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# STUDIES ON THE BIOGENIC MEDIATION OF SEDIMENT DYNAMICS IN COASTAL SYSTEMS

**Rebecca Jane Aspden**



A thesis submitted to the University of St Andrews for the degree of  
Doctor of Philosophy

School of Environmental and Evolutionary Biology  
University of St Andrews

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## Abbreviations

<b>Abs</b>	Absorbance at 485nm
<b>A<sub>662</sub></b>	Absorbance at 662nm
<b>A<sub>750</sub></b>	Absorbance at 750nm
<b><math>\tau_0</math></b>	Bed shear stress
<b>Re<sub>r</sub></b>	Boundary roughness Reynolds number
<b><math>d\bar{u}</math></b>	Change in current velocity
<b><math>d\log z</math></b>	Change in height above the bed derived from a $\log_{10}$ vertical scale
<b>C</b>	Chlorophyll <i>a</i> concentration
<b>M</b>	Co-efficient (gradient of the line)
<b>CSM</b>	Cohesive Strength Meter
<b><math>\tau_{ocrit}</math></b>	Critical bed shear stress
<b>U<sup>*</sup><sub>crit</sub></b>	Critical shear velocity
<b><math>\rho</math></b>	Density of the water
<b><i>d</i></b>	Diameter (scale component)
<b>DMF</b>	Dimethylformamide
<b><math>\epsilon</math></b>	Extinction co-efficient of Chlorophyll <i>a</i> .
<b>EPS</b>	Extracellular Polymeric Substances
<b><math>\nu</math></b>	Kinematic fluid viscosity
<b>HPLC</b>	High Performance Liquid Chromatography
<b>IPCC</b>	Intergovernmental Panel on Climate Change
<b><i>l</i></b>	Length (of filaments)
<b>Wt</b>	Sample weight
<b><math>u^*</math></b>	Shear velocity
<b>SSSI</b>	Site of Special Scientific Interest
<b>SAC</b>	Special Area of Conservation
<b>SE</b>	Standard Error
<b><i>u</i></b>	Velocity of the flow
<b><math>\nu</math></b>	Viscosity
<b><math>\kappa</math></b>	Von Karmen's constant (5.75)

## **Abstract**

Coastal areas have high ecological and economic importance and act as an efficient natural defence against the erosive power of the incoming tide. Due to climate change and anthropogenic effects these systems are under threat of decline and as such must be protected. Management strategies, produced as a result of collaborations between experts in varying fields, will only succeed if holistic and accurate interpretations of the processes occurring within the systems are carried out.

A number of techniques were utilised to determine sediment dynamics within a number of different systems. In experimental flume studies, it was found that the presence of the algal turf reduced bed load transport and that trapping of sediment by the filamentous matrix of the algae was augmented by the presence of mucilage-producing diatoms within the filaments. Frequent harvesting of the Venice Lagoon was determined to prevent the establishment of biotic communities, preventing biostabilisation and reducing the stability of the surface sediment.

Microphytobenthic biofilms within mudflat and salt marsh systems were determined to stabilise sediments through cohesive and matrix effects and by altering boundary flows. The research carried out in this thesis indicated that no single variable could be measured to determine sediment stability, thus, a suite of variables must be examined in order to obtain an accurate description of sediment dynamics within individual systems.

Stromatolite material exhibited the ability to biostabilise relatively quickly after major disturbance. The effects of cyanobacterial and diatomaceous activity within stromatolite structures were studied. Biostabilisation was significantly higher in material maintained in natural conditions compared to samples maintained in darkness. Low-temperature scanning electron microscopy revealed that samples maintained in disparate light regimes supported different microphytobenthic assemblages at the surface of the samples.

This thesis highlights the importance of the roles of functional groups within the systems and their effects upon sediment dynamics. All systems studied exhibited spatial heterogeneity on a scale of centimetres to kilometres, highlighting the complexity and site specificity of biogenic variables controlling sediment dynamics.

# **CHAPTER ONE**

## **GENERAL INTRODUCTION**

## 1.1 The importance of coastal systems

Coastal areas are complex environments created by the dynamics between wave action, tides and the coast, and as a result the physical features of the shorelines vary considerably. The ecosystems examined in this study include: estuaries; sandy shores with rocky outcrops; lagoons; salt marshes; and stromatolite reefs, all of which have important roles to play in the dynamics of coastal zones.

Sea level rise has major implications for coastlines, and the main cause for its increase is climate change. Global sea levels are likely to increase to 0.1-0.9 m over the next century (Houghton *et al* 1994) exacerbating the already erosive and destructive capabilities of the ocean. The implication to our coastlines are significant and it is important to be able predict the consequences of these occurrences (Jones *et al.* 1994). In order to be able to make these predictions we have to acquire a sound and full knowledge of the health and dynamics of the coastlines at present, and determine what roles each of the habitats play in the larger coastal scheme.

Studies in the past have not properly considered both the physical and biological coupling of processes despite the fact that many systems (e.g. stromatolites and salt marshes) are demonstrably biogenic in origin. In order to obtain an accurate representation of these dynamic systems, changes over time and space must be considered along side the physical effects of the biology, and the biotic and abiotic processes occurring within the system.

With increasing sea level rise, climate change and the associated implications for coastlines, the ability to predict changes to the coastlines will benefit socio-economic aspects as well as those of industry and ecology. The ability to make

these predictions is possible through recent advances in mathematical modelling, thereby allowing responsible decisions to be made with regard future management plans for coastal areas. Whilst mathematical modelling has been used to represent the physical changes over time and space of these systems it is only recently that these models have truly taken into account and quantified the effects of morphological and ecological aspects of the systems, in order to provide accurate predictive models (Roman *et al* 1995, Silvestri and Marani 2004).

## 1.2 Coastal dynamics

Coastal areas are dynamic environments structured by both physical and biological processes. Whilst the sediments within the various types of habitat may vary in size and composition, the forces acting upon them remain fairly similar. This may include wind, tidal currents, and wave action and these factors combine within the physical surroundings causing processes such as erosion, sediment transportation and accretion. These physical factors were traditionally thought to shape the biological components of a system, however, whilst to a certain point this is true, more recent research has shown the biological components not to be passive, and the coupling of physical and biological components to be an important part of the system.

### 1.2.1 Physical dynamics

As water flows it applies a frictional force upon the sediment bed known as the bed shear stress ( $\tau_o$ ), which is expressed per unit area. As the flow

increases the stress exerted on the bed also increases until it reaches a velocity at which the sediment particles become dislodged from the bed. At this point the sediment has reached its erosion threshold (Denny 1988, Vogel 1994). Once eroded from the bed particles are transported for varying times depending on their size and the energy of the flow. Also, as the velocity of water increases the flow will eventually change from laminar to turbulent flow. The speed and turbulence of flow determines whether particles remain in suspension or settle back onto the sediment bed. The point at which turbulence is likely to begin can be estimated by determining the Reynolds number (Equation 1.1; Vogel 1994, Jumars and Nowell 1984), which expresses the ratio of viscous to inertial forces.

$$\text{Reynolds number} = \frac{ud}{\nu} \quad \text{Equation 1.1}$$

Velocity of the flow = ( $u$ )

Diameter (scale component) = ( $d$ )

Kinematic fluid viscosity = ( $\nu$ )

The region of flow, next to the sediment surface influenced by the frictional forces, is known as the boundary layer. As distance from the boundary increases, the frictional forces opposing flow are reduced and as a result the velocity of flow increases with height above the bed until the bed has no influence on the flow (free stream velocity). This profile can be visualised by plotting a graph of flow velocity against height above the bed (Figure 1.1). From this the shear stress against the surface can be determined as units of force per unit area ( $\text{Nm}^{-2}$ ) (Equation 1.2), however when describing flow this value can be converted to the

shear velocity ( $u_*$ ), expressed as units of velocity ( $\text{ms}^{-1}$ ) (Equation 1.3) (Denny 1988, Brown *et al* 1999).

$$\tau_o = \rho u_*^2$$

Equation 1.2

$$u_* = \sqrt{\frac{\tau_o}{\rho}}$$

Equation 1.3

### 1.2.2 Biological influence on bed erosion

Grant *et al* (1982) define biogenic stabilization of sediment as “an increase of the critical value of shear stress for initiation of motion over Shields abiotic value”, similarly destabilization is defined as “an observed decrease compared to Shield’s abiotic value”. Critical shear velocity ( $U_{crit}^*$ ) (sensu Postma 1967) is determined by the movement of a particle at the lowest flow velocity possible.

Sediments are usually defined by grain size. Cohesive sediments contain more than 5-10% fine grain size (fine grain size  $< 2\mu\text{m}$ ), and non cohesive sediments contain less than 5-10% fines. Non-cohesive sediments lack any physical or chemical interactions and so the sediment particles move independently of each other (Brown *et al* 1999). The nature of non-cohesive sediments under various conditions has been well documented (Shields 1936, Gibbs *et al* 1971, Miller *et al* 1977, Soulsby and Whitehouse 1997).

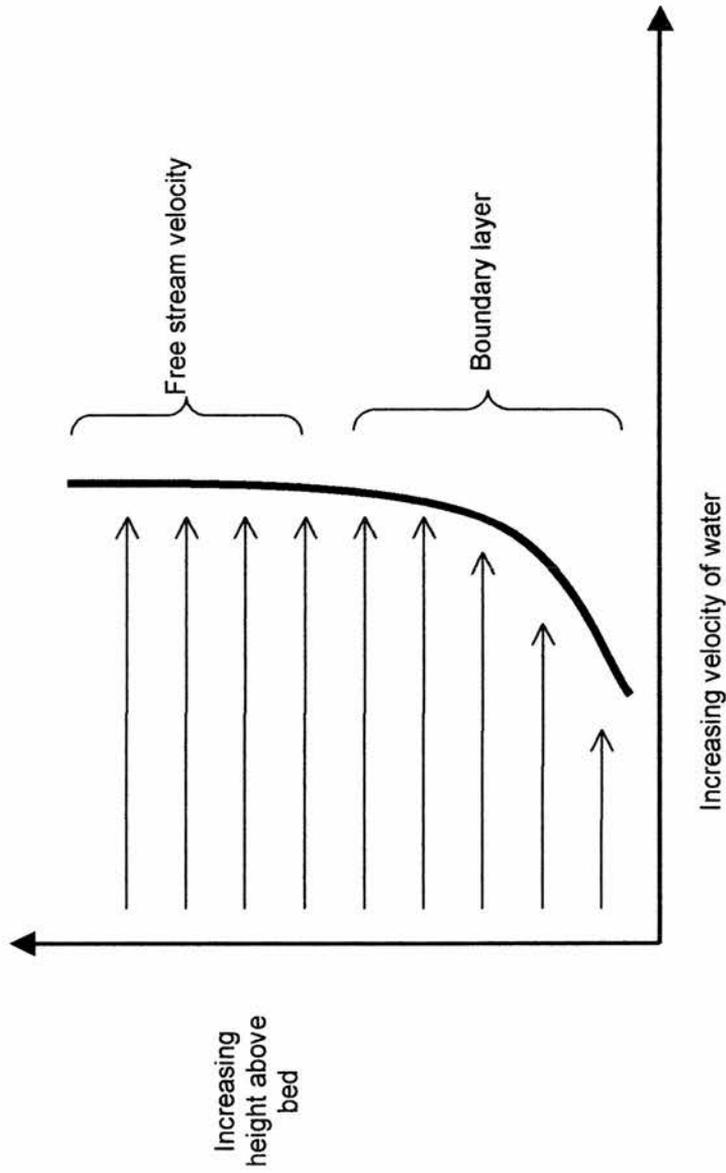


Figure 1.1: Flow of water is reduced due to the friction caused by contact with the sediment surface. A gradient of flow is created from zero flow closest to the sediment surface and increases up to a flow velocity that is no longer affected by the friction and drag forces acting upon the water below this height. The area of water with reduced velocity is known as the boundary layer, and the unaffected flow is termed free stream velocity.

The behaviour of cohesive sediments is less easily modelled due to the various forces and processes acting upon and within them. The shear stress required to erode cohesive sediment particles tends to be greater than it should for the particle size present when compared with non cohesive sediments. Cohesive sediments contain clay minerals (fine particles) increasing the surface area to volume ratio. This factor along with the effect of electrostatic forces acting upon the particles results in the sediment particles aggregating and becoming cohesive, thereby ceasing to act independently but responding as an amalgam of particles or floc.

### 1.2.3 Faunal biogenic mediation

Whilst the ecology of the depositional habitats are affected by physical aspects, the biological components of the systems must not be overlooked as they also play an integral role in habitat functioning. These processes include bioturbation, biodeposition, pelletization and biogenic stabilisation. The alteration of bed roughness at the sediment surface due to biological processes, such as the production of mounds or presence of tubes can cause the flow to vary to such a degree that erosion thresholds change (Ziebis *et al* 1996). Nowell *et al* (1981) proposed that as bed roughness doubled, due to the presence of faecal mounds, the critical erosion velocity decreased by 20%. The impedance of water flow over the sediment due to the presence of emergent polychaete tubes can dramatically change the physical effects of the flow due to changes in velocity and direction. Eckman *et al* (1981) discovered that the initial movement of sand grains on smooth beds required a higher velocity than that of the same sediment type within fields of *Owenia fusiformis* (a tube building polychaete). These

flume experiments were carried out at varying densities of tubes and the results suggested that at higher densities the erosion threshold was lower than that at lower densities. Carey carried out similar experiments in 1983 using the polychaete *Lanice conchilega*. The tubes of the polychaete caused a reduction in flow of up to 20%. Resuspension of sediments in front of the tubes occurred due to the alteration of the flow, however in the wake of the tube the flow was reduced thereby allowing the deposition of sediments previously held in suspension. The presence of tubes has been suggested to encourage bacterial and microbial colonisation within the surface sediments (Eckman 1985), thereby stabilising the sediments further due to microbial stabilisation.

#### 1.2.4 Floral biogenic mediation

It has become widely accepted that areas of coastal vegetation can act as effective sea defence by decreasing incoming wave energy and reducing the erosion of coastal sediments (King *et al* 1995). The main elements responsible for the changes in flow and erosive capabilities within areas of coastal vegetation are the root matrix and canopy. The root matrix directly enhances the stability of the sediment, while the canopy reduces the flow velocity, decreasing the shear stress exerted upon the surface sediments, and enhancing the deposition of fine sediments (van Eerd 1985). Freidrichs *et al* (2000) carried out flow experiments in stands of artificial shoots and found that as the density of surface cover increased, flow was directed towards the top of the shoots, away from the boundary layer, thereby producing a “skimming flow” and reducing the erosive effects of the flow. The flexibility of sea grass canopies intensifies the development of skimming flow at high velocities, thereby reducing turbulent

kinetic energies often found within rigid stands. Reduced flow also promotes the deposition of sediment and organics, creating a stable, but nutrient rich sediment (Eckman 1985, Fonseca and Fisher 1986). Shi *et al* (1996) demonstrated that the turbulent shear stress above and outside the canopy structure was greater than that beneath the canopy thereby increasing the probability of particle flocculation and deposition of fine sediments. Established salt marsh vegetation increase accretion rates due to the attenuation of wave energy by the canopies of the halophytic plants, allowing the deposition of sediments from suspension. The presence of salt marsh vegetation is often associated with the presence of extensive biofilms as the shoots and increased sediment stability encourage microbial growth (Shi *et al* 1995, Underwood 1997). If these biofilms persist it will lead to further stabilisation and increased diversity of organisms within the sediment (Eckman 1985).

### **1.3 The Microphytobenthos**

Whilst the previously mentioned habitats differ in structure and function, one common link among them all is the presence of bacterial and microbial biofilms that serve as the primary food resource. A biofilm is a surface accumulation of cells, organic and inorganic material bound within the surface sediments by exopolymers produced by the assemblage (Neu 1994). In sediment systems, transient and permanent biofilms are largely formed by microphytobenthos (MPB) which is the collective term for photosynthetic micro-organisms including cyanobacteria, diatoms and euglena living on or in benthic systems. When at high numbers, these organisms can be seen by the naked eye

as a green or golden brown coloured biofilm. Diatoms are usually the most dominant form of MPB. These biofilms are adapted to survive depositional and highly dynamic environments (Paterson *et al* 1998; Yallop *et al* 1994). Not only do microphytobenthic biofilms serve as primary producers in the ecosystem but also have a number of other ecosystem services (Chapin *et al* 1997) including the stabilisation of cohesive sediment.

### 1.3.1 A brief history

Centric diatoms evolved in the early cretaceous period (Gersonde and Harwood 1990) with pennate diatoms following in the late cretaceous (Harwood 1988), and many species found within this time period were morphologically similar to the species found today with around 200,000 extant species (Admiral 1984, Mann, 1999). The first pennate diatoms were araphid (non-motile), and motile forms did not appear in great numbers until the Eocene period (Medlin *et al* 1993) (Figure 1.2).

### 1.3.2 Diatom structure

The diatom is made up of a siliceous cell wall composed of 2 halves (the epitheca and the hypotheca). These halves are known as valves, made up of girdle elements and cinctures, and fit very closely together, one within the other, creating the frustule. Some diatoms exhibit a cleft running down the centre of the valve known as the raphe, however, when the raphe is present but runs along the edge of a valve it is known as a keel. Araphid diatoms exhibit a clear area known as a pseudoraphe. The valve may also contain other features which are

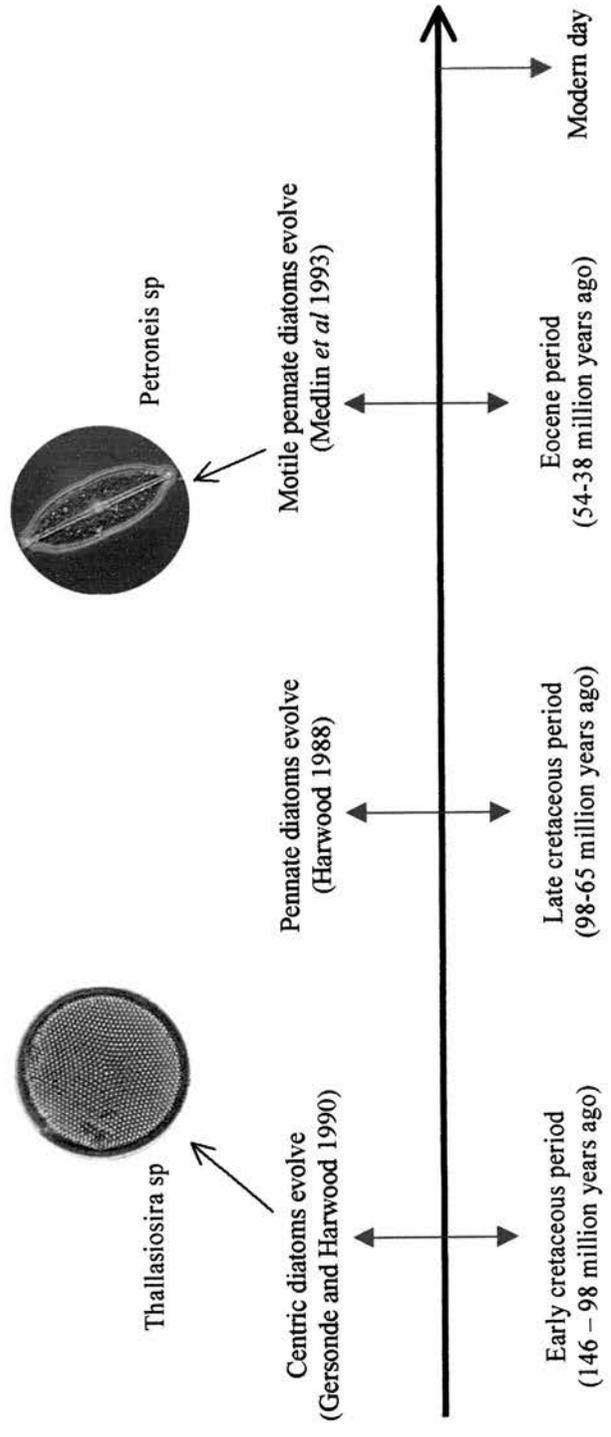


Fig 1.2: Time line representing the occurrence of major changes to the morphology and occurrence of diatomaceous species to the present day.

important for the identification of various species such as stria, punctae, spines, and central area (Round et al 1990) (Figure 1.3).

### 1.3.3 Microphytobenthos – an integral part of ecosystems?

The microphytobenthos are important primary producers and provide a significant source of autochthonous carbon within the ecosystem. The microphytobenthos found in cohesive tidal sediments are responsible for around one third of the entire estuarine systems organic budget alone (de Jonge 2000), and estimates suggest they produce 40% of total global primary productivity in marine systems (Medlin 2002). Most of the research carried out on microphytobenthic assemblages has been associated with intertidal sediments (Admiral 1984, Underwood and Kromkamp 1999, Paterson and Hagerthey 2001). Microphytobenthos play an important role in the shaping of the systems by influencing the properties of sediments in which they occur, however, on the other hand it must be considered that the physical aspects of the environment control the spatial distribution, species diversity and abundance of benthic diatoms due to the sediment types and sizes of sediment particles present (Paterson and Hagerthey 2001, Saburova *et al* 1995). Species diversity has been found to be directly related to sediment grain size on a number of occasions (Paterson and Hagerthey 2001, Cahoon et al 1999, Sabbe and Vyverman 1991). Whilst literature refers to the relationship of diatom diversity and grain size it is actually the space available between the grains that is the important factor. Intermediate interstitial grain sizes tend to host a higher diversity of diatom species than small or large interstitial spaces (Bergey 1999).

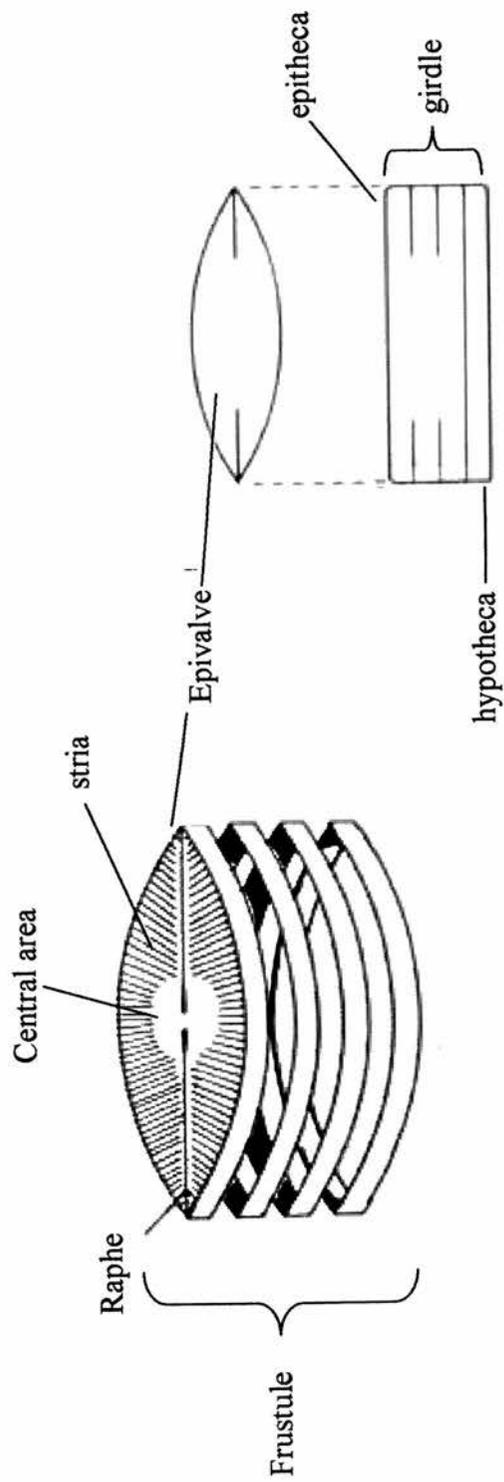


Figure 1.3: A view of an exploded pennate diatom, illustrating the presence of the entire frustule including the raphe, central area, stria, epivalve, epitheca, hypotheca, and girdles. (Figure courtesy of Professor David Paterson).

### 1.3.4 Diatom migration

Diatoms most commonly associated with coastal sediments are the epipelon (free-living within the sediment), and occur anywhere there is sufficient light to allow them to photosynthesise. MPB migrate within the top 3mm of the surface sediments so as to position themselves in optimum conditions. This migratory strategy may be an adaptation to environmental variables such as light, temperature and oxygen availability. The ability to migrate within the surface sediments allows the cells to photosynthesise (Perkins *et al* 2002, Kromkamp *et al* 1998), avoid photodamage or pigment bleaching (Kingston 1999, Cohn *et al* 1999), avoid resuspension (Kromkamp *et al* 1998, Hay *et al* 1993), or to avoid predation (Pinckney *et al* 1994). This phenomenon was originally reported by Ehrenberg (1883), and is believed to be due to geotactic, chemotactic, and phototactic influences (Round and Palmer 1966, Round *et al* 1990, and Cohn and Disparti 1994). Consalvey (2002) demonstrated that individual cells within a biofilm migrate at different times and under varying conditions (cell cycling) suggesting that individuals are capable of responding to environmental conditions separately from the rest of the biofilm. Early research into diatom motility considered many types of locomotory options such as amoeboid action, ciliary action, and jet propulsion (Cohn *et al* 1999, Cohn and Disparti 1994, and Edgar and Picket-Heaps 1984). However it was soon realised that none of these options were feasible and the most recent conclusion suggests motile diatoms (epipelon) are capable of migration within sediments by a polymer driven locomotion. This polymer, is one of the many extracellular polymeric substances (EPS) produced by microbial metabolism and found in sediments (Underwood *et al* 1995, Decho, 1990, 2003). EPS is exuded from the raphe structure of diatoms

but is also produced in the form of tubes, stalks, adhering films and cell coatings. The process of diatom locomotion, is proposed to function due to the adhesion of a strand of EPS to the substratum whilst one end remains attached to free transmembrane structures which are moved along the raphe structure regulated by associated actin bundles (Poulsen *et al* 1999, Round *et al* 1990, Underwood and Paterson, 2003). This locomotive theory was proposed by Edgar and Pickett Heaps (1983, 1984) after a hydrophobic lipid coating was identified around the raphe structure, aiding the secretion of EPS. The velocity of an individual cell and the rate of EPS exuded from the raphe were found to be comparable, and a trail of EPS was left behind individual cells during locomotion.

#### 1.3.5 Extracellular polymeric substances

EPS is a hydrated carbohydrate rich exopolymer produced by metabolic processes and whilst it is an integral part of the locomotion of individual cells, EPS also has a variety of other functions. The mucilage prevents desiccation, protects from abrasion, buffers environmental changes such as temperature, salinity or heavy metals, reduce resuspension and increases the stabilisation of surface sediments (Holland *et al* 1974, Grant *et al* 1986, Hoagland *et al* 1993, Yallop 1994, Sutherland 1996). Whilst these functions are important for the cell it must be considered that physical factors such as salinity, temperature and light will also affect the EPS itself and modify its ability to perform the above functions (Decho 1990, Smith 1999). Diatom biomass is linked to the concentration of colloidal carbohydrates found in sediments, due to the fact that EPS is mainly comprised of carbohydrates (Underwood *et al* 1995, Blanchard *et al* 2000). These substances can form interconnective strands of

mucopolysaccharides and act as a natural 'glue', causing the sediment particles to adhere together forming a biofilm (Admiraal 1984, Paterson 1989, Underwood *et al* 1993).

However, EPS has a low density similar to sea water ( $1.024 \times 10^5 \text{ Kg m}^{-3}$  at  $20^\circ\text{C}$ ) which results in it being buoyant. Combined with the fact that thick biofilms, held together by EPS secretions, may trap air bubbles beneath them due to the high levels of aerobic activity occurring within them means they may be washed away relatively easily by the incoming or out going tides. This may mean that the introduction of EPS into sediments in order to increase sediment stability may in fact have the opposite effect by reducing the erosion threshold and enhancing resuspension on highly aerobic sediment systems (Sutherland *et al* 1998).

On the other hand, EPS promotes the stabilisation of sediments due to a reduction in shear stress, Reynolds number, and resuspension of sediments, and the binding of particles by strands of EPS within the interstitial spaces (Delgado *et al* 1991, Chenu 1993, Chenu and Jaunet 1992, Yallop *et al* 1994, Paterson 1997, Austen *et al* 1999). Sediment treated to remove all organic matter was found to have erosion threshold velocities at least half that of untreated sediment (Neumann *et al* 1970, de Brouwer *et al* 2000). Natural sediment is more stable than sediment with organics removed, and the extent of this stabilisation was investigated by Manzenrieder (1983) who found that natural sediments exhibited erosion stabilities up to 300% greater than those of sediments with no organic content. This correlation between quantity of EPS and sediment stabilisation is known as epipellic stabilisation and may be attributable to the biogenic effects of

organisms such as microphytobenthos and the associated EPS secretions (Paterson and Black 1999).

#### **1.4 Areas of study**

The effects of biotic influences on sediment stabilisation can be measured using the biostabilisation index (Manzenreider 1983) and is expressed as the biotic stability divided by the abiotic stability. Abiotic sediments have been widely studied within laboratory environments (Manzenreider 1983, Grant and Gust 1987), but without taking into consideration the biotic interactions that occur in nature it is not possible to make accurate models and predictions. The only way to do this is to collect measurements from the systems over the relevant spatial and temporal scales. However this in itself poses problems including sampling error and differences in interpretation. Variations between biotic interactions and processes will be time and site dependent and so it is of great importance that systems are treated individually and the processes occurring within the site being studied are understood as fully as possible in order to obtain accurate and relevant information.

##### **1.4.1 Sandy shore with rocky outcrops**

The rocky shore is a dynamic environment presenting widely fluctuating conditions, for the flora and fauna present. Tides cause predictable cycles of floods and ebbs subjecting communities to a wide range of conditions, such as desiccation, scouring, dislodgement, and burial. Organisms present on the rocky shore are subjected to extreme variations in sea water temperature, light

intensity, salinity, and exposure, however, sediment erosion, accretion and transport are dominant factors in environments such as this, and sediment levels can vary dramatically. Competition under optimal conditions creates a space limited environment, in which local disturbances provide new niches for species to take hold. Gaps created by local disturbances such as dislodgements or scouring in high energy areas, provide sites in which more tolerant but less dominant species can thrive. Shores with high diversity of organisms tend to be areas of intermediate disturbance (Connell 1978, Lubchenco and Menge 1978). Although physical factors may be important in shaping the rocky intertidal areas, microalgae and microphytobenthos form the primary food source from which the ecosystem thrives.

#### 1.4.2 Intertidal mud flat systems

Estuaries are semi-enclosed transitional bodies of water with both seawater and freshwater inputs, and are one of the most productive systems in the world (De Jonge and Colijn 1994).

Estuarine systems can be categorised into 4 main components; those areas that are always submerged (channels); areas that emerge on extreme low tides only (tidal mud flats); areas that are only flooded on extreme high tides; and areas that are always emerged. Although intertidal mud flats serve as important protection to coastal margins against the powerful erosive forces of waves, they are also important sites with regards anthropogenic activities such as industry, fishing, shipping, recreation and farming. As fresh water from the river systems enters the estuary the flow velocity is reduced causing coarser sediment particles carried within the water column to settle out of suspension. The fine sediment is

retained within the water column at the lower flow velocities, but due to the larger surface to volume ratio, Van der Waals forces and electrostatic charges associated with silt particles, flocculation of these particles occurs and they are deposited to form mud flats. Mud flats act as a sink and source of pollutants and toxins released into the estuarine waters by local industries, due to the fact the pollutants are attracted to the charged particles within the sediment. Once the sediments have been re-suspended during a storm event the pollutants are free to re-enter the ecosystem. This has ecological implications for the ecosystem associated with the estuary/mudflats due to the fact they provide important breeding, nesting and feeding areas for wading birds and fish, and hosts a wide diversity of organisms.

#### 1.4.3 Salt marsh systems

Salt marsh systems are highly dynamic environments formed by the physical and biological forces working within and around it. The survival and health of a salt marsh is dependent upon the balance between sediment erosion and accretion. As long as the rate of accretion is equal or greater than the rate of erosion and the relative rate of sea level rise, the salt marsh, with a continual supply of fresh sediment, will survive. However, salt marsh systems are under continual threat from anthropogenic influences, and climate change. In southern England, during the period 1973-1988, 23% of salt marsh was lost due to a 4-5cm relative rise in sea level (Pethick 1993). At present the average rate of salt marsh erosion in the south east England is 40ha year<sup>-1</sup> and in reaction to this massive loss of habitat salt marshes are now a Biodiversity Action Plan habitat,

with the hope that salt marshes can be restored and maintained to the areas present in 1992 (United Kingdom Biodiversity Group, 1999).

The natural loss of salt marsh is increased due to the development of sea defence systems and the influence of coastal squeeze. The defence structures prevent the natural landward migration of salt marshes and so these areas are becoming increasingly diminished due to erosion from the rising sea level. This in itself is counter productive as salt marshes are one of the most effective sea defence mechanisms, due to the ability of the halophytic macrofauna to attenuate wave energy, thereby decreasing its erosional forces. King and Lester (1995) calculated that the total loss of salt marsh from the Essex coastline would cost £600 million per annum in sea defence maintenance, and at present the loss of salt marsh is 1% per annum. For this very reason managed re-alignment (set-back) is becoming an increasingly popular coastal defence mechanism, allowing old sea walls to be breached and accepting the loss of land. If the land is not high enough for the plants to retreat to, the sediment deposited by the incoming tide will eventually accumulate to the appropriate elevation for the salt marsh vegetation to survive (Paramour and Hughes 2004).

Salt marshes are not only valuable with regards coastal defence; they are also valuable habitats for conservation. This environment consists of a wide variety of halophytic plants, insects, macrofauna and microbes (including diatoms and bacteria) (Aspden *et al* 2004b), offers important feeding, breeding and nursery sites for fish and birds, and has a major role in carbon cycling helping to maintain the local food web. Without the geochemical processes the microbial population provides, such as the breakdown of organic matter,

oxygenation of the surface sediments and the recycling of various nutrients, salt marshes would struggle to thrive in such a dynamic environment.

#### 1.4.4 Lagoonal systems

Lagoon systems make up more than 10% of coastlines world wide (Kjerfve *et al.*, 1996). These systems are shallow bodies of water separated from the ocean by a natural or artificial barrier. Inlets within these barriers often allow the transport of water in and out of the lagoon basin by wind and tidal currents. There may also be a sediment source from riverine inputs. Lagoon systems are particularly susceptible to pollution effects as a result of limited tidal flushing of the basin due to restricted access to the ocean, and are heavily influenced by water temperature and salinity due to the fact they are shallow water systems. Lagoons can be categorised into the same 4 main components as estuaries (section 1.4.2).

#### 1.4.5 Stromatolite reef systems

Stromatolite formation is little understood, despite their presence in marine systems for 3.5 billion years (Schopf 1983). These ancient structures are living evidence that prokaryotic assemblages are capable of promoting accretion and stabilisation of sediments through the trapping and binding of sediment particles and the lithification of microbial assemblages present. The modern equivalents of these structures provide an ideal opportunity to examine these processes further. Stromatolites are created by the lithification of microphytobenthic and bacterial mats along side periods of sediment accretion and carbonate precipitation (Walter 1976, Reid *et al* 1995). Reid *et al* (2000)

carried out a two year observation of stromatolites in Exuma Sound, Bahamas and proposed three growth stages of stromatolite formation, each determined by different surface microbial communities, although this phenomenon may be site dependent. Other studies have suggested growth stages to be dependent on physical factors such as sediment accretion and position of the stromatolites within the reef (MacIntyre *et al* 1996, Golubic and Browne, 1996). Microbial mats (mostly containing cyanobacteria) form a filamentous matrix initially trapping carbonate sand grains. Photosynthetic cyanobacterial mats are capable of nitrogen fixation and therefore play an important role in the nutrient dynamics of aquatic systems. During periods of low sedimentation, layers of trapped sediment particles become bound by microbe filaments and associated exopolymers. The presence of microbes and associated microbial activity mediates precipitation and the dissolution of  $\text{CaCO}_3$  forming calcified biofilms known as micrite (lithified laminae of microcrystalline carbonate). The presence of microbes has been shown to activate calcium carbonate precipitation and dissolution (Walter 1983), and whilst sedimentation is of great importance to the dynamics of the system, without the lithification of the exopolymer associated with the bacterial and microphytobenthic populations present within the upper layers (Reid *et al* 2000), the growth of the stromatolite structures may be stunted. Micritic crusts may bridge the gap between grains, but are thin and not be strong enough to become a structural feature. However, the micritic crusts become areas of intense boring by *Solentia* sp (an endolithic cyanobacteria) and during this boring activity micrite precipitates in the boreholes creating the fusion of grains as the cyanobacteria moves amongst the grains (MacIntyre *et al* 2000).

Studies carried out by Visscher *et al* (1998) have linked sulphate reducing bacteria to the precipitation of carbonates within microbial mats.

Stromatolites are worthy of further investigation since the knowledge we could gain from existing systems can help understand how similar structures were formed in the past, and further studies could resolve the lack of knowledge regarding the formation of these systems in extreme environments such as hyper saline waters.

## **1.5 Thesis aims**

The aims of this study were to examine the biogenic processes involved in the stabilisation of sediments within various coastal habitats utilising a suite of different techniques best suited to the habitat being studied.

The following hypotheses were tested:

- sediment retention occurs within the structure of a filamentous algae.
- microphytobenthic assemblages play an integral role in the sediment stabilisation of subtidal and intertidal systems.
- spatial and temporal variations in sediment stability in tidal flats and salt marsh systems can be characterised by measuring a range of sediment properties.
- clam harvesting significantly reduces sediment stability in the Lagoon of Venice.
- To determine the influence of on the biostabilisation of stromatolite ooids is highly dependent on light levels and duration of light periods.

## **CHAPTER TWO**

### **GENERAL MATERIALS AND METHODS**

## Chapter 2 General methods

The methodologies described in this chapter provide the general material and methods used throughout the thesis. The methods are described with reference to the relevant chapters.

### 2.1 Study Sites

The main sites studied throughout the course of this thesis were situated in the Eden Estuary, Scotland, and the Venice Lagoon, Italy. The main sampling methods included grain size analysis, biomass (chlorophyll *a*), sediment stability characteristics, organic content, carbohydrate content, and microphytobenthic composition.

#### 2.1.1 East Sands

East Sands (NO 520 159 GB grid; Fig 2.1(B)) is a rocky intertidal beach on the south side of the old harbour in St Andrews, Fife, Scotland. The beach area currently holds a blue flag award (Bathing Water Directive 76/160/EEC). The rocky areas supports a healthy diversity of macrofauna and macroalgae, including the red filamentous alga, *Rhodothamniella* sp. Sediment deposition and erosion varies seasonally and the area is subjected to a tidal range of 6m. This site was used to study the influence of algal turf on the retention of sandy sediments, discussed in chapter 3.

### 2.1.2 The Eden Estuary

The Eden estuary, Scotland, UK (56°22'N, 02°51'W; Fig 2.1(C)) has an intertidal mud flat area of 9.37km<sup>2</sup> (exposed at low tide) and a total area of 10.41km<sup>2</sup> (Davidson and Buck 1997). The River Eden has a catchment area within north Fife of 400km<sup>2</sup> and flows into the sea 4km north of St Andrews. The estuary experiences low turbidity, due to the fact the hydrodynamics of the system are driven by tidal currents rather than wave action, and the tidal flats contain many drainage channels. The Estuary is a local nature reserve, an important site for the over-wintering of wildfowl and waders, has two Sites of Special Scientific Interest (SSSI) and has been appointed a Special Area of Conservation (SAC; JNCC, 2003). This site was used for the study of biogenic spatial and temporal variability in surface sediments, discussed in chapter 5.

### 2.1.3 The Venice Lagoon

The Venice lagoon is a semi enclosed body of water with limited freshwater inflows and three links to the Northern Adriatic sea at Lido, Malamocco and Chioggia (Fig 2.2). It is the widest lagoon area in the Mediterranean with an average depth of 1.5m, and an area of 550km<sup>2</sup> (Rijstenbil *et al* 1996).

Sediment dynamics play a large role in the ecological status of the lagoon and are controlled mainly by wave energy, river flow, and coastal currents. Open water and tidal channels make up 78% of the enclosed lagoon area, salt marsh areas cover approximately 37km<sup>2</sup> of the lagoon (Ravera 2000), and the general ecology of the system functions as a balance between riverine and marine influences. This site was used to study the effects of clam harvesting on the

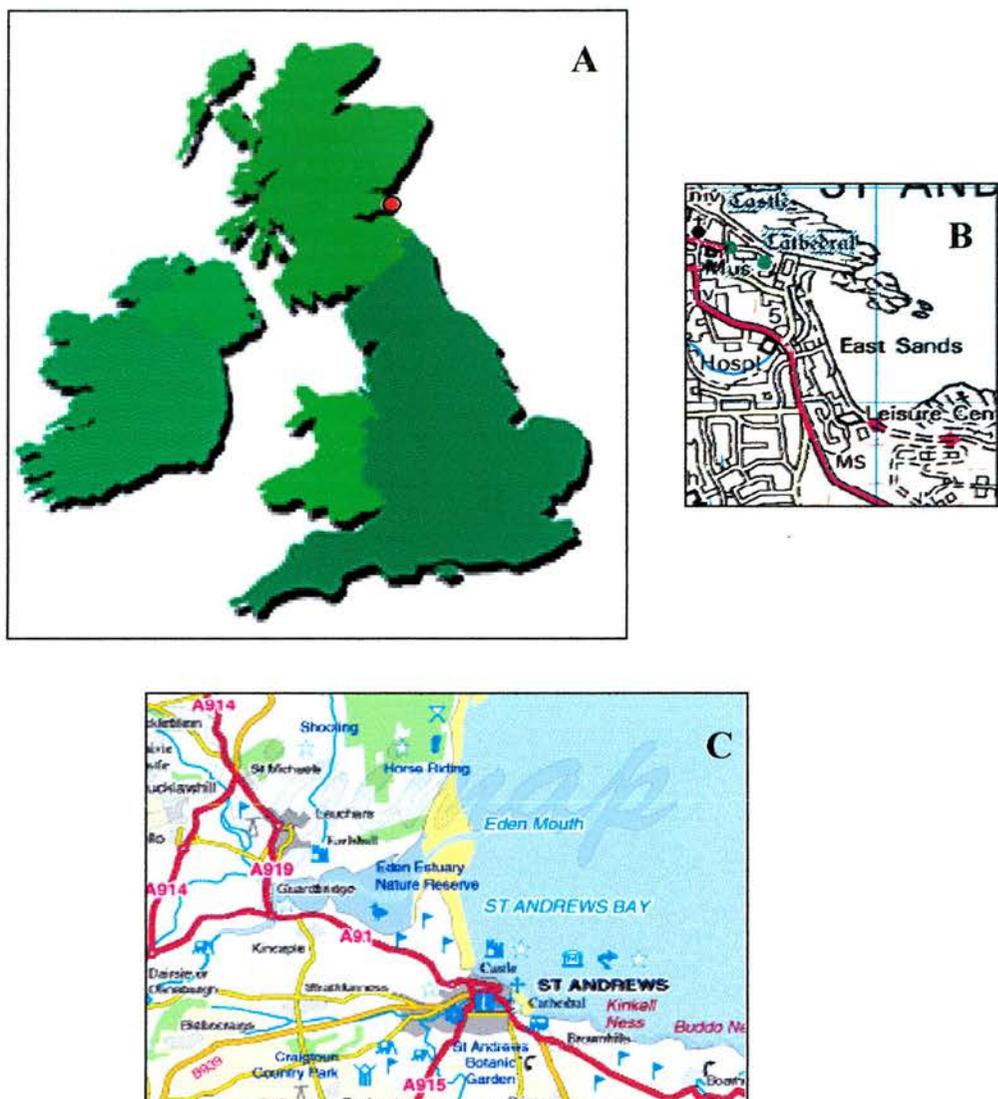


Fig 2.1 : (A) Location of study sites within the United Kingdom (B) East Sands, St Andrews and (C) The Eden Estuary (Images B and C courtesy of Digimap).



Fig 2.2: (A) The Venice Lagoon (Venice); LANDSAT-TM images (aquired 9 August 1986) (Images courtesy of Istituto Veneto di Scienze Lettere ed Arti); (B) Saltmarsh site within the lagoon; (C) Mid lagoon site.

subtidal surface sediments of the lagoon, discussed in chapter 4, and to investigate the relationship between the microphytobenthic mats and the cohesiveness of the salt marsh sediments, discussed in chapter 6.

#### 2.1.4 Highborne Cay

Highborne Cay is situated in Exuma Sound, Bahamas ( $76^{\circ} 49' W$ ,  $24^{\circ} 43' N$ ) (Fig 2.3). The main study area was of the well developed intertidal and subtidal stromatolite structures on the eastern side of the island. The seawater in which the stromatolites were present was of a normal marine salinity (36-37ppt) and the subtidal varieties grew in a seawater depth of less than 1m. This site was used for the study of retention and regeneration capabilities of stromatolite systems, discussed in chapter 6.

## 2.2 Sediment sampling

### 2.2.1 Surface microstructure

For studies of the sediment surface microstructure aluminium strips were used to gently remove the surface layers of the sediment. These samples were then quench frozen in liquid nitrogen ( $-196^{\circ}C$ ) and stored at  $-80^{\circ}C$  until low-temperature scanning electron microscopy could be carried out.

### 2.2.2 Sub-tidal core collection

The collection of subtidal sediments was carried out using cores of 10cm in diameter. The core was placed into the sediment to a depth of 15cm and the sediment lifted to the surface, using petri dishes to cover the open ends of the



Fig 2.3: (A) Location of Highborne Cay, The Bahamas (B) The study site on the East side of the Island. (Images courtesy of RIBS).

core in order to prevent loss of material or damage to the surface layers. Cores were placed in a bucket with water flush to the top of the core to prevent drainage and further analysis was carried out immediately. Samples for the determination of sediment properties (organic content and chlorophyll *a*) were taken from the cores as were sediment stability measurements, using a cohesive strength meter. Sub tidal coring was used exclusively in the study of the Venice lagoon, as described in chapter 4.

### 2.2.3 Contact coring

Contact cores consist of a metal dish of diameter 56mm with a hollow base 2mm deep (Figure 2.4A). The contact core was placed gently onto the sediment surface and liquid nitrogen was poured into the dish. This was left for 10 – 30s (dependent upon sediment type and water content) or until the sample was frozen. Any additional sediment frozen around the edge was removed. The disc of sediment was then stored at -80°C and kept for further analysis at a later date. Measurements of sediment properties (bulk density, organic content, carbohydrate content and chlorophyll *a*) were taken from the cores and used in the study of the Venice lagoon subtidal sediments, Venice lagoon salt marsh sediments, and the Eden estuary sediments.

### 2.2.4 Cryolanding

The cryolander method (Wiltshire *et al* 1997) allows a disc of frozen undisturbed sediment (10mm depth and 50mm diameter), to be removed from the sampling area allowing the surface structure and properties to be analysed at a later date.

A brass cylinder of diameter 5cm containing a layer of cotton wool placed on a nylon mesh plate (pore size 60 $\mu$ m) was placed onto the sediment surface (Figure 2.4B). Liquid nitrogen was poured through the cotton wool allowing the sinking vapour to freeze the sediment surface without disturbing the surface structure. This continues until a disc of sediment is frozen in situ and can be removed, using a plunger pushed through the brass cylinder.

## 2.3 Grain size analysis

### 2.3.1 Preparation of sediments for grain size analysis

Natural sediment was cleaned to remove any organic material prior to grain size analysis to remove any organics. Approximately 6g of each sediment sample was placed in a plastic centrifuge tube along with 2ml of distilled water. To this 5ml, of 30% hydrogen peroxide was added and placed in a rack in a 60°C water bath for 2 h. If any organic material was still present after 2h (sample still effervescing) the samples were placed in the centrifuge at 2000rpm for 10 min, the supernatant decanted and more hydrogen peroxide added for a further 2h, until the effervescing stops. Once the organics were removed the sample was placed in the centrifuge as before and the supernatant decanted. 5mls of distilled water was then added and the solution mixed thoroughly. The sample was placed in the centrifuge as before and the supernatant removed. This process was repeated four times. 10mls of distilled water and 2mls of 0.1% sodium hexametaphosphate solution (de-flocculent) was added to the sample and stored until grain size analysis could be carried out.

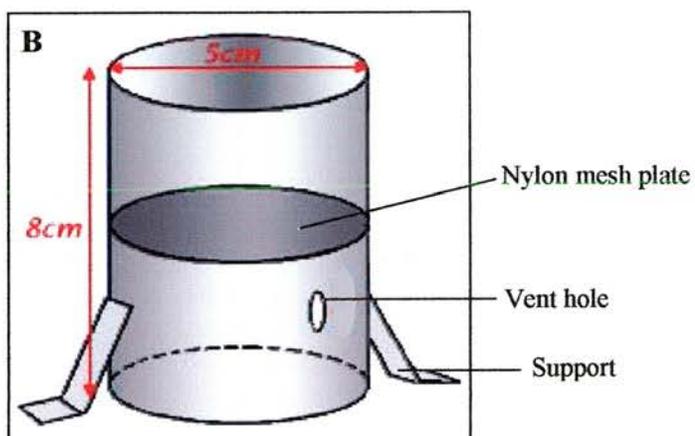
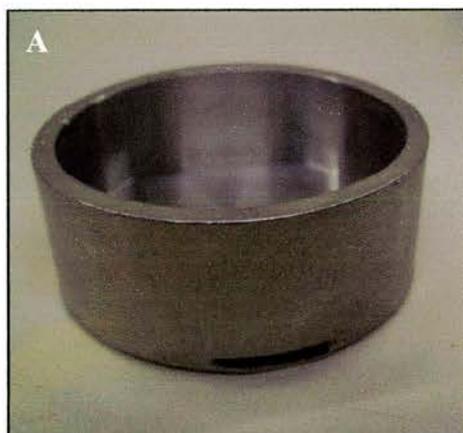


Figure 2.4: Sediment samples were removed by contact core (A) and cryolander (B) by freezing the surface sediments to ensure the data retrieved was representative of natural conditions and not a result of transport/laboratory artefacts.

### 2.3.2 Stacked shaker

Cleaned sediment samples were oven dried at 80°C for a period of 48h, after which the samples were dry sieved using a stacked shaker with mesh sizes ranging from 4.0mm to 0.063mm.

### 2.3.3 Coulter Laser Particle Sizer

Grain size analysis was carried out using a Coulter Laser Particle Sizer (LS230). This method allows the determination of particle size distribution through laser diffraction, based on the principle that particle shape, size and optical properties control the spatial variation of the diffracted beam. The cleaned sample was added to the sampling chamber and sonicated for 30s before the measurement was taken. This was repeated three times.

## 2.4 Organic content

In order to determine the organic content of sediment the loss on ignition method was used.

Lyophilised samples of known weight were ground to a fine powder and placed in a pre-weighed crucible. The crucibles were then placed in a muffle furnace for 4h at 450°C, after which time they were left to cool at room temperature in a desiccators. The samples were then reweighed (minimizing exposure to atmospheric moisture) and the organic content determined (Equation 2.1).

$$\% \text{ organic content} = 100 - \left[ \frac{\text{sediment wt after ignition (g)}}{\text{sediment wt before ignition (g)}} \times 100 \right] \quad \text{Equation 2.1}$$

## 2.5 Water content

Water content was determined as a percentage of the wet sediment weight (Equation 2.2).

$$\text{Water content (\%)} = \left( \frac{\text{Wet sediment (g)} - \text{Dry sediment (g)}}{\text{Wet sediment (g)}} \right) \times 100 \quad \text{Equation 2.2}$$

The weight of the wet sediment, in a pre-weighed and labelled plastic bag, was recorded. The samples were re weighed after lyophilisation in the dark for 24 h (or until the samples were completely dry). In order to avoid the breakdown of the thermosensitive pigments (Rowan 1989) the samples were lyophilised rather than oven dried.

## 2.6 Wet bulk density

The wet bulk density was determined as the weight of wet sample per  $\text{cm}^3$  (Equation 2.3).

$$\text{Bulk density (gcm}^3\text{)} = \frac{\text{wet sediment (g)}}{\text{Volume of sediment (cm}^3\text{)}} \quad \text{Equation 2.3}$$

## 2.7 Diatom identification

Microphytobenthic assemblages were assessed in order to determine species present and population diversity between sites and to note any changes over time

### 2.7.1 Lens tissue

In order to collect motile microphytobenthos a large piece of lens tissue was placed on the sediment surface. Further smaller pieces of lens tissue (2cm<sup>3</sup>) were placed on this base for a period of one hour (Eaton and Moss 1966). The small pieces of lens tissue were removed after this time and placed in tinted eppendorf tubes containing seawater and 4-5 drops of 1.25% glutaraldehyde solution until further analysis could be carried out.

### 2.7.1 Permanent slide preparation

In order to create permanent slides the diatom frustules were acid cleaned to remove any organic matter. Distilled water was added to the lens tissue samples, which were then agitated to break up the tissue. The distilled water and cells were removed from this solution by filtration through piece of fine netting with distilled water, into an acid cleaned centrifuge tube. The samples were centrifuged for 10 min at 2000rpm to obtain a pellet of diatoms. The supernatant was removed from the centrifuge tube, 1ml of potassium permanganate was added to the remaining diatom solution covered and left for 24 h in a fume hood. After the 24h, 2ml of hydrochloric acid was slowly added to the solution. More hydrochloric acid was added to the tubes if the samples continued to effervesce indicating the reaction was not complete. The samples were then covered with

cling film and placed in an oven at 70°C for a period of 2h, or until the solution appeared clear and yellow. The samples were allowed to cool and then centrifuged at 2000rpm for 10 min. The supernatant was removed and the remaining pellet was resuspended in distilled water and centrifuged again. This process was repeated 7 times in order to remove any remaining hydrochloric acid. The final remaining pellet was resuspended in 2ml of distilled water.

Several drops of distilled water were placed on an alcohol cleaned cover slip to which 400µl of the diatom solution was added. The cover slips were covered to avoid contamination and left to air dry for 24h.

Once dry the cover slips were mounted onto labelled acid cleaned microscope slides using the embedding material Naphrax™. Several drops of Naphrax™ were added to the centre of each slide on to which the cover slips were placed face down. The slides were then heated on a hot plate for approximately 1-2min, until the solvent, toluene, was boiled off.

### 2.7.3 Diatom identification

Slides were examined using a Zeiss Universal light microscope at x40 and x100 magnification. The identification of the diatom cells was carried out using appropriate literature (Barber and Haworth 1981, Hartley *et al* 1996, Round *et al* 1990, and van der Werff and Huls, 1976), appropriate references (Facca *et al* 2002, and Tolomio *et al* 1999) and a directory of local species found in the Eden Estuary during previous studies (SERG, unpublished data). Counts of 300 individual cells were made, unless the cell count was low, in which case timed searches of 2h were conducted. Shannon-Weaver indices were applied to the

microphytobenthos cell count data in order to compare population diversity between sites and to note any changes over time.

## 2.8 Carbohydrate analysis

### 2.8.1 Colloidal-S carbohydrate extraction

Lyophilised sediments were used in order to carry out the extraction since freeze drying has been shown to increase the yield of carbohydrates (Underwood *et al* 1995).

50mg of sediment was placed in a centrifuge tube containing 300 $\mu$ l of distilled water and left at room temperature for 15 min. The solution was centrifuged at 2000rpm for a further 15min after which 1ml of the supernatant was removed and placed in an acid cleaned glass test tube in order for the Dubois assay to be carried out. 200 $\mu$ l of 5% w/v Phenol solution was added to the supernatant and thoroughly mixed using a vortex mixer. 1ml of concentrated sulphuric acid was added to the solution and left for 35min in a fume hood. After this time the solution was decanted into a cuvette and the absorption measured using a Cecil 3000 Spectrophotometer at 486.5nm.

### 2.8.2 Glucose standard preparation

Carbohydrate concentration was expressed in terms of glucose equivalents. Standards were made from stock solutions of glucose within a range of 20-200 $\mu$ gml<sup>-1</sup>. The Dubois Assay was carried out using 1ml of each dilution, and absorbance read (as described in section 2.9.1). A new calibration was

performed with each set of samples. Linear regressions of the standards were used to calculate the constants and coefficients (Equation 2.4).

$\text{Colloidal carbohydrate } (\mu\text{g g}^{-1}) = \frac{((Abs - C) / M)(5)}{Wt}$	Equation 2.4
---------------------------------------------------------------------------------------	--------------

Abs = the absorbance at 485nm

C = the constant (intercept of the line)

M = the co-efficient (gradient of the line)

Wt = the sample weight (g)

The numerator was multiplied by 5 to correct for the total volume of sample (5ml).

## 2.9 Pigment analysis

### 2.9.1 Preparation of standards

A stock solution of chlorophyll *a* standard was prepared by dissolving 1mg of Spinach sample (Sigma<sup>TM</sup>) in 250ml of 90% DMF (Dimethylformamide). Serial dilutions were carried out to provide a range of concentrations (4, 2, 1, 0.5, and 0.25mg l<sup>-1</sup>). The standards were wrapped in tinfoil and stored at 4°C to inhibit pigment degradation.

Each standard concentration and a blank (90% DMF) was read at 662nm (the corrected peak maxima ( $\lambda$  max) of chlorophyll *a*) and 750nm (to correct for

light scattering within the sample) in a Cecil 3000 Spectrophotometer.

Chlorophyll *a* concentration was determined using Equation 2.5.

$$C = (( [A_{662}] - [A_{750}] - \text{blank} ) / \epsilon) * 1000 \quad \text{Equation 2.5}$$

C = chlorophyll *a* concentration (mg l<sup>-1</sup>)

A<sub>662</sub> = absorbance at 662nm

A<sub>750</sub> = absorbance at 750nm

ε = extinction co-efficient of Chlorophyll *a*.

### 2.9.2 Extraction of pigments

Approximately 8mg of lyophilised sample was added to a pre-weighed eppendorf and the weight recorded. 1.5 ml of 90% DMF was added to the eppendorf and re-weighed to determine the exact amount of extractant added (Equation 2.6).

$$\text{Volume of 90\% DMF (ml)} = \text{Weight of 90\% DMF added} / 0.97 \quad \text{Equation 2.6}$$

90% DMF was used instead of 100% acetone because it has been shown to be more effective at extracting chlorophyll *a* from sediment, especially if macroalgae were present within the samples (Honeywill 2001), which was thought to be the case for many of the samples collected.

The sample was left in a fume hood for 24 h to allow the extraction to take place. After this time the solvent was added to a 1ml Waters™ Amber Glass Vial by filtering the solution through a 13mm 0.2µm GFC Whatman™ Glass Filter. The samples were then covered with tin foil and stored at -80°C until further analysis could be carried out, or transferred to the HPLC (High Performance Liquid Chromatography) 4° Autosampler.

### 2.9.3 High Performance Liquid Chromatography (HPLC)

The HPLC set up included a quaternary high pressure pump (Perkin-Elmer 410), an autosampler (thermostat set to maintain a temperature of 4°C) (Waters 910), a column oven (set to maintain a temperature of 25°C) containing a reverse phase Nucleosil C18 column (Capitol HPLC Ltd) and a photo-diode Array Detector (PDA; Waters 910).

All solvents used were degassed for 5 min with helium prior to each run, and any solvent or air retained within the system was removed by purging the system. 30µl of distilled water was injected into a tertiary solvent gradient (Table 2.1) prior to 70µl of extractant at a flow rate of 1.0ml min<sup>-1</sup> for 40 min. The distilled water was added in order to refine the chromatogram peak.

