.0	3.5
01 - 02	5.8	7.8	4.5
02 - 03	5.5	8.3	6.3
03 - 04	8.0	6.3	5.5
04 - 05	7.0	7.3	4.3
6.5 - 7.5	2.8	7.5	5.5
10 - 11	10.0	8.5	3.8
15 - 16	7.5	8.5	5.5
20 - 21	8.5	7.8	4.8
25 - 26	11.0	6.3	3.5
30 - 31	10.5	8.5	4.8
40 - 41	10.3	9.5	3.5

Table 3.3.26. Concentrations of Silicon ( $\text{mg l}^{-1}$ ) at stations 6, 7 and 8 for each sediment depth.

**APPENDICES. - 4.1 and 4.2 (Tamar Estuary Survey).**

Depth (cm)	Micro-organisms $\times 10^8 \cdot g^{-1}$ sediment	
	mean	(sd)
0 - 1	6.4157	(0.4611)
1.5 - 2.5	3.9585	(0.2069)
4 - 5	3.3038	(0.4363)
6.5 - 7.5	3.5649	(0.2097)
9 - 10	4.4065	(0.2054)
14 - 15	2.1409	(0.4361)
19 - 20	1.0821	(0.3090)
29 - 30	2.4217	(0.4257)
39 - 40	2.9365	(0.5631)

Table 4.1.1. Micro-organism numbers (mean and sd) for each of the depth samples at Cotehele Quay.

Depth (cm)	micro-organisms $\times 10^8 \cdot g^{-1}$ sediment	
	mean	(sd)
0 - 1	4.5389	(0.2313)
1.5 - 2.5	4.9212	(0.2097)
4 - 5	5.0180	(0.2380)
6.5 - 7.5	9.0655	(0.7092)
9 - 10	2.6581	(0.2742)
14 - 15	1.6670	(0.2738)
19 - 20	1.7079	(0.2393)
29 - 30	1.8465	(2.5885)
39 - 40	2.1169	(0.4659)

Table 4.1.2. Micro-organism numbers (mean and sd) for each of the depth samples from Salter Mills.

Depth (cm)	micro-organisms $\times 10^8 \cdot g^{-1}$ sediment	
	mean	(sd)
0 - 1	3.2549	(0.2350)
1.5 - 2.5	5.4436	(0.3014)
4 - 5	3.3549	(0.5001)
6.5 - 7.5	2.2666	(0.1235)
9 - 10	3.5445	(0.2849)
14 - 15	2.0732	(0.1315)
19 - 20	2.3146	(0.2040)
29 - 30	1.2824	(0.1129)
39 - 40	1.1975	(0.9063)

Table 4.1.3. Micro-organism numbers (mean and sd) for each of the depth samples from Tamar Bridge.

Station	Distance from high tide (m)	micro-organisms x10 <sup>7</sup> .g <sup>-1</sup> sediment mean (sd)	Sampling time
1	42	5.9792 (0.4149)	12.26
1	42	4.1655 (0.9089)	13.35
2	50	3.6766 (0.5319)	12.27
2	50	4.3275 (0.2957)	12.39
3	65	5.5981 (0.1377)	12.32
3	65	6.6044 (0.6668)	12.53
4	79	6.0188 (0.5269)	12.48
4	79	7.0301 (0.4369)	13.28
5	95	7.5712 (0.5891)	13.11
5	95	7.0679 (0.8238)	13.41

Table 4.1.4. Distances from high tide, micro-organism numbers and sampling times for each of the stations at Sharrow point.



Nutrient	Depth (cm)			
	0-2.5	2.5-5.0	5.0-7.5	7.5-10.0
<hr/>				
$\text{NO}_3^-$ (mg l <sup>-1</sup> )				
mean	1.5265	1.6299	1.6944	1.7934
(sd)	(0.0241)	(0.0308)	(0.0750)	(0.0600)
<hr/>				
$\text{SiO}_4^{4-}$ (mg l <sup>-1</sup> )				
mean	10.0975	9.9887	9.8572	9.7689
(sd)	(0.1646)	(0.1165)	(0.0607)	(0.0475)
<hr/>				
$\text{PO}_4^{3-}$ (μg l <sup>-1</sup> )				
mean	41.1601	40.0371	38.8316	37.0593
(sd)	(0.3497)	(0.1380)	(0.1551)	(0.1656)
<hr/>				
$\text{NH}_4^+$ (μg l <sup>-1</sup> )				
mean	120.9722	117.9159	116.3339	114.9029
(sd)	(0.2673)	(0.3033)	(0.4099)	(0.3823)
<hr/>				
$\text{SO}_4^{2-}$ (mg l <sup>-1</sup> )				
mean	11.1375	11.6500	11.9500	12.3700
(sd)	(0.1599)	(0.1492)	(0.1032)	(0.1742)
<hr/>				
Salinity (g l <sup>-1</sup> )				
mean	0.00	1.00	1.50	2.00
(sd)	(0.00)	(0.00)	(0.50)	(0.00)
<hr/>				