The column was conditioned at the end of every run by pumping solvent A through the system for at least 45min (Wiltshire 2000).

<b>Solvent</b>	<b>Solvent composition</b>
Solvent A	2000ml 100% methanol (HPLC Grade) 500ml distilled water 3.75g tetrabutylammonium acetate 19.25g ammonium acetate
Solvent B	2250ml 100% methanol (HPLC Grade) 250ml 100% Acetone (HPLC Grade)
Solvent C	1412.5ml 100% methanol (HPLC Grade) 1087.5ml 100% propanol (HPLC Grade)

Table 2.1 – Tertiary solvent gradient used for the extraction of pigments using HPLC.

The various components of the HPLC set up were synchronized by “Millenium”, a Waters software programme. This programme was also used to store all chromatograms recorded.

### **2.10 Examination of sediment surface structure**

The surface structure of the sediment can be examined at a microscale with minimum disruption by using low-temperature scanning electron microscopy (LTSEM) (Paterson 1995).

Sediment samples were removed from the natural environment minimising disruption to the structural integrity of the material by using either a

aluminium strip (section 2.2.1) or cryolander methods (section 2.2.4). The samples, whilst submerged in liquid nitrogen, were secured in cryostubs (specifically designed by I Davidson) and transferred to the cryo apparatus (Oxford Instruments CT1500) of the LTSEM where they were partially freeze-dried. Once enough water had been removed and a clear image could be seen, the sample was sputter coated in gold, at  $-170^{\circ}\text{C}$ , in order to increase the definition of the image. The sample could then be studied using the scanning electron microscopy apparatus (Jeol JSM 35 CF), and records of the images were taken using an attached MAMIYA camera.

## **2.11 Sediment strength**

### **2.11.1 The shear vane**

The shear vane was held at a right angle to the sediment surface and pushed into the sediment to a known depth. Four depth measurements were taken in total (9, 13, 17, and 21cm) (Figure 2.5). Using one hand the vane head was rotated steadily at a rate of 1 revolution per 30 s. The torsion device is released as soon as the sediment shears and the maximum deflection to which the spring was subjected was recorded (Nm) by the pointer on the vane head.

### **2.11.2 The cohesive strength meter (CSM)**

The small scale spatial variations in the erosion threshold of exposed subtidal and intertidal sediments were measured using the cohesive strength meter (CSM) (Tolhurst 1999). The CSM is comprised of an on board computer,

water reservoir, filter assembly, digital and analogue pressure gauges, optical sensor head, and first stage diving cylinder with hose attached (Figure 2.5 B).

The chamber (diameter 30mm) is placed onto the sediment surface and secured using a clamp stand and filled with filtered sea water. A jet of water is directed towards the sediment surface within the chamber from a height of 2cm above the sediment surface. The velocity of the water jet is increased systematically with each jet over a period of time (dependent on which test protocol is selected). A drop in transmission of the infrared light, caused by the suspension of sediment across the chamber, determines the erosion threshold. Data is recorded directly to an onboard central processing unit and can then be downloaded to a PC for further analysis.

## **2.12 Hydrodynamics and flow studies**

Flume studies were carried out in order to study sediment dynamics and response to flow in a controlled laboratory environment.

### **2.12.1 Flume studies**

Flume experiments were carried out in an 8m tilting Armfield flume (S6 8m) (Figure 2.6). The sides are made from toughened glass supported by aluminium cantilevers connected to the bed. The length of the working section is 5 meters, the channel width is 0.3m, and the height of the working channel is 0.28m. The total volume of the working section is  $0.42\text{m}^3$ . Sections of the channel floor can be removed to integrate samples, which can then be manipulated and monitored under controlled conditions. The flume is fed from

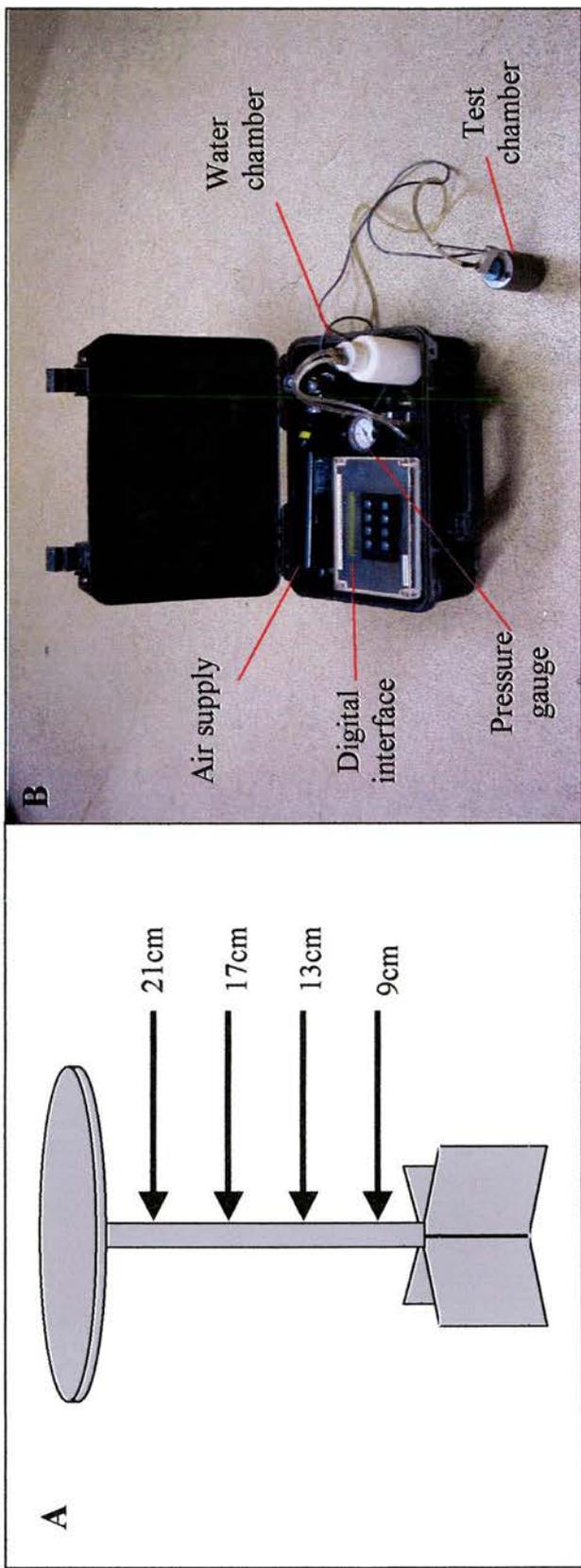


Figure 2.5: Sediment strength measuring devices (A) Diagrammatic representation of the Shear Vane and depths measured during sampling (B) the cohesive strength meter erosion device.

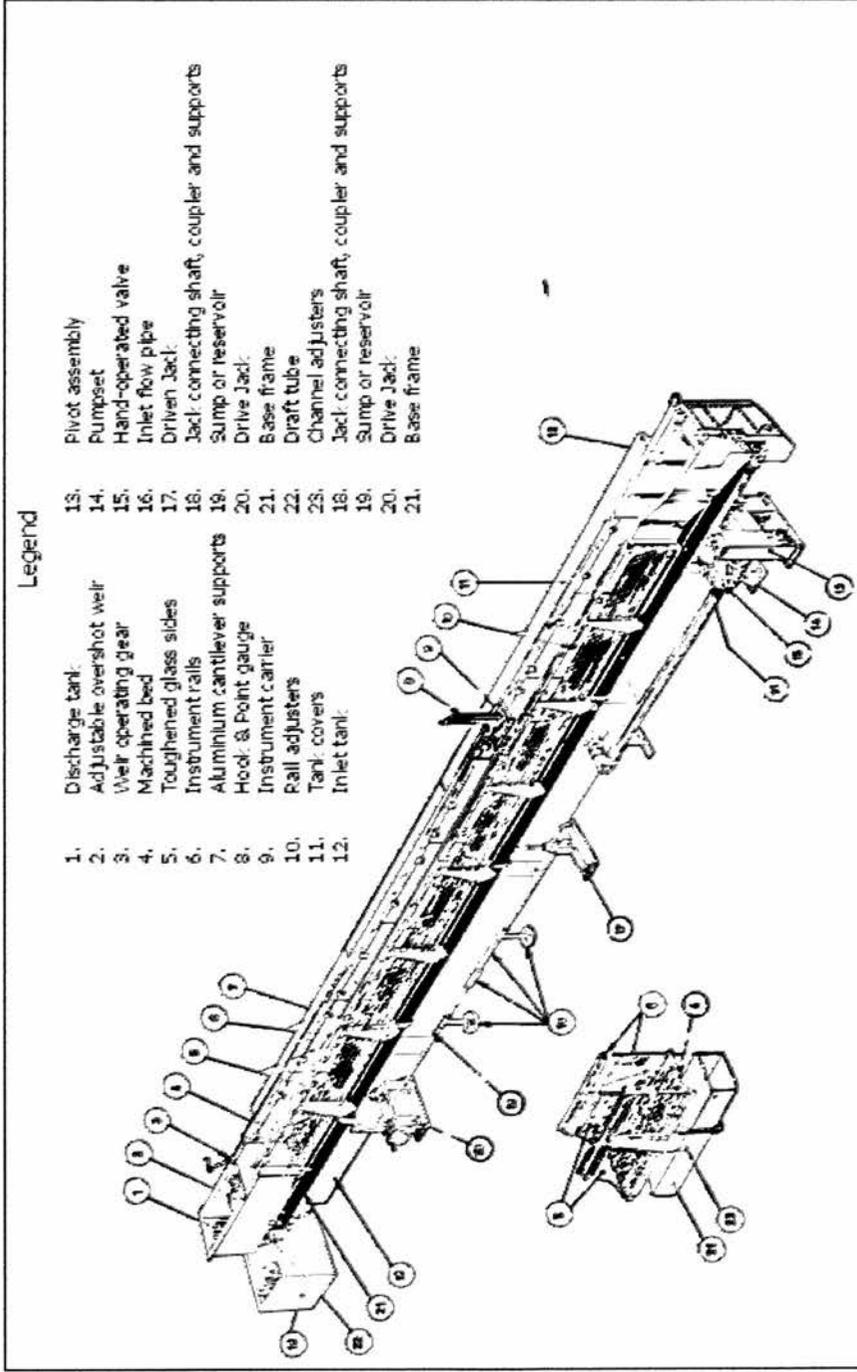


Figure 2.6: Schematic of Armfield tilting flume courtesy of Armfield Ltd.

three sump tanks via an induction grid designed to produce near uniform flow conditions. A hydrodynamic model was used on the base of the working channel in order to mimic the structure of the natural bed and entrain the flow, therefore reducing any variance in flow profile as the flow moves over the test bed of algal turf (Muschenheim *et al* 1986). Flow rate was varied by the manipulation of a valve, whilst the height of the water within the channel was controlled via a weir at the downstream end of the flume.

### 2.12.2 Acoustic Doppler Velocimeter

Flow velocity was monitored using an Acoustic Doppler Velocimeter (ADV) (Gratiot *et al* 2000) (Figure 2.7). The ADV has a measuring volume of  $1\text{cm}^3$  at a rate of 25Hz. The ADV consists of a probe with three arms at  $30^\circ$  angles, which send out acoustic pulses into the water column. These pulses are scattered by particles suspended within the water creating an echo effect. These echoes are shifted by the flow and this is known as the Doppler shift. A 3 dimensional representation of the flow can then be gained, as the Doppler shift is proportional to the velocity of the flow.

Further details of experimental procedure involving the flume and ADV can be found in Chapter 3.

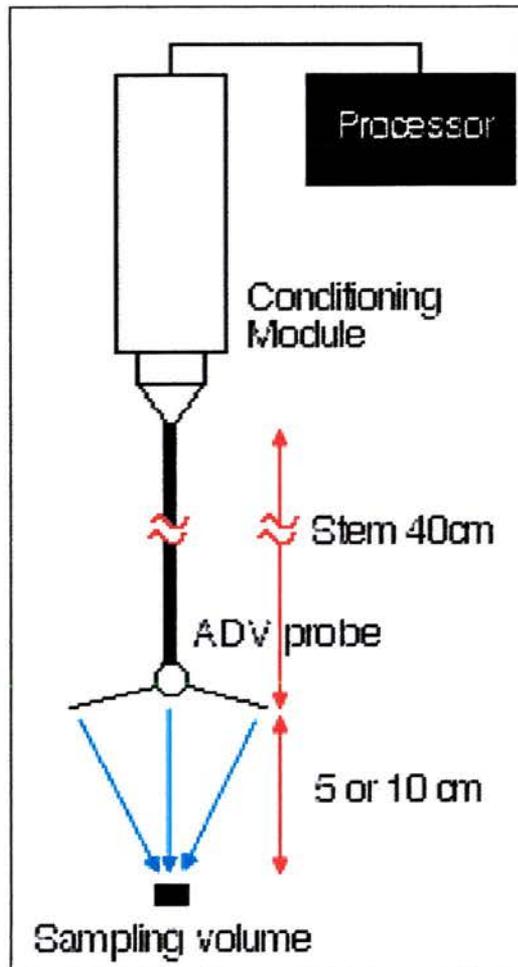


Fig 2.7: Flow velocities and boundary profiles were determined using an acoustic Doppler velocimeter. The ADV measures velocity of flow using the Doppler effect principle.

## **CHAPTER THREE**

### **INFLUENCE OF *RHODOTHAMNIELLA* SP ON THE RETENTION OF SANDY SEDIMENTS.**

### **Chapter Three - Abstract**

Rocky intertidal areas adjacent to sand systems are often subject to highly variable episodes of sedimentation and erosion due to the dynamics of the environment. Some species of epilithic turf algae, such as *Rhodothamniella*, have become adapted to these extreme environments. *Rhodothamneilla* grows on the rock surface and retains sand grains to form a “cushion” of sediment, often several cm thick over the surface of the rock. The presence of algal turf in these areas is important due to the ability/potential of these structures to provide a productive system in a stressful habitat and a habitat for other organisms to exploit. The algal turfs also promote stabilisation and decrease the occurrence of mass sediment erosion events. In experimental flume studies, it was found that the presence of the algal turf reduced bed load transport and that trapping of sediment by the filamentous matrix of the algae was augmented by the presence of mucilage-producing diatoms within the filaments. The combined turf structure acted as a hydrodynamic filter, retaining a higher proportion of fine grained sediments and allowing courser grain to pass through or over the turf matrix. This result is in keeping with measured differences in sediment composition between the natural beach sand (larger grain sizes) and the algal turf (smaller grains sizes). The turf alga preferentially retains smaller particles and a mechanism for this phenomenon may be envisaged as a filter mesh placed parallel with the flow. The “filter” allows the <250µm grains to drop into the structure of the turf but a proportion of the <425µm are too large and the majority of these grains pass over the turf or through the upper layers.

### 3.1 Introduction

Sediment deposition and erosion are major factors influencing the structure of benthic communities. High sedimentation rates and particle movement have detrimental effects on the diversity and overall richness of intertidal communities (D'Antonio 1986, Airoldi and Cinelli 1997). However, sediment movement and scour may also be responsible for promoting an increase in diversity and richness due to the creation of patches and maintenance of spatial and temporal heterogeneity, within what would otherwise be a fairly homogenous environment, (Littler *et al* 1983, McQuaid and Dower 1990, Ford *et al* 1999). In addition, many organisms have evolved to make use of sediment supply to increase their fitness within depositional environments. The relationship between sediment transport and biota is therefore varied and becoming increasingly studied (Aspden *et al*, 2004, Black *et al* 2002, Orvain *et al* 2004), and modelled (Orvain 2005, Widdows *et al* 2004).

The turf alga *Rhodothamniella* sp (Dillwyn) is a perennial rhodophyte with branched uniseriate filaments, characterised by its ability to bind sediment particles, which become an important structural component of the algal turf. The term turf has become a convenient label for mats of algae with small filamentous thalli. The ability to trap and bind sediments is an example of “ecosystem engineering” whereby organisms modify or mediate their environment in a manner that changes the nature of resource availability and therefore fitness. A single ecosystem engineer may create a rich habitat for a varied assemblage of organisms. On many intertidal shores with rocky outcrops, the level of associated sand beds are highly variable and

sand transport across and among the rock outcrops is a regular feature of the system. During high levels of sedimentation algae may suffer detrimental effects such as scour, reduced productivity due to oxygen and nutrient limitation, lack of hard substratum for settlement and recruitment. The response of turfs to physically stressful habitats has been widely studied although the effect of turfs on sediment dynamics has been largely neglected (Hay 1981, Airoidi 1998, Airoidi and Virgillio 1998, Kendrick 1991, Piazzini and Cinelli 2001). Algal turfs are able to monopolise the lower sections of rocky outcrops due to their capacity to withstand the physical and biological stresses that accompany the deposition of sediment and the associated periodical burial of the turf. For example, *Rhodomela larix* was found to be relatively undamaged after a two-week period of burial beneath 40 cm of sand (D'Antonio 1986).

For an alga, the option of turf growth is energetically expensive and when smothered by sediment the lower portions of the turf show significantly reduced apparent photosynthetic rates compared with the upper portions (Hay, 1981). The ability of a turf to reduce the energetic cost of photosynthesis by splitting its structure into separate photosynthetic regions is essential in high dynamic systems such as rocky intertidal areas. If upper layers are damaged, the branching of filaments increases causing the turf to become more compacted and uniform, however this in turn reduces the photosynthetic capability of lower filaments, but desiccation stress is lowered due to reduced water loss (Hay 1981). Therefore, continued deposition and erosion of sediments helps to maintain the branching structure of algal turfs, creating a complex matrix of filaments suited to high impact

environments (Sousa *et al* 1981, Seapy and Littler 1982, Stewart 1983), thus reducing the physical damage to the turf itself.

Despite changes in the depositional rate, the amount of sediment held within the turf structure has been shown to remain stable, suggesting that turfs assist in the stabilisation of intertidal sediments (Sousa *et al* 1981, Kendrick 1991, Airoidi and Virgillio 1998). The matrix created by the filaments forms a cohesive surface layer able to trap particles as they move along the sediment surface. As particles are bound into its structure an environment is created where grazing is inhibited and hydrodynamic stresses are reduced (Hay 1981, Airoidi *et al* 1996, Airoidi and Virgillio 1998). The presence of turf can increase drag and microturbulence due to a change in surface roughness, in turn altering the dynamics involved in sediment deposition and erosion (Phelps 1970). By creating a large area of uniform surface roughness the velocity required for the critical erosion of the mats is increased significantly. Scoffin (1970) found that turf forming *Lyngbya* sp trapped fine sediment particles by the adhesion of grains to sticky filaments due to a coating of mucilage. A similar phenomenon was observed by Neumann *et al* (1970) who observed that rhodophytes and chlorophytes relied on structural mechanisms to trap sediment whereas blue/green algae relied on mucilaginous secretions in addition to the filament structure. This study suggests that the stabilisation of sediments is a combination of structural trapping and adhesion of grains to filaments. However, the algae studied by Neumann formed widespread mats within the carbonate sediments that made up the sand flats in Abaco, Bahamas. The algal turf examined in this study grew on rocky outcrops projecting from expanses of surrounding beach,

and therefore facilitates the retention of sediment in an area that would not normally gather sand, providing an example of ecosystem engineering.

Algal turf not only withstands the stresses previously discussed, it dominates the areas in which it occurs due to the capacity of the turf to modify the growth form in order to optimise survival rate and growth potential by utilising the physical environment around it in ways that other algae competing for the same space can not. The quantity of sediment trapped by the turf will vary temporally and spatially, depending on seasonal variation, sediment deposition rates and how sheltered the area is, and in turn this will have an effect on the growth type, rate and structure of the turf.

During this research the following hypotheses were tested in order to determine the functional role of algal turf on rocky intertidal shores:

- sediment retention occurs within the filaments of the turf
- grain retention is size selective.

## **3.2 Materials and Methods**

### **3.2.1 Sediment composition**

The structure and composition of the natural turf was examined using light microscopy. Cytochemical staining was carried out to determine the presence or absence of mucopolysaccharides within the turf. The stain Alcian Blue was chosen for this procedure as it is a suitable stain for acid mucopolysaccharides (Daniel *et al* 1987). The samples were fixed in 4% formaldehyde solution for 48h, after which

small sections of the turf were removed and placed in a 1.0% solution of Alcian Blue (8GX) for 30min. The samples were then bathed in distilled water to rinse away any excess stain, mounted onto an acid cleaned slide and examined using a compound microscope.

Sections of turf material were cryofixed in liquid nitrogen in order to examine the fine detail of the surface structure by low temperature scanning electron microscopy.

Particle size was determined for the sediment bound within the turf and sediment taken from adjacent sand flats by dry sieving through graduated sieves. The two most abundant size classes were then used in the flume studies.

### 3.2.2 Flume studies

Flume studies were carried out using a linear tilting flume (Armfield 8m) to test the null hypotheses that there were no differences in particle size or quantity of sediment captured, in the sediment trap, during bed load transport with or without the presence of an algal turf. Flow velocity was monitored using an acoustic doppler velocimeter (ADV) (Gratoit *et al* 2000) and boundary profiles were measured to determine the type of flow occurring over the test bed.

#### *Retention capacity of the turf*

A hydrodynamic mimic was used in order to mimic the structure of the natural turf bed and entrain the flow, therefore reducing any variance in the flow profile over the test area of algal turf (Muschenheim *et al* 1986). The model was

domestic carpeting with a pile of 10mm, similar to the height of the algal turf. Experiments were repeated without the hydrodynamic model in order to determine that any significant differences observed were due to the presence/absence of the turf, or variation in grain size used.

The experiment consisted of three replicates of eight experimental scenarios:

- <250 $\mu\text{m}$  particles, no hydrodynamic model or turf (control)
- <425 $\mu\text{m}$  particles, no hydrodynamic model or turf (control)
- <250 $\mu\text{m}$  particles, hydrodynamic model with no turf (control)
- <425 $\mu\text{m}$  particles, hydrodynamic model with no turf (control)
- <250 $\mu\text{m}$  particles, turf without hydrodynamic model
- <425 $\mu\text{m}$  particles, turf without hydrodynamic model
- <250 $\mu\text{m}$  particles, hydrodynamic model with turf
- <425 $\mu\text{m}$  particles, hydrodynamic model with turf

A known mass of sediment was placed 0.5m in front of the test area which was placed 2m upstream of the exit, in order to ensure undisturbed flow (Muschenheim *et al* 1986). The velocity of the flow was increased in stages until mass suspension of the sediment particles occurred (between 45–50 $\text{cms}^{-1}$ ) (Figure. 3.1). Experimental scenarios were compared at two velocities: a low velocity measurement, (flow = 35  $\text{cms}^{-1}$ ) and a high velocity measurement, (flow velocity = 45  $\text{cms}^{-1}$  or 50  $\text{cms}^{-1}$ , depending on when the last measurement was taken before mass suspension of sediment particles occurred).

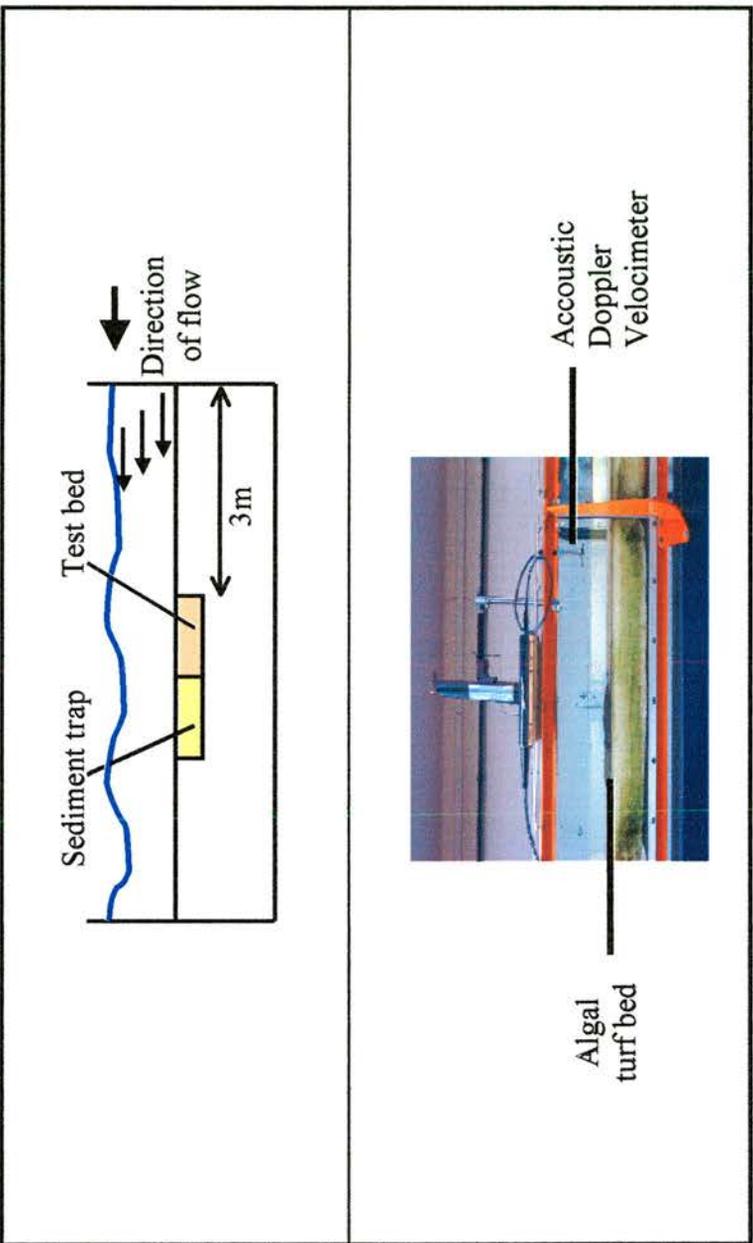


Figure 3.1: Experiments were conducted in an 8 m linear tilting flume. Experimental set up consisted of a test bed 3 metres downstream of the flow input. A sediment trap was placed directly behind the test bed in order to capture any sediment not retained by the test area.. Flow velocity was recorded using an acoustic doppler velocimeter.

During experimentation, a low and a high velocity flow was maintained for 180s (sufficient to allow test sediment to be transported across the bed (preliminary experiments, data not shown). After each velocity trial the sediment trap behind the turf was removed and the sediment was collected, dried for 48h at 80°C and the dry weight recorded.

### *Boundary layer profiles*

The shear stress acting on the flume bed surface was determined by calculations of flow velocities obtained with an acoustic doppler velocimeter. The boundary layer profile was determined by measuring flow velocity in the water column at 1cm increments from the base of the flume test section into the area of free stream velocity. These velocity values were then plotted against height to provide boundary profiles, from which the shear velocity acting upon the base was be determined. The shear velocity is related to the inverse gradient of the relationship between height and velocity (equation 1), and so the height above the bed values are plotted on a log scale.

$$U_* = \frac{1}{k} * \frac{d\bar{u}}{d \log z} \quad \text{(Equation 1)}$$

$U_*$  = Shear velocity ( $\text{ms}^{-1}$ )

$k$  = Von Karmen's constant (5.75)

$d\bar{u}$  = Change in current velocity

$d \log z$  = Change in height above the bed derived from a  $\log_{10}$  vertical scale

Once the shear velocity has been calculated this value can be used to calculate the shear stress at the sediment surface using equation 2.

$$\tau_o = \rho U_*^2 \quad \text{(Equation 2)}$$

Bed shear stress ( $\text{Nm}^{-2}$ ) =  $\tau_o$

Density of the fluid ( $\text{kgm}^{-3}$ ) =  $\rho$

Shear velocity ( $\text{ms}^{-1}$ ) =  $U_*$

From this stage the boundary roughness Reynolds number can be calculated to determine the nature of the flow (laminar or turbulent) during experimentation (Equation 3).

$$\text{Re}_r = \frac{ul}{\nu} \quad (\text{Equation 3})$$

$\text{Re}_r$  = Boundary roughness Reynolds number

$u$  = Velocity of the flow ( $\text{ms}^{-1}$ )

$l$  = Length (of filaments) (m)

$\nu$  = viscosity ( $\text{m}^2\text{s}^{-1}$ )

### 3.2.3 Statistical analysis

Data expressed as percentages was converted to proportional data and was then arcsine transformed. The Anderson –Darling test for normality and Bartlett’s test of equal variances were carried out to test whether the data were normally distributed and had equal variances. Percentage data were normalized by converting to proportional data and was then arcsine transformed. Further analysis was carried out using 2-way ANOVA (Analysis of Variance). Results were considered significant at  $p < 0.05$ .

### 3.3 Results

#### 3.3.1 Light microscopy and cytochemical staining

The morphology of the algal turf was structured by fine filaments forming an intricate meshwork. Sand grains were observed to be trapped within this interdigitated structure when viewed with a light microscope. Also attached to the filaments were stalked diatoms. Viewing the samples after staining highlighted the presence of mucopolysaccharides associated with diatoms and bacteria (stained a deep blue/green). The bacterial species and epiphytes were found throughout the matrix attached to the filaments by mucopolysaccharide secretions (Figure3.2).

#### 3.3.2 Low Temperature Scanning Electron Microscopy

LTSEM highlighted the presence of chain forming diatoms, either forming strands threaded amongst the filaments of the algal turf itself or as clusters embedded amongst EPS, within the matrix of the turf filaments (Figure3.3).

#### 3.3.3 Particle Size Analysis

The sediment found on the adjacent sand flats was comprised mostly of sediment within the 150-424 $\mu$ m size range, however it was evenly distributed between <250 $\mu$ m-424 $\mu$ m and <425 $\mu$ m-1mm. Seventy nine percent of the sediment found within the turf was comprised of much smaller grains in the 150 $\mu$ m-249 $\mu$ m size range (Figure 3.4) emphasizing the spatial variation in sediment grain size found within a relatively small area.

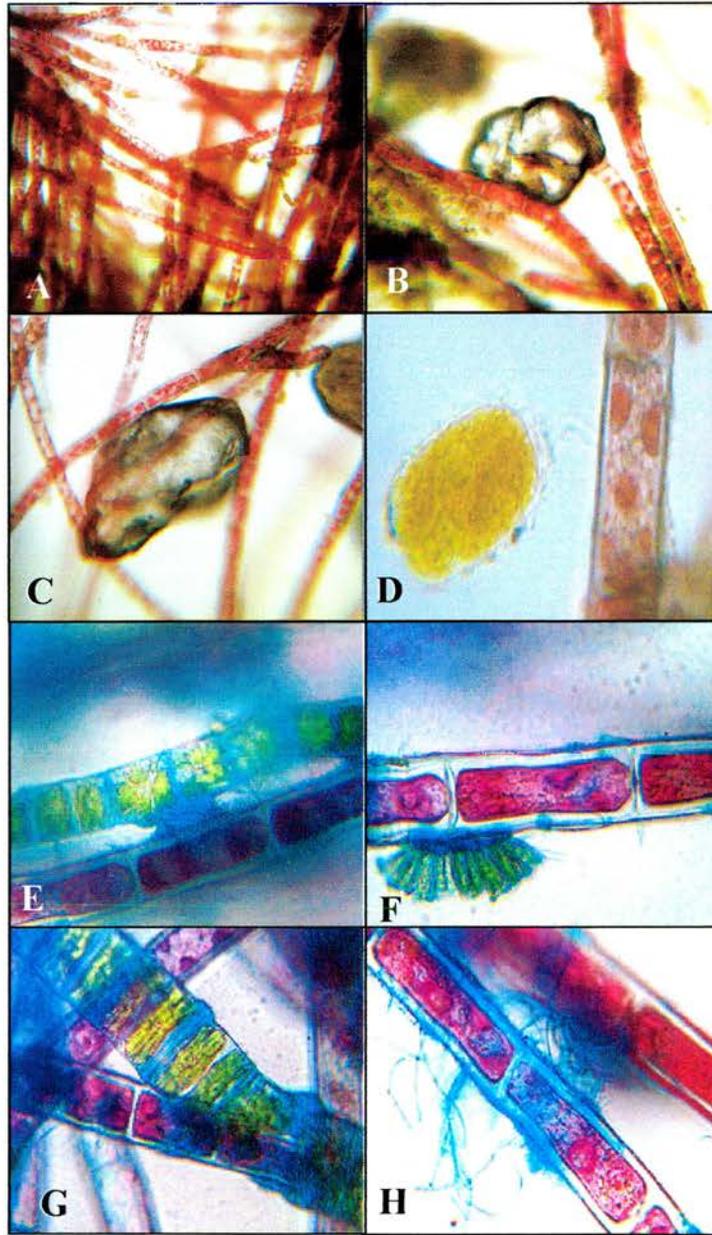


Figure 3.2: The algal turf was constructed of fine filaments that formed a mesh like structure capable of trapping sand grains within the filaments (A-C; magnification x40). Stalked and chain forming diatoms were present (D-G; magnification x250), and after cytochemical staining extracellular polymeric substances (bright green/blue) associated with the diatomaceous and bacterial assemblages, present within and attached to the filaments, could be observed (E-H; magnification x250).

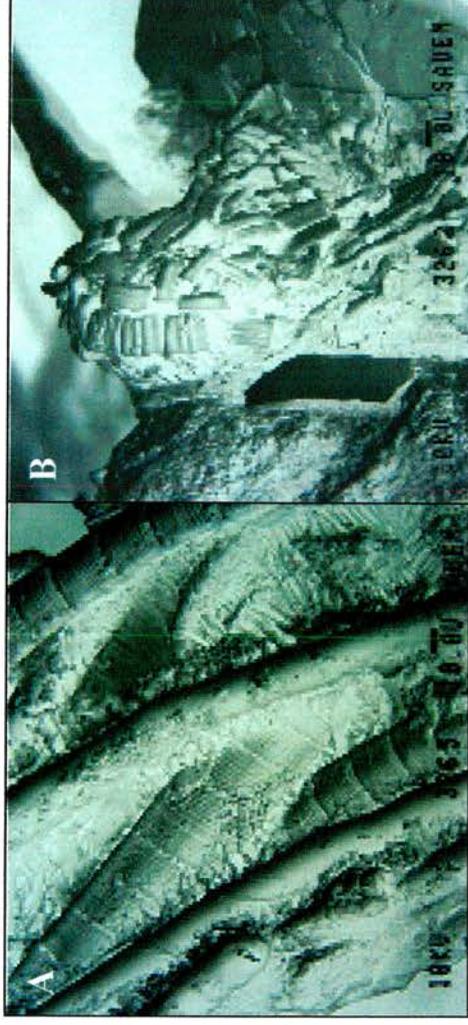


Figure 3.3: Fine scale surface structure was examined using low-temperature scanning electron microscopy. The most abundant microphytobenthic assemblages present were those of chain forming diatoms which either formed strands threaded amongst the filaments of the algal turf itself (A) or large clusters of chain forming diatoms surrounded by EPS, amongst the turf filaments (B).

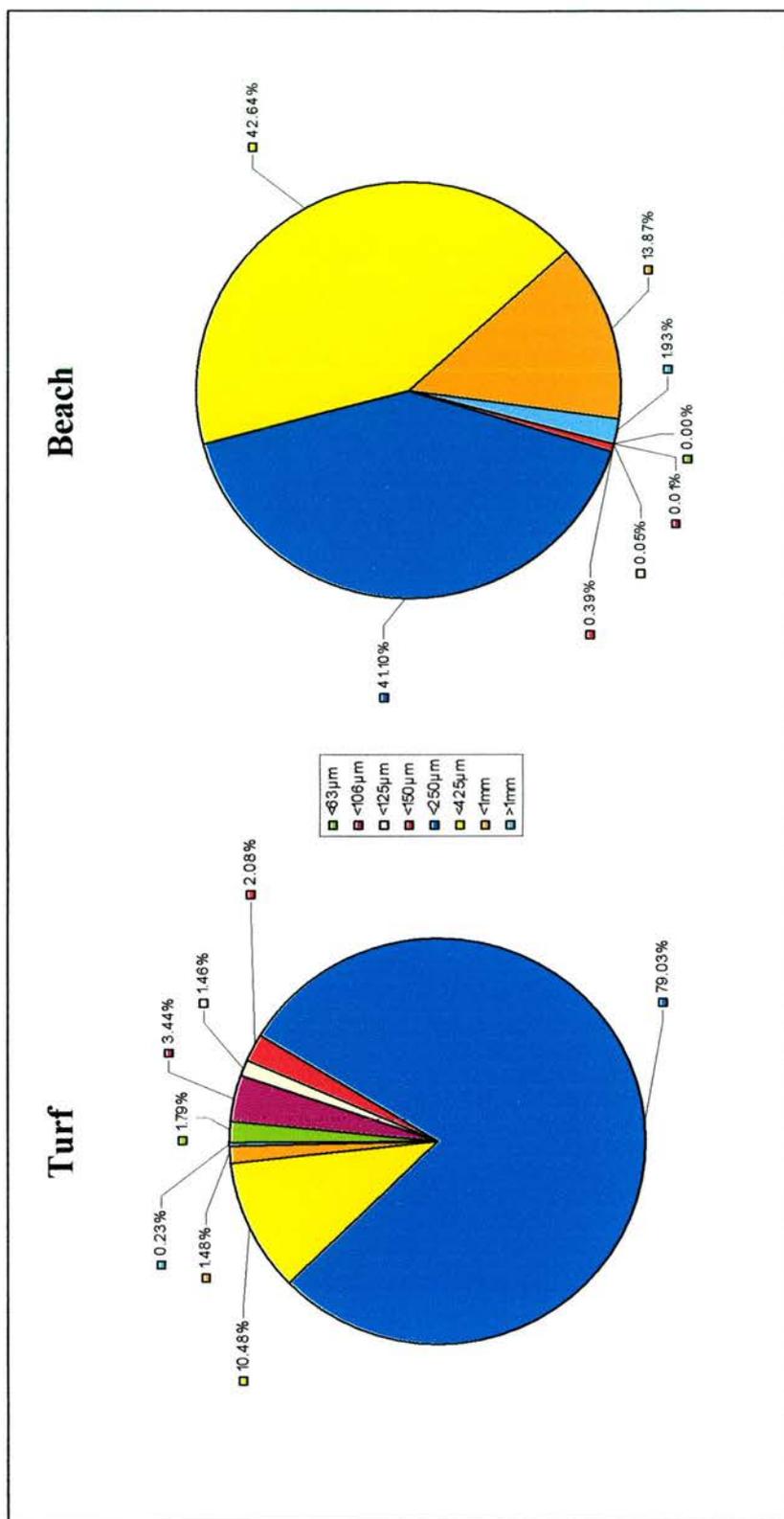


Figure 3.4: Grain size analysis expressed as a % of the total mass. The sediment within the turf was mainly comprised of grains in the 150µm-249µm size range. The sediment found on the adjacent sand flats was mostly comprised of sand grains in the <250µm-424µm size range.

### 3.3.4 Flume experiments

#### *Hydrodynamic model present: with and without turf*

The amount of sediment caught within the sediment trap increased during experimental scenarios in which the turf was absent. This difference was significant at the lower velocity (2way ANOVA  $F_{1,8} = 8.57$ ;  $p=0.019$ ;  $n=3$ ) and highly significant at the higher velocity (2way ANOVA  $F_{1,8}=755.58$ ;  $p<0.001$ ;  $n=3$ ). The least mass of sediment collected was during the scenario using  $<250\mu\text{m}$  sized sediment particles with the turf present. The greatest mass of sediment collected was during the scenario using  $<250\mu\text{m}$  sized sediment particles and no turf.

At the lower velocity there was no significant difference in mass of sediment retained when comparing the different particle sizes used (2way ANOVA  $F_{1,8}=1.69$ ;  $p=0.230$ ). During the high velocity scenarios a significantly greater mass of sediment of  $<425\mu\text{m}$  particle size was collected in the sediment trap compared with the sediments of  $<250\mu\text{m}$  (2way ANOVA  $F_{1,8}=671.32$ ;  $p<0.001$ ).

In summary, the presence of the algal turf restricted sediment transport, and the smaller particles were captured within the turf more efficiently than the larger particles (Figure 3.5).

#### *Hydrodynamic mimic absent*

The presence of the turf caused the amount of sediment trapped to decrease significantly at both low velocity ( $F_{1,8}=46.49$ ;  $p<0.001$ ) and high velocity ( $F_{1,8}=12.83$ ;  $p=0.007$ ) scenarios. The least mass of sediment caught in the trap was

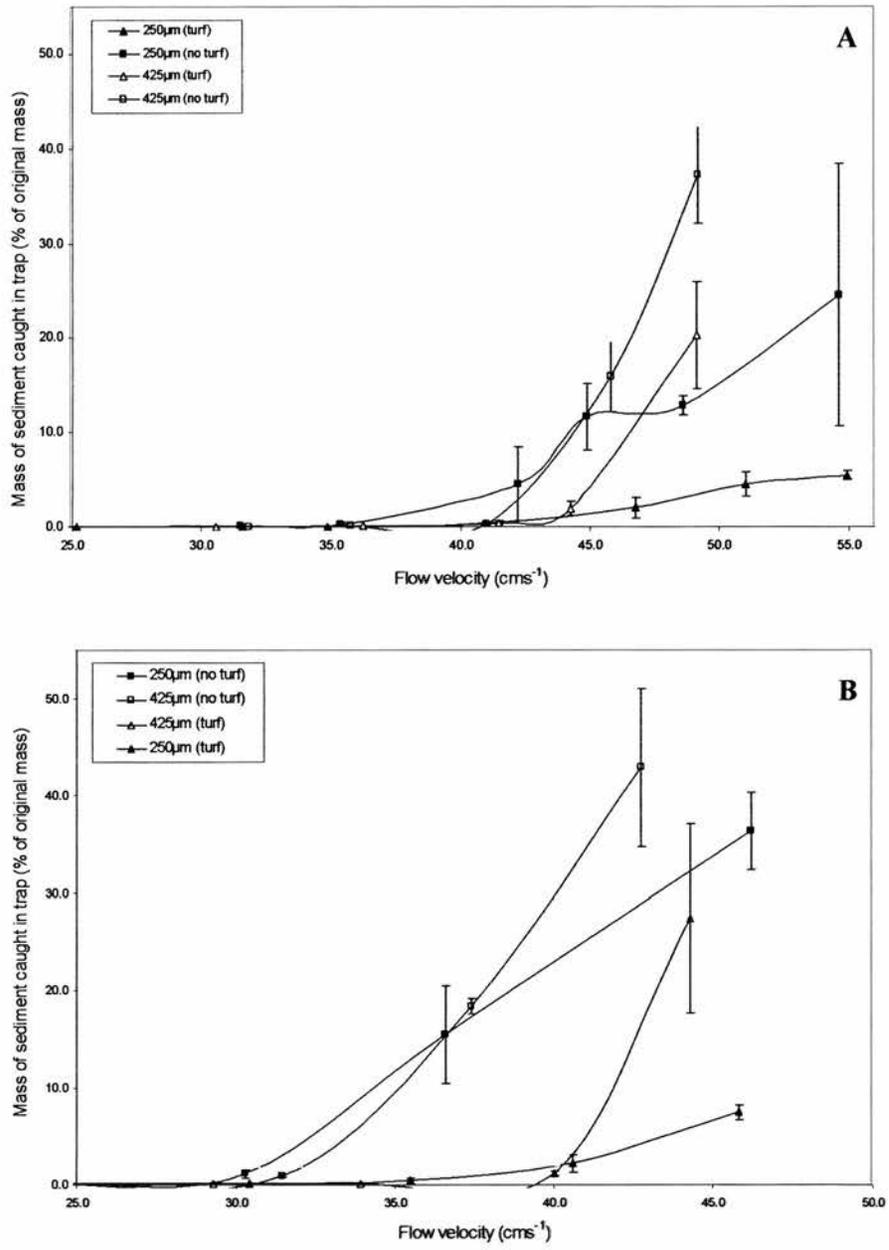


Figure 3.5: The retention of sediment by the algal turf was determined by measuring the amount of sediment collected in the sediment trap. Experiments were conducted with and without the turf present, and with 2 grain sizes (250 and 425). The experiments were repeated with (A) and without (B) a hydrodynamic model on the base of the flume track.

during the experimental scenario when the turf was present and  $<250\mu\text{m}$  sand grains were used (Figure 3.5).

*Comparisons with and without the hydrodynamic mimic*

During low velocity experimental scenarios, with no turf, a significant decrease in the amount of sediment caught in the trap was observed when the hydrodynamic model was in place ( $F_{1,8} = 49.31$ ;  $p < 0.001$ ). No significant difference was observed during the high velocity scenarios.

During experimental scenarios with the turf present a greater mass of  $425\mu\text{m}$  sediment was caught in the sediment trap than the  $250\mu\text{m}$  grain size. With the turf present a highly significant decrease in the amount of sediment caught in the trap, during the high velocity scenarios, was observed when the hydrodynamic model was used ( $F_{1,8} = 16.60$ ;  $p = 0.004$ ;  $n = 3$ ) (Figure 3.5).

*Boundary profiles within the flume*

Boundary profiles provided evidence that fast flow scenarios produced larger boundary layers and higher shear velocities than slow flow scenarios (Figure 3.6). Despite the presence of the turf experimental set ups were under hydrodynamically smooth flow during the experimental procedures as neither  $Re_r$  value was greater than 3.5 (Table 3.1).

	$U_*$ ( $ms^{-1}$ )	$\tau_0$ ( $Nm^{-2}$ )	$Re_r$
Fast flow with turf present	0.008	0.074	0.703
Slow flow with turf present	0.003	0.008	0.231

Table 3.1: Summary of shear velocity  $U_*$  ( $ms^{-1}$ ), shear stress  $\tau_0$  ( $Nm^{-2}$ ), and boundary roughness Reynolds Number ( $Re_r$ ) measurements.

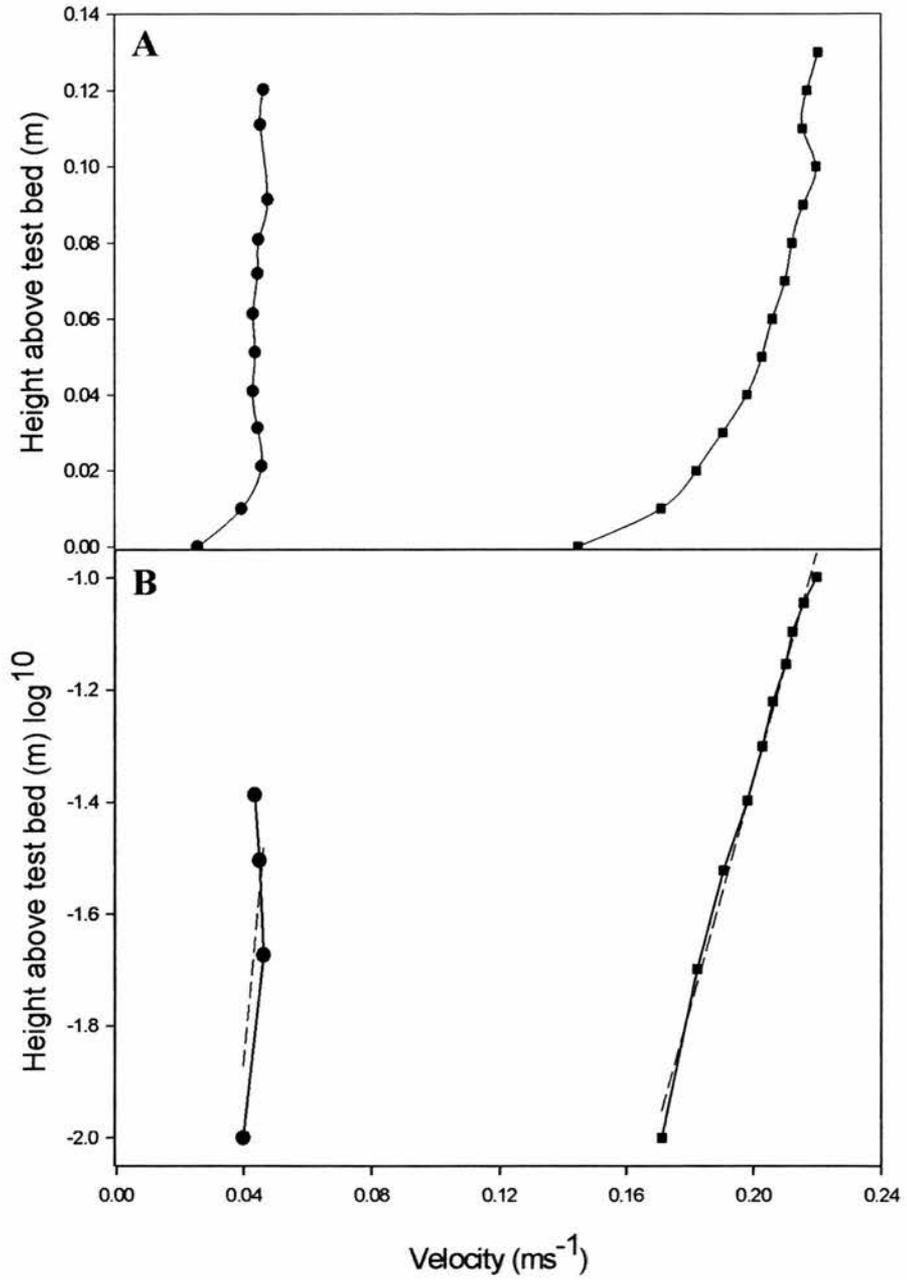


Figure 3.6: Boundary layer profiles obtained from above the turf. An increase in flow velocity can be seen (A) as height above the bed increases until the flow reaches free stream velocity. The points of measurement within the boundary layer (area below free stream velocity) can be plotted against a log scale of the height above the test bed (B), allowing shear stress to be calculated using equation 1.

### 3.4 Discussion

In dynamic habitats such as rocky intertidal areas algae can be exposed to many physical stresses, including scour and burial by sediment erosion and deposition. *Rhodothamniella* sp is an example of an alga that has adapted to thrive in harsh conditions by adopting a turf growth form. The experimental scenarios presented in this study have shown how this algal turf is an effective ecosystem engineer and has adapted to the variations in sediment deposition to which it is subjected, to its advantage by creating a stable environment on a hard rock substratum.

#### 3.4.1 The effect of algal turf on sediment transport

During the control experiments (those with no turf present), more sediment was retained in the sediment trap indicating the efficiency of the turf in retaining sediments (Fig 3.5). The flow was determined to be hydraulically smooth during all experimental scenarios. This low turbulence reduces the potential for erosion (Neuman *et al* 1970, Kendrick 1991, Airoidi 1998, Airoidi 2000). The sand grain sizes found within the natural turf were smaller than the sand grain sizes found on surrounding sand flats. During experimental scenarios a higher quantity of <250 $\mu$ m sediment was retained within the turf structure than the <425 $\mu$ m sediment therefore providing an accurate reflection of the sediment composition found in the natural turf and adjacent areas of beach.

#### 3.4.2 Advantages of sediment capture on a rock surface

The algal turf growth form may convey a number of advantages for the rock growing algae *Rhodothamniella*. Perhaps the greatest challenge for the alga is the continued action of waves. The turf growth limits the effects of wave action and erosion, since the capture of sediment forms a semi-solid matrix, which absorbs the shock of the waves, and provides physical protection from particle borne abrasion. The algal turf feels springy to the touch but the sediment within the structure is strongly retained. In addition, sediment held within the springy matrix prevents the filaments being abraded against the rock surface, by providing a solid structure in which the filaments are held firmly in place and protected against the strong hydrodynamic forces applied to them. There may also be advantages for the algae in reduced desiccation rates, nutrient retention and turnover. Sediment is believed to form an important structural constituent of the turf (Airoldi *et al* 1995) and, as the turf retains and stabilises sediment within its structure (Fig 3.7) the surface becomes more uniform, therefore reducing boundary roughness and turbulence of water as it flows over or past the turf.

#### 3.4.3 Sediment partitioning by the algal turf

The trapping of sediments is an efficient method of the turf to stabilise itself on what is a highly dynamic and physically stressful environment. Algal mat structures may modify the flow from velocities high enough to transport loose grains in saltation to velocities low enough to cause the deposition of sediments (Scoffin 1970). However, due to the hydrodynamically smooth flow observed during



Figure 3.7: Sediment is believed to form an important structural constituent of the turf. Prior to sediment deposition the turf surface is uneven (A) exposing spaces amongst the filaments. As the turf retains and stabilises sediment within its structure (B) the surface becomes more uniform, therefore reducing boundary roughness and turbulence of water as it flows over or past the turf. Sediment was observed to filter throughout the algal turf during experiments (C).

experimental scenarios it is believed that the variation in sand grain sizes held within the turf structure is not only due to the transportation of different grain sizes, but also induced by the size of the interstices within the structure of the turf. Similar results were gained by Airoidi *et al* (1996) who found the material within the turf comprised of  $<200\mu\text{m}$  sand grains, and that the amount of material present decreased with distance from the bottom layers. However, according to sediment transport theory the smaller particles should be moved more efficiently than the large particles (Allen 1992, Waugh 1995). Since both experimental set-ups were under hydrodynamically smooth flow during the experimental procedures, we can assume that the presence of the turf did not induce turbulent transition in the flow, and that any significant variations in sediment transport were not flow related. This suggests the turf selectively filters sediment during transport of grains. An analogy may be envisaged as a filter mesh placed parallel with the flow. The “filter” allows the  $<250\mu\text{m}$  grains to drop into the structure of the turf but a proportion of the  $<425\mu\text{m}$  are too large and the majority of these grains pass over the turf or through the upper layers (Figure 3.8).

#### 3.4.4 Particle retention within the turf

Once the sediment is within the turf structure it can be bound physically by the filaments of the *Rhodothamniella* sp, or by mucopolysaccharides associated with diatoms and other epiphytes which assist the retention of grains by forming cohesive attachments. Smaller grain sizes may be held more effectively by the mucilage due to their relative surface area to volume (mass) ratios (Scoffin 1970, Airoidi *et al*

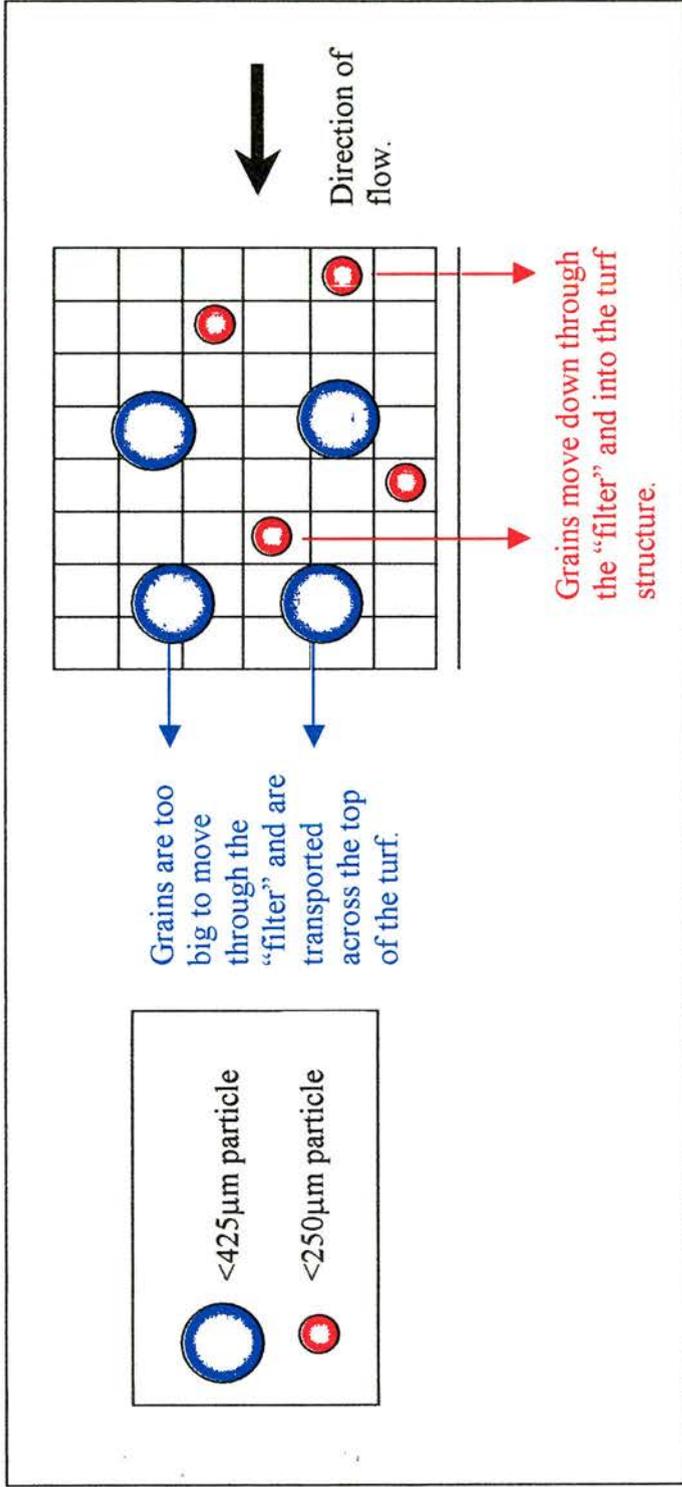


Figure 3.8: Simplistic diagram explaining the "filter theory" (viewed from above). Smaller grain sizes are retained within the turf structure more effectively than the larger grain sizes resulting in a dominant grain size retained within the turf structure.

1998). Scoffin (1970) noted that sediment was retained by adhesion to mucilage in *Lyngbya* sp, cyanobacterial mats, however it was the filaments of the turf that produced the mucilage as opposed to associated microphytobenthic communities. In the *Rhodothamniella* sp this does not seem to be the case and the mucopolysaccharides appear to be produced by bacteria and epiphytes (figure 3.2).

Studies carried out by Peterson *et al* (1990) showed that epiphytes found within turf filaments occurred at different levels and identified a basal layer, the surface layer within the filaments. For example *Nitzschia* sp was closely associated with filamentous surface layers, this was probably due to its ability to migrate vertically in order to position itself in optimum light regimes. Diatom densities on clay tiles were decreased up to 90% by large storms and it is thought that diatoms could use the turf filaments as a refuge. D'Antonio (1986) also recorded dense populations of diatoms within *Rhodomela larix* beds. However, after a long period of burial these populations decreased significantly, but a patch that was not buried maintained a dense population of the chain forming diatom *Ishmia nervosa*. This suggests that both the diatoms and the turf benefit from this relationship as host and epiphyte. The diatoms obtain a sheltered environment in which to thrive and the turf gains stability by benefiting from the mucopolysaccharides produced by the diatoms to bind sediments within its structure, and therefore become more stable and uniform.

### 3.5 Conclusion

*Rhodothamniella* sp often dominate rocky outcrops which are subjected to sporadic sand burial, due to the capacity of the turf to capture sediment and withstand long periods of burial. *Rhodothamniella* sp has been shown to effectively bind sediment into its structure. This may be enhanced by the presence of bacteria and epiphytes, and associated EPS secretions within the algal matrix. The turf has been observed to act as a selective hydrodynamic filter, the mechanism for this is unclear but may be related to the size of the interstitial spaces within the matrix of the turf. In dynamic environments such as rocky intertidal shores, species are forced to find a balance between energetic expenditure and factors such as resistance to erosion/disturbance, competition for space, and protection/tolerance from environmental stresses such as salinity, and temperature. As a result of this, species find different areas to dominate within the habitat according to the environmental stresses they have evolved to overcome, and in doing so play an important role in changing physical factors, such as local hydrodynamics, and shaping the environment around them and colonising systems where productivity and competition is low due to environmental stress. *Rhodothamniella* sp. has developed a strong engineering capacity that creates a new set of niches under extreme physical conditions, acting as a resource for epiphytes and their predators and increasing local diversity and functional capacity.