Table 4.2.1. Dissolved nutrient concentrations and salinity of the interstitial water extracted from sediment at Cotehele Quay.

Nutrient	Depth (cm)				
	0-2.5	2.5-5.0	5.0-7.5	7.5-10.0	17.5-20.0
<hr/>					
$\text{NO}_3^-$ (mg l <sup>-1</sup> )					
mean	0.7172	0.8557	0.8920	0.9660	1.0412
(sd)	(0.0322)	(0.0453)	(0.0305)	(0.0337)	(0.0182)
<hr/>					
$\text{SiO}_4^{4-}$ (mg l <sup>-1</sup> )					
mean	5.6172	5.4199	5.2507	5.1610	5.1305
(sd)	(0.0441)	(0.0594)	(0.0476)	(0.0481)	(0.0329)
<hr/>					
$\text{PO}_4^{3-}$ (μg l <sup>-1</sup> )					
mean	70.1980	70.0741	69.7982	69.6591	69.6170
(sd)	(0.0828)	(0.0389)	(0.0239)	(0.0415)	(0.0327)
<hr/>					
$\text{NH}_4^+$ (μg l <sup>-1</sup> )					
mean	90.2485	89.9830	89.7391	89.6040	89.4237
(sd)	(0.0757)	(0.0453)	(0.0850)	(0.0328)	(0.2748)
<hr/>					
$\text{SO}_4^{2-}$ (mg l <sup>-1</sup> )					
mean	1579.6025	1618.9050	1704.4950	1732.3050	1725.0225
(sd)	(12.7409)	(7.2935)	(17.3121)	(11.1171)	(5.0232)
<hr/>					
Salinity (g l <sup>-1</sup> )					
mean	24.00	25.00	25.00	25.50	26.00
(sd)	(0.00)	(0.00)	(0.00)	(0.50)	(0.00)
<hr/>					

Table 4.2.2. Dissolved nutrient concentrations and salinity of the interstitial water extracted from sediment at Salter Mills.

Nutrient	Depth (cm)			
	0-2.5	2.5-5.0	5.0-7.5	7.5-10.0
<hr/>				
$\text{NO}_3^-$ ( $\text{mg l}^{-1}$ )				
mean	0.6129	0.7038	0.7967	0.9012
(sd)	(0.0227)	(0.0245)	(0.0234)	(0.0226)
<hr/>				
$\text{SiO}_4^{4-}$ ( $\text{mg l}^{-1}$ )				
mean	3.7719	3.6197	3.4333	3.3478
(sd)	(0.0618)	(0.0484)	(0.0680)	(0.0704)
<hr/>				
$\text{PO}_4^{3-}$ ( $\mu\text{g l}^{-1}$ )				
mean	74.7559	71.4144	71.1445	68.4651
(sd)	(1.0556)	(0.9766)	(0.4567)	(0.8102)
<hr/>				
$\text{NH}_4^+$ ( $\mu\text{g l}^{-1}$ )				
mean	86.1970	83.7758	81.4052	78.8469
(sd)	(0.7483)	(0.9052)	(0.6440)	(0.7373)
<hr/>				
$\text{SO}_4^{2-}$ ( $\text{mg l}^{-1}$ )				
mean	2203.8425	2211.7550	2218.6650	2225.3650
(sd)	(2.1277)	(2.2380)	(1.8046)	(1.8117)
<hr/>				
Salinity ( $\text{g l}^{-1}$ )				
mean	32.00	32.50	33.50	33.00
(sd)	(0.00)	(0.50)	(0.50)	(0.00)
<hr/>				

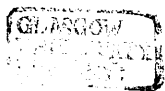


Table 4.2.3. Dissolved nutrient concentrations and salinity of the interstitial water extracted from sediment at Tamar Bridge.