### **3.6 Publications**

Data published from this chapter has been submitted to Marine Ecology Progress Series.

Aspden, R.J., and Paterson, D.M. Sediment partitioning and ecosystem engineering by the red alga, *Rhodothamniella* sp. Marine Ecology Progress Series (submitted).

## **CHAPTER FOUR**

### **THE EFFECTS OF CLAM HARVESTING ON THE SUBTIDAL SURFACE SEDIMENTS OF THE LAGOON OF VENICE, ITALY**

## **Chapter Four – Abstract**

Clam harvesting (*Tapes philippinarum*) is a socio-economically important fishery in the Venice Lagoon area, Italy. However, clam harvesting disrupts the structure of benthic communities and little is known about the effects upon sediment surface structure. These effects were investigated during four field trips. Varying frequencies of disturbance were investigated, and the study sites were assessed for the impacts of clam harvesting using direct measurements and indicators of biogenic sediment stabilisation.

During the study of immediate impacts of clam harvesting, sediment stability was found to be significantly higher at the less impacted site ( $F_{1,34}=6.23$ ,  $p<0.018$ ). Concomitant decreases in chlorophyll *a*, colloidal-S carbohydrate and dry bulk density were also observed at the less impacted site. There was no significant effect of new harvesting on the biological properties at the highly impacted site and this was attributed to the higher frequency of harvesting activity in this area.

Whilst changes were seen pre and post clam harvesting during the intermediate impact study, the changes in measured parameters tended to be increases in biogenic indicators of stabilisation, but decreases in sediment stability. This suggests that whilst the microphytobenthic communities increased as a result of the time during which disturbance did not occur, this increase had insufficient time to have any effect on the physical structure and strength of the surface sediments. The presence of a stalked filamentous diatom in a non-harvested area, was thought to be the reason for high critical erosion thresholds (CSM) compared to the rest of the sites.

Hence it was determined that frequent harvesting of the lagoon prevents the establishment of biotic communities, preventing biostabilisation and thus reduces the stability of the surface sediment.

#### 4.1 Introduction

Throughout the history of the Venice Lagoon anthropogenic pressures have caused engineers to manipulate the water flow and hydrodynamics of the lagoon and hence the ecology of the system. Sediment dynamics, controlled primarily by wave energy, river flow, and coastal currents, within the Venice Lagoon are of critical importance to the health and ecological status of system. However along with the increase in sea level rise and occurrence of the “*aqua alta*” (extreme high tides), due to climate change, this system is under increasing threat as the rate of sediment erosion is overtaking that of sediment deposition, resulting in the deepening of the lagoon and increased local erosion. The productivity of the surface sediments within the Venice Lagoon is highly significant because the dependent fishery business is of high economic importance to the surrounding areas. The clam fishery has an annual yield of 50000 tonnes, and ancillary fishery businesses employ approximately 2500 people, accounting for an annual turnover of 73 million Euros (Rosetto, 2000).

The resistance of surface sediments to erosion is of importance to the clam fishery because any change in the quality of the lagoon waters may affect the yield. For example, resuspension of sediment in the water column causes a reduction in light availability, or the release of previously bound organic material, creating an oxygen deficit. Alternatively, sediment re-suspension may increase nutrient levels promoting phytoplankton blooms (Orth, 1977). The likelihood of sediment erosion within the lagoon can be increased by the removal of biogenic stabilisers such as polychaete tube fields or microphytobenthic biofilms. These structures are removed from the sediments by the passage of commercial vessels (Vapparetto’s or water taxis), or by the direct disturbance of the sediment due to clam harvesting. Although there is limited literature

available regarding the effects of harvesting on the structure of soft sediment habitats after disturbance events of this kind, there are many references regarding the effects of biogenic stabilizers on sediment stability and faunal biodiversity, therefore providing an indication of the health of the system. Hauton and Paterson (2003) reported a reduction in sediment shear strength after dredging, whilst Jennings *et al.* (2001) found a significant decrease in infaunal and epifaunal biomass. Structures such as sea grass rhizomes and polychaete tubes (Fager, 1964; Carey, 1983; Fonseca and Fisher, 1986; Freidrichs, 2000) help to maintain sediment stability by dampening hydrodynamic forcing and promoting colonisation by microphytobenthos, and if removed or damaged by harvesting apparatus, the potential for bed erosion increases.

The Venice Lagoon is on average 1.5m deep, and therefore the presence of benthic macroalgae and microphytobenthos is integral to the structure and composition of the sediments and plays an important role in the sediment dynamics due to flow manipulation and production of metabolic exudates (EPS) (Tolomio *et al.*, 1999; Facca *et al.*, 2002). EPS has been found to play an important role in the mechanical stabilisation of sediments (Holland *et al.*, 1974; Yallop *et al.*, 1994; Austen *et al.*, 1999), by forming an extensive matrix and coating the sediment with organic material, thereby promoting inter-particle binding (Chenu and Jaunet, 1992; Chenu, 1993). Once the sediment structure has been homogenised and the biogenic content removed or reduced, the time period required for the system to recover can vary drastically depending on the scale of disturbance, sediment type, hydrological flow patterns, storm events, and the intrinsic stability of the sediment. In the harvesting areas of the Venice Lagoon the frequency and scale of disturbance depend on the intensity of harvesting practice and the harvesting mechanisms used. The success of

recolonisation, whilst site specific, is dependent upon the intensity and frequency of the disturbance events (Collie *et al.*, 2000).

The intensive harvesting practices carried out in the lagoon make it an ideal site to study the effects of mechanical harvesting practices on the biostabilisation of surface sediments. These factors should also be taken into consideration alongside the future management plans for the lagoon, such as the hydraulic flood gates, proposed in order to restrict the extreme high tides (Ravera, 2000, and references within).

The aim of studying the biostabilisation of the surface sediments of the Venice Lagoon was to determine whether sediment disturbance resulting from clam (*Tapes phillipinarum*) harvesting, could be associated with decreases in sediment stability and concomitant changes in indicators of biogenic stabilisation.

During this research the following hypotheses were tested in order to determine the effects of harvesting activity on the sediments of the Venice Lagoon:

- A site with low harvesting intensity will have higher levels of sediment stability than those subjected to high harvesting activities.
- Sites with longer periods between harvesting activity will contain more stable sediment and higher quantities of microphytobenthic biofilms, than those sites more frequently harvested.

## 4.2 Materials and Methods

### 4.2.1 Study Sites

For the first stage of the study (the immediate impact of clam harvesting) two sites, subjected to different frequencies and intensity of clam (*Tapes philippinarum*) harvesting, were selected for study; San Giacomo, situated in the Paludo area, and San Angelo della Polvere. Historically, San Giacomo has negligible harvesting intensity, due to it being an area of low clam productivity. Clam harvesting is carried out using different methods depending on the water depth. In deep water (>2 m) commercial trawling vessels (20 m in length) with larger dredge mechanisms (cage of 158cm x 38cm) can be used and are the preferred harvesting method. In shallow waters, artisanal fishermen use one or two outboard motors suspended over the side of a small boat as a means of harvesting such that the re-suspended sediment passes through nets which are placed behind the additional motors to collect the clams. These methods are referred to from this point as “dredge” or “artisanal” methods. The average water depth at San Giacomo was 1.25m, and harvesting was carried out using a small centre console vessel, with two additional outboard motors, one suspended from each side of the boat, (Figure 4.1a). The water depth at San Angelo is typically 2.25m, allowing the use of dredge harvesting (Figure 4.1b).

In order to carry out the studies to determine the intermediate effects of clam harvesting, two sites were chosen: Ca’Roman and San Angelo della Polvere, one of the areas harvested during the first stage of the study. Clam fishermen harvested both sites regularly using the dredge harvesting mechanisms. The site at Ca’Roman was previously seeded with small *Tapes philippinarum* and harvested once they had reached a suitable size. As well as

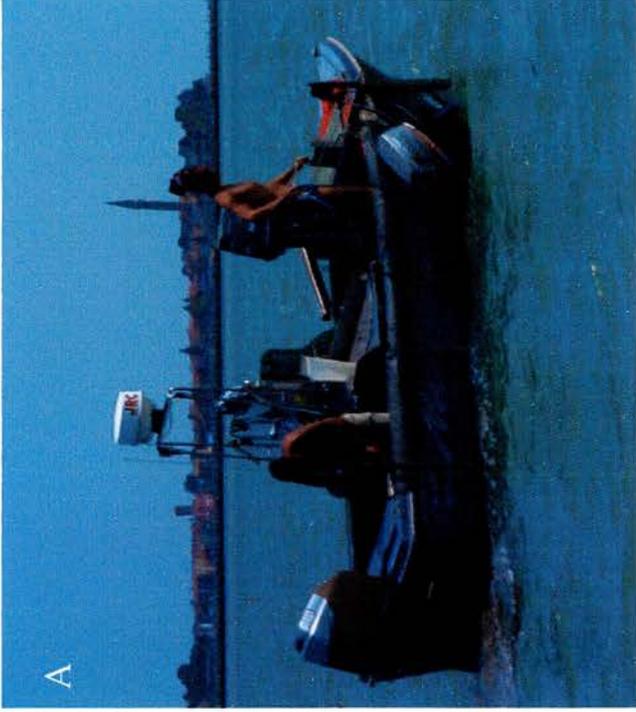


Figure 4.1: Methods of harvesting clams varied from site to site due to the differences in water depth. Water depth at San Giacomo (A) was typically 1.25m and so the artisanal method of small centre console vessels were used with additional outboard motors suspended over the sides of the vessel. The water depth at San Angelo (B) was typically 2.25m therefore allowing the use of small commercial dredge harvesting vessels.

the study sites containing clams, control sites were also subjected to the harvesting mechanisms in both areas. The control sites chosen were areas that are not normally subjected to harvesting. The control site at Ca' Roman contained a high coverage of sea grass indicating that the site had remained undisturbed for a long period of time.

#### 4.2.2 Field sampling methods

In order to carry out the first stage of the study, three transects (100 m long) were designated for dredge or artisanal harvesting (dependent upon water depth) at each study site (San Angelo della Polvere and San Giacomo). Replicate intact sediment cores (10 cm internal diameter,  $n = 4$ ) were obtained by a SCUBA diver, at 3 points (25m, 50m and 75m) along each transect line, and additionally at the same points parallel to, but 5m off each transect line. Cores were taken prior to and after the harvesting disturbance.

One core from each sample point was used to determine the critical shear stress ( $\tau_{o,crit}$ ,  $\text{Nm}^{-2}$ ) on the boat immediately after collection.  $\tau_{o,crit}$  was measured using a cohesive strength meter (CSM Mk III), an *in situ* erosion device (Tolhurst *et al*, 1999). Thus one measurement of critical erosion threshold (and presence of algal biomass) was made at 3 sample points along each of the 3 transects, both prior to and post harvesting, and on and off each transect, resulting in a total of 36 measurements.

The remaining three replicate cores were used for analysis of biogenic indicators of sediment stabilisation. The top 3-5mm of the sediment surface from each core was removed by contact freezing with liquid nitrogen-cooled metal, using the contact core method (Honeywill, 2001) and stored in liquid

nitrogen until lyophilisation prior to further sediment analysis. Thus 3 samples were taken from 3 sample points along each of the 3 transects, both prior to and post harvesting, and on and off each transect, resulting in a total of 108 samples.

Visual impacts of clam harvesting were obtained using images of the seabed taken prior to and post trawling, using Imagenix 885 side scan sonar, with a frequency of 675 kHz and range set at 100m (courtesy of Dr Richard Bates).

The study determining the intermediate effects of clam harvesting took place in three stages. During November 2002, pre-disturbance, measurements were taken from each study site and the respective controls. Due to the cold conditions and concomitant problems for the divers, the samples could not be taken entirely randomly. Therefore three sub areas were sampled within each study site, taking six 10cm drainpipe cores from each. Three of these cores were used for immediate measurements of the critical shear stress ( $\tau_{o,crit}$ ,  $Nm^{-2}$ ) using the CSM, contact cores were removed from 2 retrieved cores and the final core was used to take a surface scrape in order to study the structure of the sediment surface using low temperature scanning electron microscopy at a later date. Therefore, 9 samples were retrieved from each study area and each control area resulting in a total number of 72 samples. This sampling strategy was repeated a month after each site was disturbed by the harvesting mechanisms.

#### 4.2.3 Laboratory sampling methods

The parameters used as proxies for biogenic sediment stability (Black and Paterson, 1997; Consalvey, 2002; Paterson 1997) were chlorophyll *a* and pheophorbide content, colloidal-S carbohydrate content, dry bulk density and organic carbon content. Chlorophyll *a* and pheophorbides (pigment breakdown

products) were extracted using demethylformamide (DMF) and quantified using high performance liquid chromatography (HPLC). In order to establish an indicator of the 'health' of the surface sediments prior to trawling, ratios of chlorophyll *a* to pheophorbides were calculated.

Colloidal-S carbohydrates were extracted using the methods of Underwood *et al.* (1995) and Smith and Underwood (1998). Sediment dry bulk density was determined after lyophilisation for a period of 24h and organic carbon content was measured as ash-free dry weight. Sediment grain size was determined using a Beckman Coulter LS 230 Particle Size Analyser. Grain sizes were separated into four groups (Wentworth, 1922): <63  $\mu\text{m}$  (silt/clay), 63  $\mu\text{m}$ –125  $\mu\text{m}$  (very fine sand), 125  $\mu\text{m}$ –500  $\mu\text{m}$  (fine/ medium sand), and >500  $\mu\text{m}$  (coarse sand).

Microphytobenthic assemblages were examined using light microscopy. Counts of 300 individuals were made, unless the number of individuals was low, in which case timed searches of 2h were made. Microphytobenthos present at the sediment surface were collected over 1h using the lens tissue method (Eaton and Moss, 1966), and preserved in glutaraldehyde prior to permanent slide preparation. Permanent slide preparations were made by acid-cleaning samples to remove organic matter (Simonsen, 1974).

Cytochemical staining was carried out to determine the presence or absence of mucopolysaccharides within the Ca'Roman samples thought to contain *Licmophora* sp. The stain Alcian Blue was used as it is suitable for acid mucopolysaccharides (Daniel *et al* 1987). The samples were fixed in 4% formaldehyde solution for 48 h, after which small sections of the turf were removed and placed in a 1.0% solution of Alcian Blue (8GX) for 30 min. The samples were then bathed in distilled water to rinse away any excess stain,

mounted onto an acid cleaned slide and examined at high magnification (x40-100) under a light microscope. Low temperature scanning electron microscopy was also carried out on these samples to ensure correct species identification.

#### 4.2.4 Statistical analysis

Chlorophyll *a* content, colloidal-S carbohydrate content, dry bulk density, and organic carbon content were tested for normality and equality of variances using Anderson –Darling test for normality and Bartlett’s test of equal variances. Differences prior and post trawling were then determined, using one-way ANOVA. *Post hoc* analysis was employed using the Tukey test to identify the cause of variation at a significance level of  $p < 0.05$ . The critical erosion threshold data did not meet the criteria of ANOVA and were tested using the non-parametric Kruskal-Wallis test. Results were considered significant at  $p < 0.05$ . PRIMER (6 Beta) was used to examine significant patterns within the microphytobenthic community data, and Shannon-Wiener indices were applied to microphytobenthic cell count data, to compare diversity of species within sites.

## 4.3 Results

### 4.3.1 Immediate impacts of harvesting disturbance

#### *Comparison of sites*

##### *Microphytobenthic biomass*

A significant decrease in Chlorophyll *a* content was observed after the disturbance event on the test transects at both sites (San Angelo:  $F_{3,104} = 8.468$ ,  $p < 0.001$ ; San Giacomo:  $F_{3,103} = 28.139$ ,  $p < 0.001$ ), however, this decrease was not observed on the control sites parallel to the transects (Figure 4.2A&B). Chlorophyll *a*: pheophorbide ratio was higher at San Giacomo than at San Angelo, and was found to decrease after the disturbance event (Figure 4.3).

##### *Sediment critical erosion threshold*

$\tau_c$  did not differ significantly parallel to or on the transects prior to the disturbance event at either sampling site, and so data were pooled for statistical analysis. San Giacomo surface sediments had higher erosion thresholds compared to San Angelo prior to harvesting, but this was reduced to a similar level of stability after the disturbance event (Figure 4.4). Thus at San Giacomo, sediment stability was reduced by harvesting to levels similar to San Angelo. There was less variation in sediment stability after trawling at San Angelo.

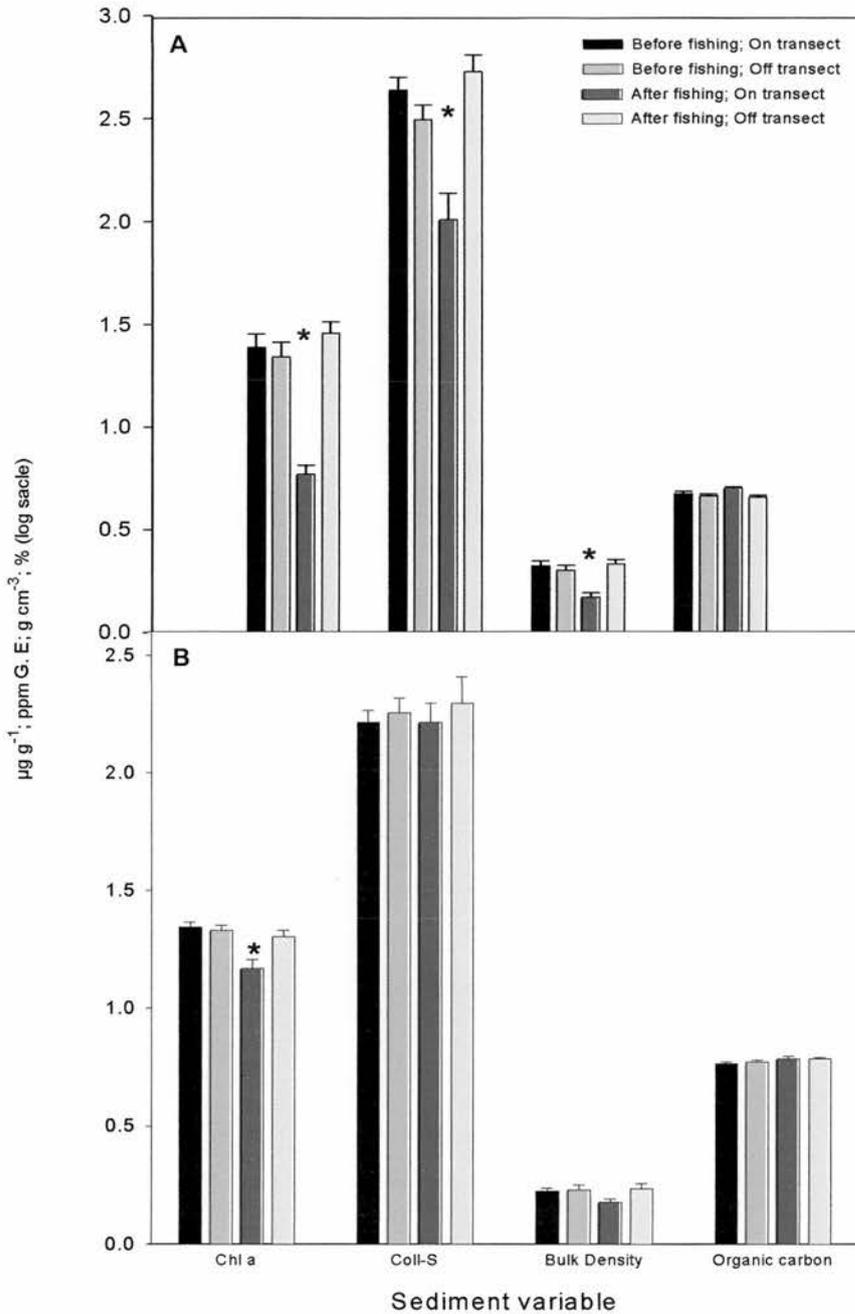


Figure 4.2: Chl *a* ( $\mu\text{g g}^{-1}$ ), colloidal-S carbohydrate (ppm glucose equivalents), bulk density ( $\text{g cm}^{-3}$ ), and organic carbon content (%) of lyophilised sediment from San Giacomo (A) and San Angelo (B) during the immediate impact of clam harvesting study. \* = significant difference at  $p < 0.05$ . Mean  $\pm$  s.e.,  $n=24-27$ .

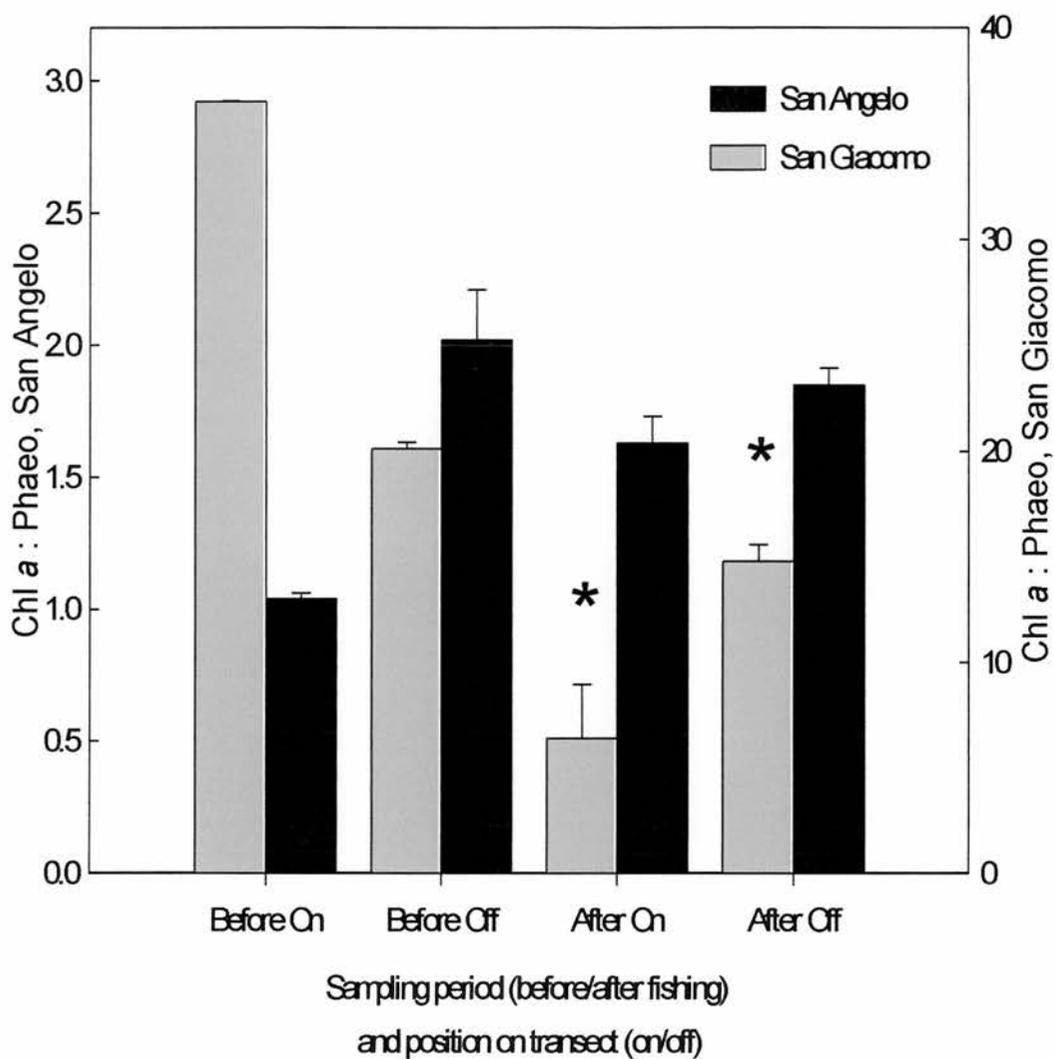


Fig 4.3: Chl *a* to phaeophorbide ratios in sediment samples from San Angelo and San Giacomo during the immediate impacts of clam harvesting study. \* = significant difference at  $p < 0.05$ . Mean  $\pm$  s.e.,  $n = 16-25$ .

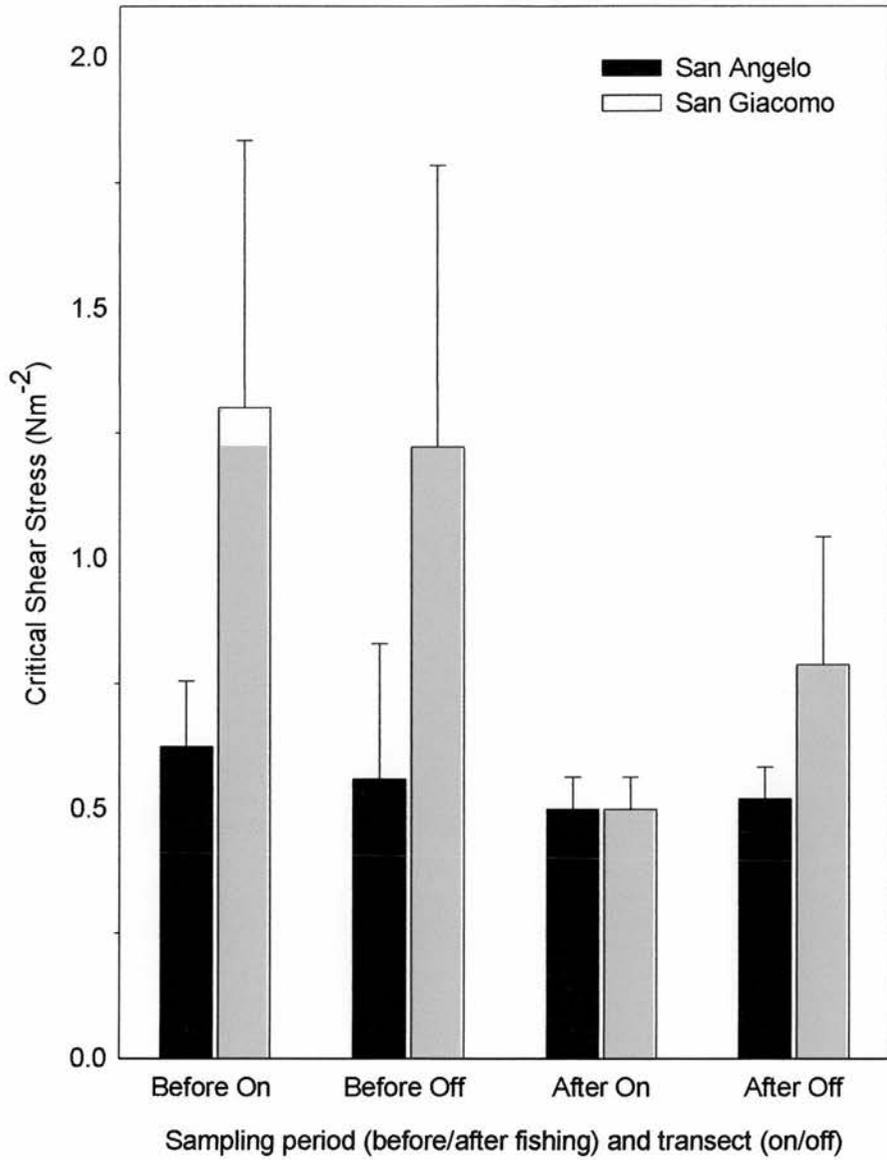


Fig 4.4: Critical erosion threshold (Nm<sup>-2</sup>), for intact sediment cores at San Angelo and San Giacomo, during the immediate impacts of clam harvesting study. Mean ± s.e., n = 9.

*Comparison within sites**San Angelo (high impact site; dredged)*

Silt/clay ( $\leq 63\mu\text{m}$ ) represented over 70% of the total sediment volume. 5-10% of the total volume exceeded a particle size of  $500\mu\text{m}$  and was comprised largely of shell fragments, probably indicating the extent of clam harvesting in this area (Figure 4.5).

Chlorophyll *a* content declined significantly on the transect after the harvesting event ( $F_{3,104} = 8.468$ ,  $p < 0.001$ ; Figure 4.2). All other measurements (carbohydrate content, dry bulk density organic carbon content, and critical shear stress) were unaffected by harvesting. The diversity of benthic algal assemblages varied from 1.82 to 1.78 (Shannon-Wiener Index), before and after harvesting respectively, suggesting a minor, possibly negligible, immediate effect of harvesting on community structure. The dominant diatom taxa found on the sediments were *Navicula cincta*, *Nitzschia dissipata*, *Nitzschia constricta*, *Coconeis scutellum*, and *Amphora* sp. Multidimensional scaling plots were used to illustrate microphytobenthic assemblage composition did not significantly differ before and after harvesting (Figure 4.6A). Side scan sonar images showed a high level of disturbance prior to harvesting activity (Figure 4.7A), and after harvesting most of these previous features had been replaced (Figure 4.7B).

*San Giacomo (low impact site; artisanal fishing)*

Over 80% of the sediment by volume at San Giacomo was represented by silt/clay ( $\leq 63\mu\text{m}$ ). The largest size class ( $>500\mu\text{m}$ ) occurred as a much lower proportion of the total sediment volume compared to sediment at San Angelo, suggesting a relatively finer sediment matrix and a lack of shell fragments (Figure 4.5).

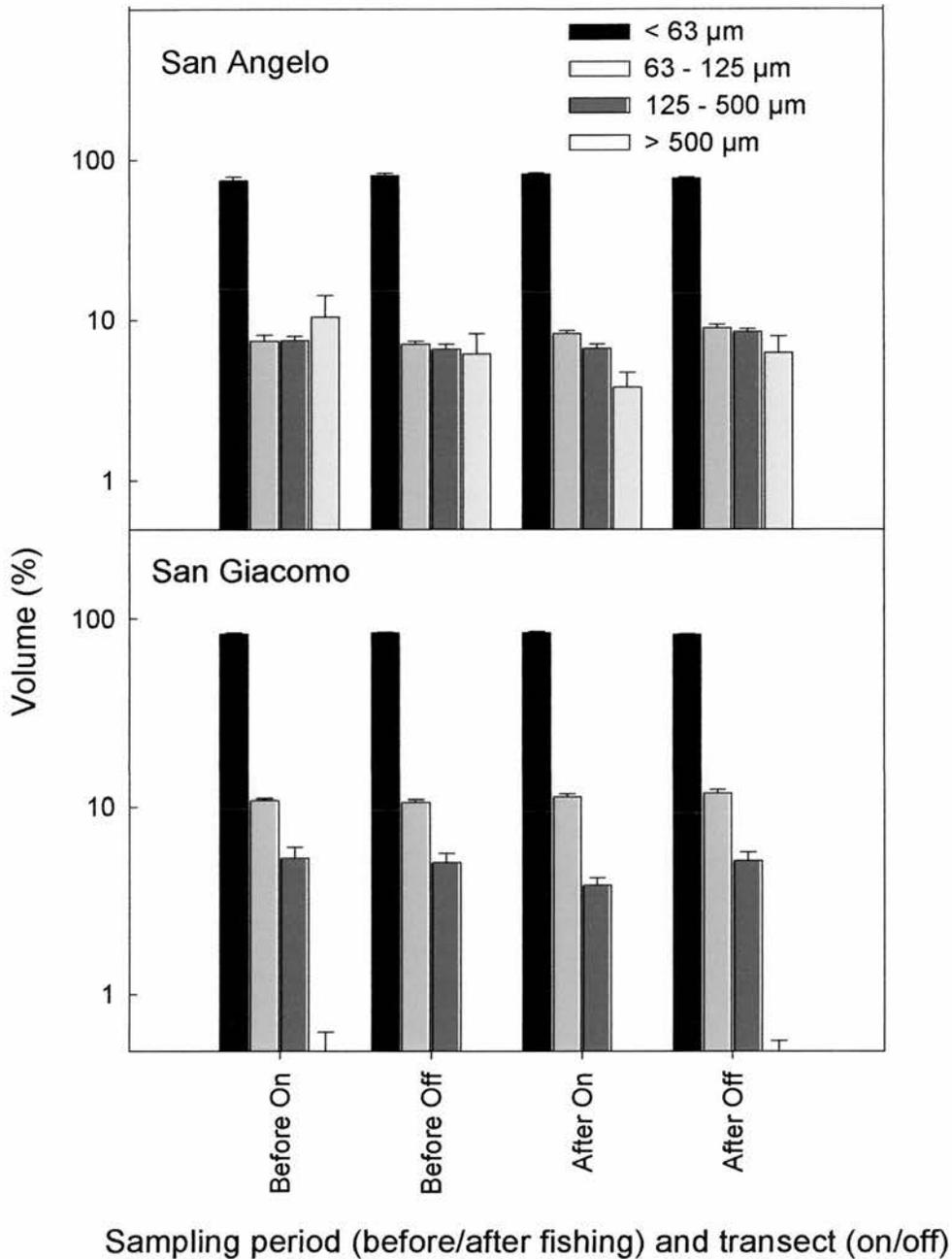


Fig 4.5: Volume distributions (%) for grain size classes for lyophilised sediment samples from San Angelo and San Giacomo during the immediate impacts of clam harvesting study (mean  $\pm$  s.e.,  $n = 24-27$ ). Size classes: <63 $\mu\text{m}$  (silt/clay), 63 $\mu\text{m}$ -125 $\mu\text{m}$  (very fine sand), 125 $\mu\text{m}$ -500 $\mu\text{m}$  (fine/medium sand), and >500 $\mu\text{m}$  (coarse sand).

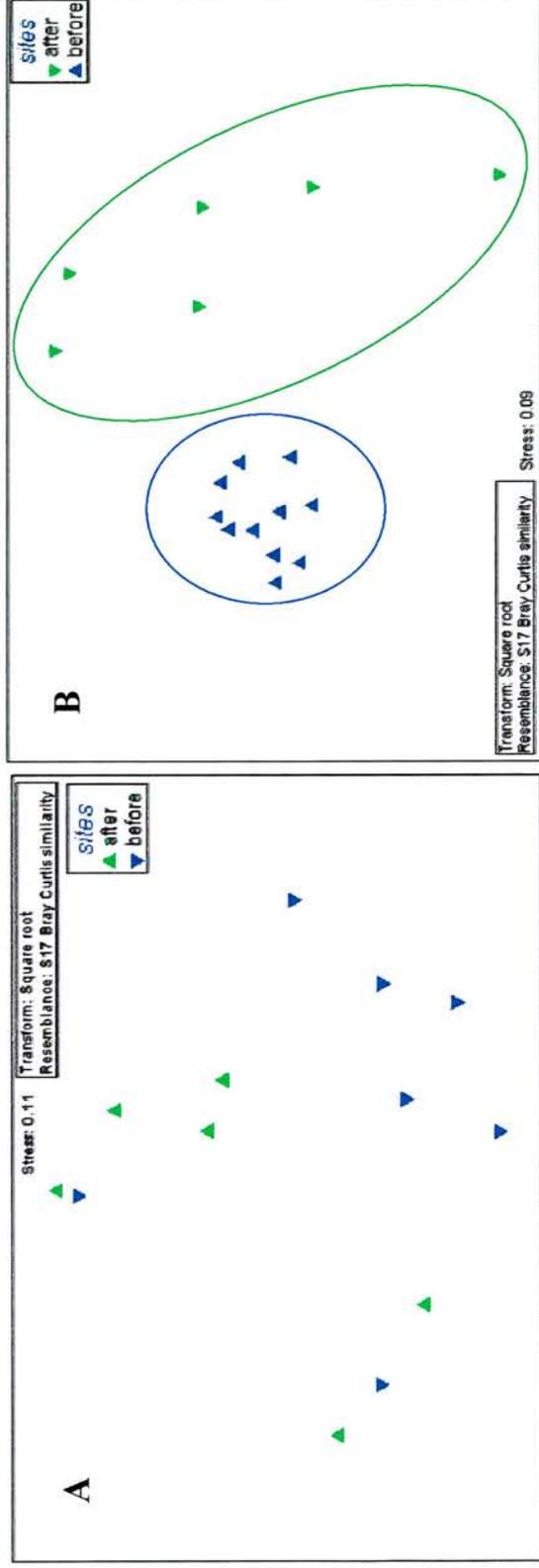


Fig 4.6: Multi-dimensional scaling plot reflecting the relative dissimilarity of the microphytobenthic community assemblage composition at San Angelo (A) and San Giacomo (B) during the immediate impacts of clam harvesting study. Circles group pre and post harvest events.

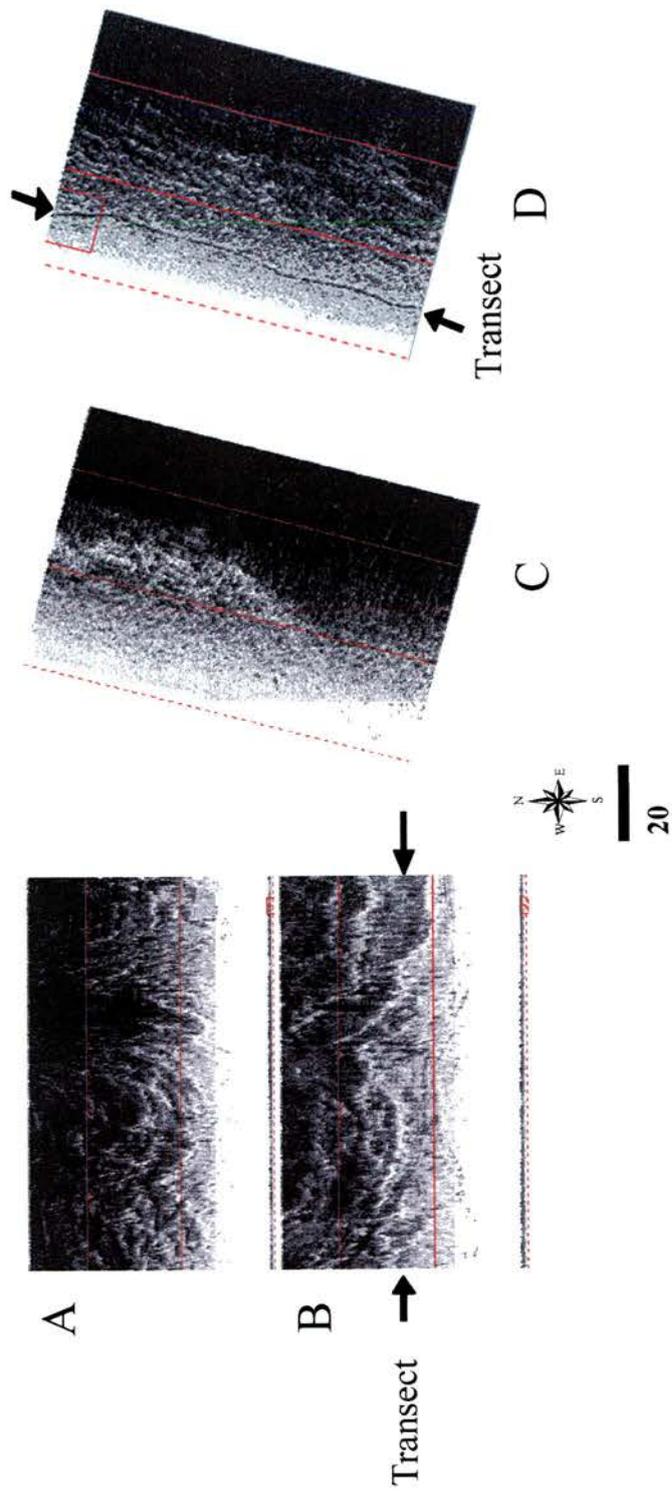


Fig 4.7: Side scan sonar images of the same area of sea bed taken at San Angelo prior to (A) and post (B) the immediate impacts of harvesting event, and at San Giacomo prior to (C) and post (D) the immediate impacts of harvesting event, aligned to a north bearing. The images of the sediment at San Angelo prior to fishing provides an excellent visual representation of the damage caused by continuous harvesting when compared to the homogeneous nature of the sediment at San Giacomo. A furrow can be seen clearly after the harvesting activity had taken place at San Giacomo.

Colloidal-S carbohydrate content and dry bulk density decreased significantly after harvesting ( $F_{3,101} = 12.748$ ,  $p < 0.001$ ) ( $F_{3,102} = 12.070$ ,  $p < 0.001$ ). This decrease only occurred on the transects and not off transects (Figure 4.2). No significant temporal differences in the content of organic carbon were observed (Figure 4.2).

The dominant diatom taxa found were *Navicula cincta*, *Nitzschia dissipata*, *Nitzschia constricta*, *Nitzschia frustulum* *Nitzschia dubiiformis*, *Coconeis scutellum*, *Amphora* sp, and *Gyrosigma acuminatum*. The diversity of the assemblage at San Giacomo was higher than at San Angelo with a range of 1.83 to 1.98 (Shannon Weaver Index) prior to and post harvesting respectively. Multidimensional scaling plots illustrated that the microphytobenthic community composition before harvesting differed from that after harvesting (Figure 4.6B). However, the overall diversity of the assemblages was unaffected

Despite a decrease in values of the indicators of biogenic stabilisation (chlorophyll *a*, colloidal-S carbohydrate, dry bulk density, and organic carbon content) after harvesting, there was no statistically significant decrease in the critical erosion threshold (Figure 4.4), although a 50% reduction did occur ( $p=0.05$ ).

Side scan sonar images showed a homogenous surface prior to harvesting (Figure 4.7C). However, a distinct track caused by the outboard motor was evident once sediment had been disturbed by the harvesting equipment (Figure 4.7D).

### 4.3.2 Intermediate impacts of harvesting disturbance

#### *Comparison within sites*

##### *San Angelo*

Chlorophyll *a* content and colloidal-S carbohydrate content showed a significant increase a month after the harvesting event ( $t = -8.93$ ,  $df = 5$ ,  $p < 0.001$  ;  $t = -3.92$ ,  $df = 7$ ,  $p = 0.006$ ), whilst total organic content decreased significantly after the harvesting event;  $t = 8.09$ ,  $df = 9$ ,  $p < 0.001$ ). No significant difference was observed in dry bulk density (Figure 4.8). The critical shear stress decreased significantly after harvesting had occurred (Figure 4.9) ( $W = 126.0$ ,  $p = 0.0002$ ).

Silt/clay ( $<63\mu\text{m}$ ) represented over 70% of the total sediment volume present at San Angelo. Roughly 12% of the total volume exceeded  $500\mu\text{m}$ , due to the presence of shell fragments (Figure 4.10).

The diversity of benthic algal assemblages varied from 2.55 to 2.50 (Shannon-Wiener Index), before and after harvesting respectively, suggesting that there was negligible effect of the harvesting activity on the benthic algal diversity. The dominant taxa found in the surface sediments were *Navicula cincta*, *Nitzschia dubiiformes*, and *Amphora* sp. Multidimensional scaling plots indicated that whilst there was little variation in diversity, there was a distinct change in abundance and species composition pre and post harvesting activity (Figure 4.11).

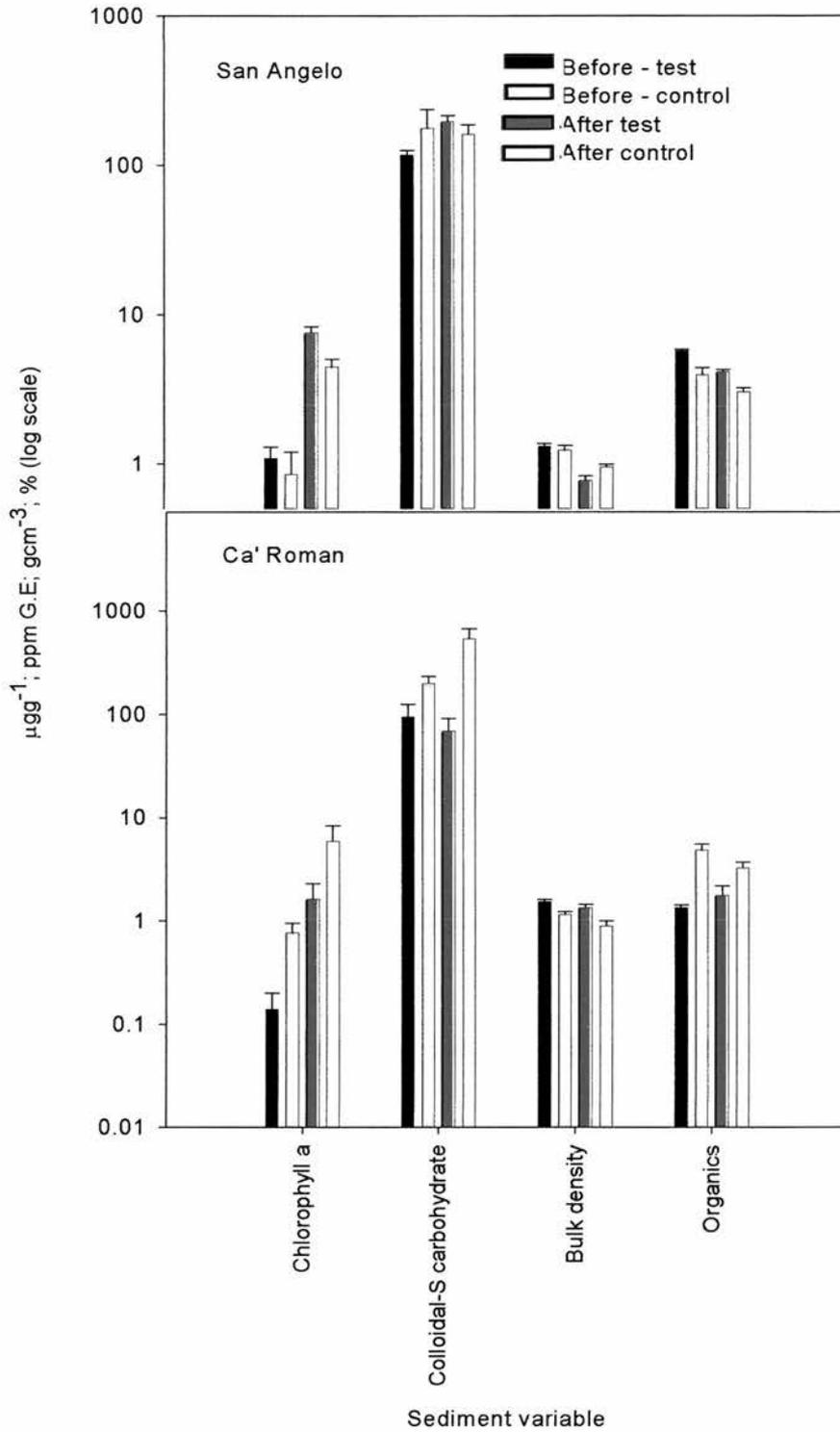


Figure 4.8: chl *a* ( $\mu\text{gg}^{-1}$ ), colloidal-S carbohydrate (ppm glucose equivalents), bulk density ( $\text{gcm}^{-3}$ ), and organic carbon content (%) of lyophilised sediment from San Angelo and Ca' Roman during the intermediate impact of clam harvesting study. Mean  $\pm$  s.e.,  $n = 6$ .

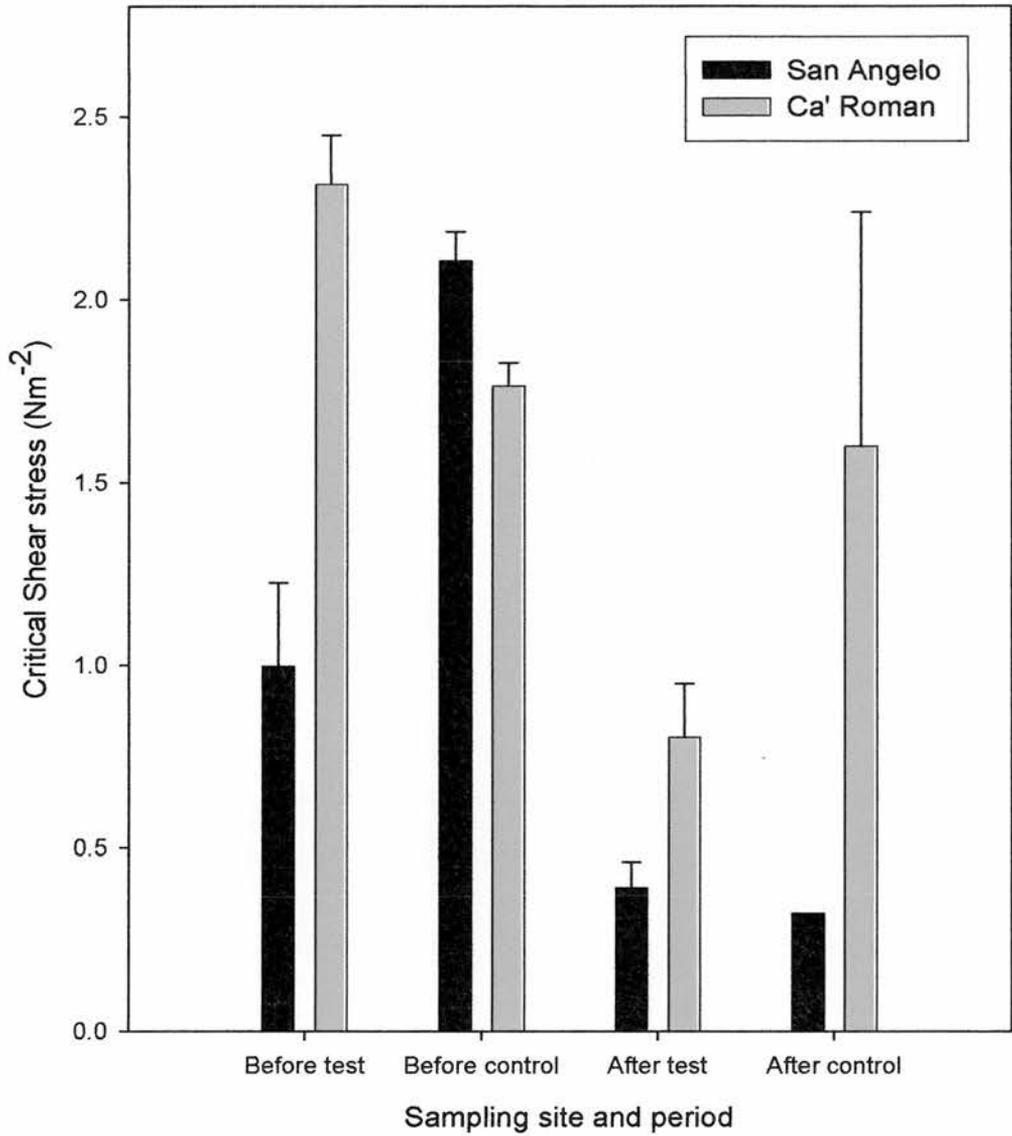


Fig 4.9: Critical erosion threshold (Nm<sup>-2</sup>), for intact sediment cores at San Angelo and Ca' Roman, during the intermediate impacts of clam harvesting study. Mean ± s.e., n = 9.

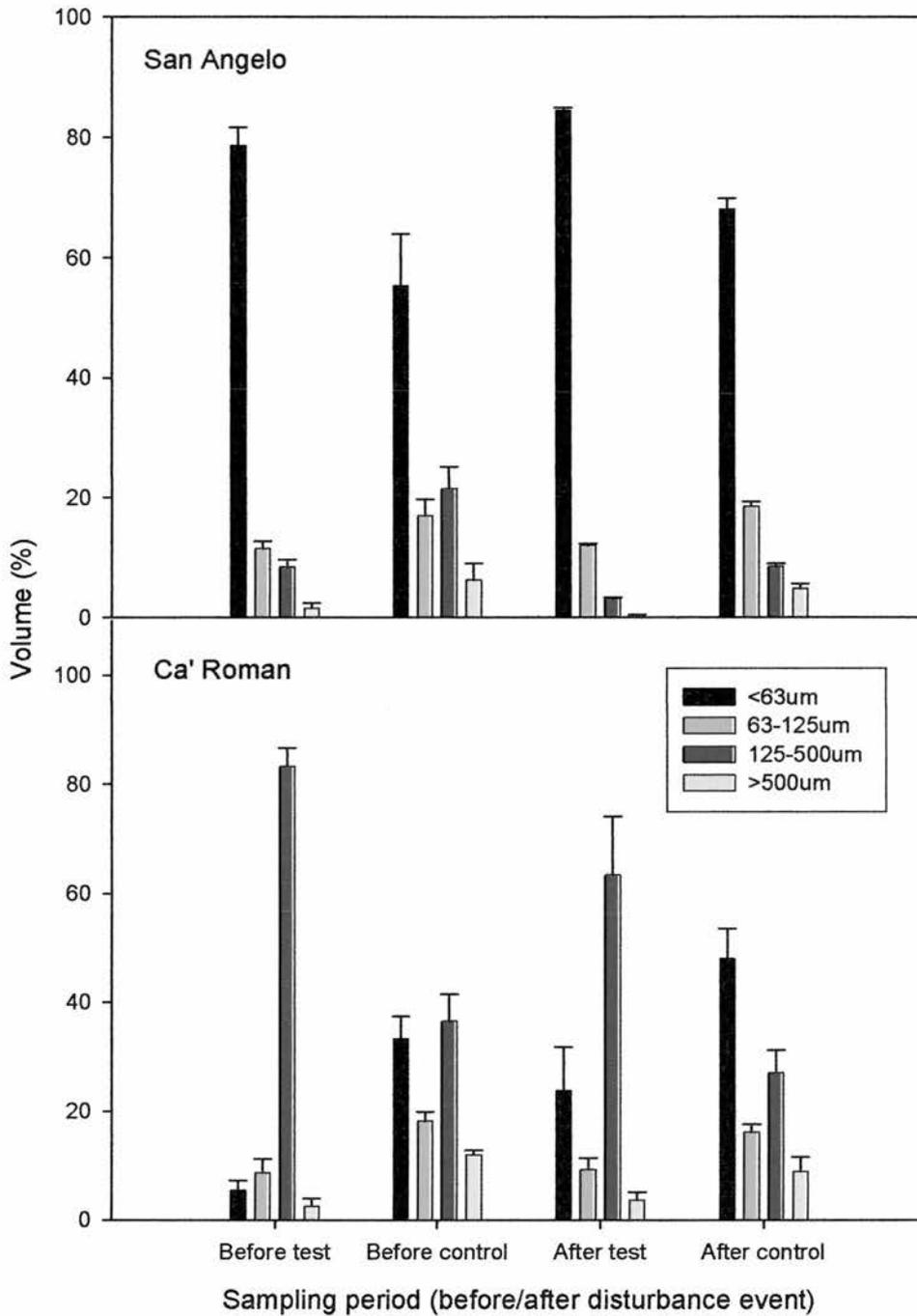


Fig 4.10: Volume distributions (%) for grain size classes for lyophilised sediment samples from San Angelo and Ca' Roman during the immediate impacts of clam harvesting study (mean  $\pm$  s.e., n = 6). Size classes: <63µm (silt/clay), 63µm-125µm (very fine sand), 125µm-500µm (fine/medium sand), and >500µm (coarse sand).

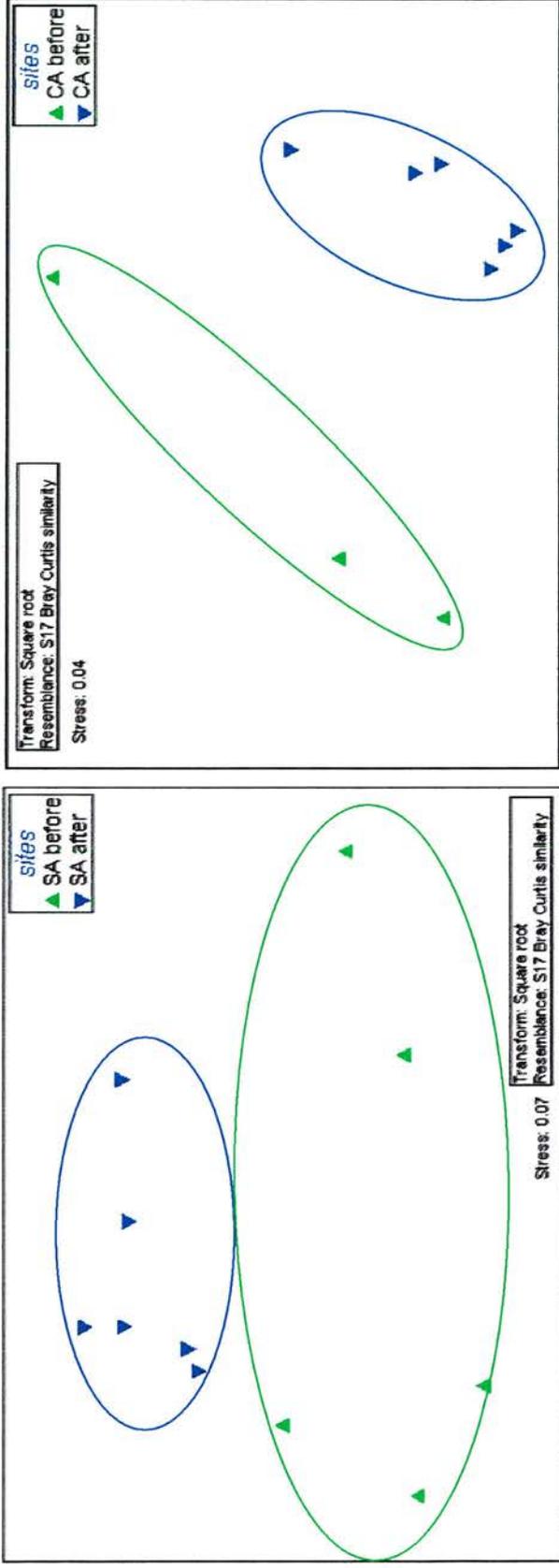


Fig 4.11: Multi-dimensional scaling plots reflecting the relative dissimilarity of the microphytobenthic community assemblage composition at San Angelo (A) and Ca' Roman (B) during the intermediate impacts of clam harvesting events. Circles group pre and post harvest events.

*Ca Roman*

Chlorophyll *a* content showed a significant increase after the harvesting event had occurred ( $t = -3.02$ ,  $df = 6$ ,  $p = 0.023$ ). No significant difference was found in colloidal-S carbohydrate, total organic content or dry bulk density values (Figure 4.8). Critical shear stress had decreased highly significantly a month after the harvesting event had taken place ( $W = 126.0$ ,  $p = 0.0004$ ) (Figure 4.9).

67% of the total sediment volume was represented by silt/clay ( $<63\mu\text{m}$ ), whilst only 3% of the total volume exceeded  $500\mu\text{m}$  (Figure 4.10).

Benthic algal diversities varied from 1.38 to 1.88 (Shannon Weaver Index), before and after harvesting respectively, and the dominant taxa found were *Navicula cincta*, *Licmophora* sp, *Nitzschia dubiiformes*, and *Coconeis scutellum*. Multidimensional scaling plots indicated the variation in abundance and diversity before and after the harvesting event (Figure 4.11). The presence of a filamentous benthic alga was investigated further as it was only found within Ca Roman sites. Observation after cytochemical staining showed the presence of acid mucopolysaccharides on the stalks. Some of the samples were acid cleaned to allow accurate identification of the frustules, and further low-temperature scanning electron microscopy confirmed the alga present was *Licmophora* sp (Fig. 4.12). Critical erosion thresholds within the sites containing *Licmophora* sp were up to 4 times higher than those without (Fig 4.13).

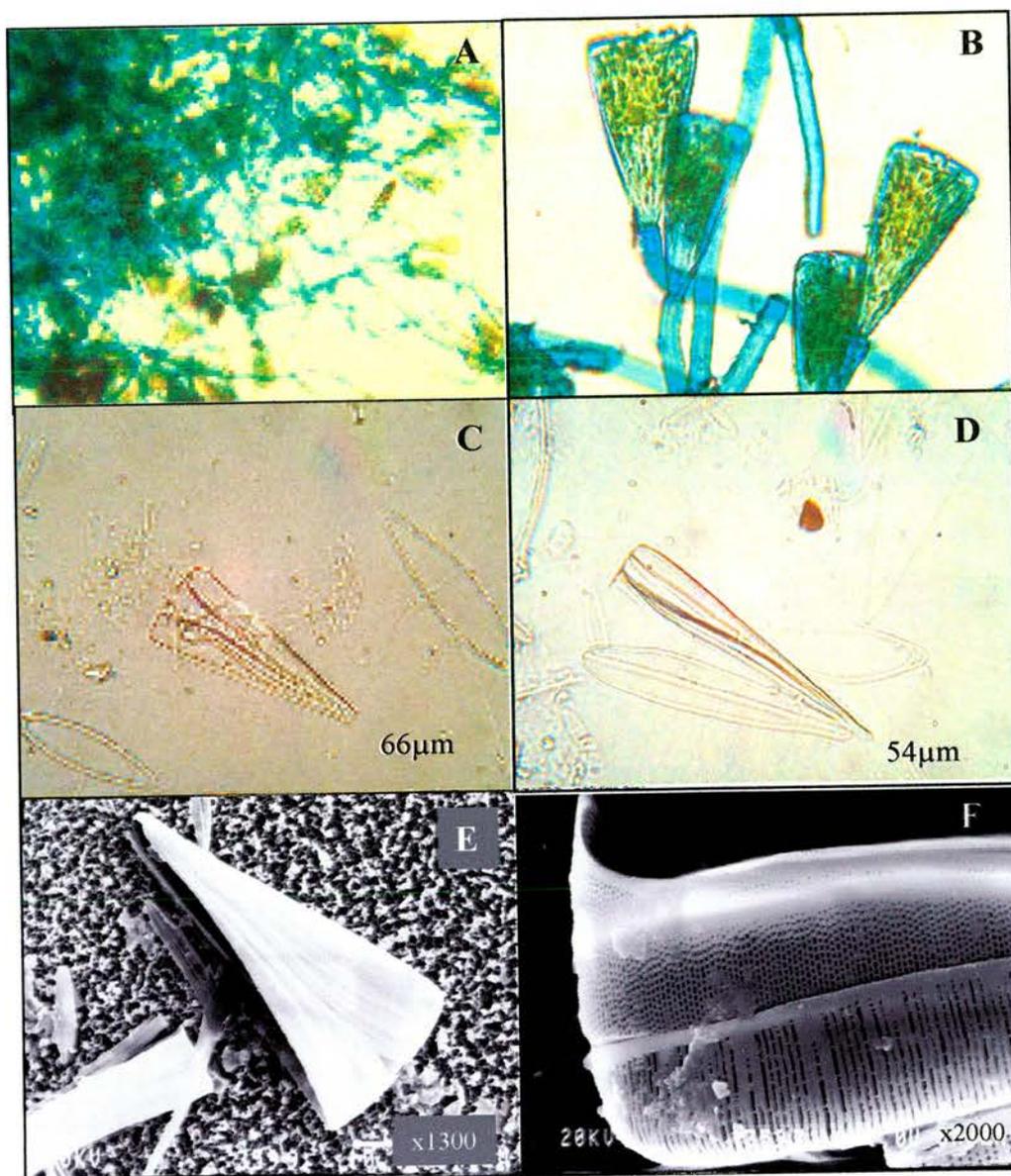


Fig 4.12: The diatom *Licmophora* sp was abundant within the control site at Ca' Roman. The long stalked cells coated with mucopolysaccharides were observed under a light microscope (A&B) after staining with 1.0% solution of Alcian Blue (8GX). After the cells were acid cleaned and mounted onto slides the cells were identified (C&D), and the identification was checked once the fine structure of the cells could be observed using low temperature scanning electron microscopy (E&F).

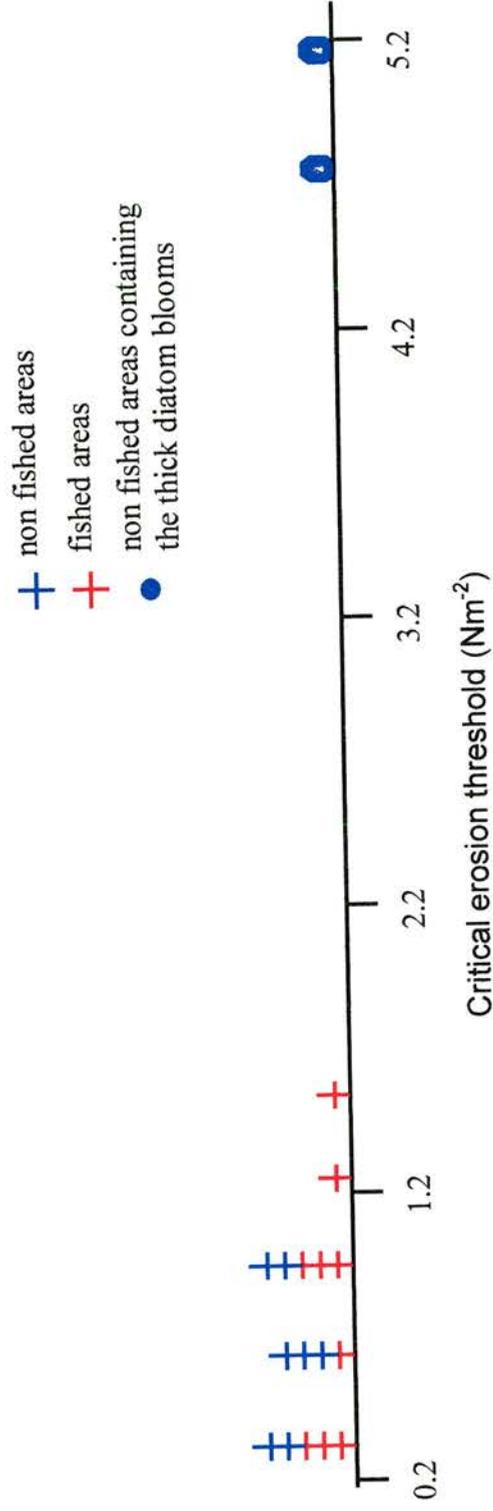


Fig 4.13: Dot plot of the critical erosion threshold values within the Ca' Roman site. Sites where *Licmophora* sp was present within the surface sediments tended to have higher critical erosion thresholds (Nm<sup>-2</sup>) than those without.

## 4.4 Discussion

The establishment of a benthic biotic community was prevented due to the high frequency of harvesting, thereby preventing the development of natural levels of biostabilisation of the sediment. Whilst areas of the lagoon, in which harvesting events occur less frequently, exhibited signs of recovery and formation of benthic microbial biofilms, areas exposed to little or no harvesting activity were highly stable compared to other areas of the lagoon due to the well-established microbial biofilms present.

### 4.4.1 Immediate effects of clam harvesting disturbance

Establishment of a microphytobenthic biofilm was impeded to such a degree that biostabilisation through biofilm growth and associated extracellular polymer production did not occur at the regularly dredged site (San Angelo). In comparison, at the low impact site (San Giacomo), some biostabilisation was observed, which was reduced by a single harvesting event using an outboard motor to re-suspend the sediment, and as such had a large effect on the properties of the sediment surface. The surface of the bed at San Giacomo become similar in erosive properties to San Angelo where disturbance was regular, after a single disturbance event. The selected indicators of biostabilisation were all significantly lower at San Angelo compared to San Giacomo, thus when fished, San Angelo showed little change in sediment stability or indices of biostabilisation, as there was little stability or sediment biota to have an impact upon. In contrast, a single harvesting pass had detrimental effects at the less impacted site, San Giacomo, where establishment of benthic biota was able to occur due to less frequent harvesting activities. It should be noted that San

Giacomo has a negligible level of harvesting, although with no quantitative data on harvesting efforts, this cannot be stated for certain, and the site is referred to as a low impact site.

Problems of using chlorophyll *a* to pigment ratios include deposit feeding, grazing pressures, bacterial breakdown, and redistribution of pigments due to disturbance events. These factors must be considered when using the ratio to indicate the health of a system. For example, Lucas and Holligan (1999) showed that grazing had a large effect upon pheophorbide measurements, although Ford and Honeywill (2002) reported that pheophorbide should not be used as a marker of macrofaunal grazing intensity. Due to the very low biomass of macrofauna, other than clams, in the Venice lagoon sediments (author pers. obs.) chlorophyll *a*: pheophorbide ratios were used in this study as an indirect measure of system health with respect to chlorophyll *a* degradation.

A high frequency of harvesting disturbance would prevent sediment consolidation, the succession of biological communities and the development of stable benthic assemblages. This hypothesis is supported by the side scan sonar images, which also confirmed the original assertion that, before the clam harvesting study, San Angelo was more heavily fished than San Giacomo (Figure 4.7 A, C). The lack of a distinct track after the harvesting event at San Angelo (Figure 4.7B) suggests the sediments were already disturbed to such a degree that further harvesting activities had no structural effect on the surface sediments compared to those at San Giacomo, either due to the type of harvesting mechanism being used or due to the homogeneity of the San Giacomo sediments prior to harvesting. However, in order to determine which factor is causal, an area of the lagoon would have to be closed off from harvesting access and left to fully recover from any prior harvesting activities before measurements could be

taken. However, the high level of disturbance prior to harvesting at San Angelo is strong circumstantial evidence that harvesting frequency at this site was responsible for the difference as opposed to harvesting methodology.

At San Angelo, the only factor that changed significantly post harvesting was the sediment chlorophyll *a* content, suggesting that microphytobenthos present on the surface were either dispersed or buried by harvesting. Otter trawling, also known as dragging, is one of the most commonly used harvesting techniques, during which, a large net is dragged along the sediment surface behind a towing vessel (Rosenberg *et al* 2003). Otter trawling has been shown to create a disturbance zone of up to 120-250m wide (Schwinghamer *et al.*, 1998), however the disturbance in the present study was less due to the smaller scale of the equipment used. Any effects seen off transect (5m from the trawling path) after harvesting would have been due to the disturbance of sediment from on transect, and the subsequent spread of re-suspended sediment. The sites adjacent to the transect were mostly unaffected showing the limited impact of the individual harvesting lines. In comparison, the results obtained from San Giacomo indicated that the re-suspension of sediment using outboard motors had a major effect on the site in terms of the biological and physical indicators of stabilisation measured. This effect may be more pronounced, as this site is less commonly fished for clams and so there has been a greater period of time in which benthic assemblages have developed, allowing biogenic stabilisation of the surface layers to take place (Rhoads *et al.*, 1978).

A change in community structure or removal of epifauna will affect the microphytobenthic biofilms present. This is important since sediment stability is affected by microphytobenthic biomass and associated sediment polymer content (Dade *et al.*, 1990; Underwood and Paterson, 1993; Taylor and Paterson, 1998;

Tolhurst, 1999). Consalvey *et al* (2002) reported that an increase in sub tidal sediment stability was positively correlated with microphytobenthic biofilm growth. The presence of microphytobenthos at San Giacomo was noted to change before and after the harvesting event, but this was not the case at San Angelo. This may have been due to the difference in historical harvesting frequency. Microphytobenthic biofilms present at San Angelo may have become disturbed, re-suspended and dispersed during the continuous harvesting activities. In addition, the high frequency of harvesting may not allow sufficient time for biofilms to recolonise sediments. At San Giacomo the decrease in biogenic indicators of sediment stabilisation suggested that a greater period of time between harvesting events could allow a biofilm to form and biostabilise the lagoon sediments, supporting the hypothesis that a greater biogenic stabilisation was occurring at the less disturbed site. Auster (1998) suggested that a threshold of disturbance may exist, and when reached, leads to significant damage to the habitat. Evidence provided by this study indicates that this threshold has not been reached at San Giacomo whereas at San Angelo it has been exceeded.

#### 4.4.2 Intermediate effects of clam harvesting disturbance

San Angelo and Ca' Roman were chosen due to the fact both sites are regularly subjected to clam harvesting activities. Both sites exhibited changes in the biogenic indicators of surface sediment stability during the study. An increase in chlorophyll *a* content was observed at both sites and colloidal-S carbohydrate levels increased at San Angelo, a month after the harvesting event took place, suggesting the establishment of a microphytobenthic community. However, the critical erosion threshold was still lower a month after the disturbance event than prior to it, leading to the assumption that whilst a month

was long enough to allow microphytobenthic biofilms to establish within the surface sediments it was not long enough for the biofilms to have an effect on the physical and structural aspects of the surface sediments. This theory is strengthened by the fact that some of the sampling sites within the control site at Ca' Roman contained the filamentous diatom *Licmophora* sp (Honeywill, 1998). The critical erosion thresholds at this site were almost 4 times as high as in areas without the diatom biofilms, thus showing how important a well-established biofilm can be to the structure and strength of subtidal sediments. Facca *et al* (2002 a) found that the percentage of fine grain size (<63µm) was strongly related to benthic diatom communities and this finding is backed up by many other studies (Barranguet *et al.* 1998, Brotas and Plant-Cuny 1998, and Cahoon *et al* 1999). This is due to the fact that silt/clay sediments have a high source of organics and nutrients. However, this may also be a disadvantage in areas of high harvesting activity as these fine sediments are easily resuspended by harvesting mechanisms leading to a loss in benthic diatom communities in such areas. Sites subjected to trawling impacts have been found to recover more quickly in sandy sediments than muddy sites in previous studies (Kaiser *et al* 1998, Collie *et al* 2000).

The changes observed in the present study may be thought to be due to environmental changes over the month, however previous studies of the Venice Lagoon showed that microphytobenthic communities were found to change very little over a seasonal cycle. However certain sites within the Lagoon were thought to be influenced by different environmental factors (Facca *et al* 2002a & b).

Homogenisation of sediments occurs after harvesting due to the destruction of healthy biofilms and structures such as burrows and mounds. In turn this

increases the amount of re-suspended sediment within the water column (Pilska *et al.*, 1998; Watling and Norse, 1998) thereby reducing the amount of nutrients available within the water column. Jennings *et al.* (2001) found that bivalve harvesting decreased infaunal and epifaunal biomass, although the biomass of polychaetes was unaffected. This indicated that the life strategies of different infauna affect their ability to survive periodic disturbance, suggesting that frequent harvesting will select for specific life strategies and perhaps functional groups. Therefore, if periods between harvesting activities were to change, it makes sense that the communities present would also change. A similar phenomenon was observed in Hamilton Harbour (Bermuda). Large cruise liners would frequently disturb the sediments in the shipping lanes, resulting in major changes to the macrobenthic and meiobenthic communities (Warwick *et al.* 1990). Both direct and indirect factors may be influential, and in turn this may have varying affects on the infauna of the surface sediments. Defew *et al.*, (2002) showed that *Nereis diversicolor* increased sediment stability, but *Arenicola marina* decreased the stability of surrounding sediments. These differences could be due to many site-specific factors, including bioturbation effects, sediment type (e.g. grain size), drainage of sediments, burrow formation and grazing pressure upon microphytobenthic biofilms. At present, there is very little information on the rate of biofilm formation under sub-tidal conditions and this is worth further investigation. There is no data available suggesting the recovery time of the Lagoon subtidal sediments after regular harvesting events, and before management plans can be put into place this must be addressed. Studies done in the past on different habitats show that recovery times can vary dramatically over a number of years (Spencer *et al.*, 1998, Sainsbury *et al.* 1997). Whilst this study examines this aspect to some degree it only shows that during

intermittent disturbance events some degree of recovery can take place. However, this does not indicate how long the harvested areas would take to recover to the same biological status as those containing sea grasses and benthic diatom biofilms, such as the control sites at Ca' Roman. Consalvey *et al.* (2001) demonstrated the ability of benthic diatoms to recover and re-establish within 5 days following a simulated disturbance event. However, this was only one single disturbance event, and only the surface sediments were removed. Whilst this study exhibits the potential of microphthobenthic communities to re-establish within sediments, a strict comparison cannot be made to the sediments of the lagoon following the clam harvest. Regular harvesting disturbs the structural integrity of the sediment bed and increase the potential for resuspension, which in turn will have an adverse effect on light penetration and conditions for biofilm development. Thus a negative feedback could occur, such that high harvesting frequency prevents establishment of a benthic algal community, which in turn increases water column turbidity through increased sediment re-suspension, which in turn reduces light penetration and inhibits benthic algal growth. Studies done on *Tapes philippinarum* cultivation in the River Exe estuary, Devon, demonstrated the recovery of sediment structure and infaunal community 12 months after the harvest (Spencer *et al* 1998).

Clam harvesting, therefore, is likely to have a significant affect on ecosystem function and turnover within the system (Emmerson *et al.*, 2001). Whilst other authors suggest that biofilms have an important role to play in the cohesion and stabilisation of sediments (MacIntyre *et al.* 1996, Austen *et al.* 1999), the continued disturbance of the Lagoon beds in the harvested sites studied negates the importance of benthic diatom biofilms. However, this study has also shown that if the surface sediments are not disturbed and left to establish

healthy benthic diatom blooms and the associated extracellular polymeric substances, the stability can increase dramatically. A crucial question for the management of the lagoon is the critical time between harvesting events at particular sites. The period required for this recovery is likely to be site-specific dependant upon factors such as sediment type, hydrography, flow patterns, and colonisation of macrofauna, and although this data is limited, some relevant literature is available (e.g. Spencer *et al*, 1997; Collie *et al*, 2000). This is a hypothesis that can be tested readily within a system such as the Venice lagoon.

#### 4.5 Conclusion

The results of this study on clam harvesting impacts suggest that frequent harvesting within the Venice lagoon acts to reduce the stability of the surface sediments due to the removal of microphytobenthos. The presence of microphytobenthos contributes to the sediment stability through the adhesion of fine particles by the associated EPS, thereby increasing the critical shear velocity required for the entrainment or resuspension of surface sediments. However, due to the difficulty of finding an undisturbed site in order to carry out true control comparisons, and the natural complexity of the benthic sea habitat, quantifying the disturbance effects will continue to be far from simple. This study has illustrated the importance of determining the effects of harvesting methods on soft-bottomed systems. The frequency of sediment disturbance is of great importance with respect to time to allow establishment of benthic biotic communities, which can aid sediment stability. Future studies should include the establishment of areas protected from seabed disturbance by clam harvesting for

varying periods of time, allowing them to revert to a natural disturbance frequency, based on episodic storm and flow events, as more representative control sites.

If the Venice Lagoon was allowed to revert to a natural state, it would most likely become a less commercial, less turbid system, dominated by sea grass beds such as those found at the control site at Ca' Roman. Whilst this scenario may be deemed preferable by some in order to preserve the unique habitat and wildlife associated with it, this form of management is not a socio-economically viable solution for the area as a whole. The consequences of this for the economy of the area would be catastrophic. Both the fishery business itself and the ancillary businesses would be largely affected resulting in the loss of many jobs, and important economic input to the area. In order to preserve the unique and valuable habitat of the lagoon, depended upon by the local and migrant wildlife, whilst maintaining the important socio economic implications of the fishery business, it is essential that strong links are forged between fishery officials and environmental organisations. The close association between these bodies must lead to production and implementation of management strategies that will allow both the environmental and economic aspects of the lagoon to thrive, without jeopardising one or the other.

#### **4.6 Publication**

Data from this chapter has been published in Hydrology and Earth Systems Sciences.

See Aspden, R.J., Vardy, S., Perkins, R.G., Davidson, I.R., Bates, R., and Paterson, D.M. 2004. The effects of clam fishing on the properties of surface sediments in the lagoon of Venice, Italy. *Hydrology and Earth Systems Sciences* 8(2):160-169.

## **CHAPTER FIVE**

**THE USE OF BIOGENIC VARIABLES TO DESCRIBE  
SPATIAL AND TEMPORAL VARIATIONS IN THE  
SURFACE SEDIMENTS OF INTERTIDAL MUD  
FLATS IN THE EDEN ESTUARY, SCOTLAND.**

## **Chapter Five – Abstract**

Intertidal mud flats have enormous ecological and economic importance and are situated at the interface of marine and terrestrial environments. In order for accurate models and predictions to be made for intertidal systems, thorough field measurements must be carried out to allow this data to be incorporated into the models effectively.

This chapter details the measurement of variables within the sediments. *In situ* measurement of sediment stability using systems such as the cohesive strength meter are rapid and accurate, proxy measurements (such as chlorophyll *a* content, colloidal carbohydrates, organic content) can also be used. These measurements can be used to generate maps of stability over a large scale at any given time. The data presented here was collected to determine whether proxy measurements could in fact be used for this purpose. No single parameter could be used to determine the stability of intertidal mud flats. However, stability was primarily dependent on two factors: the sediment grain size and chlorophyll *a* content, however this was determined to be highly site dependent. Microphytobenthic assemblages varied considerably from site to site and this was determined to be due to variations in grain size and dry bulk density. Within the same sites seasonal variations were also observed in microphytobenthic assemblages. Sediment stability also varied significantly between sites, and high stabilities were observed to occur at sites with grains  $>125 \leq 500 \mu\text{m}$ , and high dry bulk densities, suggesting a compact sediment with low water and organic content. The results gained from this study emphasise the importance of examining intertidal systems holistically.

## 5.1 Introduction

Estuaries are semi-enclosed transitional bodies of water with both seawater and freshwater inputs, and are one of the most productive systems in the world (De Jonge and Colijn 1994). Tidal mud flats are characteristic intertidal habitats of estuarine systems created by the deposition of fine sediments in low energy coastal environments, particularly in estuaries and other sheltered areas. The deposited sediment consists mostly of silts and clays with a high organic content.

### 5.1.1 The importance of intertidal mud flats

Estuaries have enormous ecological and economic importance (Kennish 2000, Underwood and Kromkamp 1999), and approximately 15% (265,000 ha) of northwest European estuarine habitats are located in the UK (UK BAP, 2002). Intertidal mudflats are situated at the interface of marine and terrestrial environments and as such form a natural barrier against the erosive forces of tides and waves, thereby reducing coastal erosion and damage to sea defences (King and Lester 1995). Intertidal mudflats are one of the most productive marine ecosystems (Underwood and Kromkamp 1999) and the high levels of primary production that occur within the system sustain the coastal food web. Mud flats often occur on the seaward side of areas of salt marsh, due to the fact mud flats attenuate wave energy and reduce the flow velocity of incoming tides, thereby allowing the deposition of fine sediments, enabling salt marsh to thrive. Intertidal mud flats support a large number of invertebrates, and serve as an important resource for migrant wildfowl and the low energy waters provide the ideal habitat for the development of many shell fish (Heip *et al* 1995). Estuaries

therefore have huge economic importance in terms of recreation, fishing, tourism and industry, all of which utilise the natural resources provided by the estuary.

### 5.1.2 The implications of climate change

Surface temperatures in Scotland are predicted to rise by approximately 0.1 to 0.3°C per decade due to global warming, and coastal water temperatures around Scotland have risen by 1°C since 1970 (Scottish Executive 2005), in keeping with the UK predictions. Global warming is predicted to cause an increase in temperature but also an increase in sea level rise and storm frequency (IPCC 2001). The extent of the impact will depend on the local geomorphology and climate of the area. A loss of 8000 to 10,000ha of UK intertidal mud flats is estimated due to sea level rise by 2013, and although the majority of this loss is expected in the south of England, major firths in Scotland will also be affected by the rise in sea level (UKBAP, 2002). The IPCC (Intergovernmental Panel on Climate Change) has predicted several key aspects in which climate change will affect coastal zones. These aspects are: the inundation of lowland, increased erosion of shorelines, increased occurrence of storm surges, altered intertidal ranges, alteration in sedimentation patterns and decreased light penetration in coastal waters due to increased suspension of sediment. All these factors will have major impacts on the ecosystem functioning of intertidal mud flats.

### 5.1.3 Anthropogenic influences

It is estimated that half the world's population is situated within 60Km of the coast, and estuaries are no exception. Estuaries are important areas in terms of industrial shipping lanes, tourism, and recreational activities. However, these

uses can have adverse effects on the ecosystem. It has been estimated that the use of sea defences could result in the loss of over 10,000 hectares of intertidal mud flats in England by 2012, due to the prevention of landward migration (coastal squeeze) (English Nature). In the past, land claim has removed about 25% of UK intertidal mudflats (UKBAP, 2002), although the rate of land claim has slowed due to the realisation of the ecological and environmental importance of these systems.

To meet the obligations of the Habitats Directive and the UK Biodiversity Action Plan, the UK must create new intertidal mud flat habitat at a rate of 740 hectares each year for the next 15 years (RSPB, 2000), indicating the importance of these areas as feeding grounds for wading and migratory wildfowl. In order to carry out obligations such as this the use of dredged material, although as yet not widely applied, is becoming an increasingly popular method of habitat creation. Dredging produces up to 50 million tonnes of material from coastal areas around the UK every year. Previously most of this material was deposited at offshore locations as a waste product. A recent drive to use this material as a resource rather than waste, in order to prevent coastal erosion in a natural way, is in the experimental stages but seems promising. However the implications of smothering and consequent compaction are also under investigation (Fletcher *et al*, 2001).

Protection for mudflats is provided by various international and EU agreements including, Special Protection Areas, and Special Areas of Conservation. In Scotland, Scottish National Heritage is leading the Firths Initiative and shoreline management plans, including areas of intertidal mudflats, are also being developed.

#### 5.1.4 Sediment dynamics

Intertidal mud flats mainly consist of fine cohesive sediments ( $<63\mu\text{m}$ ). Generally the size of the sediment particle determines the duration and type of transport of sandy sediments, however, the stability of fine cohesive sediments is strongly governed by the relationship between the physical, biological and chemical processes occurring within the ecosystem. Whilst many studies have attempted to determine the behaviour of cohesive sediments (Neumann 1970, Paterson and Black 1999, Widdows *et al* 1998), the difficulty in obtaining accurate and reliable results is determined by the fact that more than one process affects the behaviour of the sediment at any one time. Sediment composed of fine cohesive particles creates a substratum with high bulk density and low permeability, resulting in limited diffusion and so physicochemical gradients tend to be steep. As a result only the first few millimetres of the sediment surface are aerobic, rapidly becoming anaerobic due to a lack of oxygen, thereby creating a harsh environment to which specialist microbial assemblages have adapted to and exploited (Aspden *et al* 2004b). Physico-chemical forces must be considered when studying fine cohesive sediments due to the Van der Waals forces forming bonds of attraction between individual particles, and as such the sediment dynamics can no longer be based on individual particles, but the bed must be considered as a whole. As well as the physical and chemical effects upon the sediment, biological components are equally important, and can in turn mediate the physical environment, through processes such as bioturbation (Eckman *et al* 1981, Willows *et al* 1998, Widdows *et al* 2002) and biogenic stabilisation (Eckman 1985, Shi *et al* 1995, Ziebis *et al* 1996, Underwood 1997, Paterson *et al* 1998, Yallop *et al* 1994, Aspden *et al* 2004a, Aspden *et al* 2004b).

### 5.1.5 Benthic microbial assemblages

Intertidal mudflats are generally void of any higher plant vegetation (Figure 5.1), however microphytobenthic mats, composed of diatoms, cyanobacteria and euglanoids are common and often form extensive biofilms across the sediment surface (Paterson *et al* 1998, Underwood and Paterson 1993) which can be seen by the naked eye as a golden brown film across the surface sediments (Figure 5.1(B)). In estuarine systems such as the Eden estuary, the microphytobenthic mats are mainly composed of diatoms. Diatoms are single celled photosynthetic algae estimated to produce 4% of total global primary productivity within marine systems (Medlin 2002). The most common sediment inhabiting forms (epipelton) of diatom are generally biraphid, and move through the sediment by exuding extracellular polymeric substances (EPS) through the raphe structure (Edgar and Picket-Heaps 1984). EPS are long chain molecules that can be produced by cellular metabolism as a by product of photosynthesis.

Little is known about what controls the migration of cells, but it is believed to be manipulated by geotactic, chemotactic and phototactic cues. Decreases in locomotory behaviour have been observed during periods of low light, however the migratory patterns during periods of full illumination under laboratory conditions have also been noted (Palmer and Round 1965, Admiraal 1984, Paterson 1986, and Consalvey *et al* 2004), strengthening the importance of endogenous rhythms. The migration of diatoms tends to occur within the upper 2 mm of the sediment surface. This is due to the fact that 90% of light is attenuated in the top 400µm of the fine cohesive estuarine mud in which diatoms thrive (Kingston 1999, Consalvey 2002). These organisms are well adapted to a



Figure 5.1: Higher plant vegetation on the Eden Estuary is sparse, however areas of the estuary are covered in *Enteromorpha* sp (can be seen in the background of (A)). Patches of microphytobenthic biofilm can often be seen by the naked eye on the surface of Eden Estuary sediments (B). The biofilm appears as golden brown patches, exhibiting the spatial heterogeneity of the assemblages.

harsh environment in which they are subjected to limited periods of light exposure and highly variable temperatures (Blanchard and Guarini 1996, Serôdio and Catarino 1999), and play a very important role in the ecosystem functioning of estuarine systems.

#### 5.1.6 Biogenic stabilisation of inter tidal mud flats

Many studies of sediment transport have been carried out in the laboratory on abiotic sediments (Manzenreider 1983, Grant and Gust 1987), but without taking biotic interactions into account these findings cannot be used to determine sediment dynamics *in situ*. For example, three months of natural sediment compaction was found to be less effective at stabilising sediments than a biofilm developed over 24h. This emphasizes that physical factors such as salinity and compaction cannot be used to define the stability of sediments *in situ*. Biogenic activity within sediments was shown to increase the erosion threshold of abiotic sediments by 25-770% (Paterson and Daborn 1991). Paterson (1994) separated biogenic stabilisation into five main categories consisting of network effects, flow effects, cohesive effects, and matrix effects. However it shouldn't be assumed that stabilisation of sediments occurs because of one factor alone. It is more likely that stabilisation occurs as a result of a combination of biological and physical factors.

Microphytobenthic biofilms are one of the main primary producers in the estuarine systems but also provide a number of other ecosystem services (Chapin *et al* 1997) including the stabilisation of cohesive sediment. The stabilisation of sediments by microbial assemblages was first recorded experimentally by Holland *et al* (1974), who determined that the presence of biofilms producing

large quantities of EPS caused greater sediment stabilisation. Since then a great deal of research in the stabilisation of intertidal areas due to the exudates of diatoms has been carried out, often showing a significant correlation between EPS and sediment stability (Dade 1990, Amos *et al* 1998, Blanchard *et al* 2000, Honeywill and Paterson *et al* 2000). The importance of EPS in the sediment dynamics of intertidal mud flat sediments has been highlighted (Chapter 1). Although the importance of EPS in the biostabilisation process is widely accepted, its use on a large scale is limited as EPS cannot be discerned from Remote Sensing. However, concentrations of colloidal carbohydrates have shown to be strongly correlated with chlorophyll *a* content, which as a proxy for diatom biomass (Underwood *et al* 1995, Underwood and Smith 1998), can be estimated using remote sensing techniques. This technique would lead to the ability to produce large scale maps of sediment stability and hopefully aid the development of accurate and successful coastal management plans.

During this research the following hypotheses were tested in order to investigate the relationship between the microphytobenthic mats and the stability of the tidal mud flat sediments:

- Sites with high microphytobenthic biomass will have high sediment stability.
- Biogenic indicators of sediment stability are correlated with sediment stability.

## 5.2 Materials and Methods

### 5.2.1 Study Sites

Five areas within the Eden Estuary were sampled over a 2d period during September 2002, April 2003, July 2003 and March 2004 (Figure 5.2). The five areas were split between two sites: Site A was situated on the south shore; Site B was situated on the north shore, located beside the Guardbridge Paper Mill. Within each of the sampling areas a 25 point grid (5x5) was arranged, with 2 metres between each point, 8 m total length (Figure 5.2). Points 1-5 were placed so that they faced east. The designated sampling areas were 0.5m radius around each point.

### 5.2.2 Field sampling methods

During 2002 the field sampling carried out at points 1- 25 included critical erosion shear stress measurements ( $n=1$ ) using the cohesive strength meter (Tolhurst 1999), and contact core measurements ( $n=3$ ) at each point within the grid. Shear vane measurements ( $n=5$ ) were taken at four depths, from points 1, 5, 13, 21, and 25. At point 13 cryolander samples were obtained ( $n = 3$ ) along with surface scrape samples ( $n = 3$ ). At 5 random positions within the grid, samples of mobile microphytobenthos samples were collected using the lens tissue method.

The same field sampling methods were repeated in April 2003, July 2003, and March 2004, but due to the amount of time taken up with laboratory analysis in 2002, the number of nodes sampled within the grid was decreased in order to reduce the number of samples.

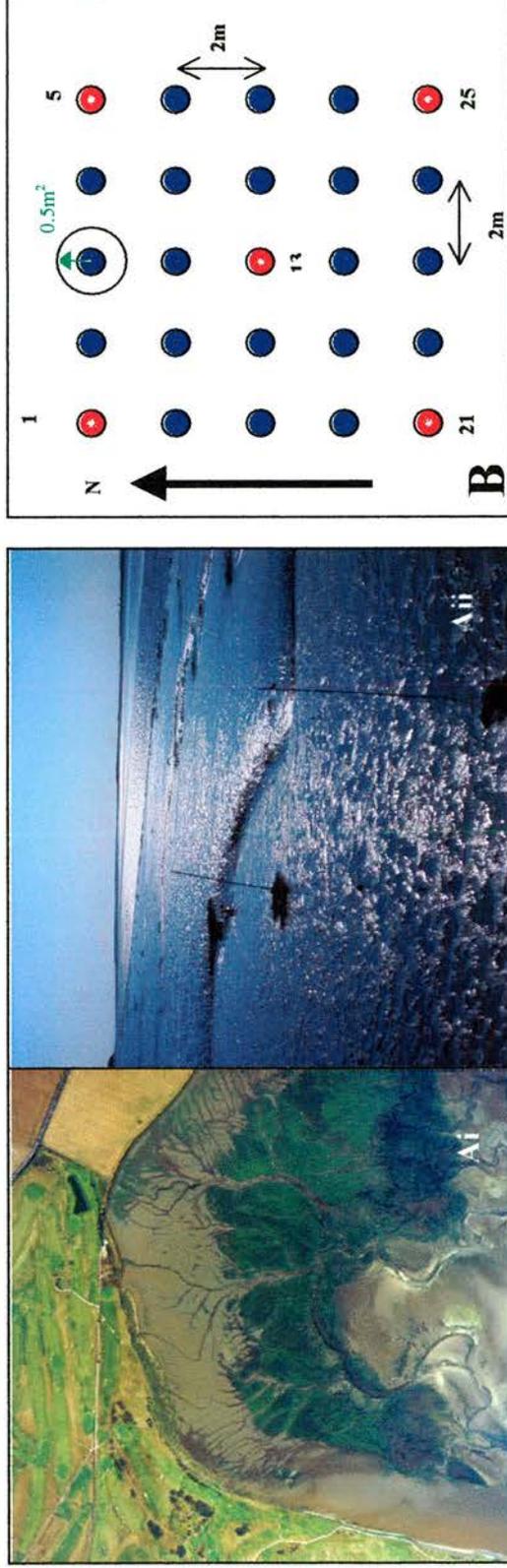


Figure 5.2 – Two sites were sampled within the Eden estuary (A): Site A was situated on the north shore (i), Site B was situated on the south shore (ii) located besides the Guardbridge Paper Mill. Within each of the sampling areas a 25 point grid (5x5) was arranged (B), 2 metres between each point, 8 m total length.



and Mann-Whitney test (Dytham 2003, Zar 1999). Results were considered significant at  $p < 0.05$ . Spearman rank order correlations were used to determine any relationships between measured parameters.

Assemblage analysis was carried out by multidimensional scaling (MDS) using PRIMER (6 Beta) software in order to examine the relative dissimilarity of the microphytobenthic community assemblage composition between sites. Shannon-Wiener diversity indices were applied to microphytobenthic cell count data, to compare diversity of assemblages within sites.

## **5.3 Results**

### **5.3.1 September 2002**

#### **5.3.1.1 Sediment variables**

The organic content, colloidal-S carbohydrate content, dry bulk density, sediment stability and chlorophyll *a* were examined in the surface of the mud flat sediments and are indicated by Figures 5.3-5.8. Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, shear strength, and critical shear stress from intertidal mud flat sediments collected are indicated in Table 5.1. Where a significant difference was found between individual sites during the survey in July, 2002 this is indicated in Table 5.2.

Significant variation of organic content was found at all sites ( $H = 257.12$ ;  $d.f = 4$ ;  $p < 0.001$  (Figure 5.3). A significant difference between sites was observed in colloidal-S carbohydrate content ( $H = 147.29$ ;  $d.f = 4$ ;  $p <$

	site A			site B		
	top shore	mid shore	low shore	mid shore	low shore	
Colloidal carbohydrate content (ppm G.E)	614.48 (14.62) n = 75	2695.40 (255.07) n = 73	918.42 (57.76) n = 74	2414.36 (215.12) n = 74	1213.12 (100.85) n = 75	
Organic content (%)	2.65 (0.02) n = 75	13.34 (0.97) n = 71	2.28 (0.06) n = 75	9.04 (0.13) n = 75	7.58 (0.21) n = 75	
Dry Bulk density (gcm <sup>-1</sup> )	1.55 (0.03) n = 75	0.50 (0.05) n = 70	1.30 (0.03) n = 75	0.55 (0.03) n = 75	0.65 (0.02) n = 75	
Chlorophyll a content (mgm <sup>-2</sup> )	94.18 (7.13) n = 70	112.33 (20.54) n = 63	78.77 (3.82) n = 74	121.15 (5.29) n = 72	112.69 (18.49) n = 73	
Shear strength (kPa)	18.88 (1.16) n = 14	/	/	5.60 (1.33) n = 15	8.03 (0.77) n = 15	

Table 5.1: Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, and shear strength, from intertidal mud flat sediments collected during September 2002.

Dry bulk density		site A			site B	
		top shore	mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	<b>0.000</b>				
	low shore	<b>0.000</b>	<b>0.000</b>			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	

Colloidal-S carbohydrate		site A			site B	
		top shore	mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	<b>0.000</b>				
	low shore	<b>0.000</b>	<b>0.000</b>			
site B	mid shore	<b>0.000</b>	0.402	<b>0.000</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	<b>0.039</b>	<b>0.000</b>	

Organic carbon content		site A			site B	
		top shore	mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	<b>0.000</b>				
	low shore	<b>0.000</b>	<b>0.000</b>			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	

Chlorophyll <i>a</i> content		site A			site B	
		top shore	mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	<b>0.021</b>				
	low shore	<b>0.003</b>	0.109			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
	low shore	0.571	<b>0.015</b>	<b>0.003</b>	<b>0.000</b>	

Table 5.2: Descriptive statistics carried out to compare between sites studied during September 2002. Mann-Whitney was used to determine significant differences ( $p < 0.050$  - indicated in bold).

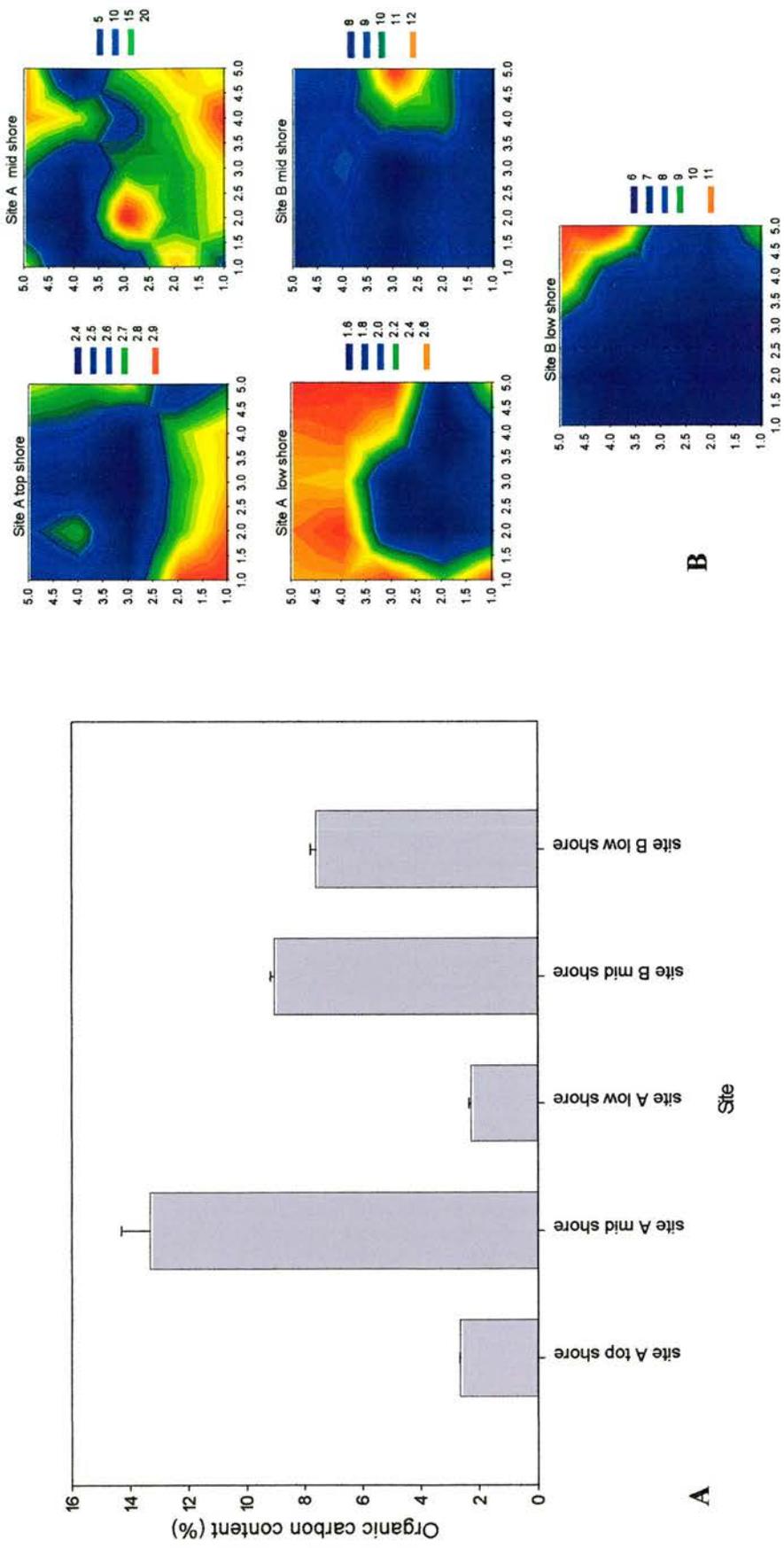


Figure 5.3: Organic carbon content (%) (A) for samples taken during the September 2002 survey. Contour plots (B) indicate the spatial variation of organic carbon content over the grids at each site during the September 2002 survey. Mean  $\pm$  s.e, n = 63-73.

0.001) (Figure 5.4), except between the mid-shore sites ( $W = 5619.0$ ;  $p = 0.4016$ ). A significant difference between all sites was observed for dry bulk density ( $H = 258.44$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.5). A significant difference between all sites was observed in chlorophyll *a* content ( $H = 53.85$ ;  $d.f = 4$ ;  $p = 0.000$ ), except between site A mid shore/low shore ( $W = 3975.0$ ;  $p = 0.109$ ) and site A top shore/site B low shore ( $W = 4899.0$ ;  $p = 0.571$ ) (Figure 5.6). Sediment grain size did not vary significantly between sites. Site A sediment was mostly within the  $>125 \leq 500 \mu\text{m}$  range, the majority of site B sediments were  $<63 \mu\text{m}$  (Figure 5.7).

Principle components analysis ordination indicates the surface sediments at site B mid/low shore and site A mid shore were most influenced by colloidal-S carbohydrate content and organic content, whereas Site A top shore and low shore were most influenced by dry bulk density (Figure 5.8).

### 5.3.1.2 Relationship between variables

Correlations carried out between variables indicated that dry bulk density was negatively correlated with chlorophyll *a* content ( $r_s = -0.108$ ;  $p = 0.043$ ) and colloidal-S carbohydrate content ( $r_s = -0.485$ ;  $p < 0.001$ ), organic carbon content was positively correlated with chlorophyll *a* content ( $r_s = 0.124$ ;  $p = 0.020$ ), colloidal-S content ( $r_s = 0.475$ ;  $p < 0.001$ ), and negatively correlated with dry bulk density ( $r_s = -0.678$ ;  $p < 0.001$ ).

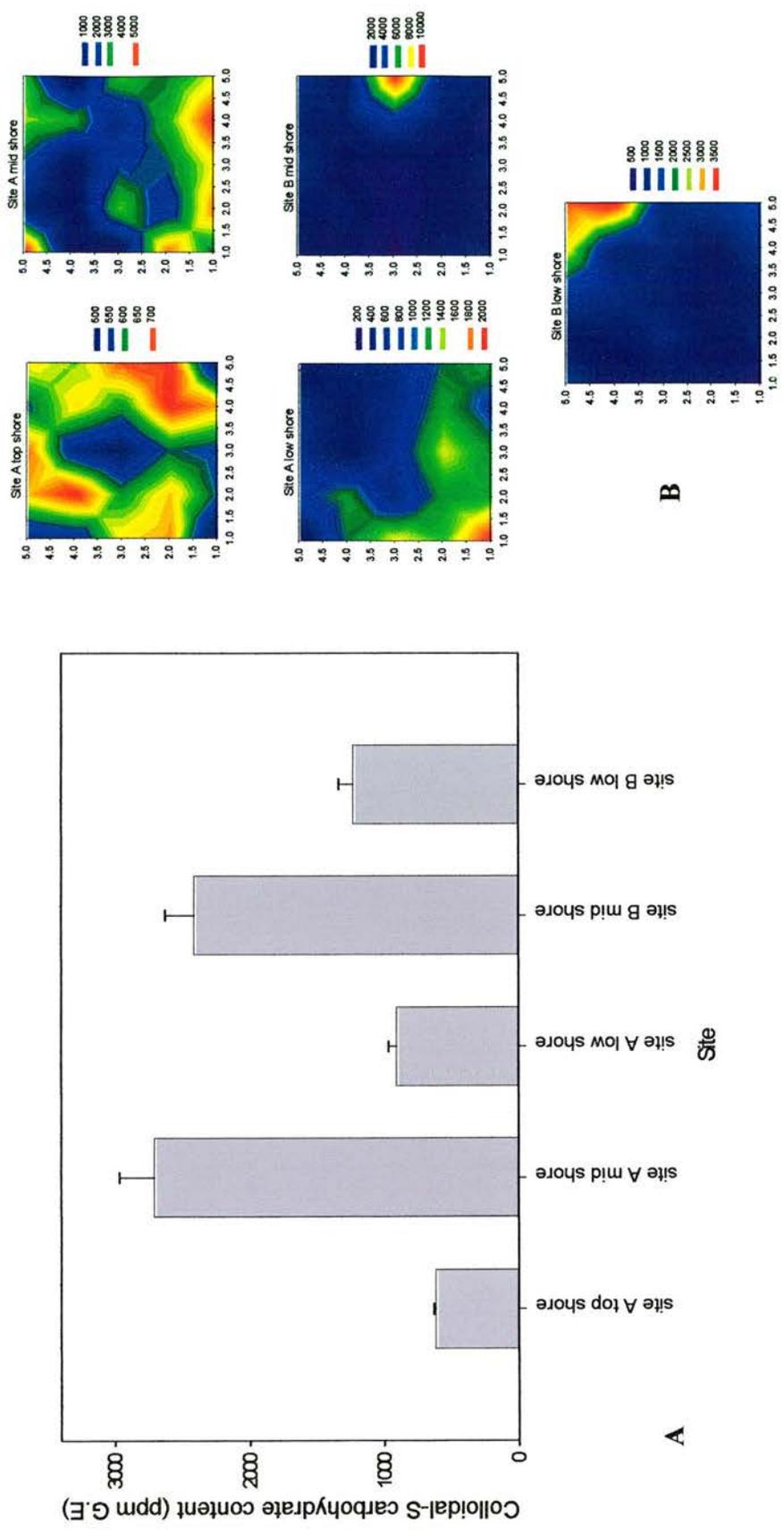


Figure 5.4: Colloidal-S carbohydrate content ( $\text{mgm}^{-2}$ ) (A) for samples taken during the September 2002 survey. Contour plots (B) indicate the spatial variation of colloidal carbohydrate content over the grids at each site during the September 2002 survey. Mean  $\pm$  s.e.,  $n = 73-75$ .

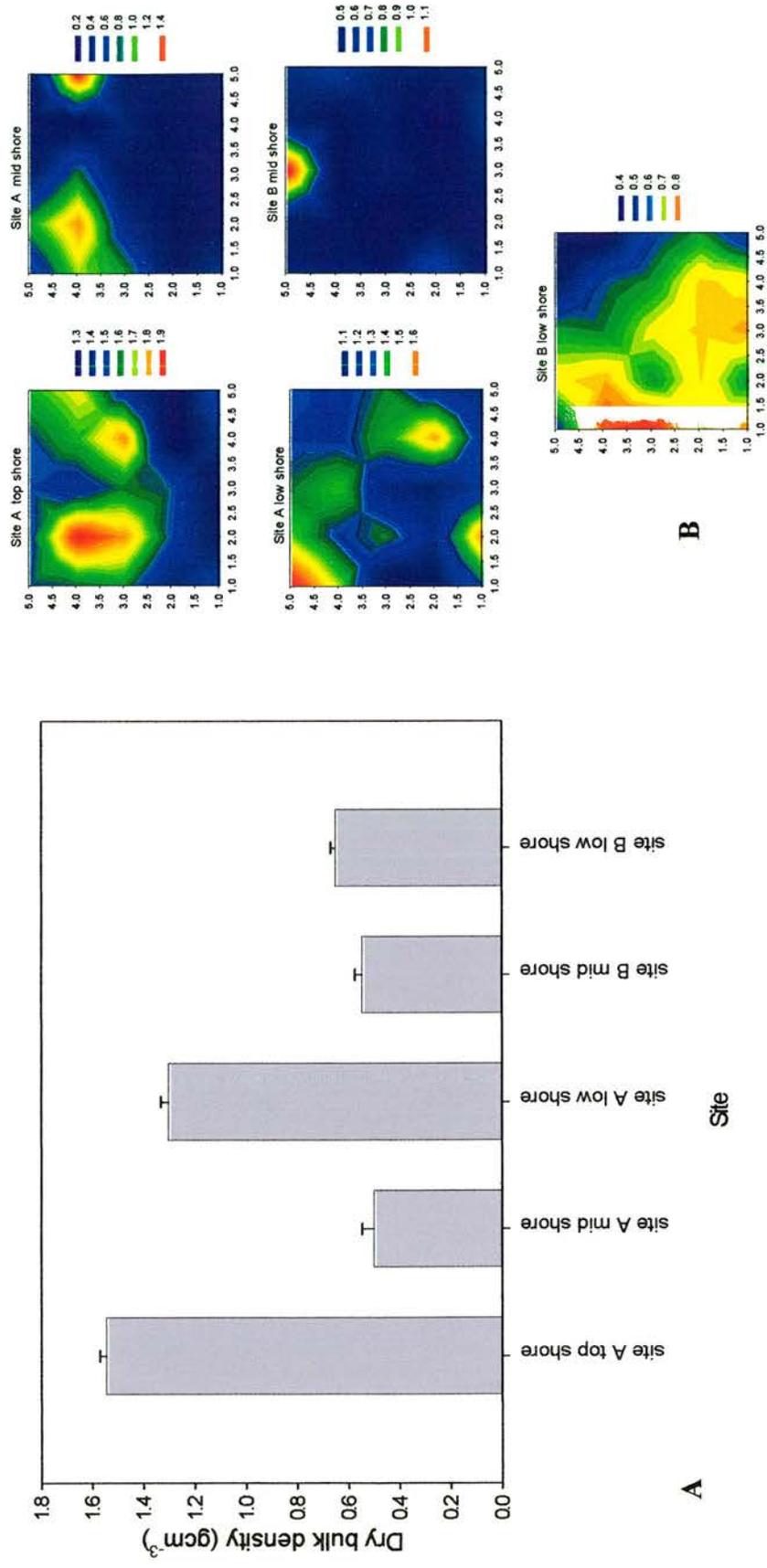


Figure 5.5: Dry bulk density (gcm<sup>-3</sup>) (A) for samples taken during the September 2002 survey. Contour plots (B) indicate the spatial variation of organic carbon content over the grids at each site during the September 2002 survey. Mean  $\pm$  s.e., n = 70-75.

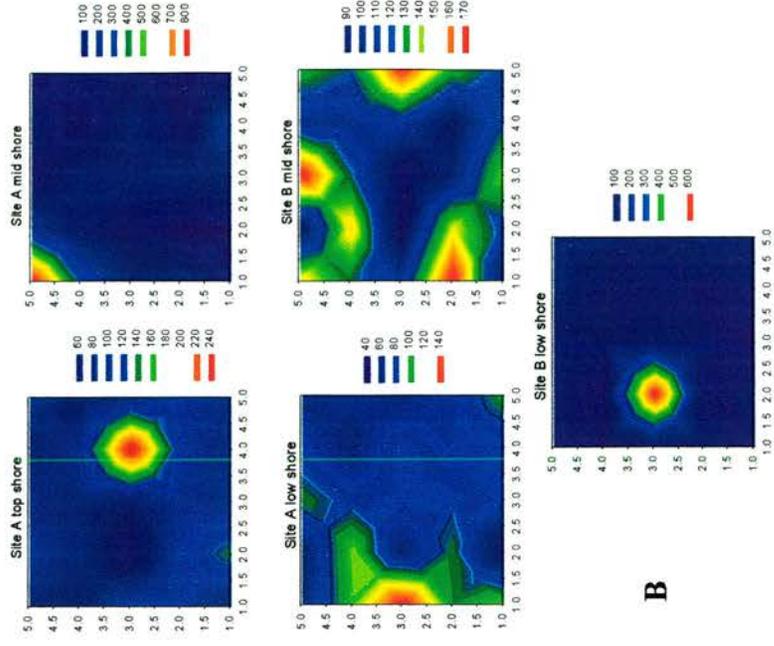
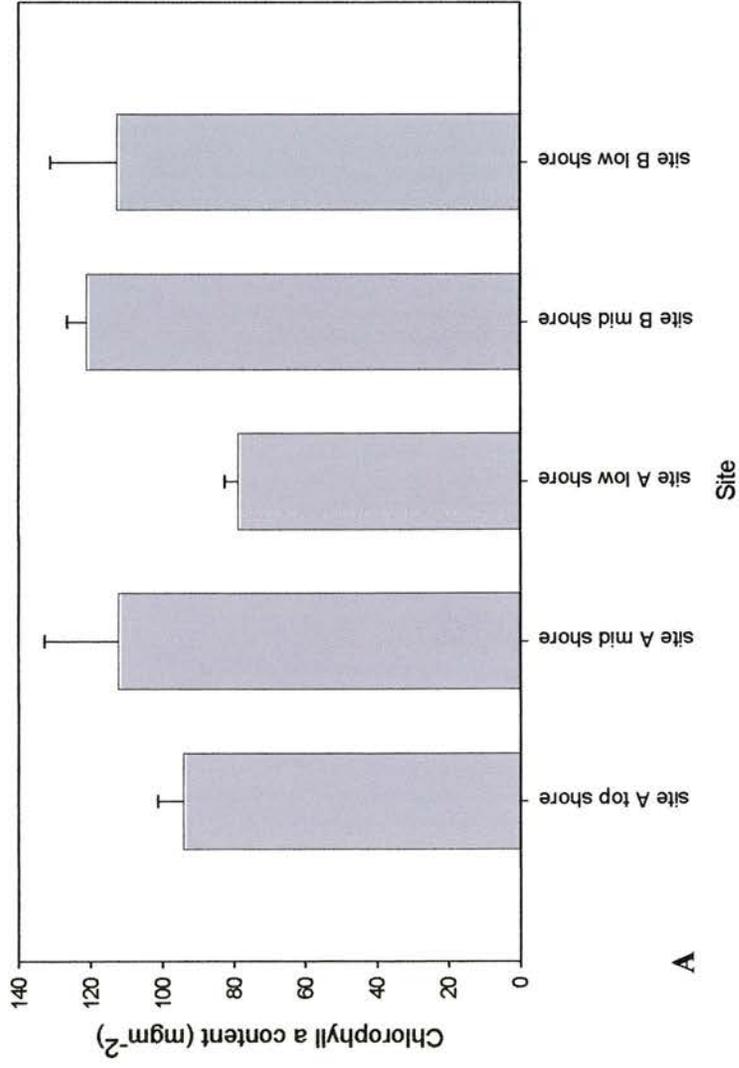


Figure 5.6: Chlorophyll a content (mgm<sup>-2</sup>) (A) for samples taken during the September 2002 survey. Mean  $\pm$  s.e, n = 63-73. Contour plots (B) indicate the spatial variation of chlorophyll a content over the grids at each site during the September 2002 survey.

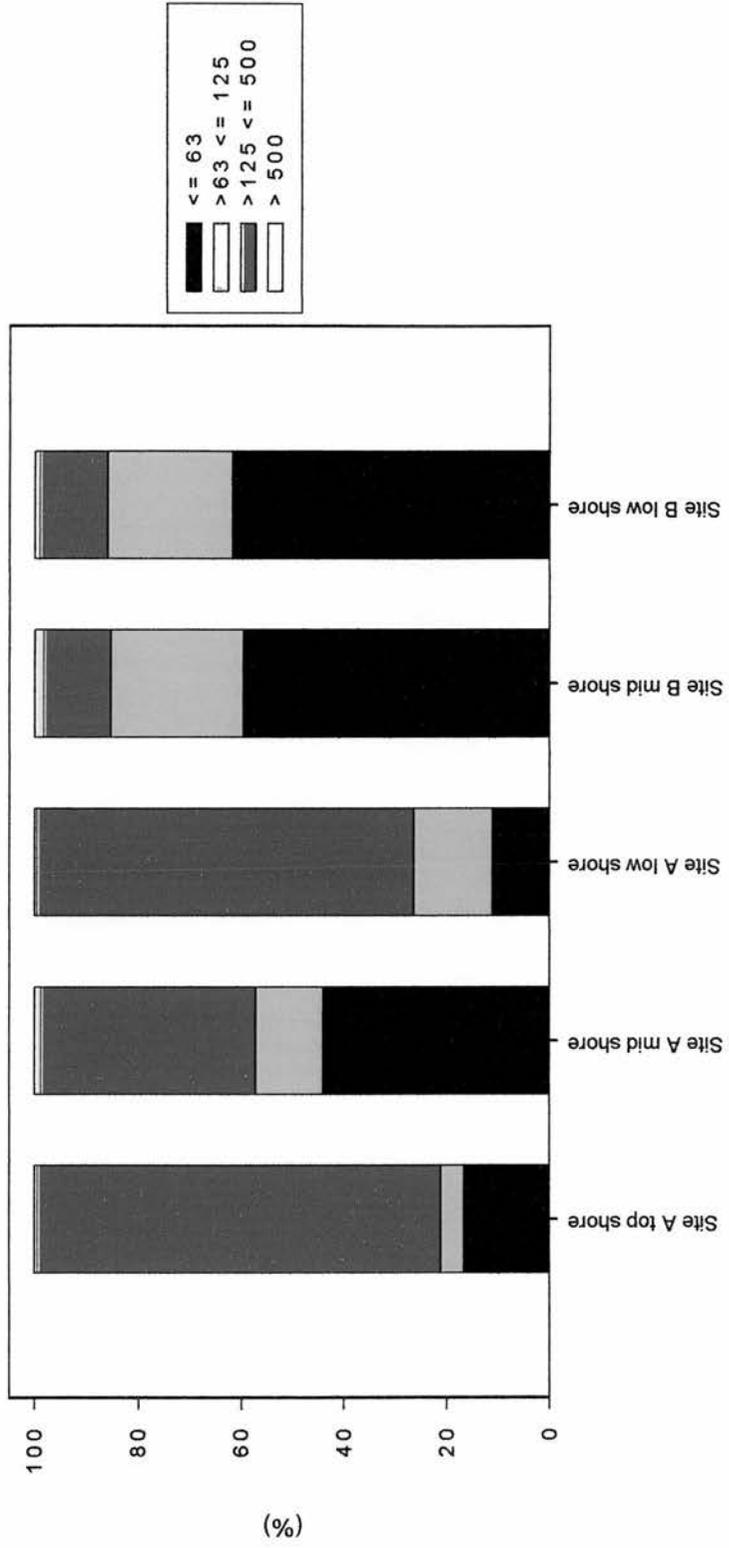


Figure 5.7: Percentage of grain sizes found at each site during the September 2002 survey. Site A was mostly composed of sediment within the  $125 < \leq 500$   $\mu\text{m}$  range. Site B mostly composed of sediments within the  $\leq 63$   $\mu\text{m}$  range.

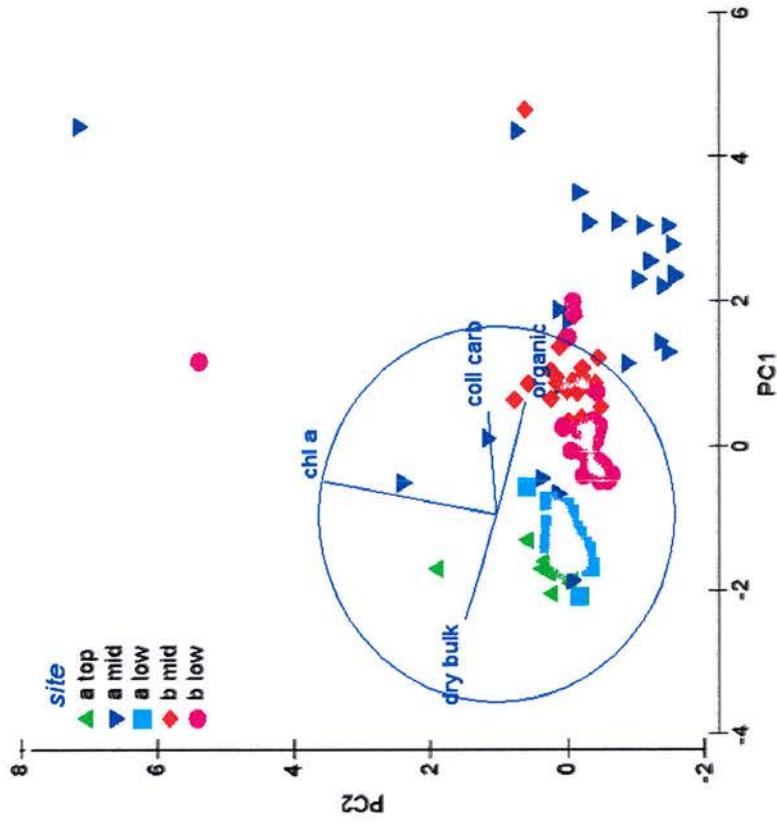


Figure 5.8: Two dimensional principle components analysis ordination of the parameters measured at each site during September 2002. The ordination indicates the surface sediments at site B mid/low shore and site A mid shore were most influenced by colloidal-S carbohydrate content and organic content. Site A top shore and low shore were most influenced by dry bulk density.

### 5.3.2 April 2003

#### 5.3.2.1 Sediment variables

The organic content, colloidal-S carbohydrate content, dry bulk density, sediment stability, shear strength and chlorophyll *a* content were examined in the surface of the mud flat sediments (Figure 5.9-5.16). Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, shear strength, and critical shear stress from intertidal mud flat sediments collected are given (Table 5.3). Where a significant difference was found between individual sites during the survey in April 2003 this is indicated (Table 5.4).

Significant variation of organic content was found at all but three sites studied ( $H = 70.75$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.9). A significant difference between all but three sites was observed in colloidal-S carbohydrate content ( $H = 32.32$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.10). A significant difference in dry bulk density was observed in all but 2 site combinations ( $F_{4,127} = 126.94$ ;  $p < 0.001$ ) (Figure 5.11). A significant difference between 3 combinations of sites was observed in chlorophyll *a* content ( $F_{3,99} = 271.86$ ;  $p < 0.001$ ), (Figure 5.12). A significant difference between half the site combinations was observed in critical shear stress ( $H = 22.75$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.13) and at a depth of 9cm, significant differences were observed in sediment shear strength at all but two site combinations ( $H = 58.66$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.14). Sediment grain size did not vary significantly between sites. Site A sediment was mostly within the  $>125 \leq 500 \mu\text{m}$  range, the majority of site B sediments were  $<63 \mu\text{m}$  (Figure 5.15).

	site A			site B		
	top shore	mid shore	low shore	mid shore	low shore	low shore
Colloidal carbohydrate content (ppm G.E)	613.70 (162.29) n = 26	1098.96 (78.09) n = 27	628.56 (63.33) n = 26	1276.74 (264.14) n = 27	943.25 (102.39) n = 27	
Organic content (%)	6.25 (0.25) n = 27	4.69 (0.33) n = 27	1.92 (0.07) n = 26	7.59 (0.48) n = 27	6.21 (0.48) n = 24	
Dry Bulk density (gcm <sup>-1</sup> )	1.17 (0.03) n = 26	0.76 (0.03) n = 27	1.18 (0.03) n = 27	0.51 (0.02) n = 27	0.62 (0.02) n = 27	
Chlorophyll a content (mgm <sup>-2</sup> )	162.41 (17.27) n = 23	65.85 (3.68) n = 27	128.25 (28.05) n = 26	118.04 (21.17) n = 26	/	
Shear strength (kPa)	10.50 (0.64) n = 15	11.71 (0.60) n = 15	8.10 (0.48) n = 15	3.17 (0.34) n = 15	2.26 (0.30) n = 15	
Critical shear stress (Nm <sup>-2</sup> )	1423.04 (286.59) n = 9	185.46 (25.29) n = 8	756.02 (251.05) n = 9	199.57 (29.42) n = 9	338.40 (118.58) n = 9	

Table 5.3: Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, shear strength, and critical shear stress from intertidal mud flat sediments collected during April 2003.

Dry bulk density		top shore	site A mid shore	low shore	site B mid shore	low shore
site A	ton shore					
	mid shore	<b>&lt;0.05</b>				
	low shore	>0.05	<b>&lt;0.05</b>			
site B	mid shore	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>		
	low shore	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	>0.05	
Organic content		top shore	site A mid shore	low shore	site B mid shore	low shore
site A	ton shore					
	mid shore	<b>0.001</b>				
	low shore	<b>0.000</b>	<b>0.000</b>			
site B	mid shore	0.078	<b>0.000</b>	<b>0.000</b>		
	low shore	0.254	<b>0.002</b>	<b>0.000</b>	0.412	
Colloidal carbohydrate		top shore	site A mid shore	low shore	site B mid shore	low shore
site A	ton shore					
	mid shore	<b>0.000</b>				
	low shore	0.127	<b>0.000</b>			
site B	mid shore	<b>0.032</b>	0.406	0.124		
	low shore	<b>0.000</b>	0.059	<b>0.018</b>	0.986	
Chlorophyll a		top shore	site A mid shore	low shore	site B mid shore	low shore
site A	ton shore					
	mid shore	<b>&lt;0.05</b>				
	low shore	>0.05	<b>&lt;0.05</b>			
site B	mid shore	>0.05	<b>&lt;0.05</b>	>0.05		
	low shore	>0.05	>0.05	>0.05	>0.05	
Critical shear stress		top shore	site A mid shore	low shore	site B mid shore	low shore
site A	ton shore					
	mid shore	<b>0.002</b>				
	low shore	0.153	<b>0.005</b>			
site B	mid shore	<b>0.004</b>	0.654	<b>0.020</b>		
	low shore	<b>0.012</b>	0.233	0.110	0.526	
Shear strength		top shore	site A mid shore	low shore	site B mid shore	low shore
site A	ton shore					
	mid shore	0.393				
	low shore	<b>0.009</b>	<b>0.001</b>			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.058	

Table 5.4: Descriptive statistics carried out to compare between sites studied during April 2003. Mann-Whitney was used to determine significant differences ( $p < 0.050$  - indicated in bold) for organic content, colloidal carbohydrate, critical shear stress and shear strength. ANOVA and Tukey post hoc were used to determine significant differences ( $p < 0.05$  - indicated in bold) for dry bulk density, and chlorophyll a content.

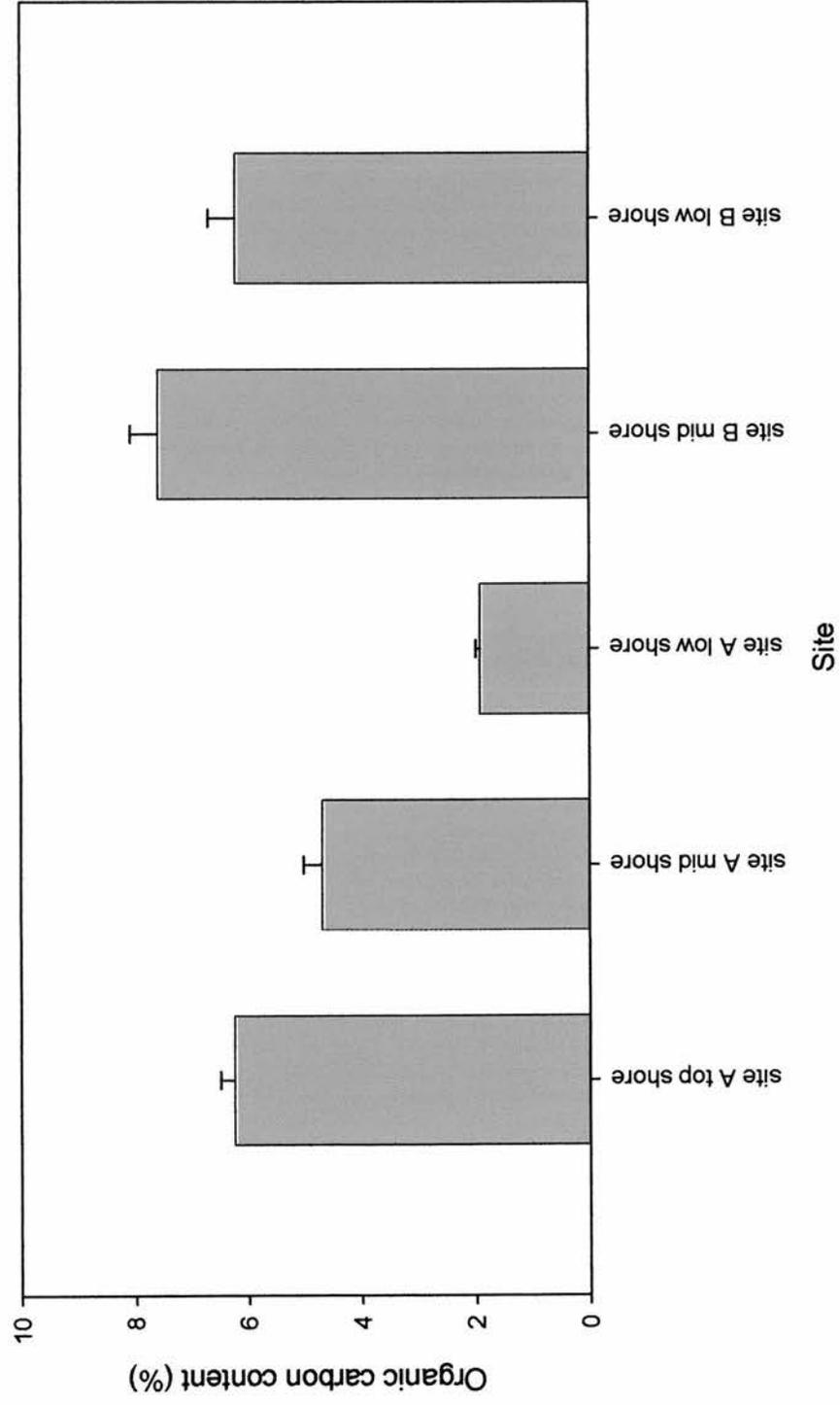


Figure 5.9: Organic carbon content (%) for samples taken during the April 2003 survey. Mean  $\pm$  s.e., n = 24-27.

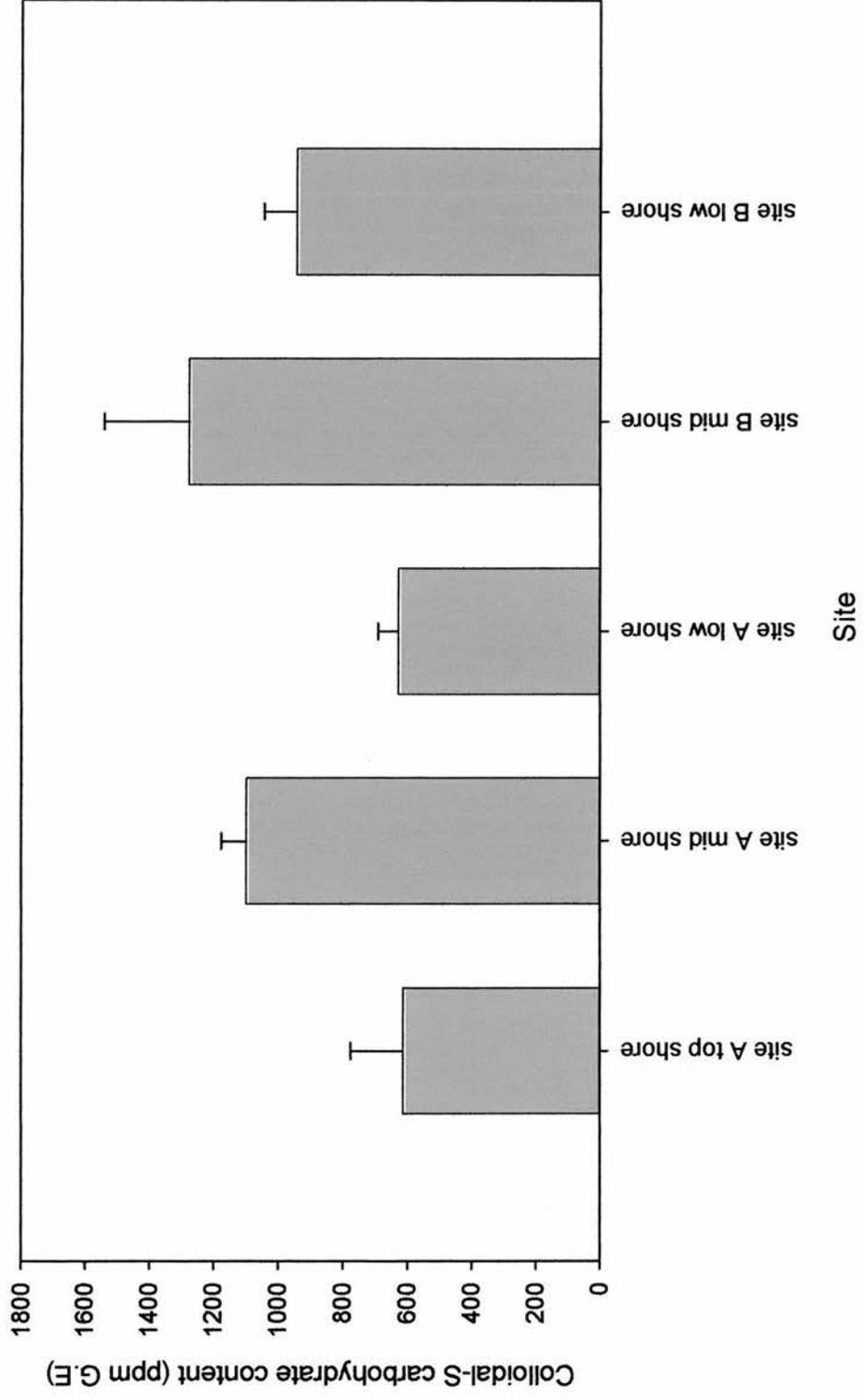


Figure 5.10: Colloidal-S carbohydrate content (ppm G.E) for samples taken during the April 2003 survey. Mean  $\pm$  s.e, n = 26-27.

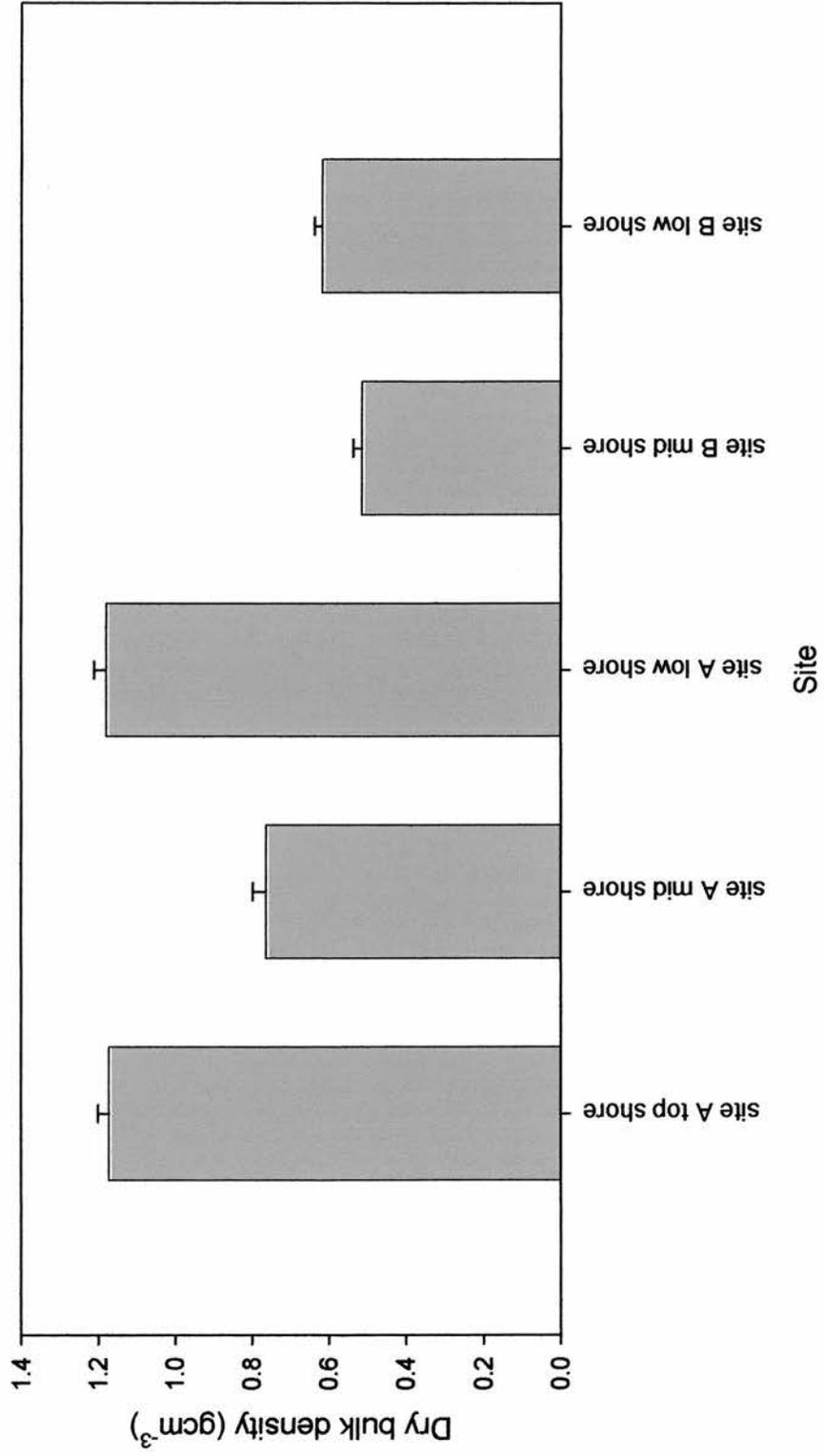


Figure 5.1.1: Dry bulk density (gsm<sup>-3</sup>) for samples taken during the April 2003 survey. Mean  $\pm$  s.e., n = 26-27.

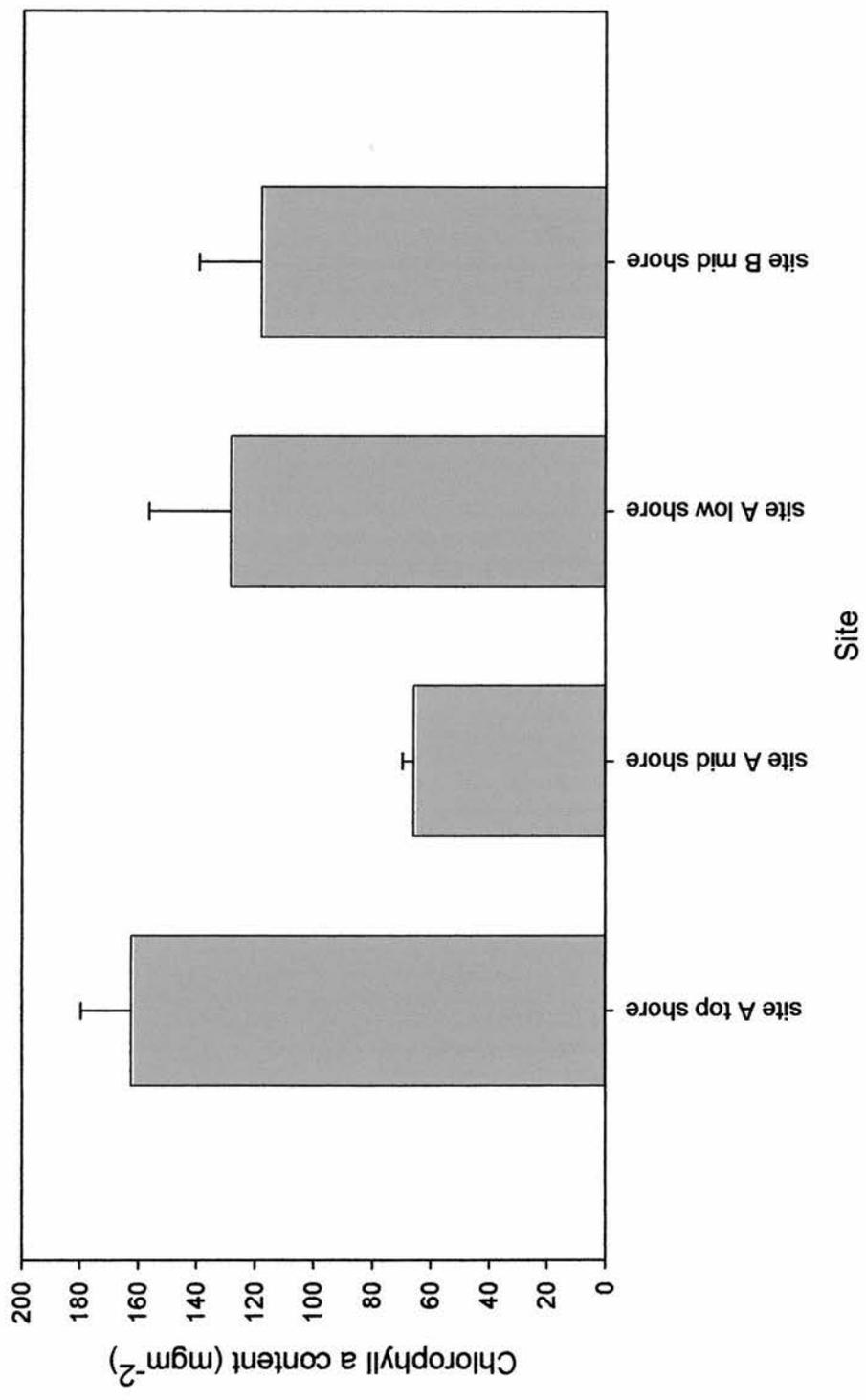


Figure 5.12: Chlorophyll a content (mgm<sup>-2</sup>) for samples taken during the April 2003 survey. Mean  $\pm$  s.e, n = 23-27.

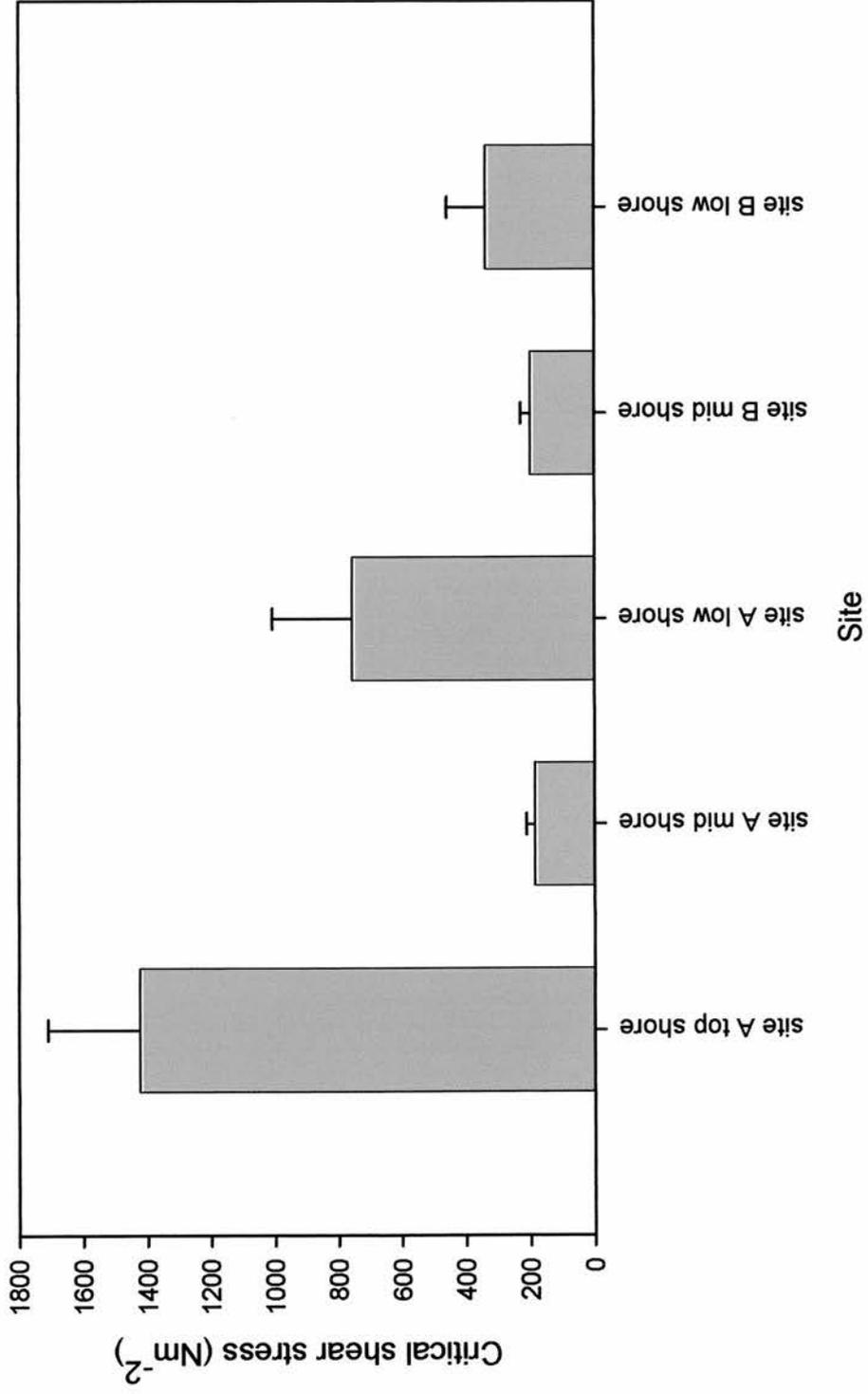


Figure 5.13: Critical shear stress (Nm<sup>-2</sup>) for samples taken during the April 2003 survey. Mean  $\pm$  s.e., n = 8-9.

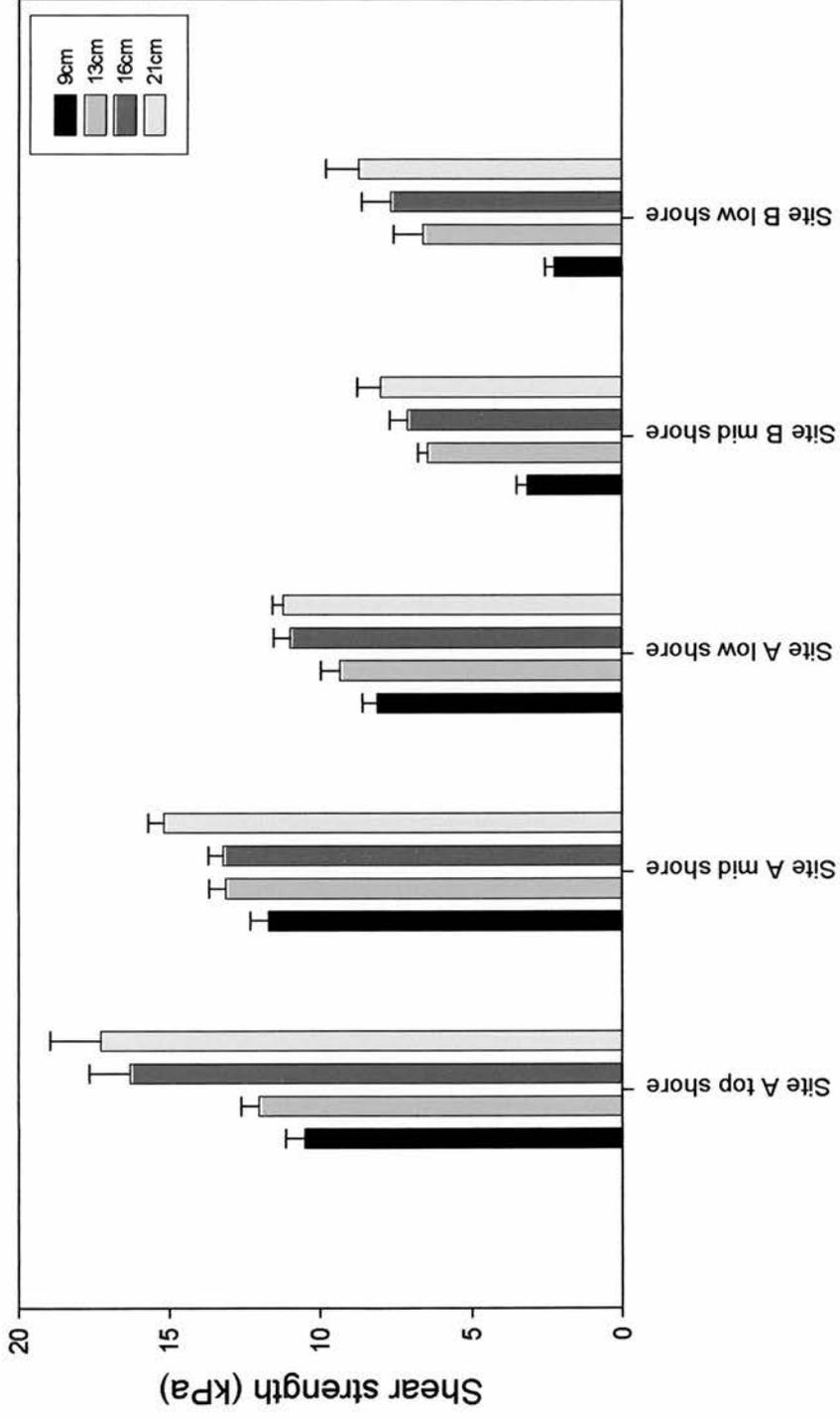


Figure 5.14: Shear strength (kPa) for samples taken during the April 2003 survey. Mean  $\pm$  s.e., n = 15.

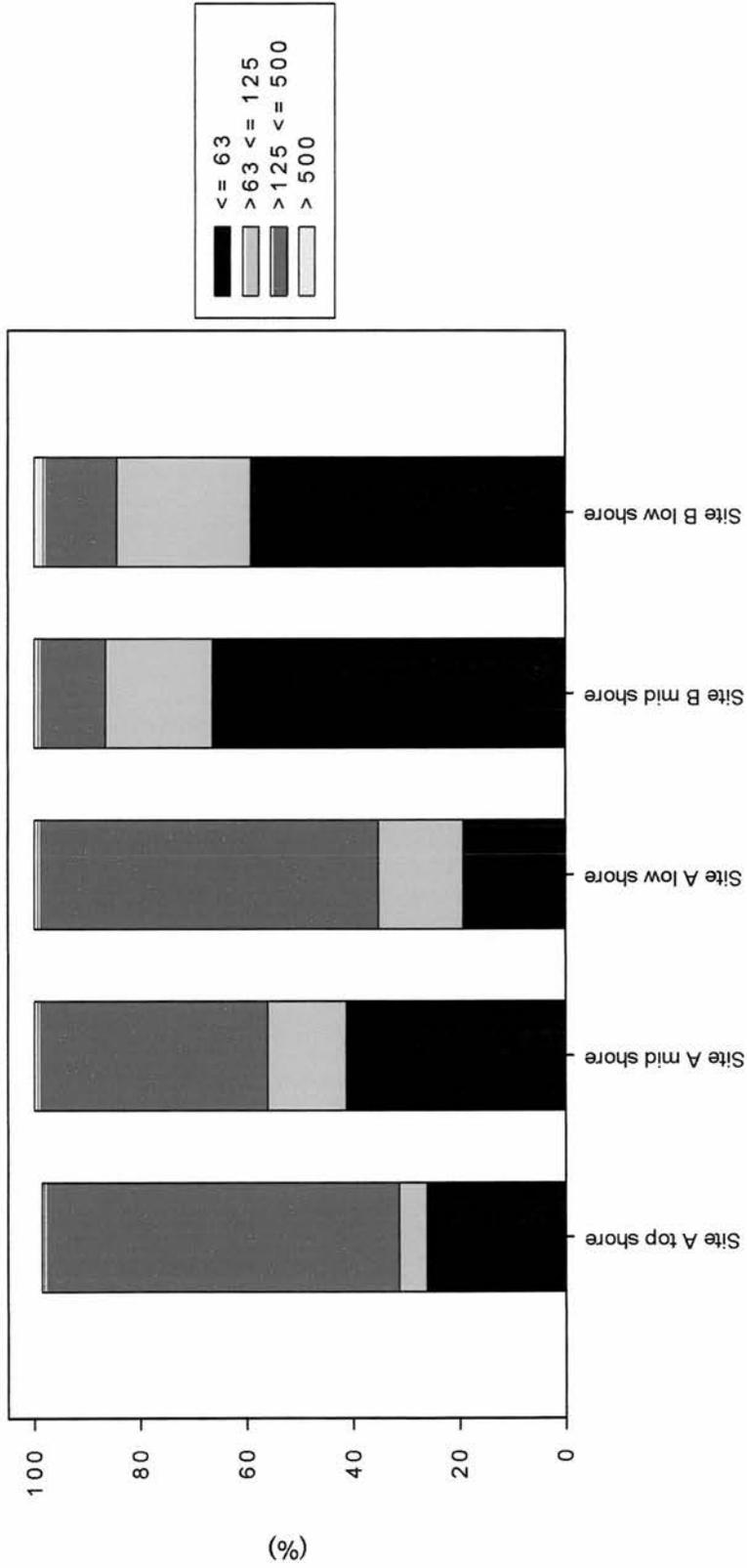


Figure 5.15: Percentage of grain sizes found at each site during the April 2003 survey. Site A was mostly composed of sediment within the >125<=500µm range. Site B mostly composed of sediments within the <=63µm range.

Principle components analysis ordination indicates the sediments of all sites were most influenced by colloidal-S carbohydrate content and organic content and least influenced by chlorophyll *a* (Figure 5.16).

### 5.3.2.2 Relationship between variables

Correlations carried out between variables indicated that dry bulk density was negatively correlated with chlorophyll *a* content ( $r_s = -0.678$ ;  $p < 0.001$ ) and colloidal-S carbohydrate content ( $r_s = -0.568$ ;  $p < 0.001$ ), colloidal-S carbohydrate content was positively correlated with chlorophyll *a* content ( $r_s = 0.488$ ;  $p < 0.001$ ), and critical erosion shear stress was positively correlated with dry bulk density ( $r_s = 0.324$ ;  $p = 0.032$ ).

### 5.3.3 July 2003

#### 5.3.3.1 Sediment variables

The organic content, colloidal-S carbohydrate content, dry bulk density, sediment stability, shear strength and chlorophyll *a* content were examined in the surface of the mud flat sediments (Figure 5.17-5.24). Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, shear strength, and critical shear stress from intertidal mud flat sediments were obtained (Table 5.5). Where a significant difference was found between individual sites during the survey in July 2004, this is indicated in Table 5.6.

Significant variation of organic content was found at all sites studied ( $H = 82.70$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.17). A significant difference in colloidal-S

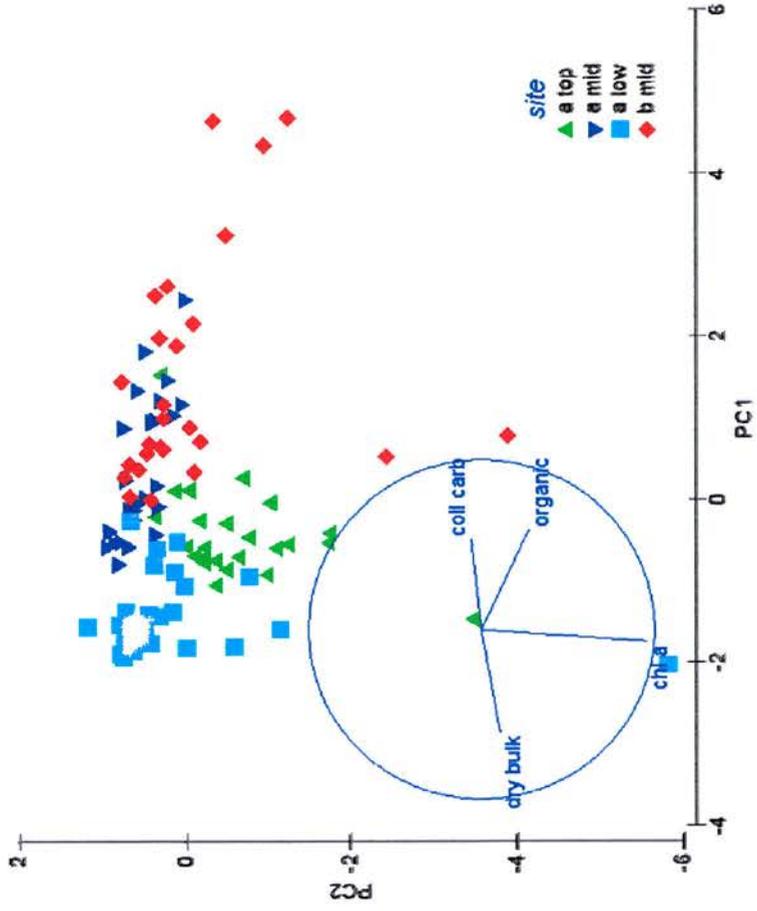


Figure 5.16: Two dimensional principle components analysis ordination of the parameters measured at each site during April 2003. The ordination indicates the surface of all sites were most influenced by colloidal-S carbohydrate content and organic content and least influenced by chlorophyll a.

	site A			site B		
	top shore	mid shore	low shore	mid shore	low shore	
Colloidal carbohydrate (ppm G.E)	1231.78 (252.00) n = 27	2911.780 (460.87) n = 27	434.39 (40.22) n = 26	283.89 (25.80) n = 27	455.91 (46.57) n = 27	
Organic content (%)	4.79 (0.83) n = 27	11.79 (0.83) n = 27	0.96 (0.02) n = 26	5.36 (0.10) n = 27	4.86 (0.25) n = 27	
Dry Bulk density (gcm <sup>-1</sup> )	0.97 (0.06) n = 27	0.38 (0.06) n = 27	1.28 (0.03) n = 27	0.63 (0.01) n = 27	0.62 (0.03) n = 27	
Chlorophyll a content (mgm <sup>-2</sup> )	160.98 (19.75) n = 27	141.07 (31.88) n = 27	50.05 (2.78) n = 25	70.24 (2.26) n = 27	51.64 (1.96) n = 27	
Shear strength (kPa)	10.00 (0.80) n = 15	10.03 (0.49) n = 15	9.57 (0.33) n = 15	2.00 (0.52) n = 15	1.93 (0.40) n = 15	
Critical shear stress (Nm <sup>-2</sup> )	711.70 (95.71) n = 9	107.80 (21.362) n = 9	40.44 (5.38) n = 8	78.15 (0.00) n = 3	78.15 (0.00) n = 5	

Table 5.5: Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, shear strength, and critical shear stress from intertidal mud flat sediments collected during July 2003.

Dry bulk density		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	ton shore					
	mid shore	<b>0.000</b>				
	low shore	<b>0.000</b>	<b>0.000</b>			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.311	
Organic content		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	ton shore					
	mid shore	<b>0.000</b>				
	low shore	<b>0.000</b>	<b>0.000</b>			
site B	mid shore	<b>0.000</b>	<b>0.026</b>	<b>0.000</b>		
	low shore	<b>0.002</b>	<b>0.001</b>	<b>0.000</b>	<b>0.001</b>	
Colloidal-S carbohydrate		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	ton shore					
	mid shore	<b>0.002</b>				
	low shore	<b>0.000</b>	<b>0.000</b>			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.012</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	0.569	<b>0.005</b>	
Chlorophyll a content		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	ton shore					
	mid shore	>0.05				
	low shore	>0.05	>0.05			
site B	mid shore	< <b>0.05</b>	< <b>0.05</b>	< <b>0.05</b>		
	low shore	< <b>0.05</b>	< <b>0.05</b>	< <b>0.05</b>	< <b>0.05</b>	
Critical shear stress		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	ton shore					
	mid shore	<b>0.001</b>				
	low shore	<b>0.001</b>	<b>0.002</b>			
site B	mid shore	<b>0.014</b>	0.450	<b>0.012</b>		
	low shore	<b>0.003</b>	0.335	<b>0.002</b>	0.844	
Shear strength		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	ton shore					
	mid shore	0.662				
	low shore	0.349	0.630			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.882	

Table 5.6: Descriptive statistics carried out to compare between sites studied during July 2003. Mann-Whitney was used to determine significant differences ( $p < 0.050$  - indicated in bold) for organic content, colloidal carbohydrate, dry bulk density, critical shear stress and shear strength. ANOVA and Tukey post hoc were used to determine significant differences ( $p < 0.05$  - indicated in bold) for chlorophyll a content.

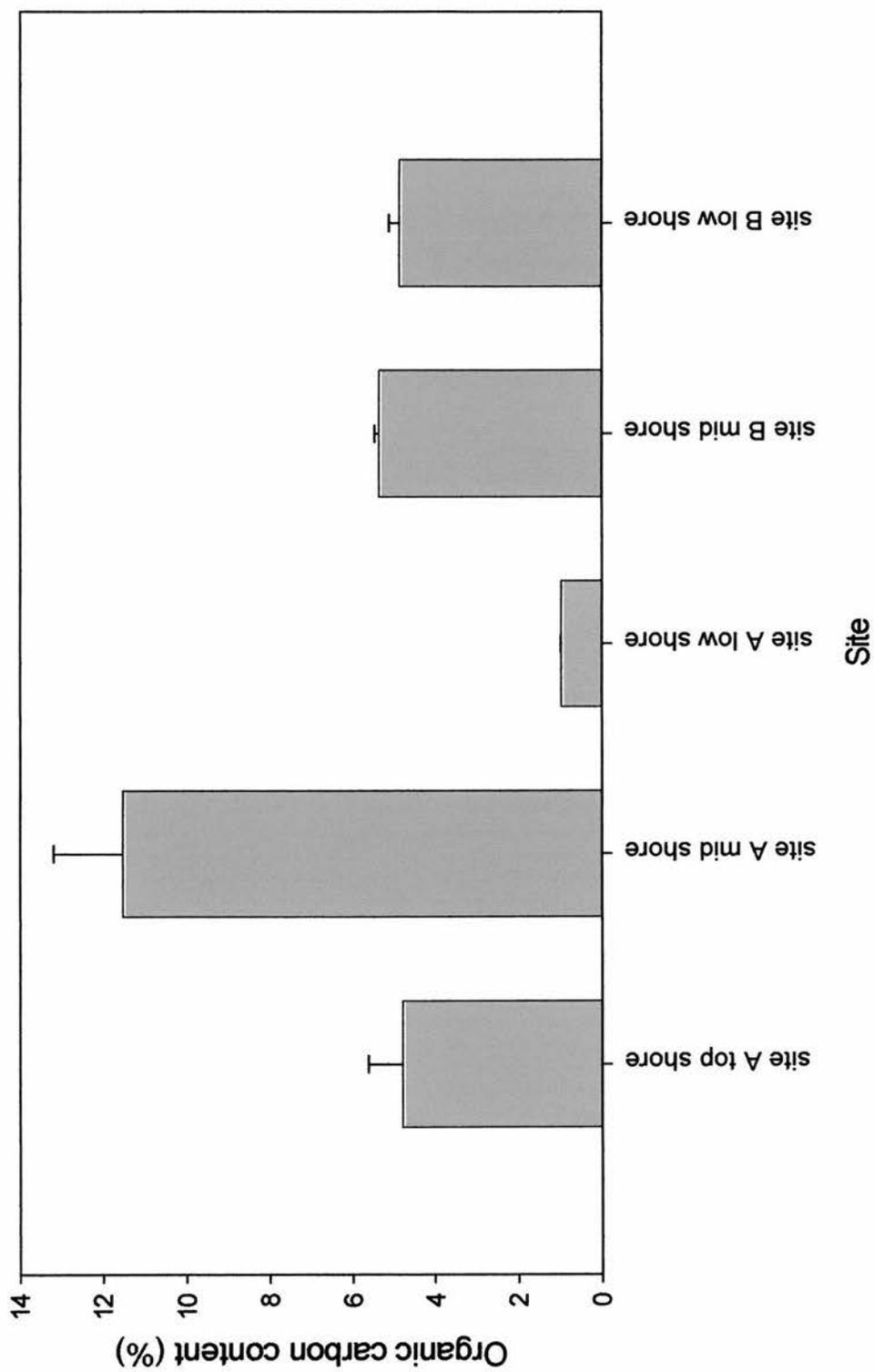


Figure 5.17: Organic carbon content (%) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 26-27.

carbohydrate content was observed between all sites ( $H = 70.46$ ;  $d.f = 4$ ;  $p < 0.001$ ), except site A low shore/ site B low shore ( $W = 669.5$ ;  $p = 0.5691$ ) (Figure 5.18). A significant difference in dry bulk density was observed at all sites ( $H = 84.62$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.19) with the exception of site B mid shore/site B low shore ( $W = 683.5$ ;  $p = 0.311$ ). A significant difference was observed in chlorophyll *a* content ( $F_{4,129} = 641.77$ ;  $p < 0.001$ ) for all sites except any combinations within site A (Figure 5.20). A significant difference between sites was observed in critical shear stress ( $H = 27.37$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.21), except for the combination of site B mid/low shore and both site B areas with site A mid shore. At a depth of 9cm significant differences were observed in sediment shear strength ( $H = 52.68$ ;  $d.f = 4$ ;  $p < 0.001$ ) however no differences in shear strength was found within site A or within Site B (Figure 5.22). Sediment grain size did not vary significantly between sites. Site A sediment was mostly within the  $>125 \leq 500 \mu\text{m}$  range, the majority of site B sediments were  $<63 \mu\text{m}$  (Figure 5.23).

Principle components analysis ordination indicates the surface sediments at all sites were most influenced by dry bulk density. Some samples at site B mid shore were influenced by colloidal-S carbohydrate and organic carbon content (Figure 5.24).

### 5.3.3.2 Relationship between variables

Correlations carried out between variables indicated that dry bulk density was negatively correlated with colloidal-S carbohydrate content ( $r_s = -0.473$ ;  $p = 0.005$ ) and organic carbon content ( $r_s = -0.748$ ;  $p = 0.000$ ). Chlorophyll *a* content was negatively correlated with colloidal-S carbohydrate ( $r_s = -0.367$ ;  $p =$

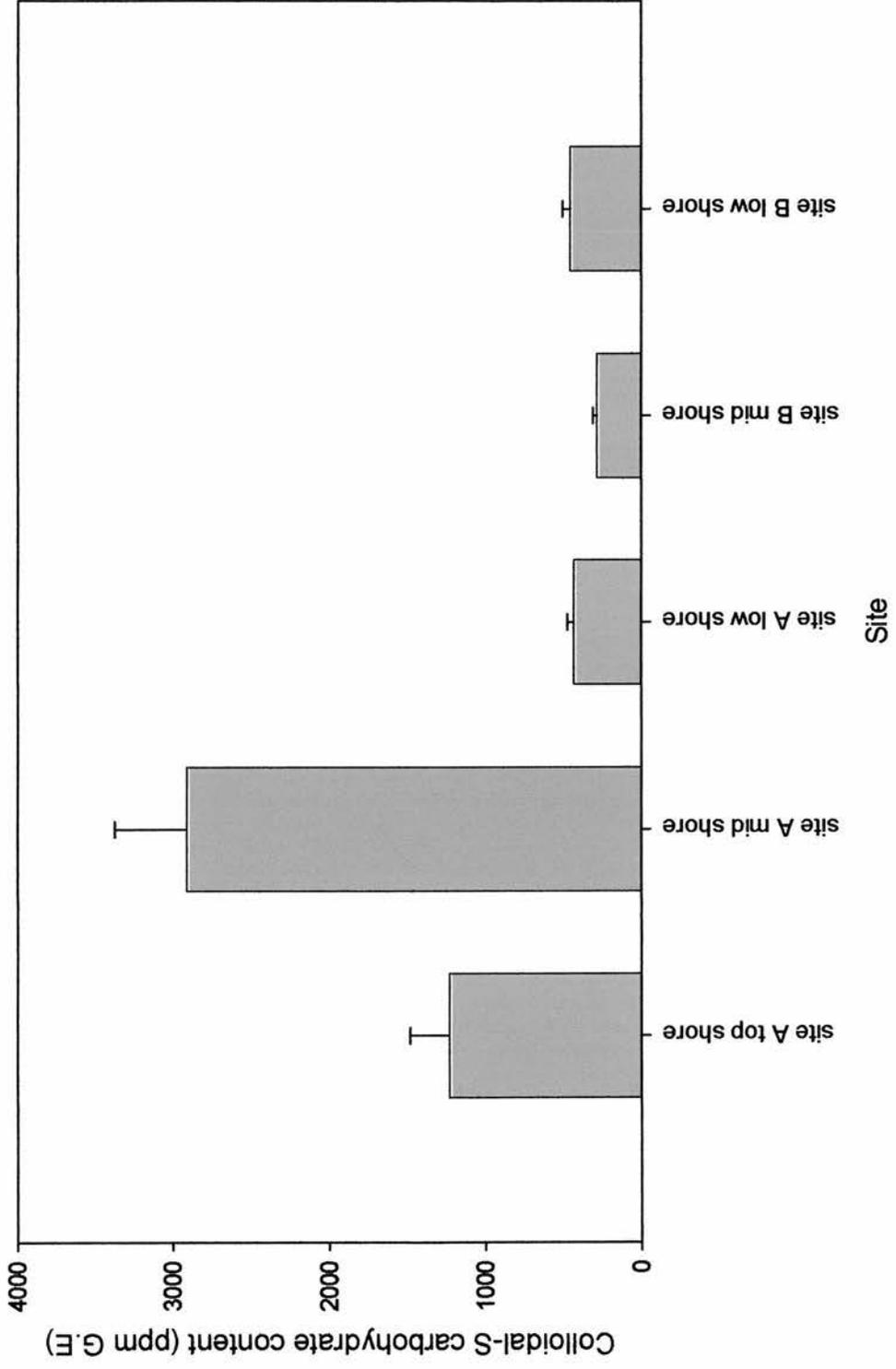


Figure 5.18: Colloidal-S carbohydrate content (ppm G.E.) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 26-27.

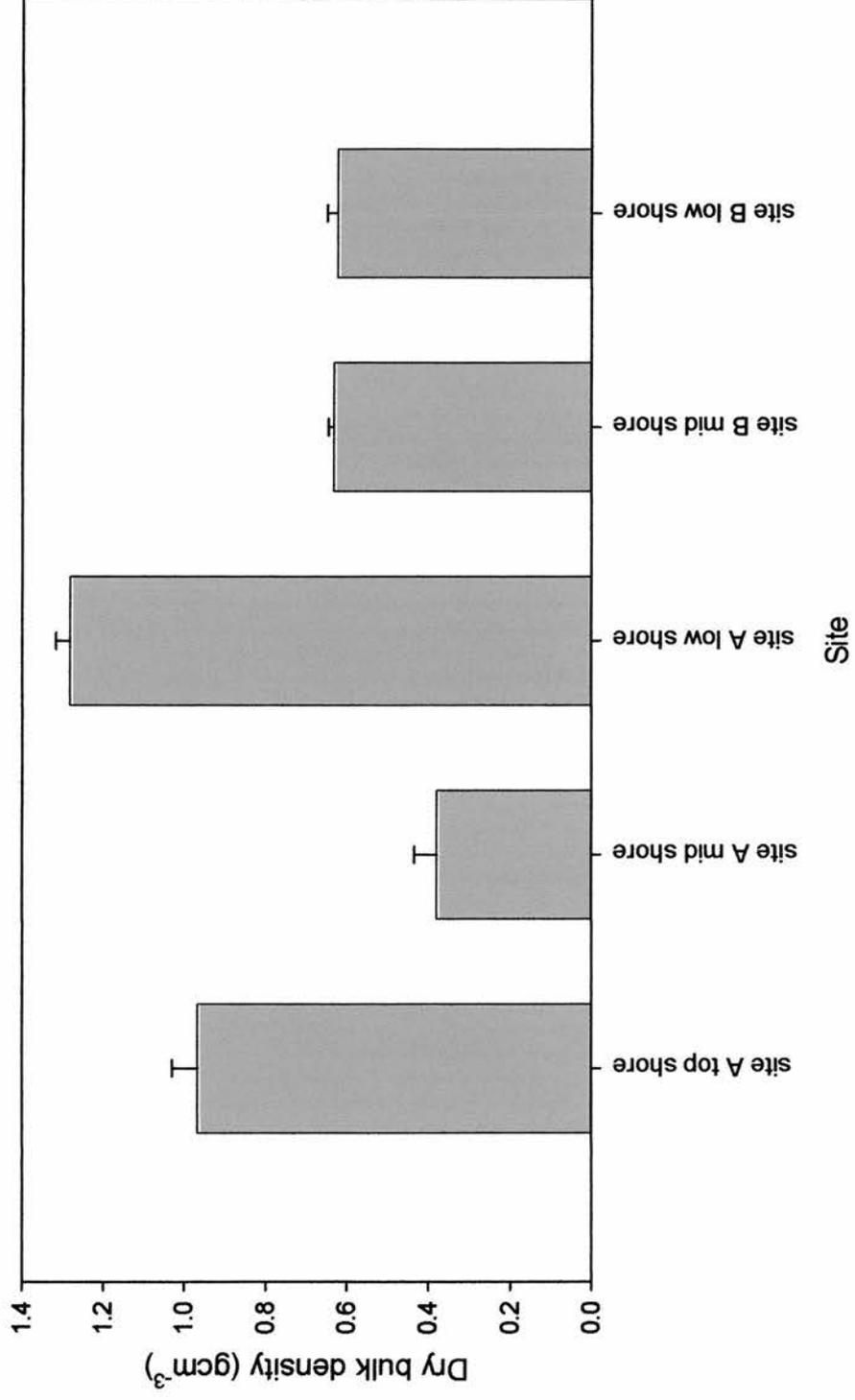


Figure 5.19: Dry bulk density (gcm<sup>-3</sup>) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 27.

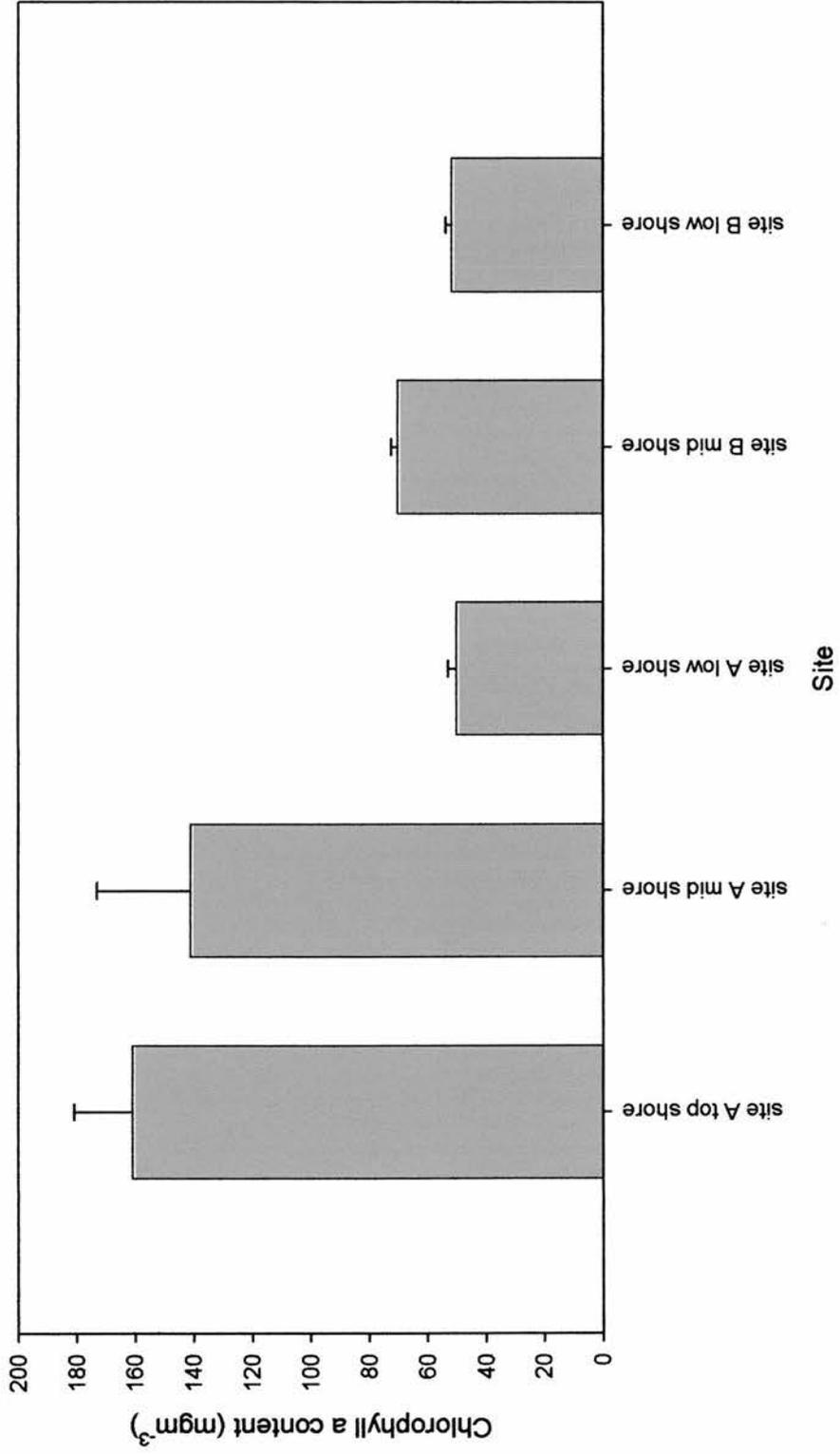


Figure 5.20: Chlorophyll a content (mgm<sup>-3</sup>) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 25-27.

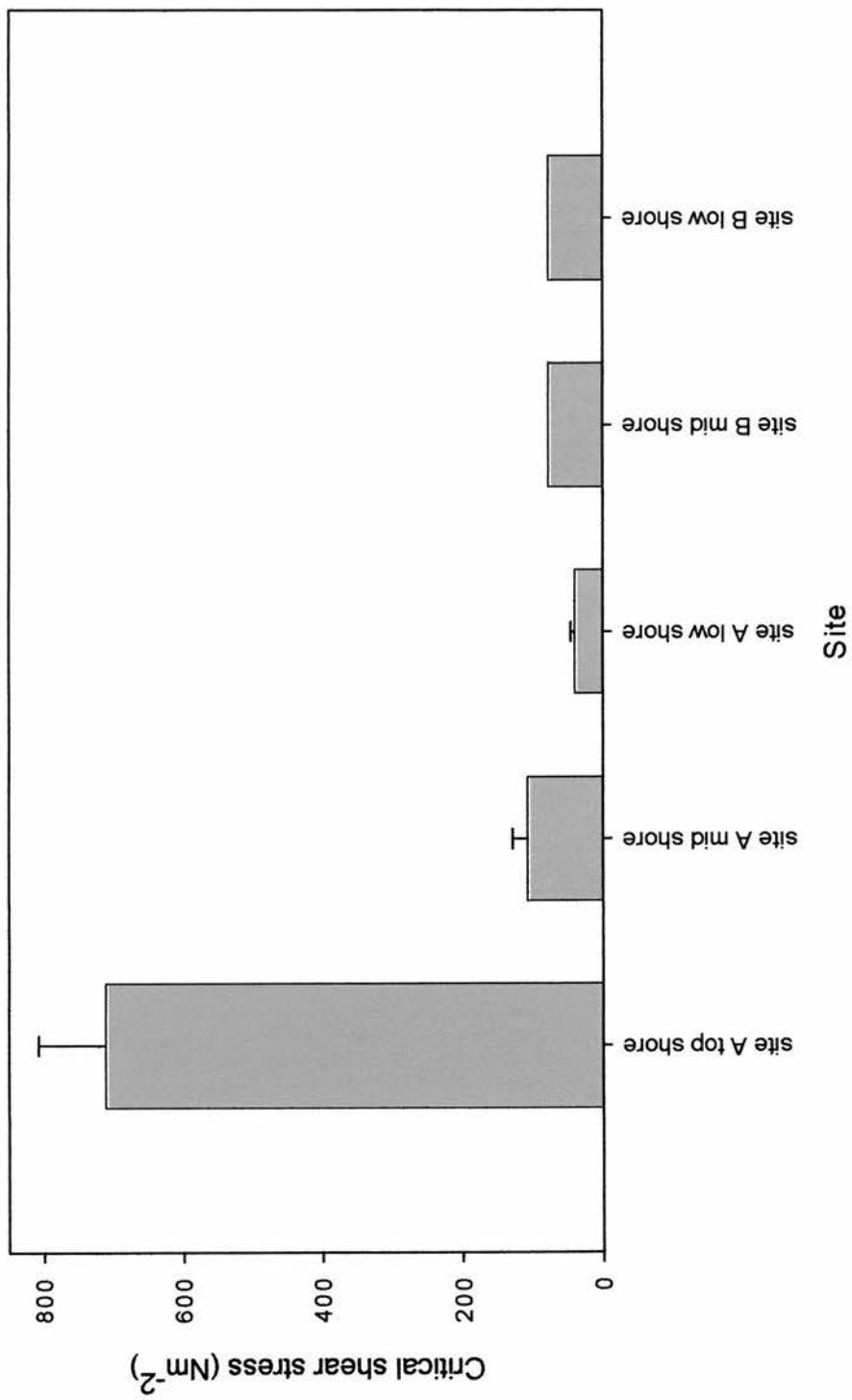


Figure 5.21: Critical shear stress ( $\text{Nm}^{-2}$ ) for samples taken during the July 2003 survey. Mean  $\pm$  s.e.,  $n = 3-9$ .

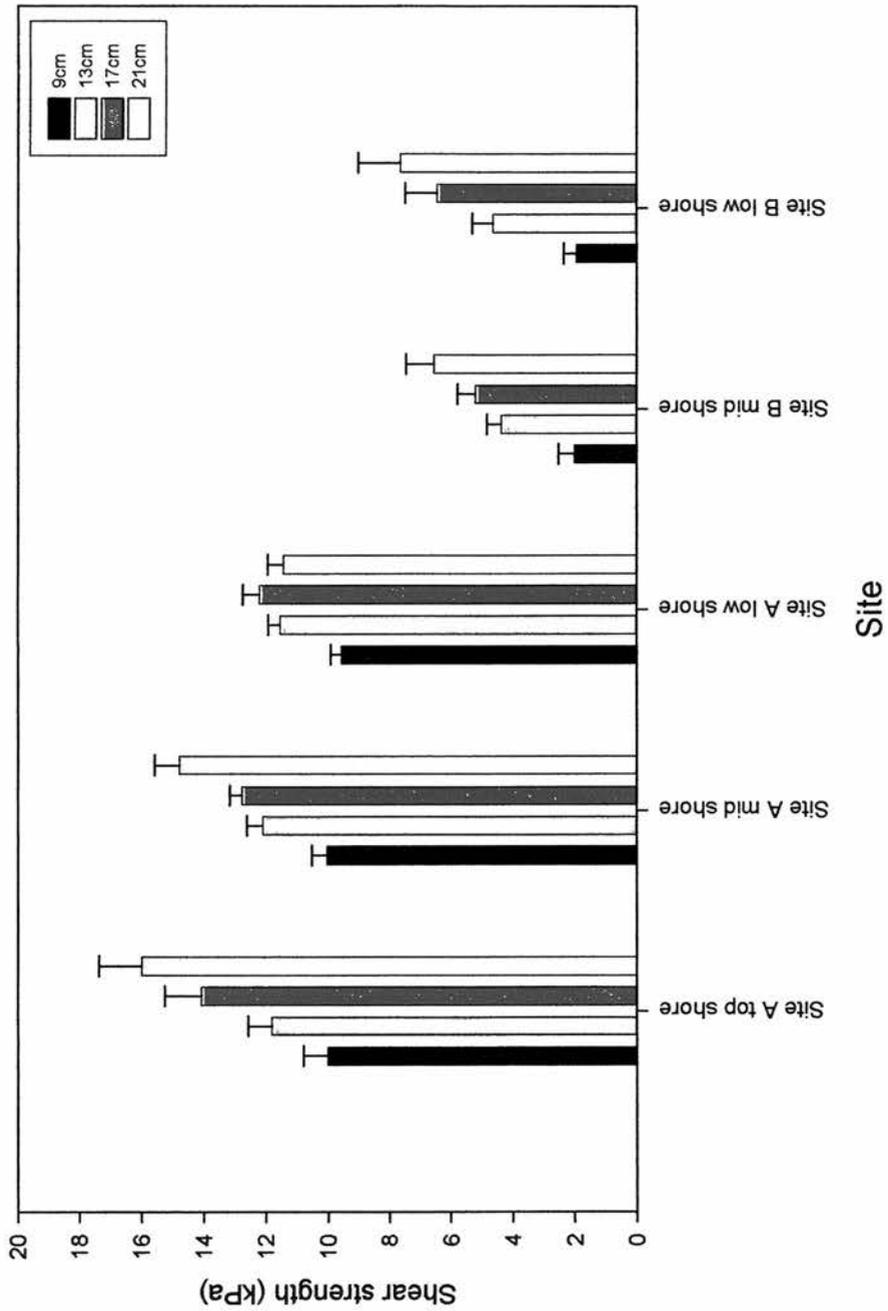


Figure 5.22: Shear strength (kPa) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 15.

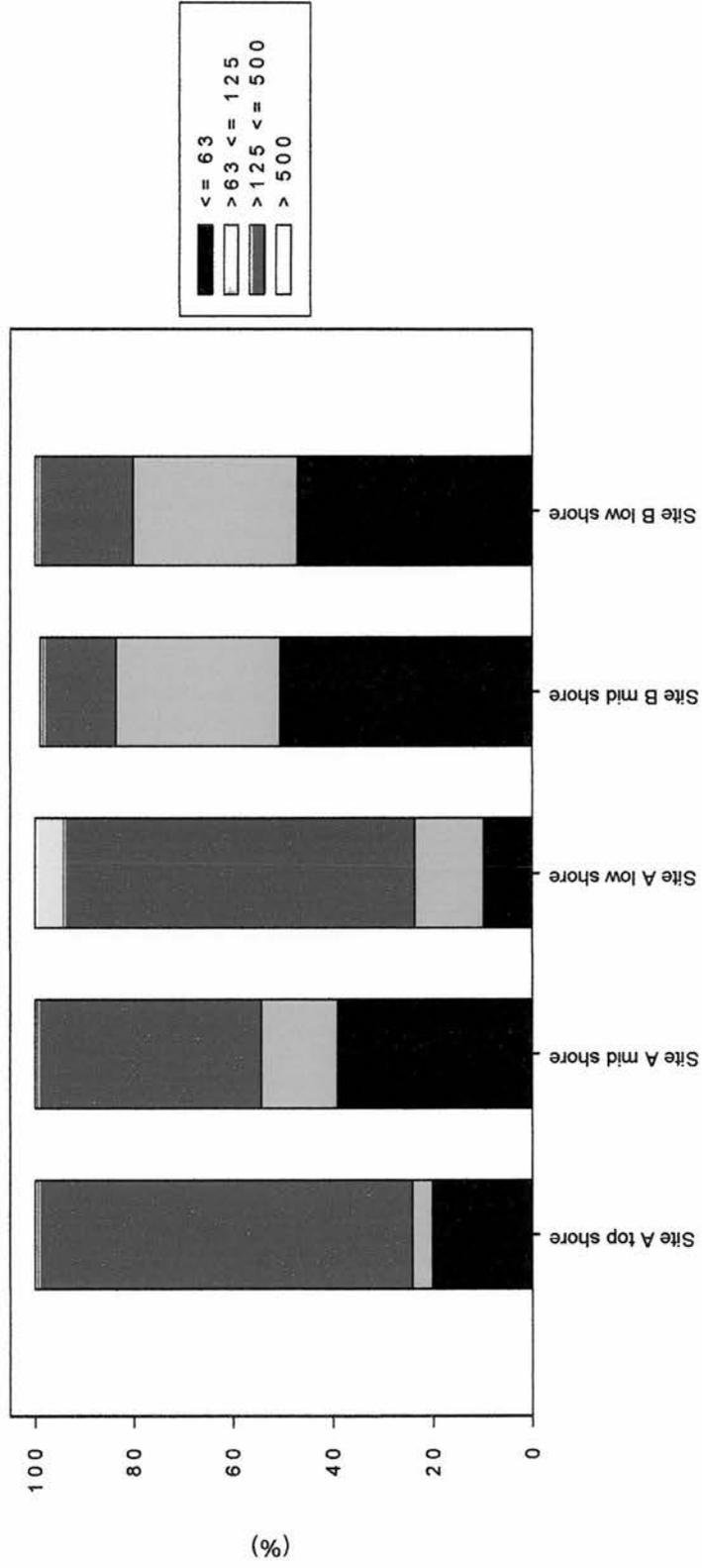


Figure 5.23: Percentage of grain sizes found at each site during the July 2003 survey. Site A was mostly composed of sediment within the >125<=500 $\mu$ m range. Site B mostly composed of sediments within the <=63 $\mu$ m range.

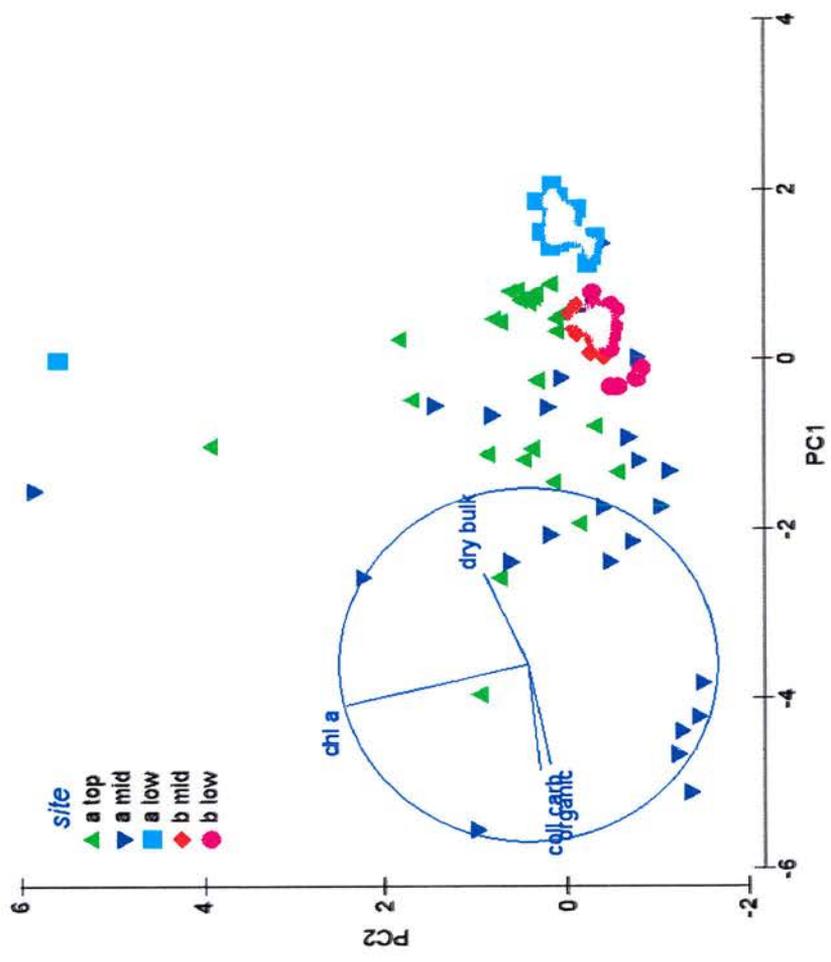


Figure 5.24: Two dimensional principle components analysis ordination of the parameters measured at each site during July 2003. The ordination indicates the surface sediments at all sites were most influenced by dry bulk density. Some samples at site B mid shore were influenced by colloidal-S carbohydrate and organic carbon content.

0.033), and organic carbon content ( $r_s = -0.399$ ;  $p = 0.020$ ). Colloidal-S carbohydrate content was positively correlated with organic carbon content ( $r_s = 0.614$ ;  $p < 0.001$ ).

#### 5.3.4 March 2004

##### 5.3.4.1 Sediment variables

The organic content, colloidal-S carbohydrate content, dry bulk density, sediment stability, shear strength and chlorophyll *a* content were examined in the surface of the mud flat sediments (Figure 5.25-5.32). Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, shear strength, and critical shear stress from intertidal mud flat sediments were determined (Table 5.7). Where a significant difference was found between individual sites during the survey in March 2004 this is indicated in Table 5.8.

Significant variation of organic content was found between all sites ( $H = 111.24$ ;  $d.f = 4$ ;  $p < 0.001$ ) except the comparison of the site B sites ( $W = 791.0$ ;  $p = 0.115$ ) (Figure 5.25). A significant difference between all but four comparisons of sites was observed in colloidal-S carbohydrate content ( $H = 38.32$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.26). A significant difference in dry bulk density was observed in all but 2 site combinations ( $F_{4,121} = 115.11$ ;  $p < 0.001$ ) (Figure 5.27). A significant difference between 3 combinations of sites was observed in chlorophyll *a* content ( $H = 33.34$ ;  $d.f = 3$ ;  $p < 0.001$ ), (Figure 5.28) (site B mid values are lacking, no statistics could be carried out for this site). A significant difference in all but two of the site comparisons was observed in

	site A			site B		
	top shore	mid shore	low shore	mid shore	low shore	low shore
Colloidal carbohydrate (ppm G.E)	561.28 (45.84) n = 25	419.70 (54.35) n = 24	235.00 (22.62) n = 26	483.73 (47.33) n = 25	942.55 (210.43) n = 27	
Organic content (%)	2.76 (0.17) n = 25	2.11 (0.13) n = 27	1.27 (0.04) n = 26	5.83 (0.11) n = 26	6.23 (0.43) n = 27	
Dry Bulk density (gcm <sup>-1</sup> )	1.30 (0.02) n = 25	1.20 (0.03) n = 26	1.41 (0.03) n = 22	0.63 (0.02) n = 27	0.70 (0.03) n = 27	
Chlorophyll a content (mgm <sup>-2</sup> )	155.04 (12.73) n = 25	100.56 (6.70) n = 25	82.89 (4.63) n = 21	/	84.36 (4.15) n = 27	
Shear strength (kPa)	48.27 (2.46) n = 15	51.33 (1.24) n = 15	45.87 (2.21) n = 15	12.13 (2.58) n = 15	13.73 (2.70) n = 15	
Critical shear stress (Nm <sup>-2</sup> )	685.47 (173.07) n = 9	78.15 (0.00) n = 9	86.82 (8.67) n = 9	104.21 (26.37) n = 9	77.84 (3.18) n = 9	

Table 5.7: Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, shear strength, and critical shear stress from intertidal mud flat sediments collected during March 2004.

Dry bulk density		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	<b>&lt;0.05</b>				
	low shore	>0.05	<b>&lt;0.05</b>			
site B	mid shore	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>		
	low shore	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	>0.05	

Organic content		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	<b>0.000</b>				
	low shore	<b>0.000</b>	<b>0.000</b>			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.115	

Colloidal-S carbohydrate content		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	0.065				
	low shore	<b>0.000</b>	<b>0.009</b>			
site B	mid shore	0.217	0.361	<b>0.000</b>		
	low shore	0.194	<b>0.006</b>	<b>0.000</b>	<b>0.022</b>	

Chlorophyll a content		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	<b>0.000</b>				
	low shore	<b>0.000</b>	0.082			
site B	mid shore					
	low shore	<b>0.000</b>	0.107	0.787		

Critical shear stress		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	<b>0.000</b>				
	low shore	<b>0.000</b>	0.374			
site B	mid shore	<b>0.001</b>	<b>0.002</b>	<b>0.003</b>		
	low shore	<b>0.002</b>	<b>0.000</b>	<b>0.000</b>	0.374	

Shear strength		top shore	site A		site B	
			mid shore	low shore	mid shore	low shore
site A	top shore					
	mid shore	0.393				
	low shore	0.506	<b>0.041</b>			
site B	mid shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
	low shore	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.723	

Table 5.8: Descriptive statistics carried out to compare between sites studied during March 2004. Mann-Whitney was used to determine significant differences ( $p < 0.050$  - indicated in bold) for organic content, colloidal carbohydrate, chlorophyll a content, critical shear stress and shear strength. ANOVA and Tukey post hoc were used to determine significant differences ( $p < 0.05$  - indicated in bold) for dry bulk density.

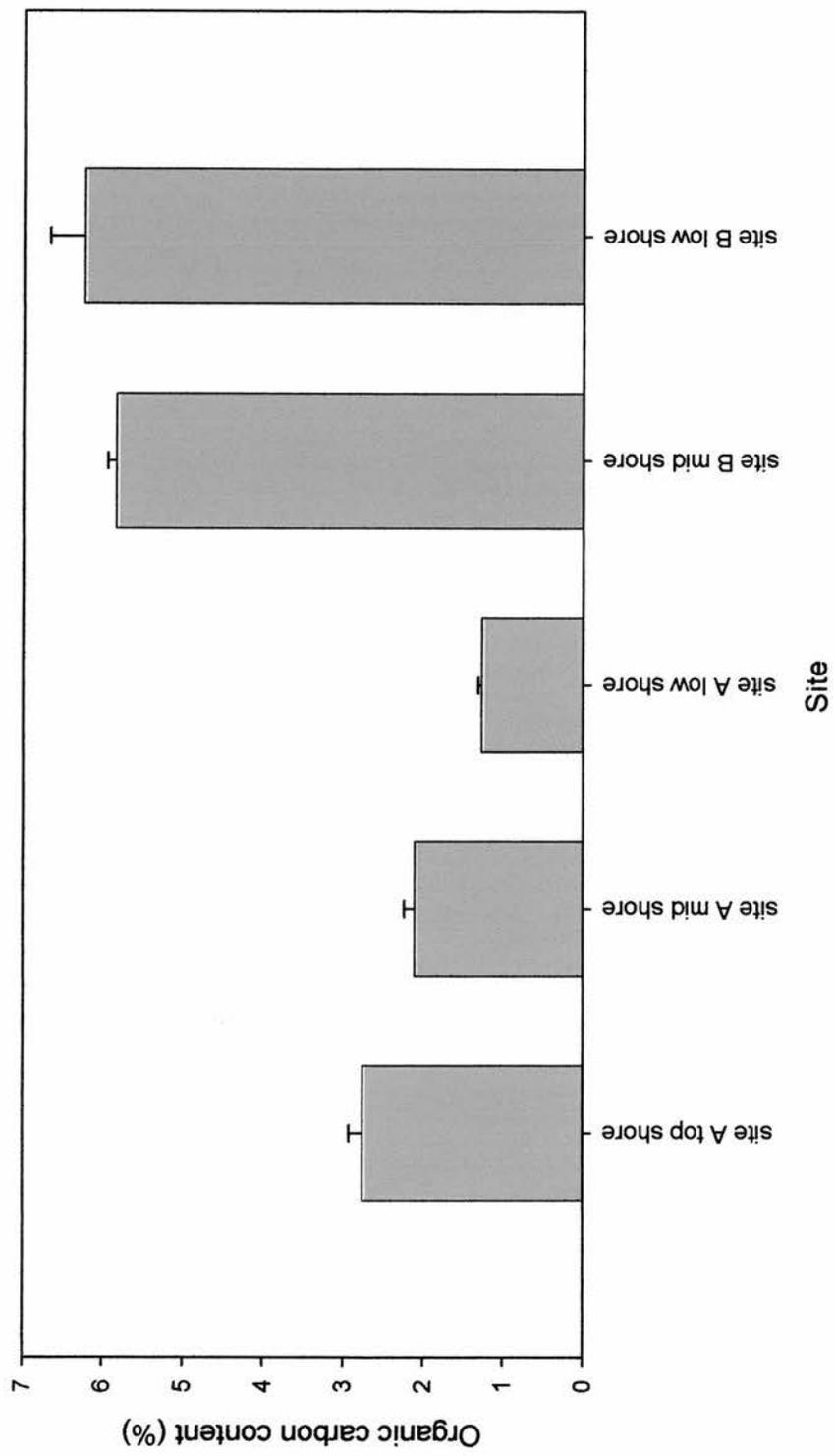


Figure 5.25: Organic carbon content (%) for samples taken during the March 2004 survey. Mean  $\pm$  s.e, n = 25-27.

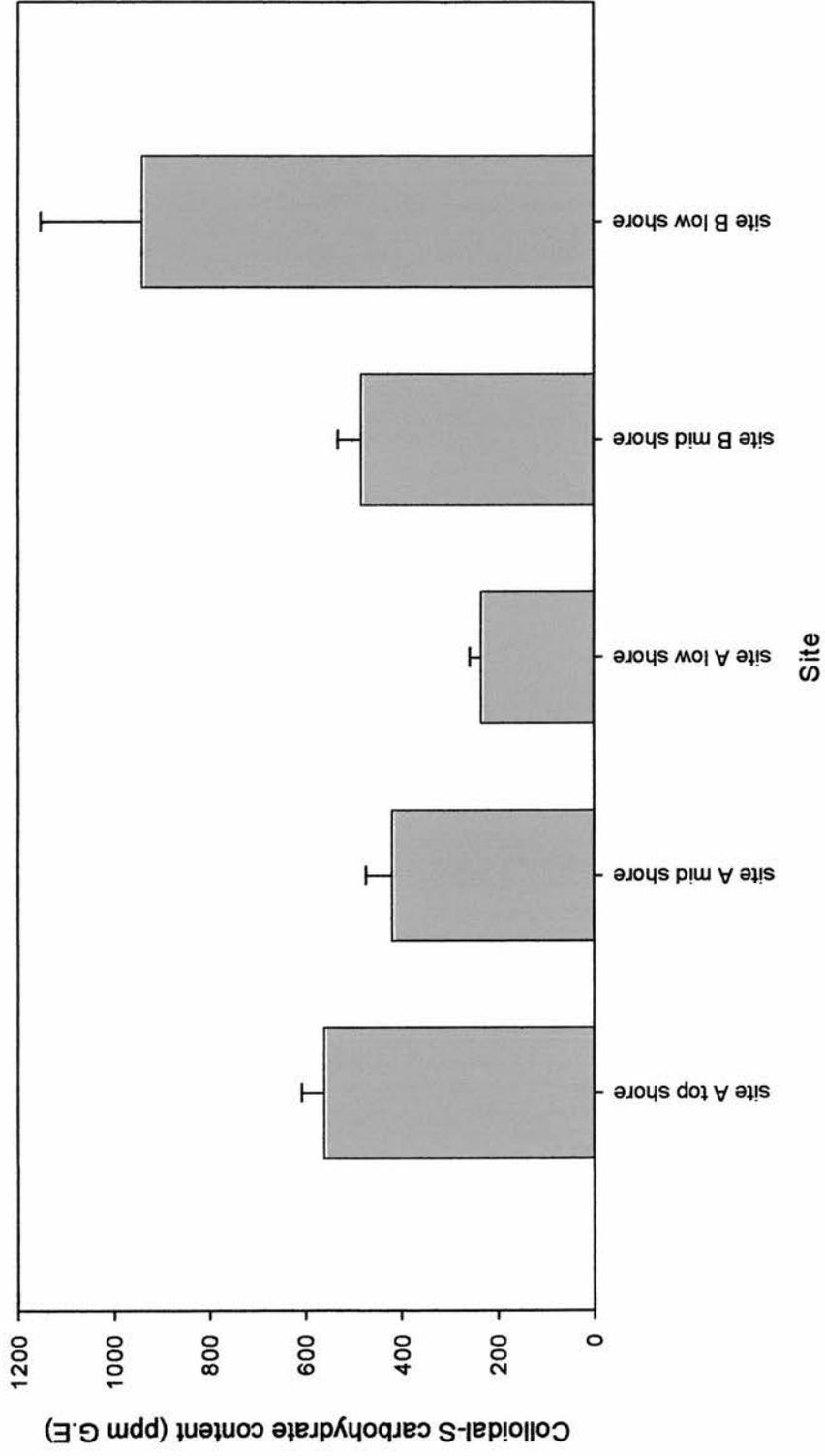


Figure 5.26: Colloidal-S carbohydrate content (ppm G.E) for samples taken during the March 2004 survey. Mean  $\pm$  s.e, n = 24-27.

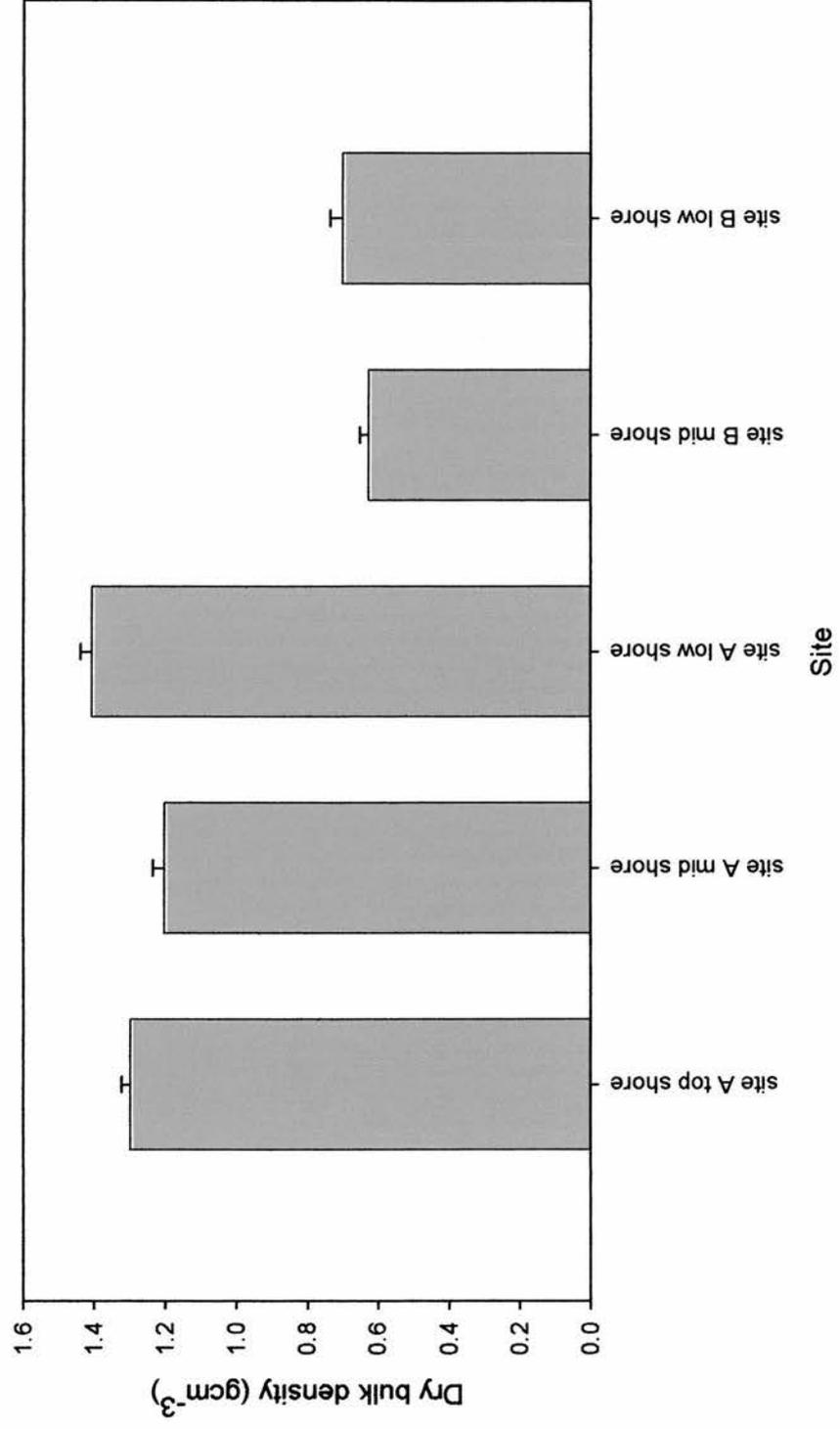


Figure 5.27: Dry bulk density (gcm<sup>-3</sup>) for samples taken during the March 2004 survey. Mean  $\pm$  s.e, n = 24-27.

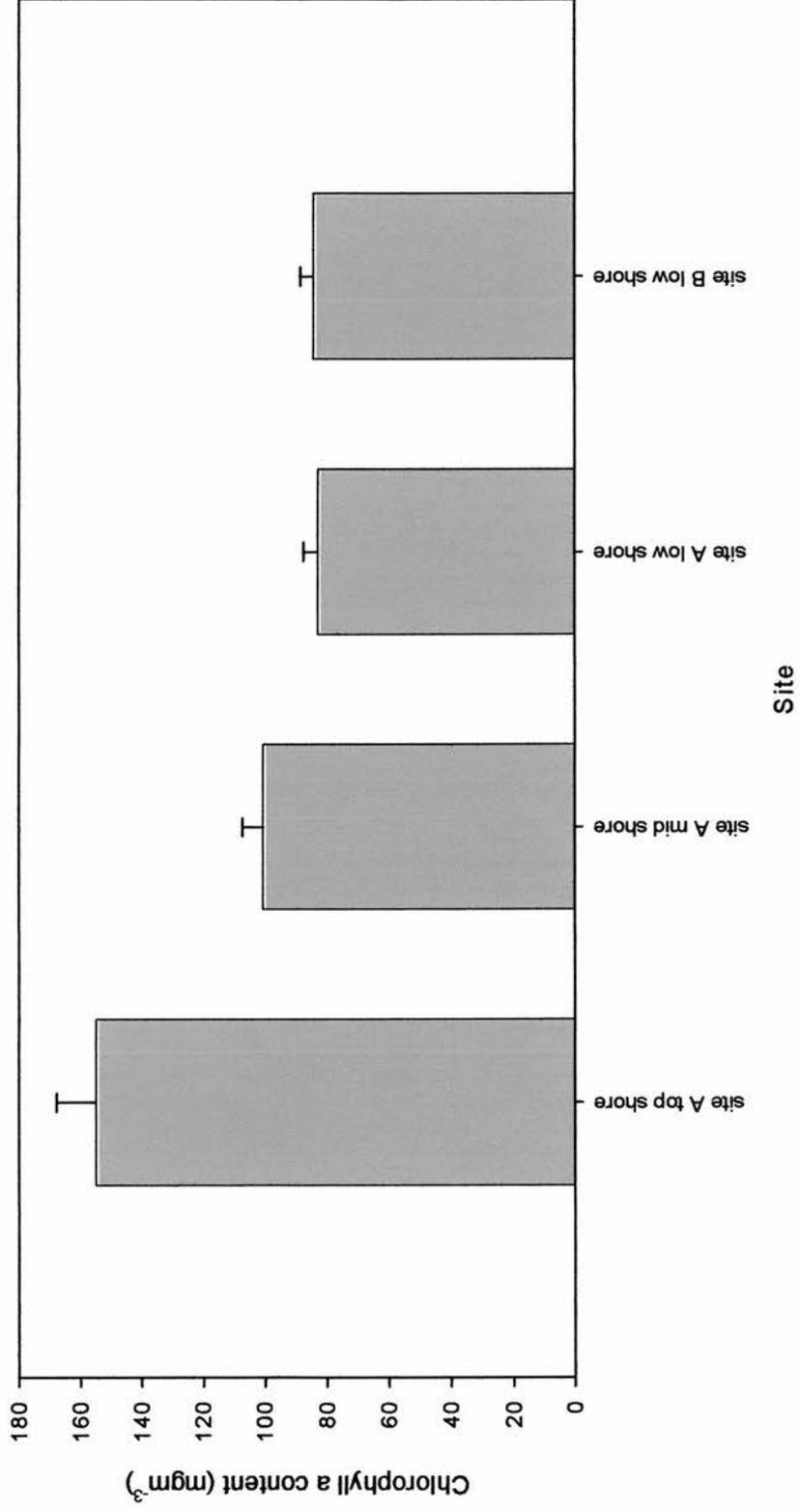


Figure 5.28: Chlorophyll a content (mgm<sup>-3</sup>) for samples taken during the March 2004 survey. Mean  $\pm$  s.e, n = 25-27.

critical shear stress ( $H = 36.37$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.29) and at a depth of 9cm, significant differences were observed in sediment shear strength at all but three site combinations ( $H = 58.66$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 5.30). Sediment grain size did not vary significantly between sites. Site A sediment was mostly within the  $>125 \leq 500 \mu\text{m}$  range, the majority of site B sediments were within the  $<63 \mu\text{m}$  range (Figure 5.31).

Principle components analysis ordination indicates the surface sediments at all sites were most influenced by dry bulk density (Figure 5.32).

#### 5.3.4.2 Relationship between variables

Correlations carried out between variables indicated that chlorophyll *a* content was positively correlated with organic carbon content ( $r_s = 0.374$ ;  $p = 0.011$ ) and critical shear stress ( $r_s = 0.477$ ;  $p = 0.001$ ). Critical shear stress was positively correlated with organic carbon content ( $r_s = 0.652$ ;  $p < 0.001$ ).

#### 5.3.5 Changes in measured variables over time

The organic content, colloidal-S carbohydrate content, dry bulk density, sediment stability, shear strength and chlorophyll *a* content were examined in the surface of the mud flat sediments and are indicated (Figure 5.33-5.39).

Significant differences in colloidal-S carbohydrate content were observed between the three years studied at site A top shore ( $H = 27.80$ ;  $d.f = 3$ ;  $p < 0.001$ ), site A mid shore ( $H = 52.21$ ;  $d.f = 3$ ;  $p < 0.001$ ), site A low shore ( $H = 59.20$ ;  $d.f = 3$ ;  $p < 0.001$ ), site B mid shore ( $H = 91.84$ ;  $d.f = 3$ ;  $p < 0.001$ ) and site B low shore ( $H = 37.33$ ;  $d.f = 3$ ;  $p < 0.001$ ) (Figure 5.33).

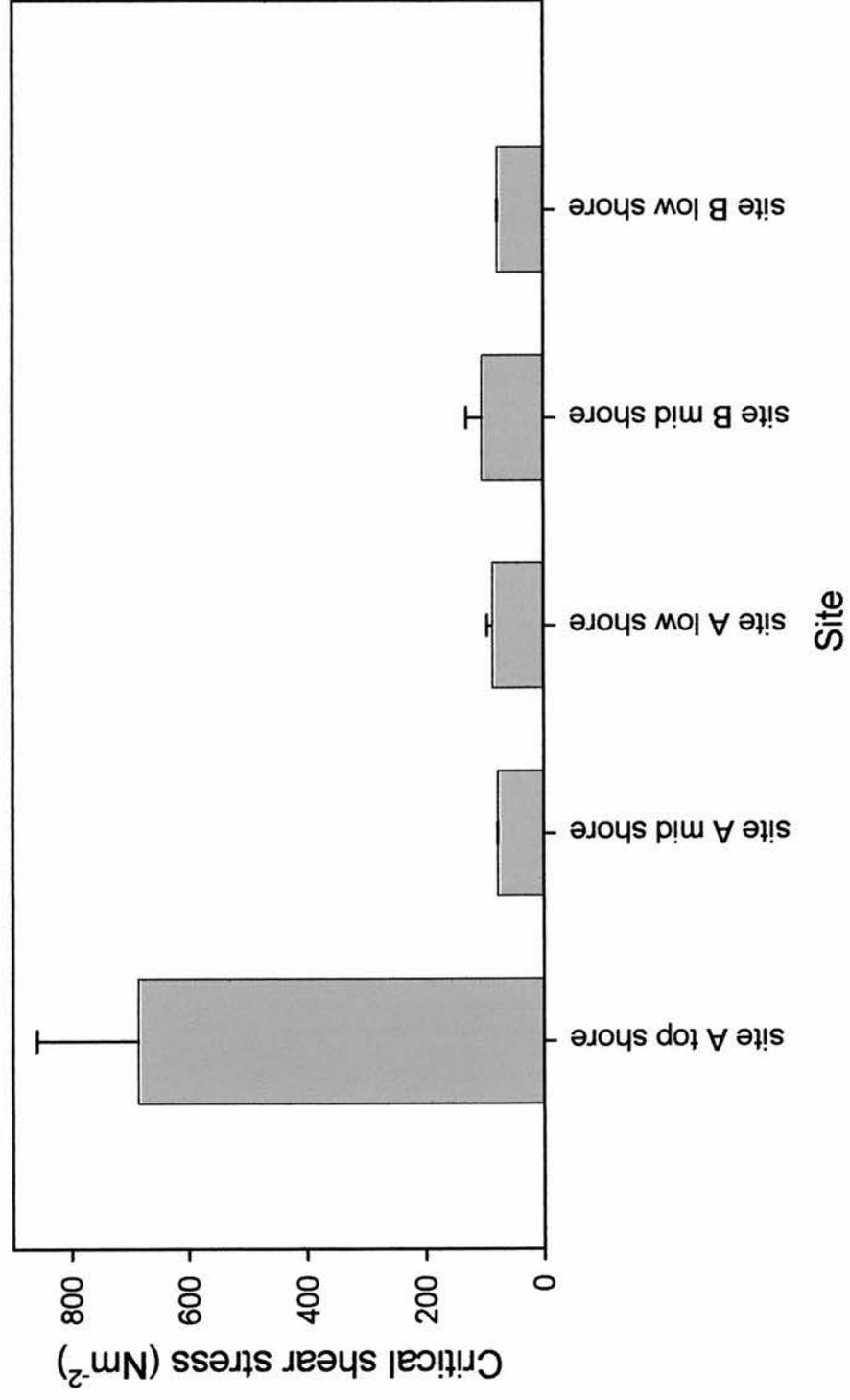


Figure 5.29: Critical shear stress (Nm<sup>-2</sup>) for samples taken during the March 2004 survey. Mean  $\pm$  s.e, n = 9.

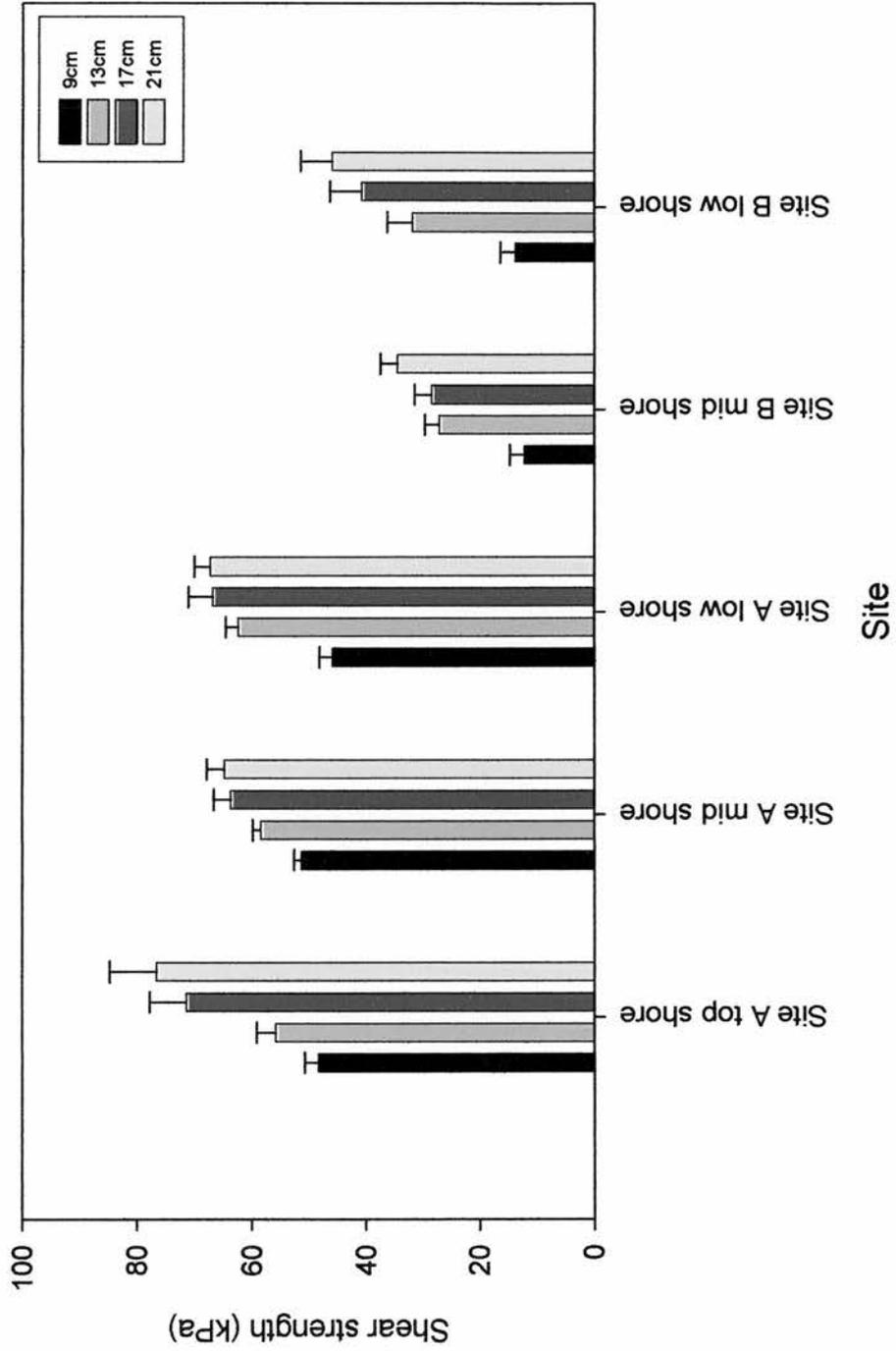


Figure 5.30: Shear strength (kPa) at 4 measured depths, for samples taken during the March 2004 survey. Mean  $\pm$  s.e, n = 15.

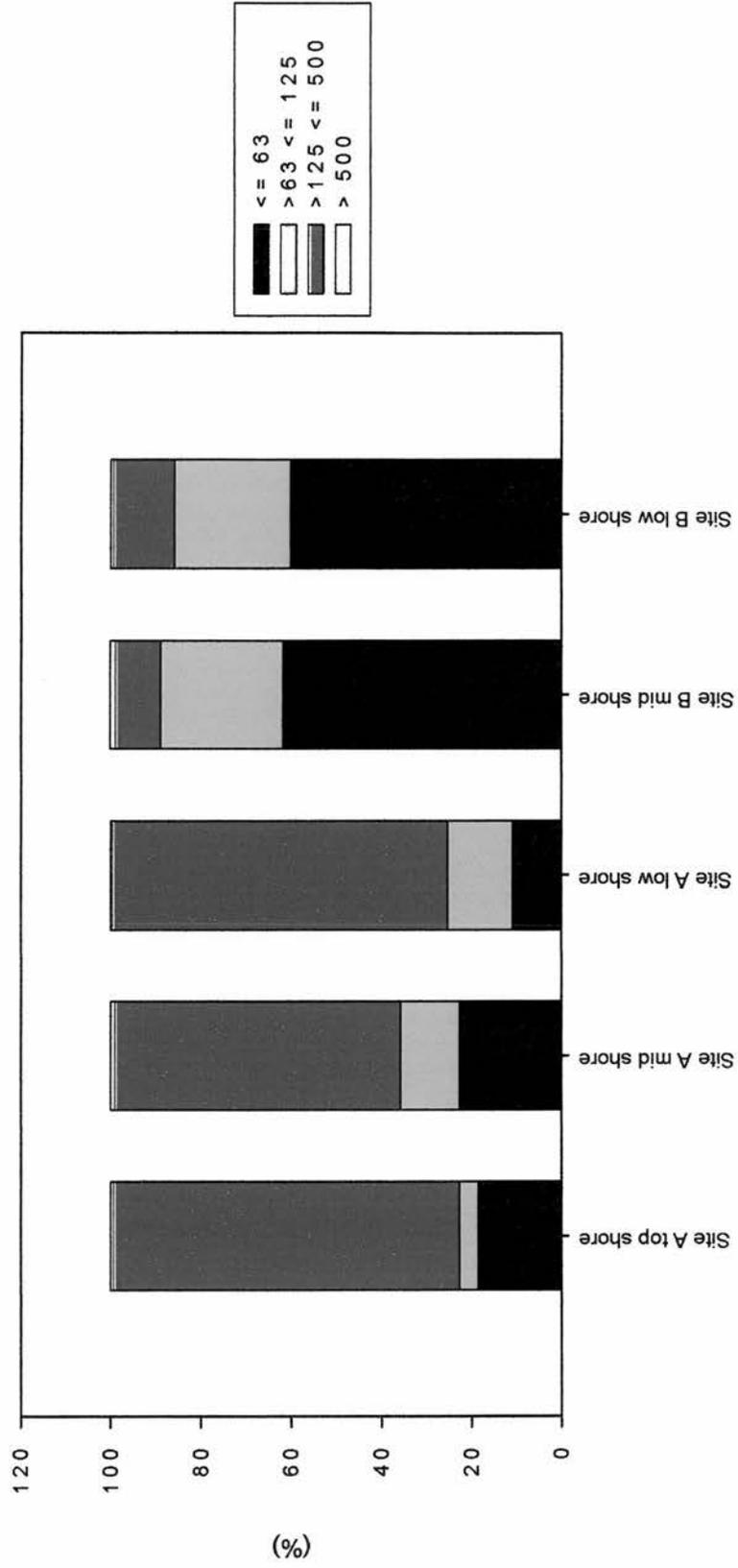


Figure 5.31: Percentage of grain sizes found at each site during the March 2004 survey. Site A was mostly composed of sediment within the  $>125 \leq 500 \mu\text{m}$  range. Site B mostly composed of sediments within the  $\leq 63 \mu\text{m}$  range.

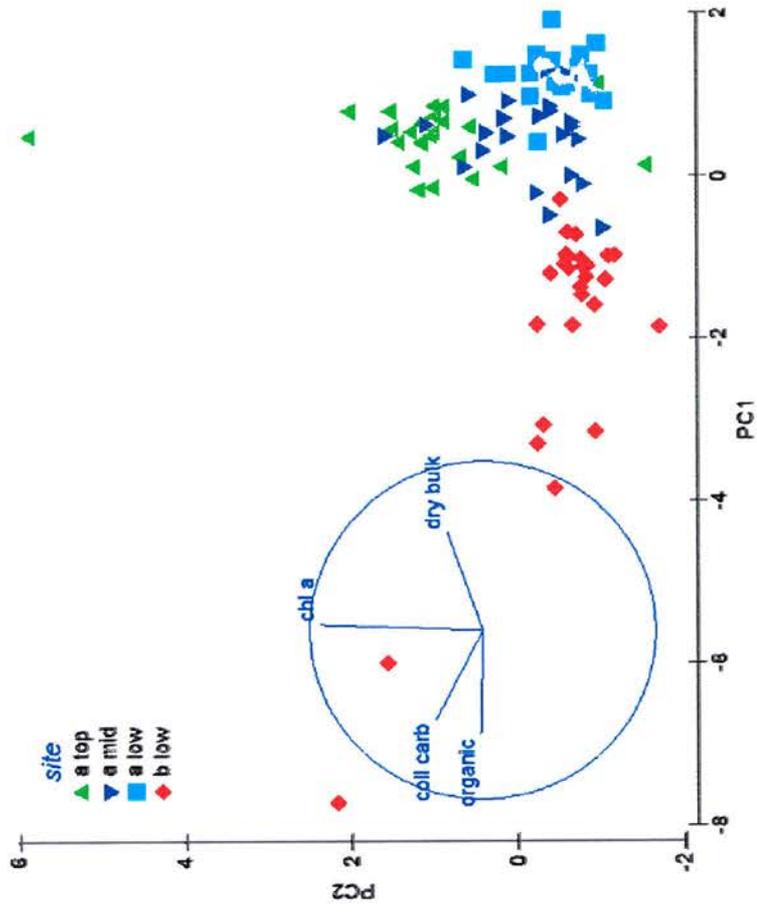


Figure 5.32 : Two dimensional principle components analysis ordination of the parameters measured at each site during March 2004. The ordination indicates the surface sediments at all sites were most influenced by dry bulk density.

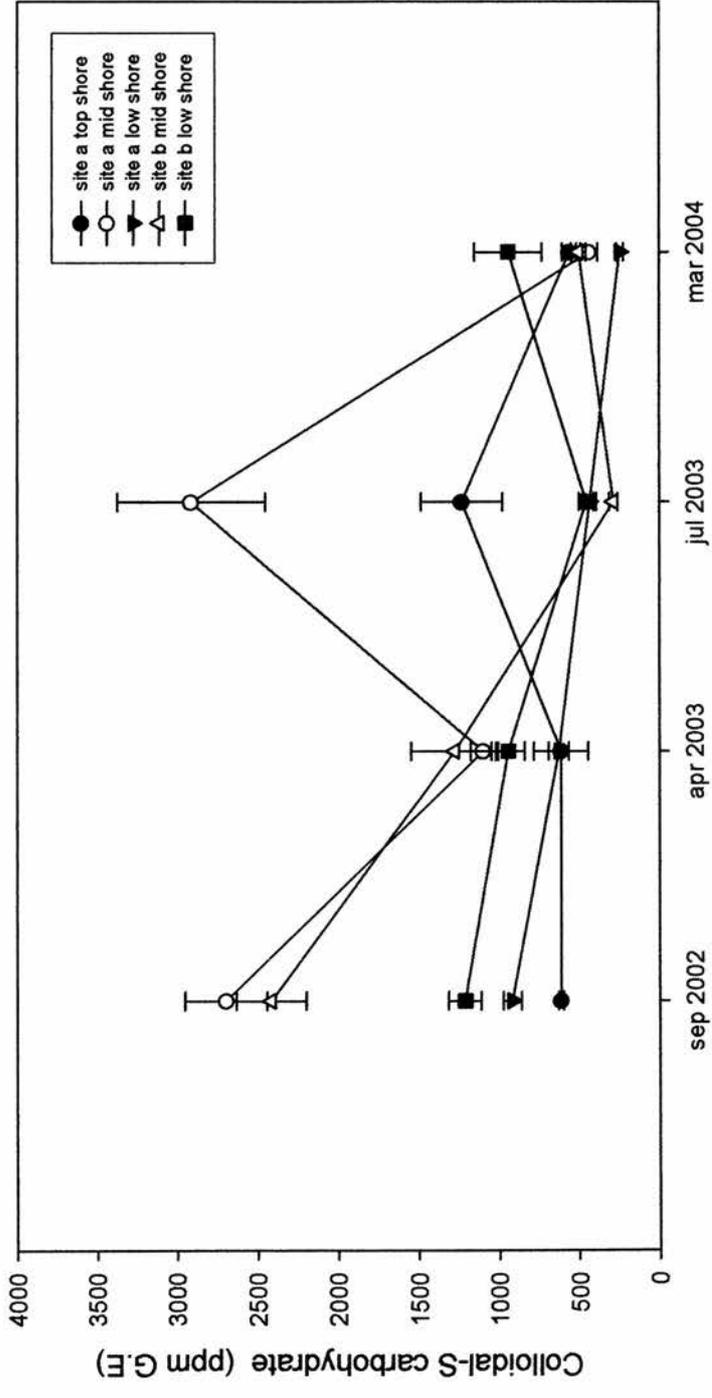


Fig 5.33: Changes in colloidal-S carbohydrate content (ppm G.E) over the period of study at each site.

Significant differences in organic carbon content were observed over the three years at site A top shore ( $H = 78.48$ ;  $d.f = 3$ ;  $p < 0.001$ ), site A mid shore ( $H = 72.22$ ;  $d.f = 3$ ;  $p < 0.001$ ), site A low shore ( $H = 98.78$ ;  $d.f = 3$ ;  $p < 0.001$ ), site B mid shore ( $H = 98.66$ ;  $d.f = 3$ ;  $p < 0.001$ ) and site B low shore ( $H = 48.39$ ;  $d.f = 3$ ;  $p < 0.001$ ) (Figure 5.34).

Significant differences in dry bulk density were observed between the three years at site A top shore ( $H = 95.07$ ;  $d.f = 3$ ;  $p < 0.001$ ), site A mid shore ( $H = 64.92$ ;  $d.f = 3$ ;  $p = 0.000$ ), site A low shore ( $H = 17.46$ ;  $d.f = 3$ ;  $p < 0.001$ ), and site B mid shore ( $H = 44.41$ ;  $d.f = 3$ ;  $p < 0.001$ ). Site B low shore exhibited no significant difference over during the three years of study (Figure 5.35).

Significant differences in chlorophyll *a* content were observed between the three years studied at all sites sampled; at site A top shore ( $H = 50.15$ ;  $d.f = 3$ ;  $p < 0.001$ ), site A mid shore ( $H = 10.42$ ;  $d.f = 3$ ;  $p = 0.015$ ), site A low shore ( $H = 59.20$ ;  $d.f = 3$ ;  $p < 0.001$ ), site B mid shore ( $H = 39.57$ ;  $d.f = 2$ ;  $p < 0.001$ ) and site B low shore ( $H = 42.83$ ;  $d.f = 2$ ;  $p < 0.001$ ; Figure 5.36).

Critical shear stress differed significantly over the three years at site A mid shore ( $H = 10.95$ ;  $d.f = 2$ ;  $p = 0.004$ ), site A low shore ( $H = 23.12$ ;  $d.f = 2$ ;  $p < 0.001$ ), site B mid shore ( $H = 10.62$ ;  $d.f = 2$ ;  $p = 0.005$ ) and site B low shore ( $H = 18.79$ ;  $d.f = 2$ ;  $p < 0.001$ ). The top shore sampling area at site A showed no significant difference in critical shear stress over the three years of study (Figure 5.37).

Sediment shear strength differed significantly over the three years at site A top shore ( $H = 29.49$ ;  $d.f = 2$ ;  $p < 0.001$ ), site A mid shore ( $H = 30.02$ ;  $d.f = 2$ ;  $p < 0.001$ ), site A low shore ( $H = 32.22$ ;  $d.f = 2$ ;  $p < 0.001$ ), site B mid shore ( $H$

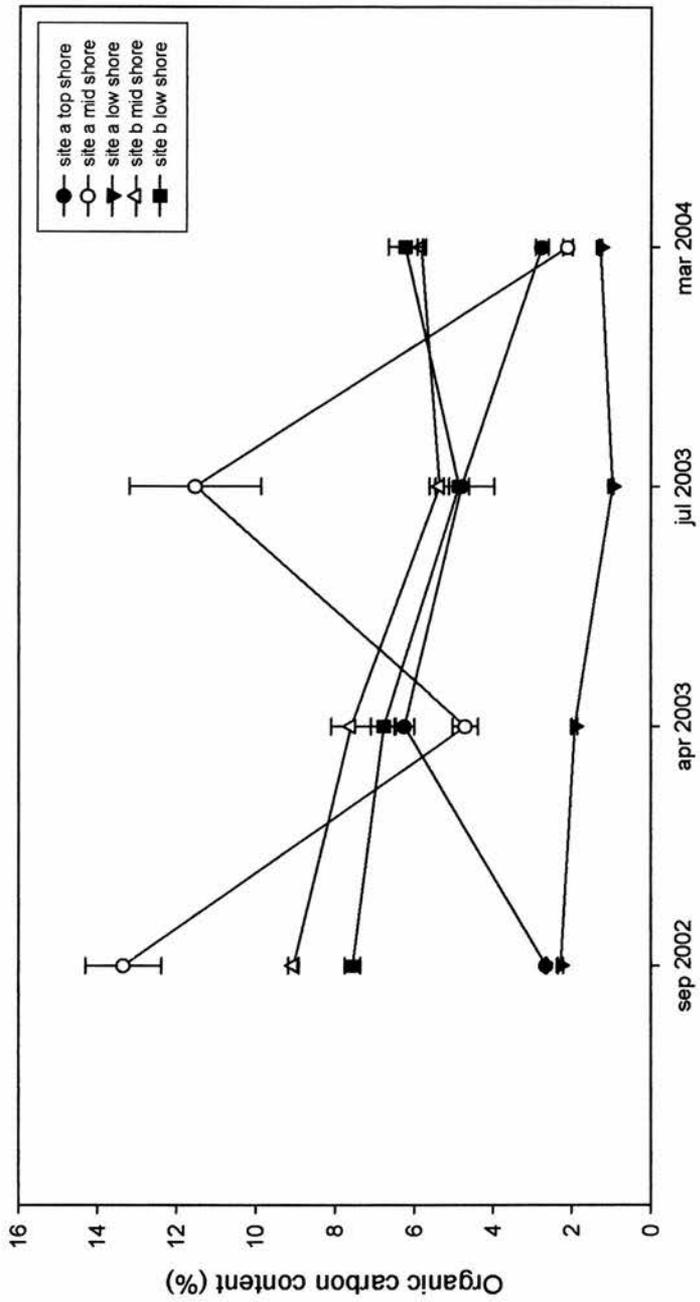


Fig 5.34: Changes in organic carbon content (%) over the period of study at each site.

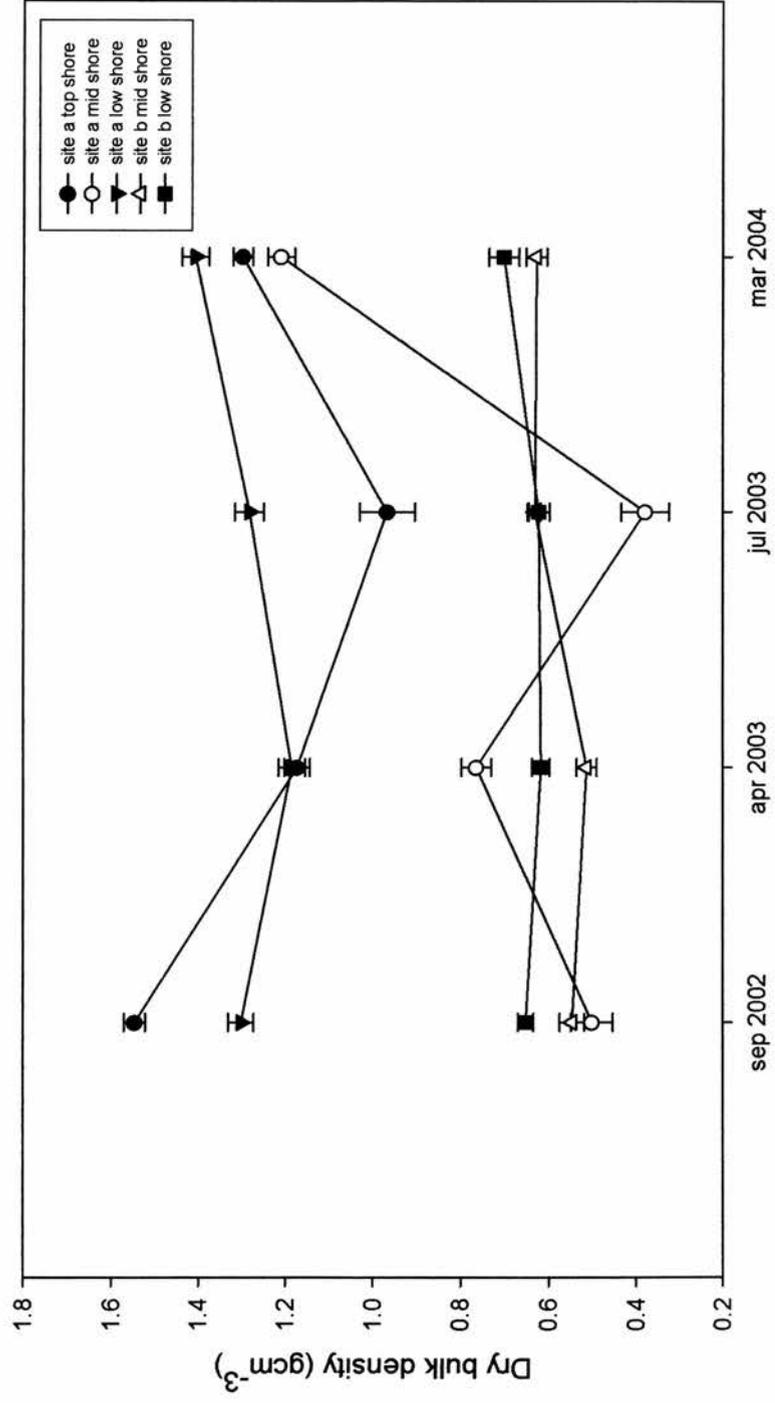


Fig 5.35: Changes in dry bulk density (gcm<sup>-3</sup>) over the period of study at each site.

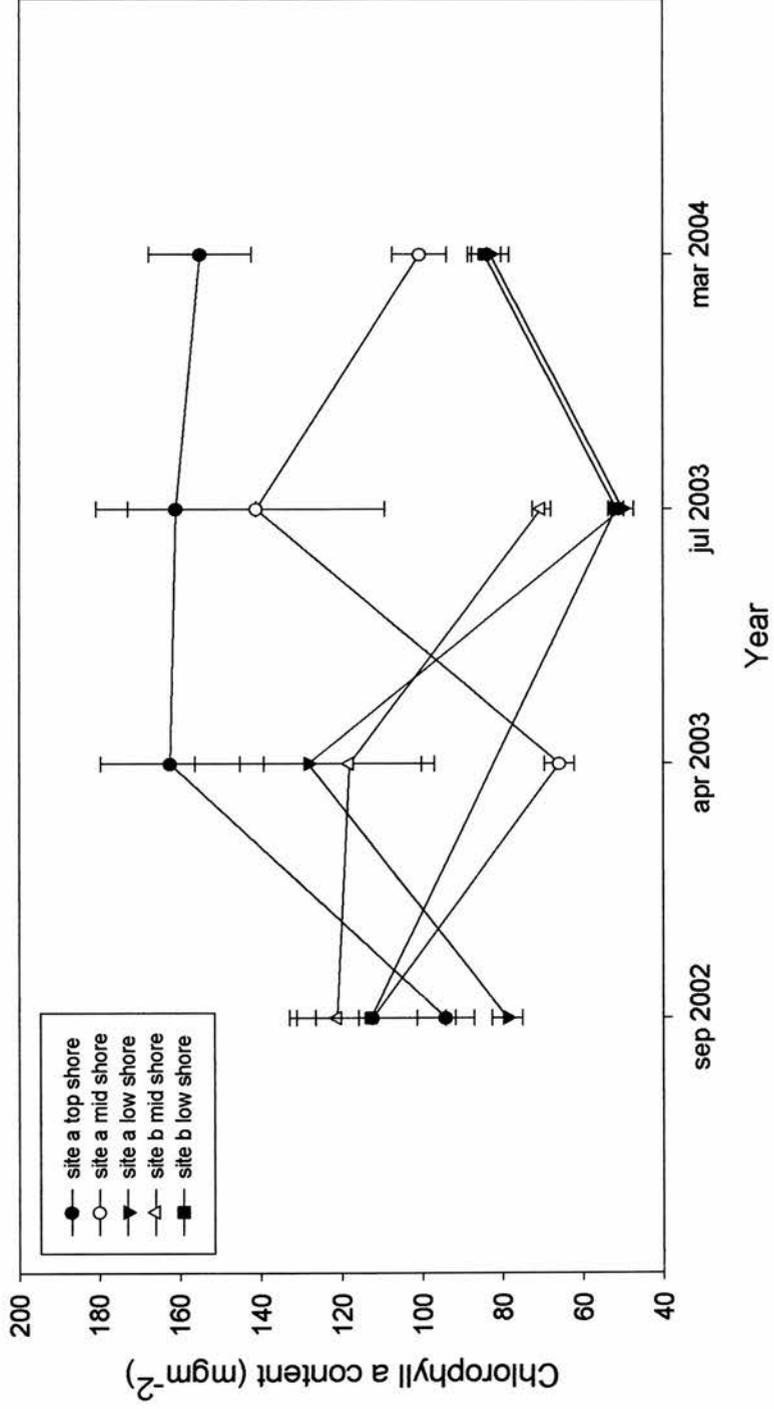


Fig 5.36: Changes in chlorophyll a content (mgm<sup>-2</sup>) over the period of study at each site.

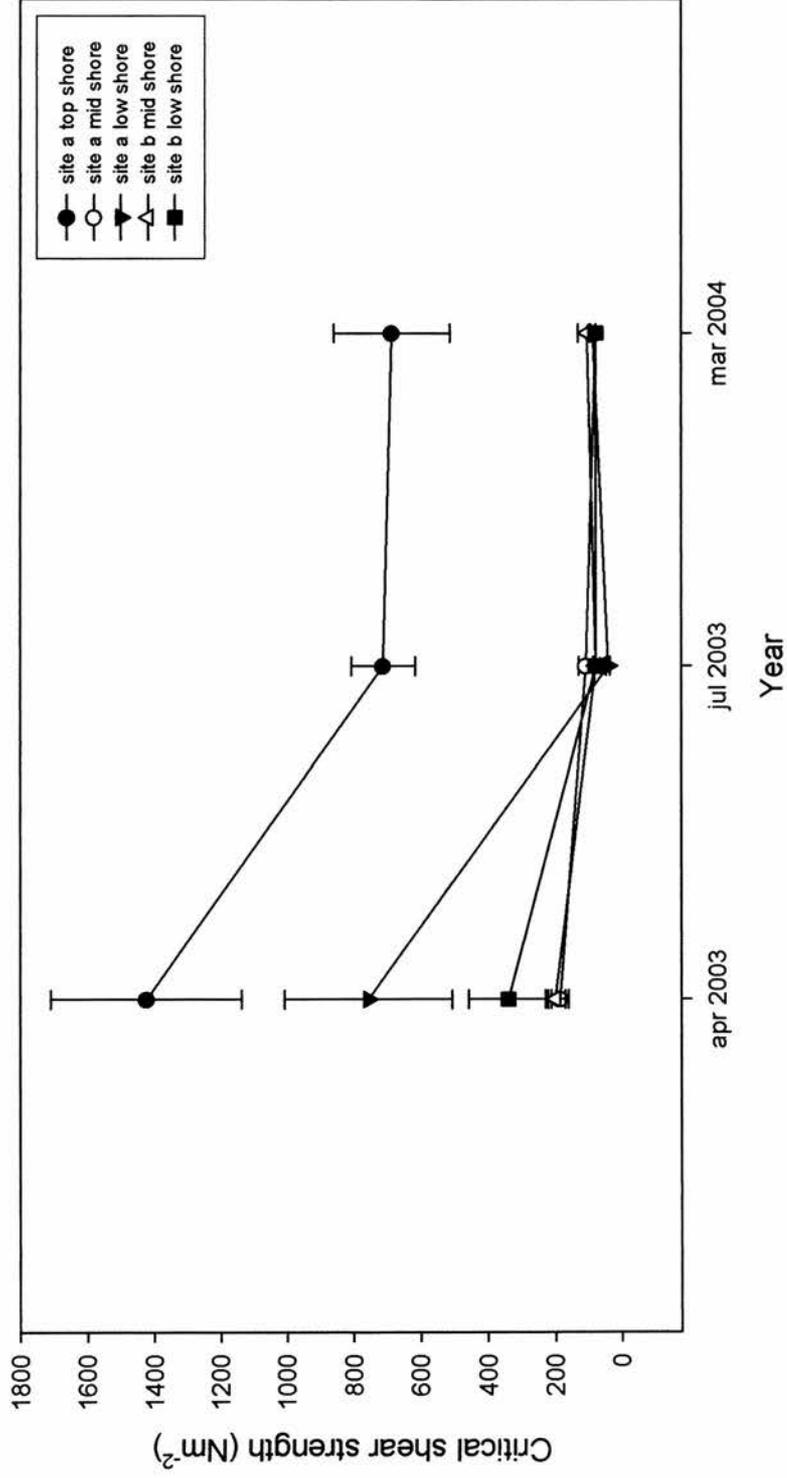


Fig 5.37: Changes in critical shear stress ( $\text{Nm}^{-2}$ ) over the period of study at each site.

= 12.44; d.f = 2; p = 0.002) and site B low shore (H = 12.44; d.f = 2; p = 0.002) (Figure 5.38).

#### 5.3.5.1 Microphytobenthic assemblages

Examination of microphytobenthic assemblages present within the sediments showed variation in composition between sites (Figure 5.39) between the 2 years (September 2002 and July 2003). These variations were most obvious between September 2002 site A top shore and the following sites: September 2002 site B low shore, July 2003 site A top shore, and July 2003 site B mid shore, all of which had ANOSIM R values of 1. The diatom species most responsible for the dissimilarities between assemblages composition were *Navicula cincta*, *Amphora ovalis*, *Achnanthes delicatula*, *Nitzschia dissipata*, *Raphoneis ampiceros*, and *Cocconeis molesta*. Site A top shore (2002) and site A mid shore had the most similar assemblages (ANOSIM R value = -0.111). Low temperature scanning electron micrographs demonstrated that surface sediments contained a greater density of mixed diatom assemblages at the sediment surface at site B than site A (Figure 5.40). No significant difference was observed in assemblage diversity during the September 2002 and July 2003 surveys. Assemblage diversity values (Shannon H') during the July 2003 survey was 1.89, compared to 1.30 during the September 2002 survey. In September 2002 site B had an assemblage diversity value of 1.41 and site A had an assemblage diversity value of 1.22, whereas in July 2003 both sites had similar assemblage diversity values (site A = 1.90; site B = 1.88). A list of species found is available (Table 5.9).

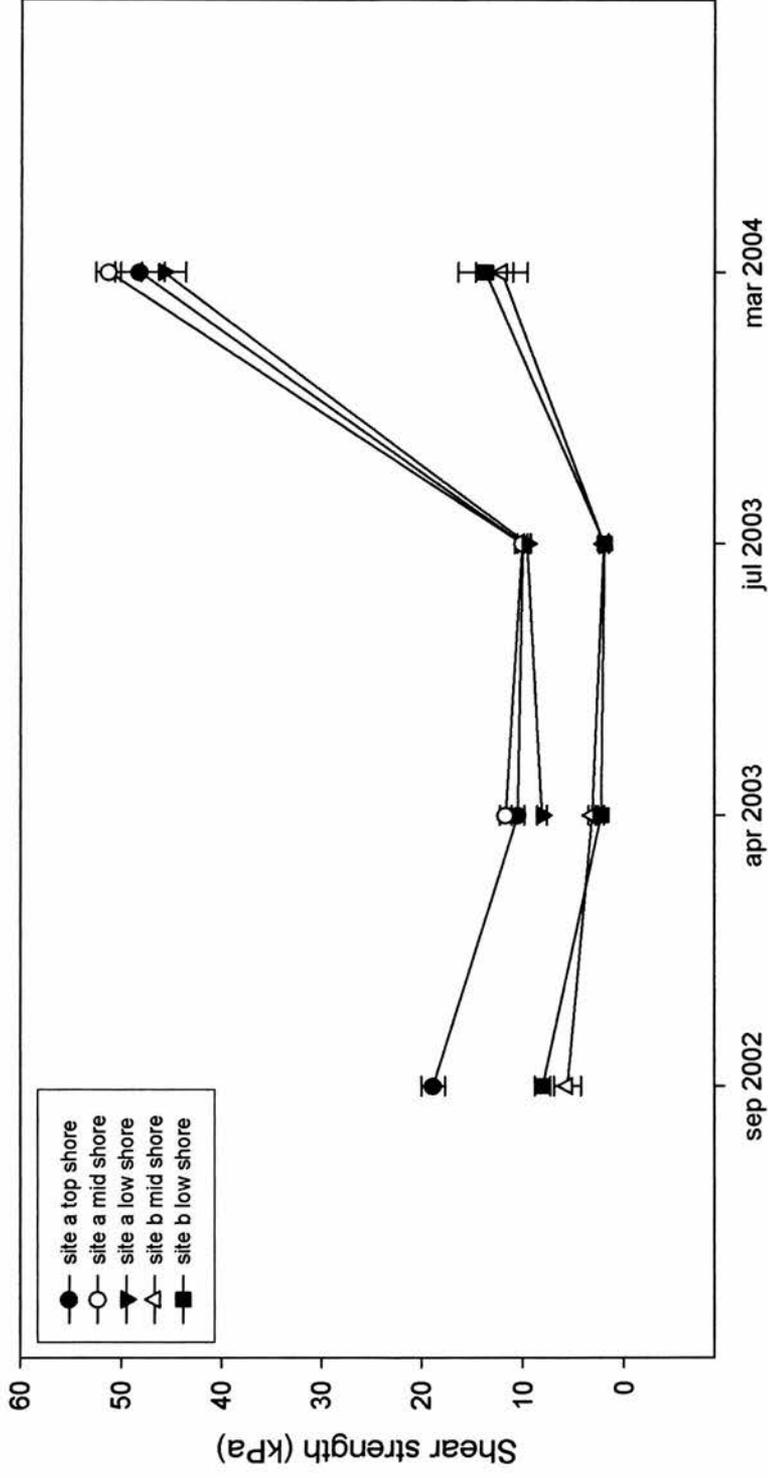


Fig 5.38: Changes in shear strength (kPa) over the period of study at each site.

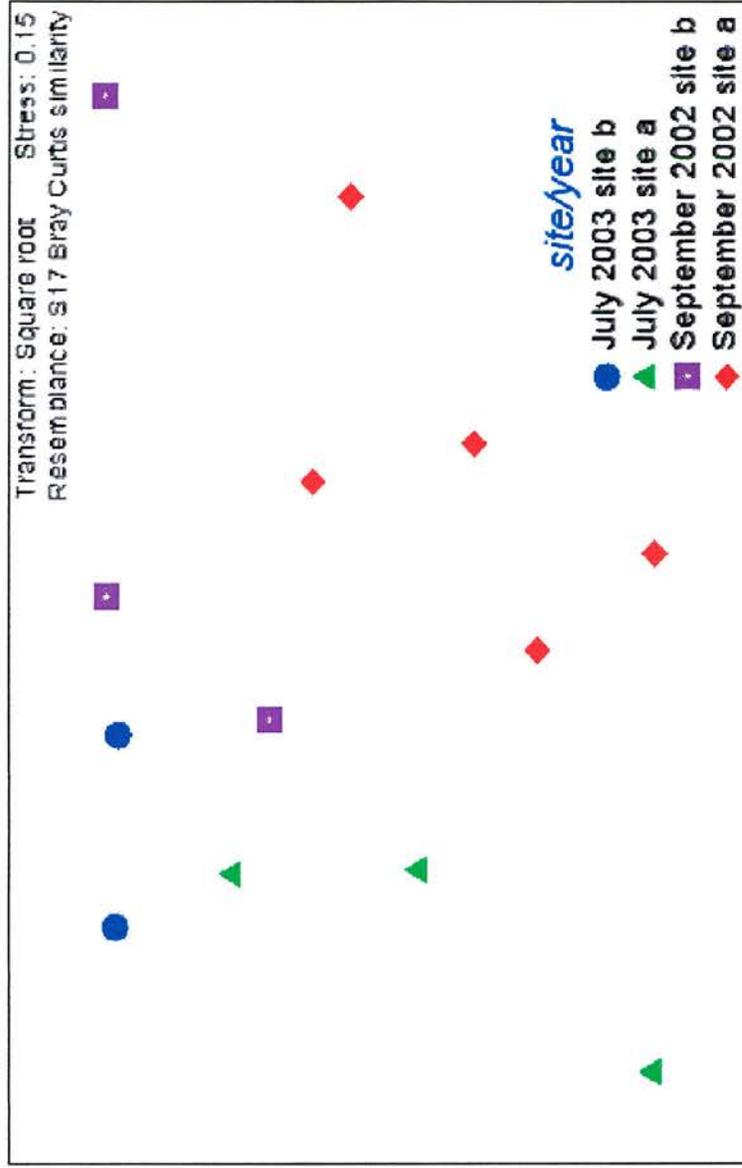


Figure 5.39: Multi-dimensional scaling plots of the microphytobenthic community assemblages present at study sites in the Eden Estuary.

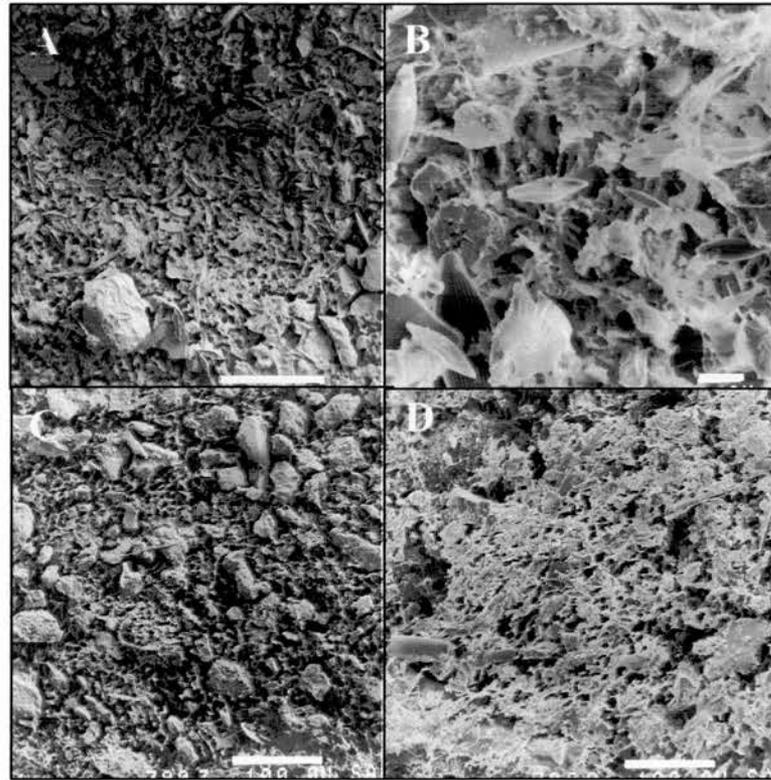


Figure 5.40: Low temperature scanning electron micrographs of surface sediments demonstrated that, during both the September 2002 and July 2003 surveys, surface sediments contained a greater density of mixed diatom assemblage at site B (A-September 2002; B-July 2003) than at site A (C-September 2002; D-July 2003). Bar marker B = 10µm; bar marker A,C,D = 100µm.

<i>Achnanthes brevipes</i>
<i>Achnanthes delicatula</i>
<i>Amphora paludosa</i>
<i>Amphora</i> sp
<i>Amphora rhombica</i>
<i>Cocconeis molesta</i>
<i>Cocconeis scutellum</i>
<i>Cyclotella</i> sp
<i>Cyclotella closterium</i>
<i>Diploneis crabro</i>
<i>Falacia forcipata</i>
<i>Gyrosigma acuminatum</i>
<i>Gyrosigma fasciola</i>
<i>Mastogloia</i> sp
<i>Navicula cincta</i>
<i>Navicula digitoradiata</i>
<i>Navicula gregaria</i>
<i>Navicula virens</i>
<i>Navicula bilobata</i>
<i>Nitzschia constricta</i>
<i>Nitzschia dissipata</i>
<i>Nitzschia frustulum</i>
<i>Nitzschia obtusa</i> var. <i>scalpelliformis</i>
<i>Nitzschia sigma</i>
<i>Opephora</i> sp
<i>Petrodictyon</i> sp
<i>Petroneis latissima</i>
<i>Pleurosigma</i> sp
<i>Psammodictyon panduriforme</i>
<i>Raphoneis amphiceros</i>
<i>Stauroneis</i> sp
<i>Surirella brebonissi</i>
<i>Synedra</i> sp
<i>Thalassiosira</i> sp
<i>Tryblionella punctata</i>

Table 5.9: Motile diatom species collected and identified from intertidal mud flat sediments in the Eden Estuary, during surveys in 2002, 2003 and 2004.

## 5.4 Discussion

Estuarine systems including intertidal mud flats are important areas in terms of environmental, socio-economic factors. The importance of estuarine sites has been recognised by schemes such as the Habitats Directive, the UK Biodiversity Action Plan and the International Ramsar Convention on Wetlands. In order to monitor and manage these habitats to the best ability, systems must be put in place to develop and validate comprehensive dynamic models, incorporating both physical and ecological processes. Such models are being produced by the TIDE project (an EU funded multidisciplinary project) in the hope to better understand the ecosystem functioning of the system as a whole.

The data presented in this chapter represents a small proportion of the work being carried out, but details the measurement of variables within the sediments in order to help develop these models. Whilst *in situ* measurement of sediment stability using systems such as the CSM are rapid and accurate (Tolhurst *et al* 1999, Black and Paterson 1997), proxy measurements (such as chlorophyll *a* content, colloidal carbohydrates, organic content) can also be used (Underwood and Smith 1998, Riethmüller *et al* 2000). These measurements such as chlorophyll *a* content can be easily mapped by ground truthing or remote sensing and can be used to generate maps of stability over a large scale at any given time. The data presented here was collected to determine whether proxy measurements could in fact be used for this purpose.

### 5.4.1 Is the Eden Estuary a biogenic system?

The results gained from this analysis highlight how varied and diverse the two sites within the Eden Estuary are, in terms of both physical properties (dry

bulk density, grain size, and critical shear stress), and biological properties (chlorophyll *a* content, organic content, colloidal-S carbohydrate content, and microphytobenthic assemblage occurrence). Sites A and B both exhibited varying property characteristics, the most obvious being the presence of a different range of grain sizes, which may be the reason for many of the variations found within the other variables measured. This suggests that the variables measured may be most greatly influenced by the physical aspects of the site, as opposed to biological influences, and these results conflict with those from previous studies (Paterson *et al* 2000, Riethmüller *et al* 2000, Riethmüller *et al* 1998).

At the majority of sites dry bulk density was negatively correlated with chlorophyll *a* content, organic carbon content, and colloidal-S carbohydrate content. The areas of highest dry bulk density were sites with a higher proportion of sandy grains compared to the other sites, suggesting these sites were well-drained with low water and organic content. Dry bulk density was the most important variable in terms of influencing the sediments at the Eden Estuary sites, and this was exhibited by the principle components analysis (Fig 5.8, 5.24, & 5.32). Principle components indicated that there was a temporal change in the influence of certain parameters. During the September 2002 study Site A top and low shore were strongly influenced by dry bulk density, and Site B samples were influenced most strongly by colloidal-S carbohydrates and organic content. In April 2003 colloidal-S carbohydrates and organic content influenced all the sites. This then changed and for the last two studies, July 2003 and March 2004, dry bulk density was the most influential factor for all sites. In previous studies chlorophyll *a* had been found to correlate very well with

sediment stability (Austin *et al* 1999, Riethmüller *et al* 1998, and Paterson *et al* 2000). However although this was the only variable found to correlate positively with sediment stability during the present study, the correlation was only evident during the March 2004 study. Riethmüller *et al* (1998) found that the correlation between sediment stability and chlorophyll *a* content became weaker, as the fine grain size fractions decreased, which is concurrent with the grain size fractions found at Site A (dominated by grains in the range  $>125 \leq 500 \mu\text{m}$ ). Sediment stability only increased on intertidal sand flats when chlorophyll *a* content was greater than  $500 \text{mgm}^{-2}$  during studies carried out by Paterson *et al* (1994). Again this can be explained by the larger grain size, and the need for a higher biomass to fill the inter particle spaces before a cohesive effect could occur.

#### 5.4.2. Spatial heterogeneity

The spatial heterogeneity of the sediment surface is highly variable from site to site. These variations may be due to the aspects such as migration of microphytobenthic biofilms from the surface sediments, or variations in sediment size, therefore the formation of relationships between variables such as chlorophyll *a* content and sediment stability is highly site specific due to the spatial variability (Defew *et al* 2002). Figure 5.1 illustrates perfectly the patchy nature of biofilms, and therefore determining if a relationship exists between microbial assemblages and sediment stability over a large scale may be masked by variations in the data set, due to spatial heterogeneity, which itself is a result of biotic and physical interaction within the environment.

#### 5.4.3 Microphytobenthos in intertidal mudflats

The biogenic mediation of intertidal sediments by microphytobenthic assemblages has been well documented (Paterson 1986, 1989, 1994, Underwood and Paterson 1993, Yallop *et al* 1994, Tolhurst 1999). Although assemblage diversities did not vary, the microbial assemblage compositions were most similar at site A top and mid shores, and these sites exhibited large differences when compared to site B, which may be attributed to the sediment grain size in these areas. The grain size at site A was mostly composed of grains  $>125\leq 500\mu\text{m}$ , in comparison with the sediment at Site B which was mostly composed of grains  $\leq 63\mu\text{m}$ . However a large variation in assemblage composition was also observed at site A top shore between September 2002 and July 2003, suggesting that the assemblages underwent a seasonal change. This finding is concurrent with the work done by Underwood (1994), who determined that seasonal changes in diatom assemblage composition occurred on the upper shores of intertidal mudflats.

#### 5.4.4 The erosion of intertidal mud flat sediments

Sediment stability was greater at site A top than any of the other sites. This site was dominated by grains  $>125\leq 500\mu\text{m}$ , and had high dry bulk densities, suggesting a compact sediment with low water and organic content. This may lead to sediment with a high critical shear stress because of both physical and biological factors. Sediments at the upper shores of the intertidal mud flats are exposed for longer periods and as such microphytobenthic biofilms will react to this by producing more EPS in an effort to prevent desiccation of the cells. However desiccation of the sediments and in particular the desiccation of

mucilage (EPS) has been shown (Paterson 1988) to lead to increased sediment stability. Physical factors such as water loss and compaction will also affect the stability of the surface sediments. Perkins *et al* (2003) determine some problems and potential errors associated with measurements of Chlorophyll *a* and EPS as dewatering has been shown to result in the compaction of sediment grains therefore resulting in an increase of dry bulk density (Fleming and Delafontaine 2000). These results highlight the importance of monitoring a suite of variables when examining the sediments of estuarine systems, rather than depending on a single variable, which may be affected spatially and temporally by other environmental variables.

## **5.5 Conclusions**

The results gained from this study emphasise the importance of examining intertidal systems holistically. No single parameter can be used to determine the stability of intertidal mud flats. From this study it appears that stability is dependent on two factors: the sediment grain size and chlorophyll *a* content, and that this is highly site dependent. Although this study goes some way to examining the system as a whole, it by no means considers all parameters involved in the functioning of the system. In order to understand the complex interactions occurring between the biotic and physical processes a large scale survey and extensive multivariate analysis would allow a more accurate description of the estuary to be made, and determine which variables are responsible for shaping the environment on a site specific basis.

If relationships between the microphytobenthic assemblages, stability, and other measured variables are to be used to determine and predict sediment transport through the use of remote sensing much more work needs to be carried out, in order to establish whether this kind of relationship indeed exists, and if so to what scale can it be used. The analysis carried out has shown the collection of data over small spatial scales would have little use in terms of large scale remote sensing projects, due to the small scale heterogeneity of the sediments within estuarine tidal flats. The use of remote sensing to determine vegetation patterns over large areas has been proven successful (Silvestri *et al* 2002), and as such I believe that with more research this could lead to the development of rough descriptions of surface sediments due to associated relationships (ie, elevation and water content). However, the analysis carried out during this study suggest that due to lack of relationships between optical and non optical variables the prediction of accurate descriptions is less likely to be achieved at the present time. I suggest the use of remote sensing for this type of analysis would be most successfully utilized when examining ecosystems in a holistic manner (for example, rather than determining variations within tidal mud flats, sediment transport or stability patterns could be determined on a larger scale by comparing variations from the tidal flat to established salt marsh), and determining patterns and relationships on a larger scale.

Future work to be carried out should involve a more detailed analysis of the microphytobenthic assemblages present and determine relationships between these assemblages to associated variables in order to provide detailed and accurate data for the use of validation of comprehensive dynamical models, allowing the future prediction of the overall system behaviour.

## **CHAPTER SIX**

**SPATIAL AND TEMPORAL VARIATION IN SALT  
MARSH SEDIMENTS, VENICE LAGOON, ITALY.**

## **Chapter six – Abstract**

The salt marsh examined in this study was situated in the Venice Lagoon, Italy. Salt marsh ecosystems are highly sensitive to change and the health and stability of these systems are greatly dependent on the balance between deposition, accretion, and erosion of sediments. The Venice lagoon system is no exception. Halophytic angiosperms may appear to dominate the salt marsh; the relatively stable sediment in which they grow provides a nutrient rich substratum, which is ideal for the survival and growth of microbial assemblages. These microbes are essential for the success of salt marsh ecosystems, which would not function without the essential biogeochemical processes driven by the microbial metabolism provided by microbial assemblages. The purpose of this study was to determine relationships between stability of the salt marsh sediments and biogenic variables measured, a relationship rarely addressed.

Stabilisation of the salt marsh sediments was found to be highly variable within and between sites. However, the grain size distribution across the sites was constant removing the possibility that this was the cause of the variation. Thus the variation between sites and within sites may have more in keeping with the biological nature of the sediment and hence the inherent spatial variability of biological assemblages. Microphytobenthic identification exhibited distinct assemblage composition at each site. The shear stress results obtained throughout the study exhibited three steps to the erosion process, which were related to a stratified microbial layer, changing with depth.

The data suggests that dry bulk density appears to influence the salt marsh sediments to a greater degree than the other measured parameters, however the stability of the salt marsh could not be related to any individual measured

parameter. Either the system is too variable to predict with our current knowledge or a more holistic sampling approach might be required, including the nature of the higher salt marsh plants present at each site.

## 6.1 Introduction

Salt marshes usually occur in relatively sheltered locations between the heights of mean high water neap tides and mean high water spring tides. These ecosystems occur in five main habitats: estuaries, saline lagoons, behind barrier islands, at the heads of sea lochs, and on beach plains. The salt marsh examined in this study was situated in the Venice Lagoon, Italy. The Venice Lagoon is a semi enclosed body of water with limited freshwater inflows and three links to the Northern Adriatic sea at Lido, Malamocco and Chioggia. Sediment dynamics play a large role in the ecological status of the lagoon, including the salt marsh areas, and are controlled mainly by wave energy, river flow, and coastal currents. Open water and tidal channels make up 78% of the enclosed lagoon area, whilst the areas of salt marsh cover approximately 37km<sup>2</sup> of the lagoon (Ravera 2000). The general ecology of the system functions as a balance between riverine and marine influences.

### 6.1.1 The importance of salt marsh systems

Salt marshes are dynamic and complex ecosystems that have a multitude of functions and are highly important in sustaining the ecology of coastal areas. These ecosystem functions include acting as barriers between land and sea by absorbing wave energy (thereby decreasing coastal erosion), serving as nurseries for fish, important areas for migrating birds, and providing sites of primary production that sustain the coastal food web. As well as providing these ecosystem services salt marshes are rare and valuable habitats in their own rights with respect to faunal and floral conservation (Paramor and Hughes 2004, Hughes and Paramor 2004, Adam 2002, King and Lester 1995). An estimate of

the economic value of 50m width of salt marsh has been calculated as £6000 per hectare (King and Lester 1995) and whilst there are many criticisms regarding such socio-economic valuations the point is made that salt marshes are valuable habitats worthy of our protection, so much so that they are a priority habitat in European Biodiversity Action Plans.

#### 6.1.2 The implications of climate change

Salt marsh ecosystems are highly sensitive to change (Doody 2000) and the health and stability of these systems are greatly dependent on the balance between deposition, accretion, and erosion of sediments. This balance is under threat due to climate change and the associated rise in sea surface temperature (which will be exacerbated in a lagoonal system due to an average depth of 1.5m), an increase in salinity, a rise in sea levels and an increase of storm frequency (IPCC 2001). The combination of these factors in the Venice Lagoon will lead to increased flooding, extended periods of tidal inundation, loss of salt marsh habitat, and accelerated erosion. The erosional process is exacerbated in some locations by a reduced supply of sediment, since only three freshwater inputs now carry sediment into the lagoon. The extent of these impacts will depend greatly on the rate of change relative to sediment supply and rate of sediment deposition. In the south of England relative sea level rise was recorded as 4-5mm per year during 1973-1988, and during this period 23% of salt marsh area was lost (Pethick 1993).

### 6.1.3 Anthropogenic influences

The placement of sea walls often increases the rate of salt marsh loss by preventing natural landward migration, also known as coastal squeeze. These defences are still in use today despite the high costs associated with the initial construction and continued maintenance. This seems ironic, as recent research has shown an increase in the width of salt marsh present is directly related to a decrease in the construction cost for coastal defence barriers (King and Lester 1995). As a result of findings such as this and concern by environmental agencies because of the rate of habitat loss, salt marsh ecosystems are being re-established by accepting the loss of land and allowing the natural landward migration of the salt marsh species. In the UK recent work led by the Environment Agency has promoted the role of salt marshes as wave energy dissipaters prior to reaching sea wall defences thereby reducing the costs of coastal defence. Flood defence costs can therefore be reduced in the long term by setting back lines of defence and allowing salt marsh development on the seaward side of obsolete man made defences (UK Biodiversity Action Plan 2004). The Rural Development Service (part of the Department for Environment, Food and Rural Affairs) have listed coastal salt marsh as one of the key areas which land owners can gain stewardship awards by managing the land in such a way that it can revert to a more natural habitat. For management strategies such as managed realignment to be successful it is important to understand the ecology and processes involved in the formation of salt marsh systems due to the difficulties involved in predicting the type of habitat that would emerge from different geographical location and management plans.

#### 6.1.4 Sediment dynamics

Salt marshes require continual deposition of sediment in order to persist (Aspden et al 2004b, Day *et al* 1999, Shi *et al* 1996). The sediment dynamics within a salt marsh habitat are complex. Variation in surface flow leads to the hydrodynamic sorting of particles so that sediment particles of different size classes will be deposited at various places within the salt marsh area. Due to the fact that flow velocity is impeded by existing vegetation, the sediment found within the centre of the salt marsh tends to be fine cohesive particles. Once sediment has been deposited it undergoes dewatering, compaction and biogeochemical processes thereby becoming part of the sediment surface. Sediment composed of fine cohesive particles creates a substratum with high bulk density and low permeability, resulting in limited diffusion and so physicochemical gradients tend to be steep. Therefore only the first few millimetres of the sediment surface are aerobic, rapidly becoming anaerobic due to a lack of oxygen, thereby creating a harsh environment to which specialist microbial assemblages have adapted to and exploited (Aspden et al 2004b).

Traditionally salt marsh ecology and dynamics were believed to be driven by physical processes that put restraints upon the biology of the habitat. However, more recently it has been acknowledged that whilst the physical dynamics are an integral part of the system, the biological components are equally important, and can in turn mediate the physical environment, by processes such as bioturbation, biogenic stabilisation, and the manipulation of flow by vegetation (Shi *et al* 1996, Shi *et al* 1995, Fonseca *et al* 1986).

### 6.1.5 Salt marsh vegetation

Salt marsh vegetation is dominated by a number of halophytic (salt tolerant) angiosperms adapted to regular immersion by the tides. Salt marsh communities are affected by changes in the environment such as temperature, salinity or physical factors such as the particle size of the sediment. Most salt marsh systems exhibit a clear zonation pattern of plant species adapted to varying periods of inundation by the tides. For example at the lowest levels the glassworts, *Salicornia* spp can withstand immersion by as many as 600 tides per year, while transitional species of the upper marsh can only withstand occasional inundation (UK Biodiversity Action Plan 2004). The presence of salt marsh vegetation attenuates the wave energy of incoming tides, thereby promoting the deposition of sediments amongst the stems, and decreasing the erosional power of the flow. The physical presence of a root structure within the sediment increases stability also. Although the halophytic angiosperms may appear to dominate the salt marsh, the relatively stable sediment in which they grow provides a nutrient rich substratum, which is ideal for the survival and growth of microbial assemblages. These microbes are essential for the success of salt marsh ecosystems, which would not function without the essential biogeochemical processes driven by the microbial metabolism provided by microbial assemblages. The majority of these processes occur within the nutrient rich sediments and contribute to sediment oxygenation, organic matter breakdown, nutrient recycling, and sediment dynamics.

### 6.1.6 Benthic microbial assemblages

Due to the steep physicochemical gradients present within the surface layers of the sediment, the microbial assemblages present vary accordingly. The upper layers are inhabited by anoxygenic phototrophs, and with depth heterotrophic forms become dominant. The microbial assemblages within salt marsh systems are essential to functioning and ecosystem services of the system (Chapin *et al* 1997), through carbon and nitrogen fixation, to the capture and retention of sediments. Whilst most studies have concentrated on microbial assemblages found within intertidal cohesive sediments (Figure 6.1) (Admiral 1984, Underwood and Krompkamp 1999, Paterson and Hagerthy 2001) these organisms can occur anywhere where light levels are great enough to support photosynthesis.

Diatoms are single celled photosynthetic algae estimated to produce 4% of total global primary productivity within marine systems (Medlin 2002). The majority of diatoms found within salt marsh systems are less than 30µm in length (Paterson 1986) and usually migrate within the upper 1-3 mm of the sediment surface (Honeywill 2001, Paterson 1986). They occur at these depths due to the need to obtain the optimal light in order to photosynthesise (Palmer and Round 1965, Paterson 1986) and are capable of locomotion (see Chapters 1 and 5).

Cyanobacteria, like diatoms, photosynthesise and move through the sediment by exuding polymeric material (Stal 2001). Cyanobacteria are present in salt marsh sediments in filamentous or unicellular forms and can accumulate in the top layers of the sediment surface forming dense mats. These dense mats are capable of stabilising sediments by trapping sediment within the filamentous structure, or by creating a smooth surface layer thereby promoting skimming



Figure 6.1: Salt marsh systems are dominated by halophytic angiosperms (1) but the sediment among and between the plants is colonised by a highly productive microbial assembles. This microbial development can colour the surface of the sediment and is particularly pronounced in wet salt pan regions (2). On the surface of drier sediment there is often little obvious microbial development, however removal of the surface layer, even by scuffing a shoe over the surface, reveals a coloured subsurface layer (3). This layer usually comprises filaments of cyanobacteria that are responsible for carbon fixation, nitrogen fixation and can also bind and retain sediment against hydrodynamic stress. Note the bubbles and grains bound in the matrix shown in the image (4). Diatoms are also common component of the microbial assemblage (5 & 6) usually found in more moist regions and lying in a layer above the cyanobacterial zone. This is not always the case since the assemblage may be mixed and both diatoms and cyanobacteria are capable of migration in response to environmental conditions (5) = *Surirella fastuosa*, (6) = *Amphiprora paludosa*, and *Stauroneis* sp.

flow (Paterson 1994). Cyanobacteria are also capable of migration through the salt marsh sediments, and during periods of lower light levels they accumulate at the sediment surface and migrate deeper into the sediment as light levels increase (Stal 2000). Different triggers may cause this migrational behaviour. As light levels decrease the opportunity for photosynthesis is reduced and anoxic conditions spread toward the sediment surface. This increases the level of sulphide in the sediment, which is toxic to cyanobacteria and may induce the upward migration of the cells. Cyanobacteria appear to be adapted to low levels of light and as light levels increase they migrate down away from the surface stimulated by a negative phototaxis. The diversity of cyanobacteria is not as great as for diatoms in salt marsh systems, and a number of common genera regularly occur in the sediment matrix including *Oscillatoria*, *Microcoleus*, and *Schizothrix* (Stal 2000). Whilst diatoms and cyanobacteria tend to have similar functional roles within salt marsh systems, cyanobacteria are also capable of nitrogen fixation and provide an important ecosystem service in terms of nutrient cycling within the system.

#### 6.1.7 Biogenic stabilisation of salt marsh sediments

Sediment stabilisation can be enhanced by the presence of biotic influences such as the presence of microbial assemblages and higher salt marsh plants. Many studies have been carried out in the laboratory on abiotic sediments (Manzenreider 1983, Grant and Gust 1987), but without taking biotic interactions into account these findings cannot be used to determine sediment dynamics *in situ*.

Organisms such as cyanobacteria and filamentous algae are capable of trapping and retaining sediment within filaments, thereby structurally modifying the environment around them (Airoldi *et al* 1996, Paterson 1997, Aspden 2005 submitted). This stabilisation of the sediment surfaces greatly reduces the potential for surface erosion. The presence of higher plants, increases the stabilisation of sediments also due to the structural support provided by roots and stems (van Eerdt 1985). The presence of salt marsh canopies can promote skimming flow over the tops of shoots and away from the sediments surface, and also causes the reduction in flow velocity and promotes the deposition of fine sediments (Fonseca *et al* 1986, Huettel *et al* 2002).

The exudates produced by the microbial assemblages present within salt marsh systems, increase the mechanical stability of sediments (Yallop *et al* 1994, Paterson 1997, Austen *et al* 1999) by the cohesion of sediment particles due to the EPS produced, and the associated increase in inter particle binding (Chenu and Jaunet 1992, Paterson 1994, Yallop *et al* 1994). As the production of EPS increases the stability of the sediment increases correspondingly (Frankel and Mead 1973, Holland *et al* 1974), and as diatom biomass can potentially double in a day (Underwood and Paterson 1993), it is obvious that the presence of microbial assemblages are important to the formation and growth of salt marsh systems.

During this research the following hypotheses were tested:

- Sites with high microphytobenthic biomass will have high sediment stability.
- Microphytobenthic assemblages will vary between sites depending on the physical nature of the sediment.

## 6.2 Materials and Methods

### 6.2.1 Study Sites

Five sites within the Venice Lagoon were sampled over a period of 5 days during July 2002, July 2003, and February 2004 (Figure 6.2). The sites sampled were San Felice, Salina Norde, Palude Maggiore, Trombetta, and Passarini. Within each of these sites a 25 point grid (5x5) was arranged, with 2m between each point, and 8m total length (Figure 6.2). Points 1-5 were always placed so that they faced east. The designated sampling areas were 0.5m radius around each point.

### 6.2.2 Field sampling methods

During 2002, the field sampling carried out at points 1- 25 included critical erosion shear stress measurements ( $n = 1$ ) using the cohesive strength meter (Tolhurst 1999, Vardy *in press*), and contact core measurements ( $n=3$ ) at each point within the grid. At point 13 cryolander samples were obtained ( $n = 3$ ) along with surface scrape samples ( $n = 3$ ), and at 5 random positions within the grid mobile microphytobenthic samples were collected using the lens tissue method. Shear stress analysis was modified by using a new CSM calibration in order to account for inconsistencies found at higher pressures between different models of CSM system. A description of the new calibration can be found in Vardy *in press*).

The same field sampling methods were repeated in July 2003, and February 2004, but the number of nodes sampled within the grid was decreased in order to reduce the number of samples.

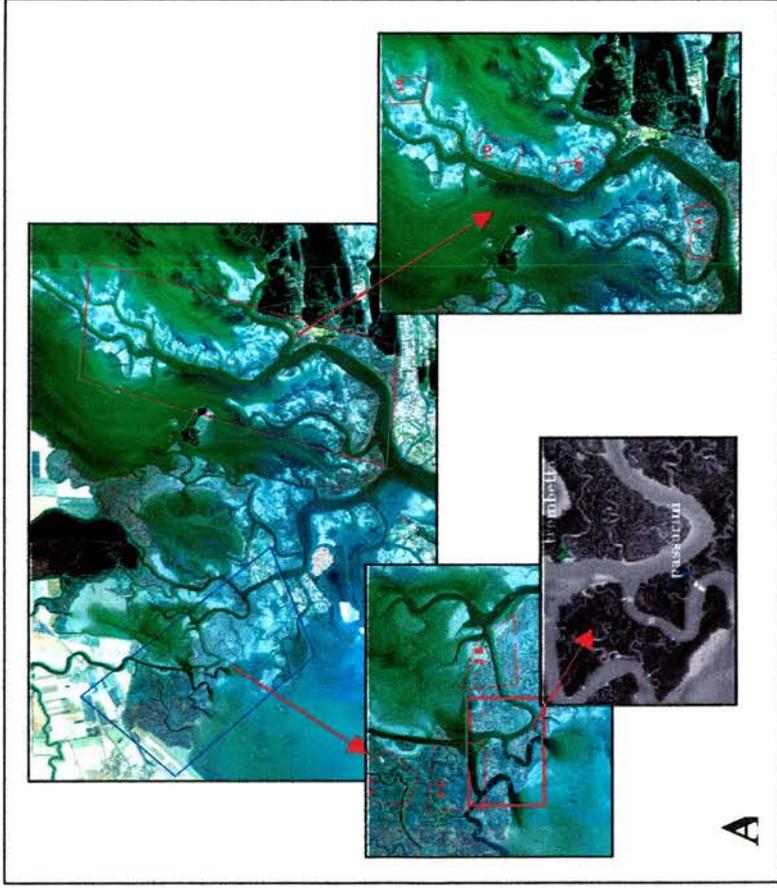


Figure 6.2: A: Images of the Venice Lagoon indicating sites of study areas; San Felice (1A), Salina Nord (1C), Palude Maggiore (1D), Trombetta and Passarini. B: Diagrammatic representation of sampling grid. Each node (25 nodes in total) placed 2 m apart, around which the sampling area was 0.5m<sup>2</sup>.

Field sampling in 2003, and 2004 included critical erosion shear stress measurements (n =1), contact core measurements (n=3) and in addition shear vane measurements (n = 5) at four depths, from points 1, 5, 13, 21 and 25.

### 6.2.3 Laboratory sampling methods

The parameters used as proxies for sediment stability (Black and Paterson, 1997; Consalvey, 2002; Paterson 1997) were chlorophyll *a* content, colloidal-S carbohydrate content, dry bulk density and organic carbon content. Chl *a* was extracted using demethylformamide (DMF) and quantified using high performance liquid chromatography (HPLC). Colloidal-S carbohydrates were extracted using the methods of Underwood *et al.* (1995) and Smith and Underwood (1998). Sediment dry bulk density was determined after lyophilisation for a period of 24h and organic carbon content was measured as ash-free dry weight. Sediment grain size was determined using a Beckman Coulter LS 230 Particle Size Analyser. Microphytobenthic assemblage composition was determined using light microscopy. Low-temperature scanning electron microscopy was also carried out on surface scrape samples to correct species identification, and to examine the surface structure of the sediment. See Chapter 2 for individual technique methodologies.

### 6.2.4 Statistical analysis

The Anderson–Darling test for normality and Bartlett’s test of equal variances were carried out to test for normality and equality of variances. If data fulfilled the requirements One way ANOVA, Tukey post hoc tests and the t-test were used to determine variations within sites and over time. If data did not

fulfil these requirements it was transformed using a box-cox transformation, and retested for normality and equal variances. If after the transformation data still did not express normality and equal variances further analysis was carried out using the Kruskal Wallis test and Mann-Whitney test (Dytham 2003, Zar 1999). Results were considered significant at  $p < 0.05$ . Spearman rank order correlations were carried out to determine any relationships between measured parameters. Assemblage analysis was carried out by multidimensional scaling (MDS) using PRIMER (6 Beta) software in order to examine the relative dissimilarity of the microphytobenthic community assemblage composition between sites. Shannon-Wiener diversity indices were applied to microphytobenthic cell count data, to compare diversity of assemblages within sites.

## **6.3 Results**

### 6.3.1 July 2002

#### 6.3.1.1 Sediment variables

The organic content, colloidal-S carbohydrate content, dry bulk density, sediment stability, sediment grain size and chlorophyll *a* were examined in the surface of the salt marsh sediments and are indicated by figures 6.3-6.8. Where a significant difference was found within individual sites during the survey in July, 2002 this is indicated in Table 6.1.

Significant variation of organic content was found at all sites studied ( $H = 286.47$ ;  $d.f = 6$ ;  $p < 0.001$ ) except Paulde Maggiore (B) and Passarini ( $W = 5601.0$ ;  $p = 0.358$ ) (Figure 6.3). A significant difference between sites was

Organic content	San Felice(A)	San Felice (B)	Palude Maggiore (A)	Palude Maggiore (B)	Passarini	Trombetta
San Felice (B)	0.000					
Palude Maggiore (A)	<b>0.000</b>	<b>0.002</b>				
Palude Maggiore (B)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>			
Passarini	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.358		
Trombetta	<b>0.036</b>	<b>0.000</b>	<b>0.000</b>	<b>0.025</b>	<b>0.003</b>	
Salina Norde	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
Colloidal-S carbohydrate content	San Felice(A)	San Felice (B)	Palude Maggiore (A)	Palude Maggiore (B)	Passarini	Trombetta
San Felice (B)	0.491					
Palude Maggiore (A)	<b>0.001</b>	<b>0.000</b>				
Palude Maggiore (B)	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>			
Passarini	0.051	0.111	0.189	<b>0.000</b>		
Trombetta	<b>0.000</b>	<b>0.000</b>	0.058	<b>0.018</b>	<b>0.006</b>	
Salina Norde	<b>0.011</b>	<b>0.028</b>	0.820	<b>0.004</b>	0.438	0.170
Critical shear stress	San Felice(A)	San Felice (B)	Palude Maggiore (A)	Palude Maggiore (B)	Passarini	Trombetta
San Felice (B)	<b>0.000</b>					
Palude Maggiore (A)	<b>0.000</b>	<b>0.001</b>				
Palude Maggiore (B)	<b>0.000</b>	0.185	<b>0.028</b>			
Passarini	0.095	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		
Trombetta	0.831	<b>0.000</b>	0.173	<b>0.006</b>	0.194	
Salina Norde	<b>0.019</b>	0.070	0.691	0.375	<b>0.002</b>	<b>0.049</b>
Dry bulk density	San Felice(A)	San Felice (B)	Palude Maggiore (A)	Palude Maggiore (B)	Passarini	Trombetta
San Felice (B)	<b>0.000</b>					
Palude Maggiore (A)	<b>0.000</b>	<b>0.000</b>				
Palude Maggiore (B)	0.520	<b>0.000</b>	<b>0.000</b>			
Passarini	0.677	<b>0.000</b>	<b>0.000</b>	0.346		
Trombetta	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.002</b>	
Salina Norde	<b>0.000</b>	0.560	<b>0.015</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
Chlorophyll a content	San Felice(A)	San Felice (B)	Palude Maggiore (A)	Palude Maggiore (B)	Passarini	Trombetta
San Felice (B)	<b>&lt;0.05</b>					
Palude Maggiore (A)	>0.05	<b>&lt;0.05</b>				
Palude Maggiore (B)	>0.05	<b>&lt;0.05</b>	>0.05			
Passarini	>0.05	<b>&lt;0.05</b>	>0.05	>0.05		
Trombetta	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	
Salina Norde	>0.05	<b>&lt;0.05</b>	>0.05	>0.05	>0.05	<b>&lt;0.05</b>

Table 6.1: Descriptive statistics carried out to compare between sites studied. A Mann-Whitney test was used to determine significant differences ( $p < 0.050$ ), which are indicated in bold (One way ANOVA, and Tukey post hoc was used for chlorophyll a content).

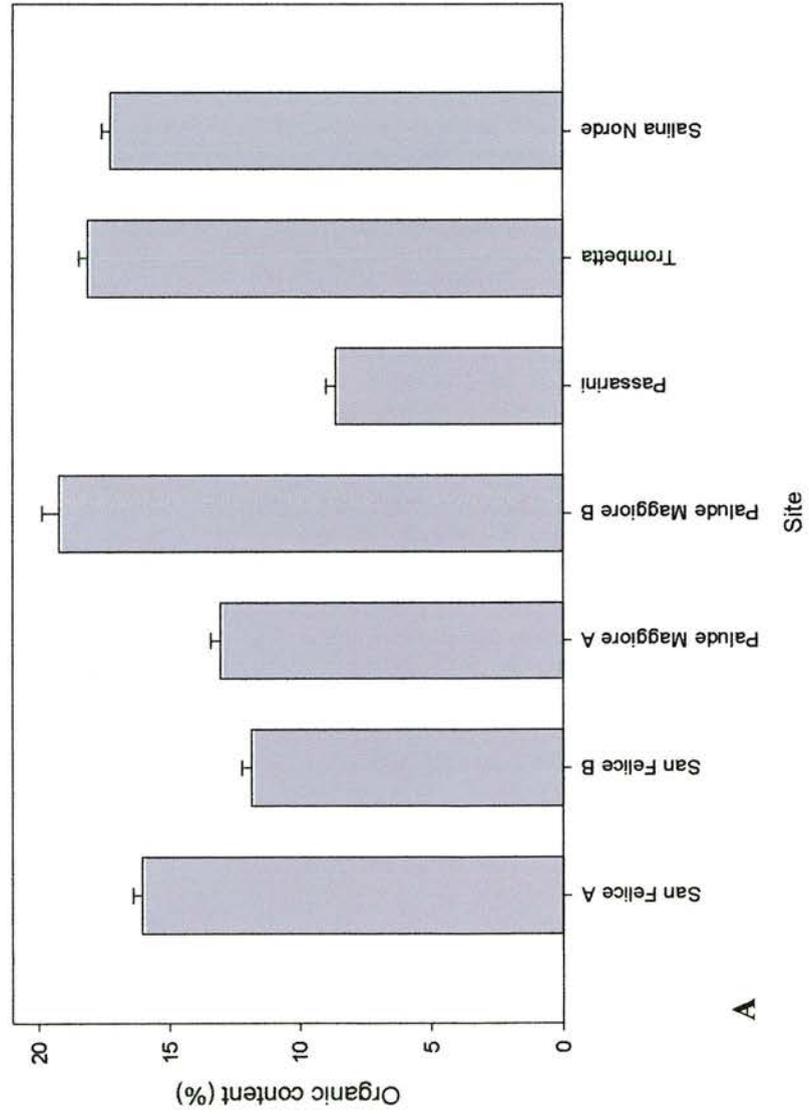


Figure 6.3: Organic carbon content (%) (A) for samples taken during the July 2002 survey. Mean  $\pm$  s.e.,  $n = 75$ . Contour plots (B) indicate the spatial variation of organic carbon content over the grids at each site during the July 2002 survey.

observed in colloidal-S carbohydrate content ( $H = 51.15$ ;  $d.f = 5$ ;  $p < 0.001$ ) (Figure 6.4). A significant difference between all but four sites was observed for dry bulk density ( $H = 188.34$ ;  $d.f = 6$ ;  $p < 0.001$ ) (Figure 6.5). A significant difference between sites was observed in chlorophyll *a* content ( $F_{6,483} = 213.99$ ;  $p < 0.001$ ) (Figure 6.6). A significant difference between sites was observed in critical shear stress ( $H = 55.45$ ;  $d.f = 6$ ;  $p < 0.001$ ) (Figure 6.7). The significant differences shown in all variables measured indicates significant variations of sediment stabilisation, and indicators of microbial biogenic stabilisation of the sites within the lagoon (Table 6.2). Grain size at Passarini, Trombetta and Salina Norde was entirely composed of sediment  $< 63\mu\text{m}$  in diameter. At least 90% of the sediment at San Felice A and B, and Palude Maggiore B was composed of  $< 63\mu\text{m}$  grain size, however only 77% of sediment sampled from Palude Maggiore A contained sediment of  $< 63\mu\text{m}$  grain size diameter (Figure 6.8).

#### 6.3.1.2 Relationship between variables

Correlations carried out between parameters indicated that dry bulk density and chlorophyll *a* content were positively correlated ( $r_s = 0.365$ ;  $p < 0.001$ ), organic content and chlorophyll *a* content were negatively correlated ( $r_s = -0.443$ ;  $p < 0.001$ ), and organic content and dry bulk density were negatively correlated ( $r_s = 0.616$ ;  $p < 0.001$ ). Significant relationships between the variables are described (Figure 6.9). Principle components analysis ordination indicates the surface sediments at San Felice A and B, Palude Maggiore A, Trombetta and Salina Norde were most influenced by dry bulk density. San Felice was least influenced by chlorophyll *a* content. Palude Maggiore B and Passarini were

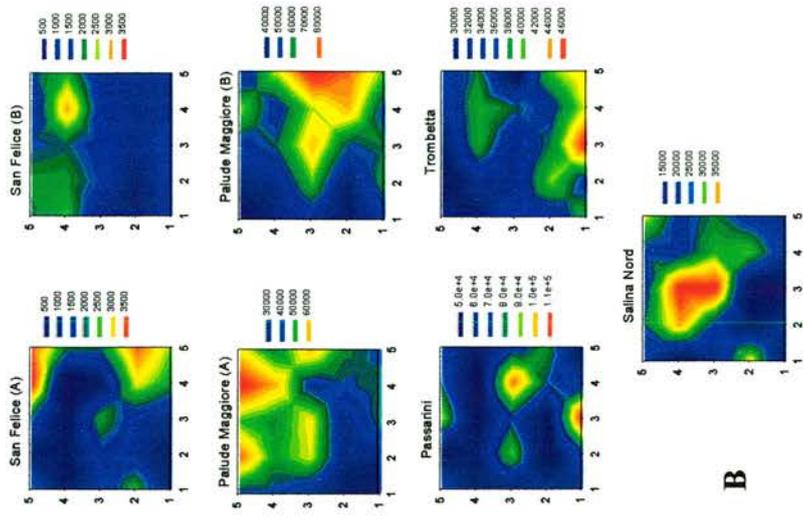
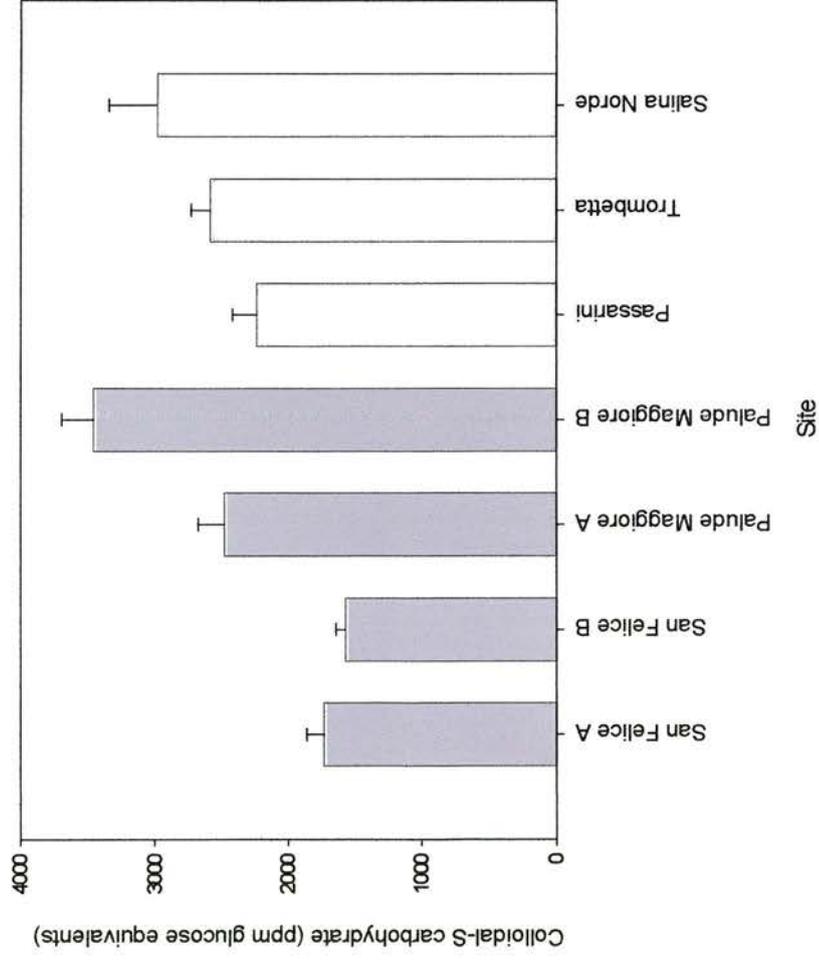


Figure 6.4: Colloidal-S carbohydrate content (ppm G.E) for samples taken during the July 2002 survey (A). Mean  $\pm$  s.e,  $n = 75$ . Contour plots (B) describing the spatial variation of colloidal-S carbohydrate over the grids at each site during the July 2002 survey

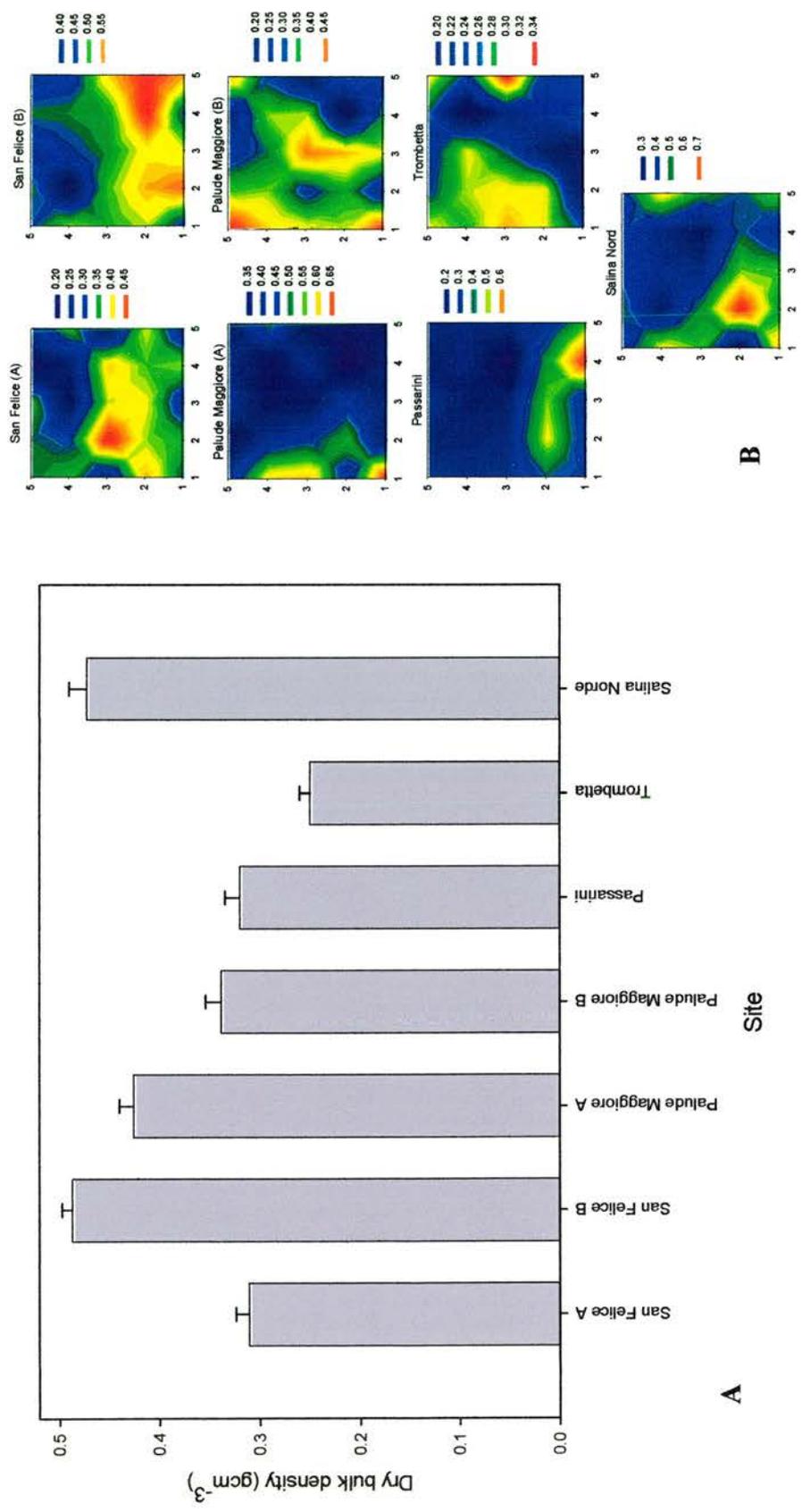


Figure 6.5: Dry bulk density (gcm<sup>-3</sup>) for samples taken during the July 2002 survey. Mean  $\pm$  s.e, n = 75. Contour plots (B) describing the spatial variation of dry bulk density over the grids at each site during the July 2002 survey

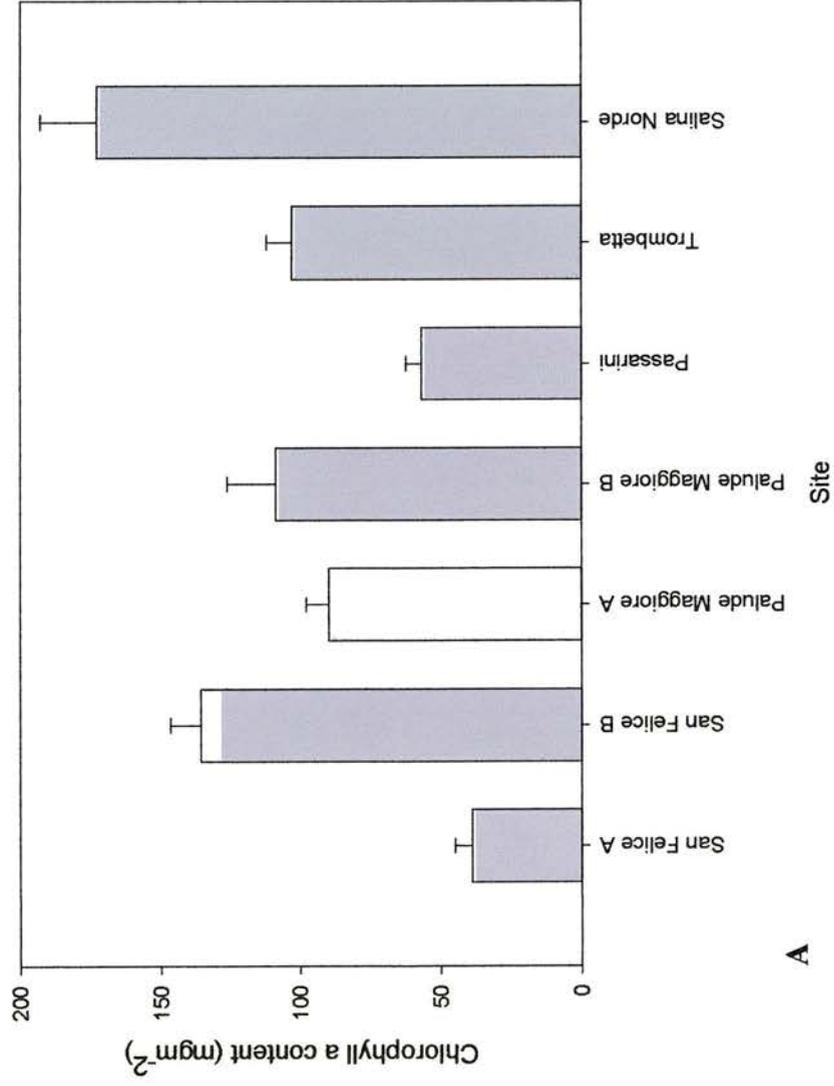


Figure 6.6: Chlorophyll a content (mgm<sup>-2</sup>) for samples taken during the July 2002 survey. Mean  $\pm$  s.e, n = 75. Contour plots (B) describing the spatial variation of chlorophyll a content over the grids at each site during the July 2002 survey.

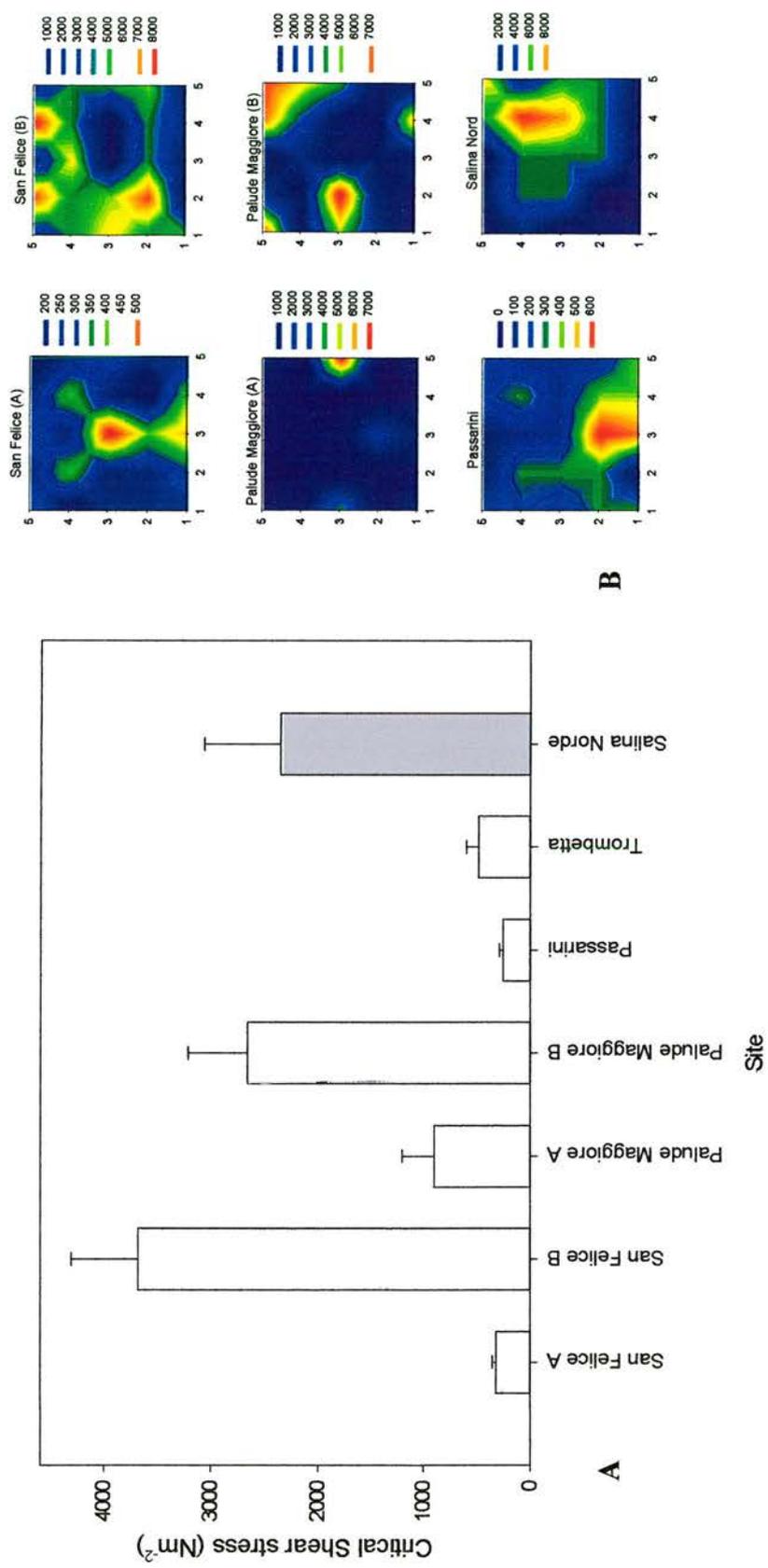


Figure 6.7: Critical shear stress (Nm<sup>-2</sup>) for samples taken during the July 2002 survey. Mean  $\pm$  s.e.,  $n = 25$ . Contour plots (B) describing the spatial variation of critical shear stress over the grids at each site during the July 2002 survey.

	San Felice (A)	San Felice (B)	Palude Maggiore (A)	Palude Maggiore (B)	Passarini	Trombetta	Salina Nord
Colloidal-S carbohydrate content (ppm G.E)	1729.00 (130.70) n = 75	1571.00 (69.90) n = 75	2480.31 (194.44) n = 75	3454.78 (237.33) n = 75	2237.33 (182.33) n = 75	2588.80 (140.67) n = 75	298.97 (359.10) n = 75
Organic content (%)	16.06 (0.35) n = 75	11.87 (0.36) n = 75	13.05 (0.37) n = 75	19.24 (0.63) n = 75	8.64 (0.36) n = 75	18.13 (0.34) n = 75	17.28 (0.31) n = 75
Dry Bulk density (gcm <sup>-1</sup> )	0.31 (0.01) n = 75	0.49 (0.01) n = 75	0.43 (0.01) n = 75	0.34 (0.02) n = 75	0.32 (0.02) n = 75	0.25 (0.01) n = 75	0.47 (0.02) n = 75
Chlorophyll a content (mgm <sup>-2</sup> )	38.91 (5.96) n = 70	135.52 (10.97) n = 68	89.72 (8.05) n = 73	108.71 (17.30) n = 67	56.70 (5.63) n = 69	102.83 (8.97) n = 71	172.59 (20.13) n = 73
Critical shear stress (Nm <sup>-2</sup> )	319.60 (31.81) n = 33	3683.25 (624.95) n = 20	900.81 (300.30) n = 24	2658.28 (554.61) n = 25	256.54 (31.96) n = 21	485.29 (110.19) n = 14	2350.47 (712.48) n = 18

Table 6.2: Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll *a*, and critical shear stress, from surface salt marsh sediments collected during July 2002.

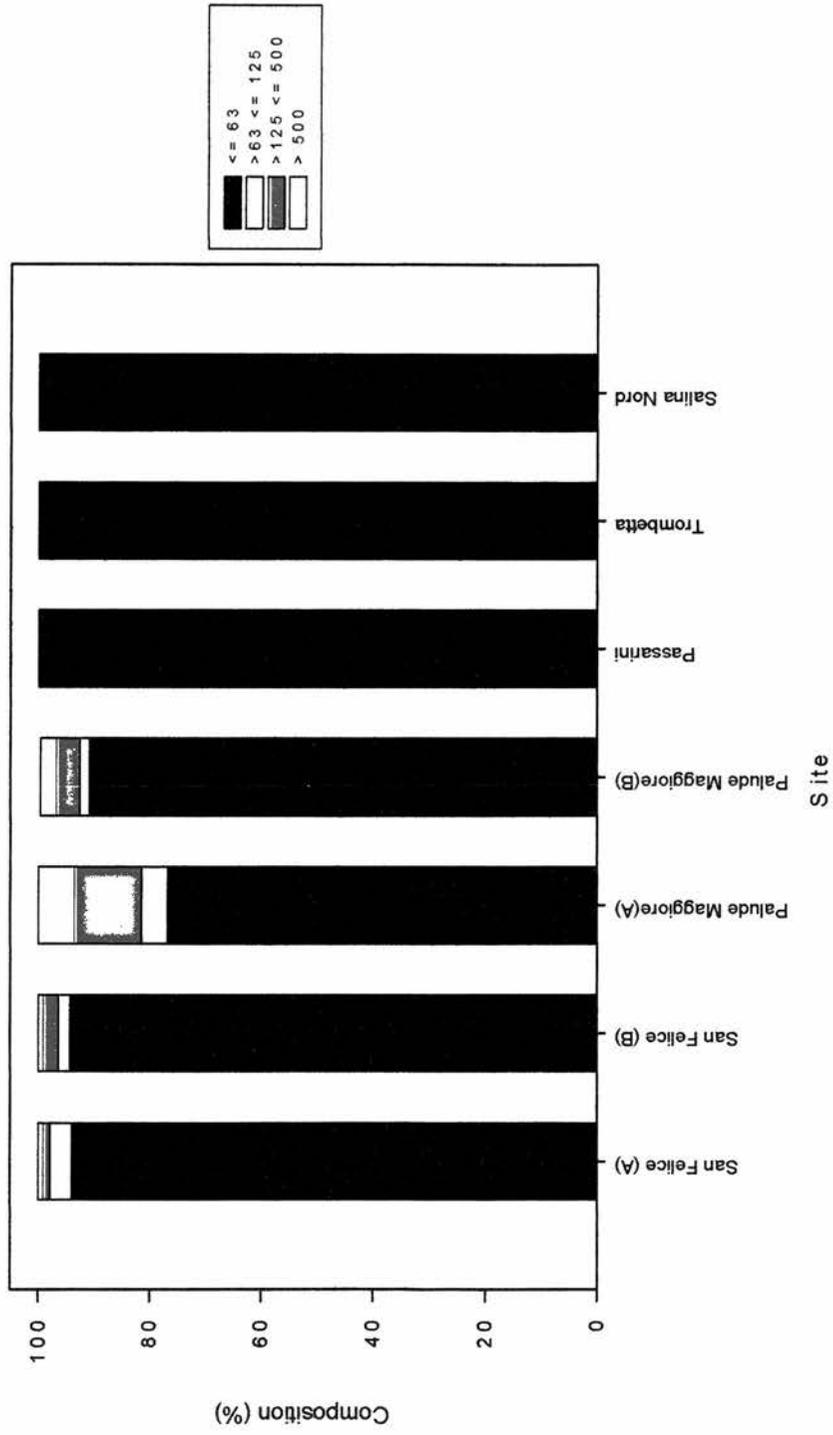


Figure 6.8: Percentage of grain sizes found at each site during the July 2002 survey. The majority of sediment at all sites was within the  $\leq 63 \mu\text{m}$  range.

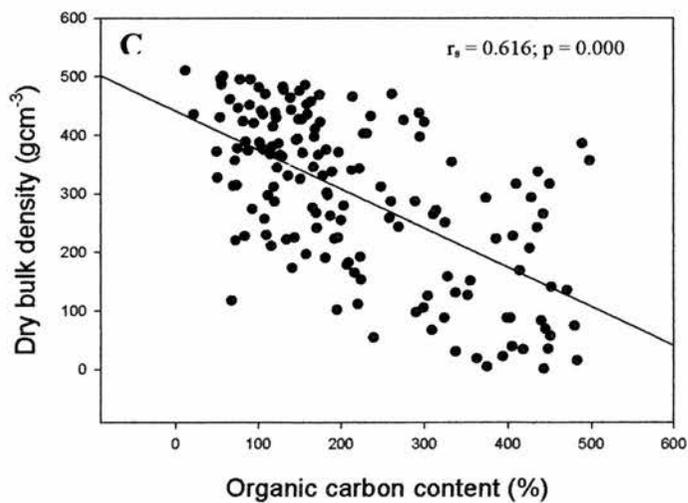
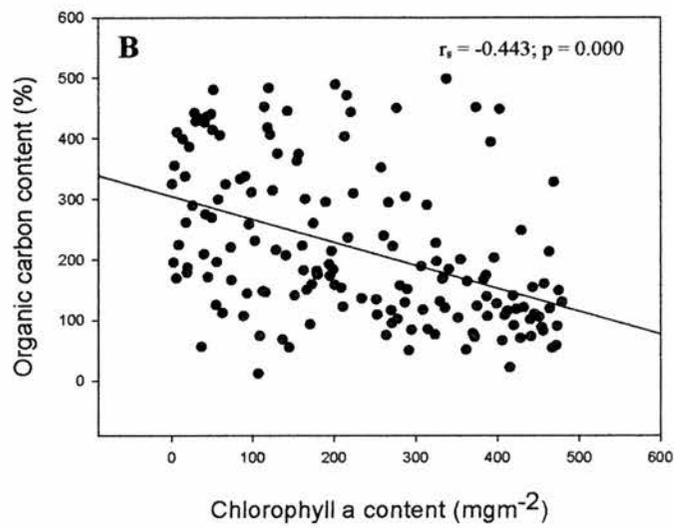
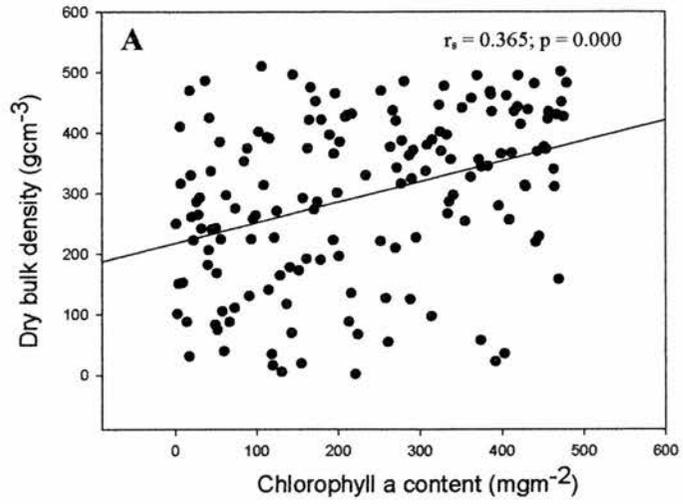


Figure 6.9: The relationship between parameters measured during the July 2002 survey. A) chlorophyll a and dry bulk density, B) chlorophyll a and organic carbon content, and C) organic carbon content and dry bulk density.

influenced by all measured variables. Principle components 1 and 2 together account for 78% of the total sample variability (Figure 6.10).

### 6.3.1.3 Microphytobenthic assemblages

Examination of microphytobenthic assemblages present within the sediments (Table 6.3) showed variation in composition between sites (Figure 6.11). These variations in assemblage composition, during the July 2002 survey, were most obvious between Passarini and Salina Nord; San Felice (B) and Salina Nord; San Felice (B) and Palude Maggiore (B); San Felice (A) and Palude Maggiore (B); and San Felice (A) and San Felice (B) all of which exhibited ANOSIM (Analysis of Similarity) R values of 1. The diatom species most responsible for the dissimilarities between assemblages composition were *Navicula cincta*, *Nitzschia obtusa* var. *scalpelliformis*, *Navicula cryptocephala*, *Amphora ovalis*, *Amphora* sp and *Diploneis crabro*. Palude Maggiore (A) and Palude Maggiore (B) had the most similar assemblages, (ANOSIM R value = 0.394). A significant difference between sites was observed in assemblage diversity ( $H = 23.44$ ; d.f = 6;  $p = 0.001$ ) during the July 2002 survey. Assemblage diversity values (Shannon  $H'$ ) ranged from 2.1850 at Salina Norde, to 2.9233 at San Felice A. Low temperature scanning electron micrographs demonstrate established diatomaceous biofilms at all sites studied. The biofilms were dominated by *Nitzschia obtusa* var. *scalpelliformis* and the images exhibit the presence of EPS amongst the diatoms themselves (Figure 6.12).

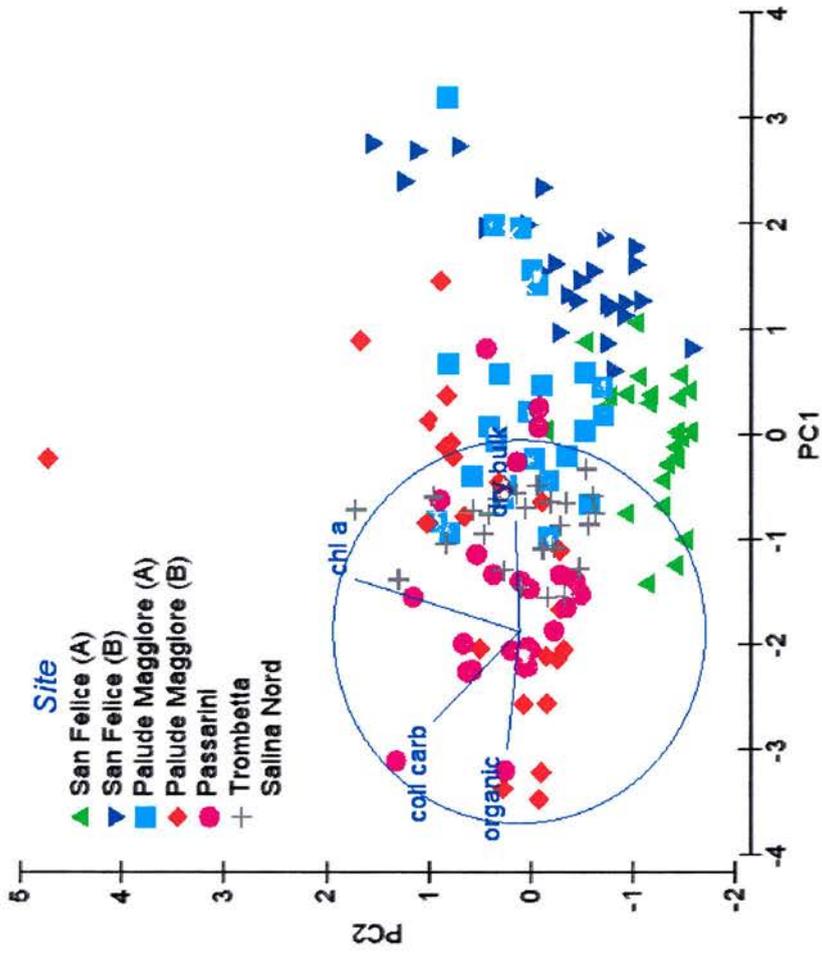


Figure 6.10: Principle components ordination indicates the surface sediments at San Felice A and B, Palude Magglore A, Trombetta and Salina Nord were most influenced by dry bulk density. San Felice was least influenced by chlorophyll *a* content. Palude Magglore B and Passarini were influenced by all measured variables. Principle components 1 and 2 together account for 78% of the total sample variability.

<i>Achnanthes brevipes</i>	<i>Navicula cincta</i>
<i>Achnanthes</i> sp	<i>Navicula cryptocephala</i>
<i>Amphiprora paludosa</i>	<i>Navicula digitoradiata</i>
<i>Amphora ovalis</i>	<i>Navicula viridula</i>
<i>Amphora rhombica</i>	<i>Nitzschia constricta</i>
<i>Amphora</i> sp	<i>Nitzschia dissipata</i>
<i>Cocconeis molesta</i>	<i>Nitzschia dubiiformis</i>
<i>Cocconeis scutellum</i>	<i>Nitzschia frustulum</i>
<i>Cyclotella</i> sp	<i>Nitzschia obtusa</i> var. <i>scalpelliformis</i>
<i>Cylindrotheca closterium</i>	<i>Nitzschia reversa</i>
<i>Diatoma vulgare</i>	<i>Nitzschia sigma</i>
<i>Dimerogramma</i> sp	<i>Opephora</i> sp
<i>Diploneis crabro</i>	<i>Petroneis latissima</i>
<i>Diploneis domblittensis</i>	<i>Petrodictyon</i> sp
<i>Diploneis interrupta</i>	<i>Pleurosigma</i> sp
<i>Fallacia forcipata</i>	<i>Psammodictyon panduriforme</i>
<i>Fragilaria</i> sp	<i>Raphoneis amphiceros</i>
<i>Gyrosigma acuminatum</i>	<i>Stauroneis</i> sp
<i>Gyrosigma balticum</i>	<i>Surirella brebbonisi</i>
<i>Gyrosigma eximium</i>	<i>Surirella fastuosa</i>
<i>Gyrosigma fasciola</i>	<i>Synedra</i> sp
<i>Licmophora</i> sp	<i>Thallasiosira</i> sp
<i>Mastogloia</i> sp	<i>Terpsinoe americana</i>
<i>Melosira</i> sp	<i>Tryblionella punctata</i>

Table 6.3: Motile diatom species collected and identified from salt marsh surface sediments in the Venice Lagoon, during surveys in 2002, 2003 and 2004.

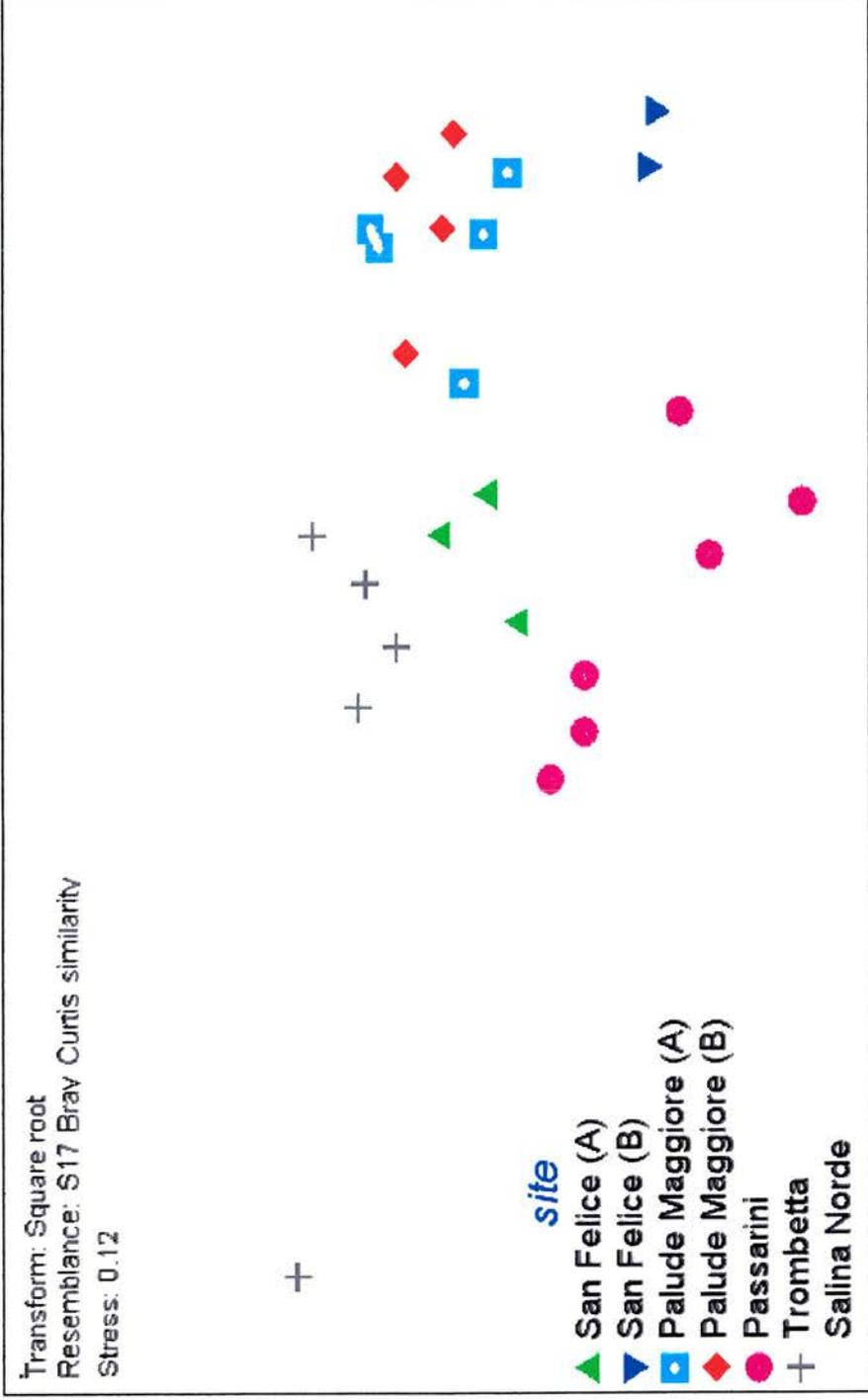


Figure 6.11: Multi-dimensional scaling plots of the microphytobenthic community assemblages present at study sites during the July 2002 survey.

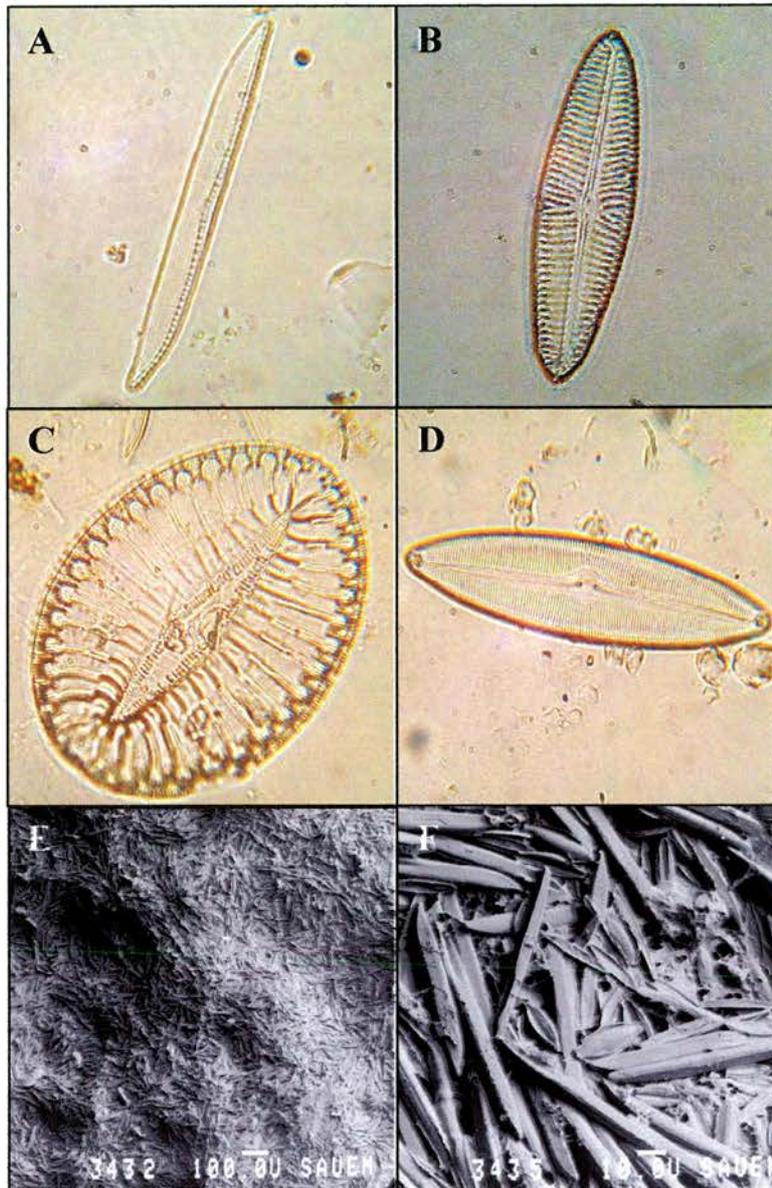


Fig 6.12: Diatoms are one of the most dominant forms of microphytobenthos found within salt marsh sediments. Examples species found within the sediments studied during the July 2002 survey include *Nitzschia obtusa* var. *scalpelliformis* (A), *Navicula digitaradiata* (B), *Surirella fastuosa* (C), and *Navicula viridula* (D). The diatoms form dense biofilms on the surface sediments migrating within the top layers (E). This movement is aided by the release of extra cellular polymeric substances (EPS) from the raphe structure in the silica frustule, and can be seen to occur as strands and sheets amongst the cells (F) under low temperature scanning electron microscopy.

### 6.3.2 July 2003

#### 6.3.2.1 Sediment variables

The organic content, colloidal-S carbohydrate content, dry bulk density, sediment stability, shear strength, sediment grain size and chlorophyll *a* were examined in the surface of the salt marsh sediments and are indicated by figures 6.13-6.19. Where a significant difference was found within individual sites during the survey in July 2003, this is indicated in Table 6.4

Significant variation of organic content was found at all sites studied ( $H = 91.08$ ;  $d.f = 4$ ;  $p < 0.001$ ) except San Felice and Palude Maggiore ( $W = 768.0$ ;  $p = 0.151$ ) (Figure 6.13). A significant difference between all but three sites was observed in colloidal-S carbohydrate content ( $H = 40.390$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 6.14). A significant difference in dry bulk density was observed ( $F_{4,125} = 1196.51$ ;  $p < 0.001$ ) (Figure 6.15). A significant difference between sites was observed in chlorophyll *a* content ( $F_{4,125} = 51.25$ ;  $p < 0.001$ ) (Figure 6.16). A significant difference between sites was observed in critical shear stress ( $H = 21.63$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 6.17). At a depth of 9cm significant differences were observed in sediment shear strength at all sites compared with San Felice ( $H = 13.11$ ;  $d.f = 4$ ;  $p = 0.011$ ) (Figure 6.18). The significant differences shown in all parameters measured, indicates significant variations of sediment stabilisation, and indicators of microbial biogenic stabilisation of the sites within the lagoon (Table 6.5). Sediment at San Felice and Palude Maggiore was entirely composed of grains  $< 63\mu\text{m}$  in diameter. At least 85% of the sediment at Salina Norde and Passarini was composed of  $<63\mu\text{m}$  grain size, however only 70% of sediment sampled from Trombetta contained sediment of  $<63\mu\text{m}$  grain size diameter (Figure 6.19).

Chlorophyll a content	San Felice	Salina Nord	Palude Maggiore	Trombetta
Salina Nord	<b>&lt;0.05</b>			
Palude Maggiore	<b>&lt;0.05</b>	<b>&lt;0.05</b>		
Trombetta	<b>&lt;0.05</b>		<b>&lt;0.05</b>	
Passarini	<b>&lt;0.05</b>	<b>&lt;0.05</b>		<b>&lt;0.05</b>
Critical shear stress	San Felice	Salina Nord	Palude Maggiore	Trombetta
Salina Nord	<b>0.001</b>			
Palude Maggiore	0.182	<b>0.006</b>		
Trombetta	<b>0.020</b>	0.055	0.206	
Passarini	<b>0.002</b>	0.749	<b>0.012</b>	0.095
Shear strength	San Felice	Salina Nord	Palude Maggiore	Trombetta
Salina Nord	<b>0.012</b>			
Palude Maggiore	<b>0.037</b>	0.210		
Trombetta	<b>0.012</b>	0.835	0.210	
Passarini	<b>0.012</b>	0.835	0.144	0.835
Organic carbon content	San Felice	Salina Nord	Palude Maggiore	Trombetta
Salina Nord	<b>0.000</b>			
Palude Maggiore	0.151	<b>0.000</b>		
Trombetta	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	
Passarini	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.001</b>
Colloidal carbohydrate content	San Felice	Salina Nord	Palude Maggiore	Trombetta
Salina Nord	0.9635			
Palude Maggiore	0.978	0.681		
Trombetta	<b>0.000</b>	<b>0.010</b>	<b>0.001</b>	
Passarini	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.021</b>
Dry bulk density	San Felice	Salina Nord	Palude Maggiore	Trombetta
Salina Nord	<b>&lt;0.05</b>			
Palude Maggiore	<b>&lt;0.05</b>	<b>&lt;0.05</b>		
Trombetta	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	
Passarini	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>	<b>&lt;0.05</b>

Table 6.4: Descriptive statistics carried out to compare between sites studied. Mann-Whitney was used to determine significant differences ( $p < 0.050$ ), which are indicated in bold (One way ANOVA, and Tukey post hoc was used for chlorophyll a content and dry bulk density).

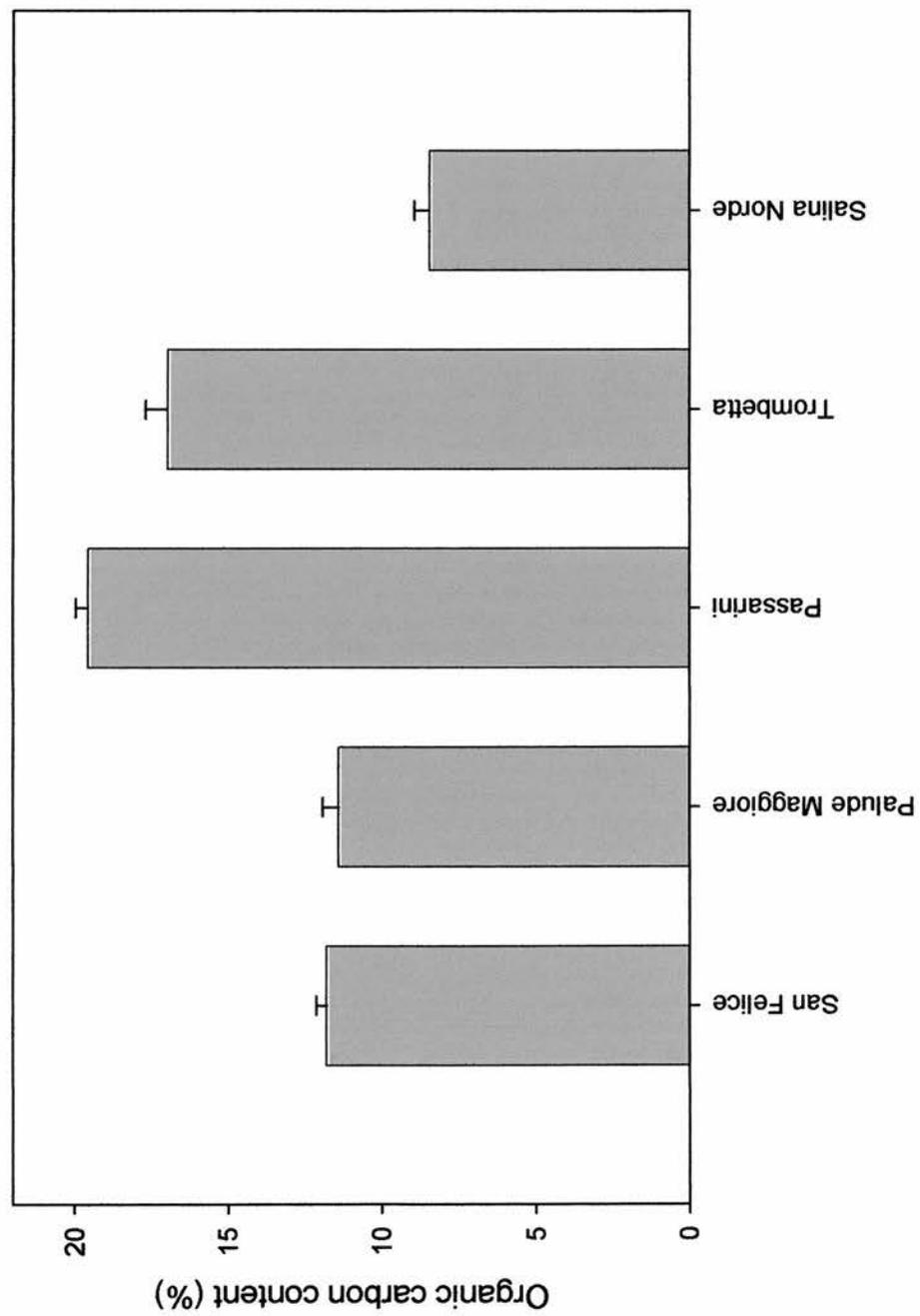


Figure 6.13: Organic carbon content (%) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 27.

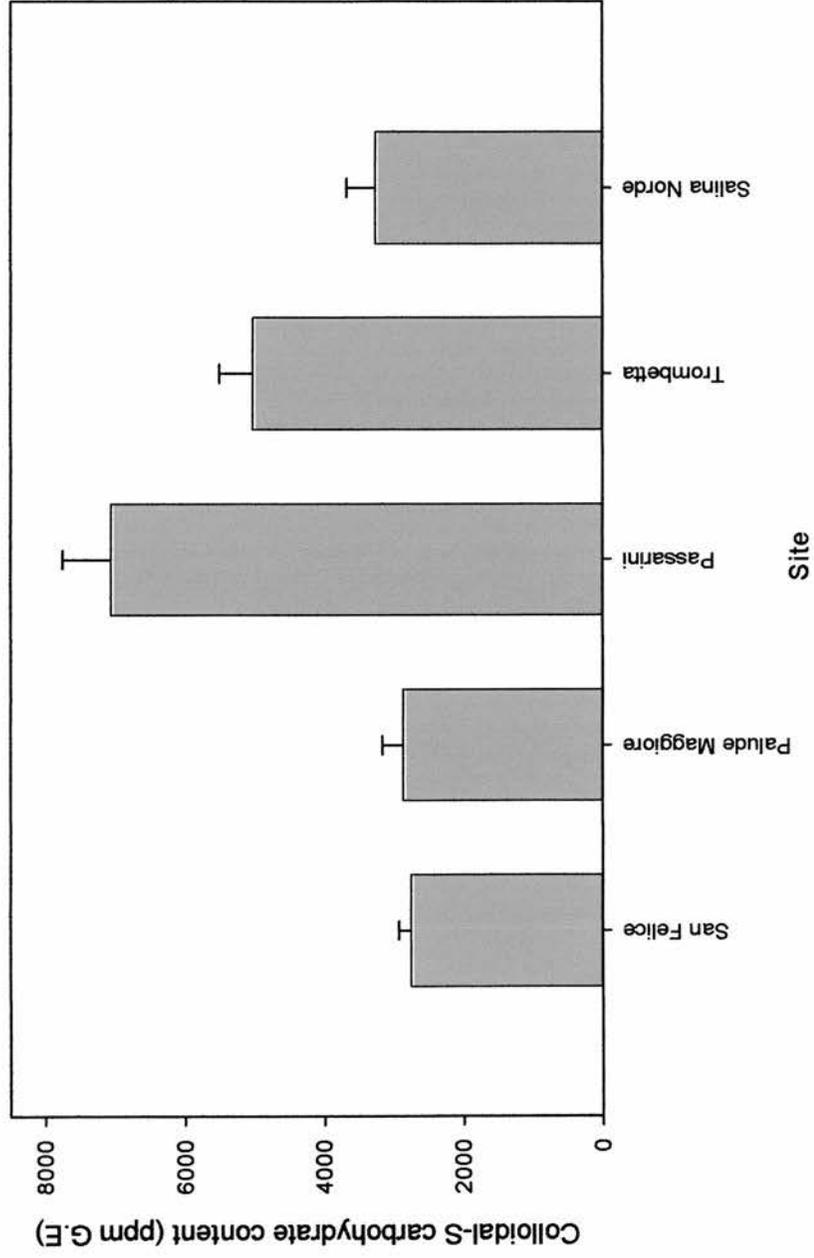


Figure 6.14: Colloidal-S carbohydrate content (ppm G.E) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 26-27.

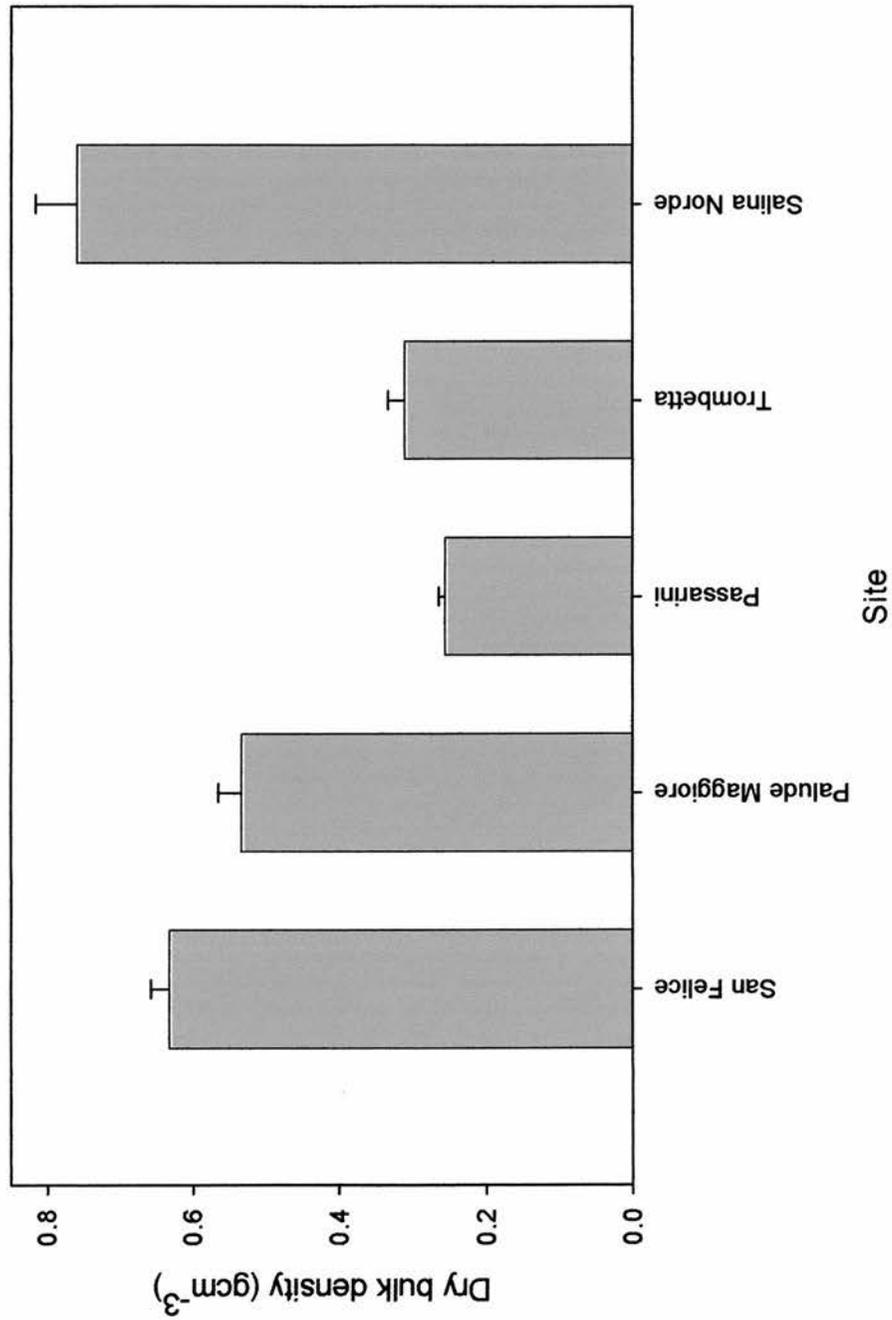


Figure 6.15: Dry bulk density (gcm<sup>-3</sup>) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 26-27.

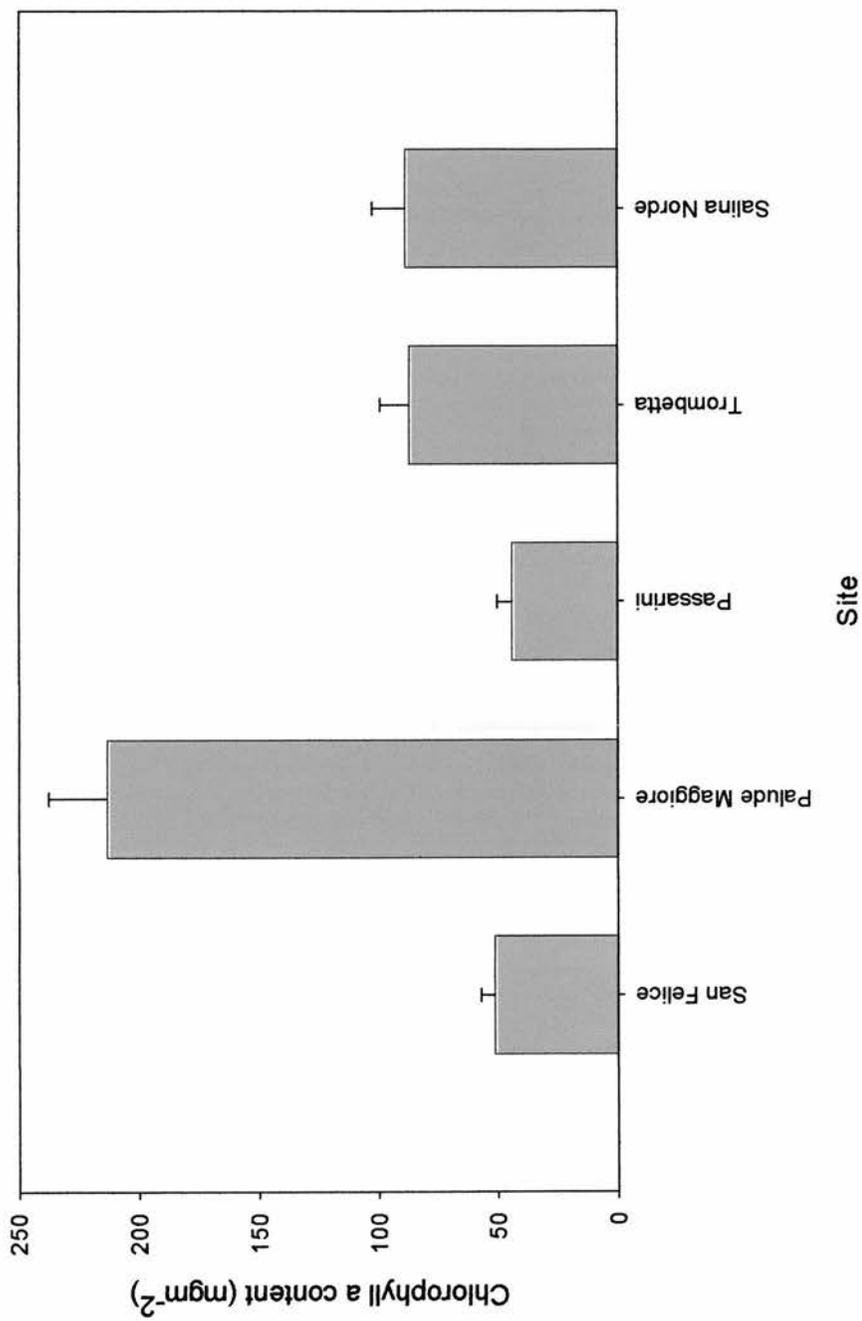


Figure 6.16: Chlorophyll a content (mgm<sup>-2</sup>) for samples taken during the July 2003 survey. Mean  $\pm$  s.e, n = 26-27.

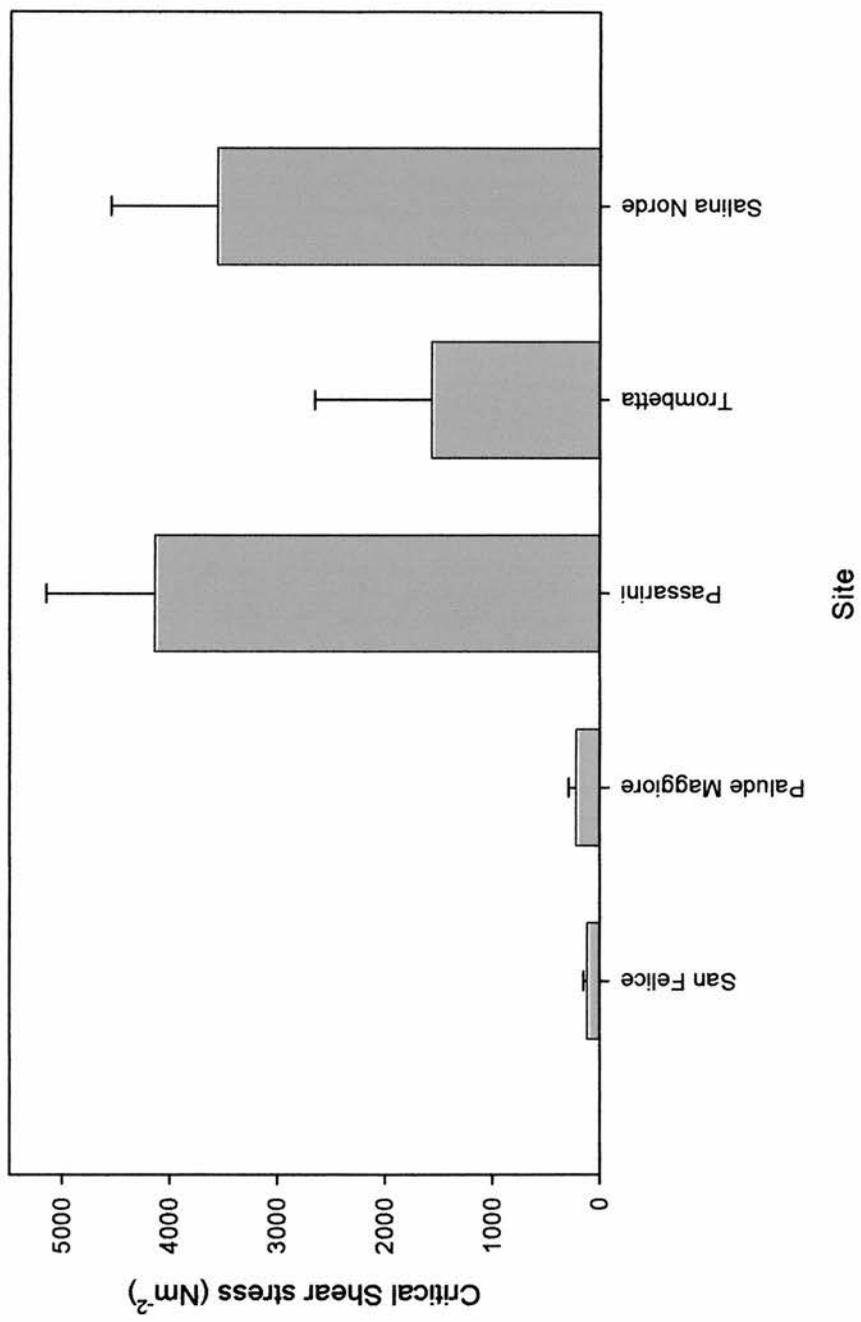


Figure 6.17: Critical shear stress (Nm<sup>-2</sup>) for samples taken during the July 2003 survey. Mean  $\pm$  s.e., n = 5-9.

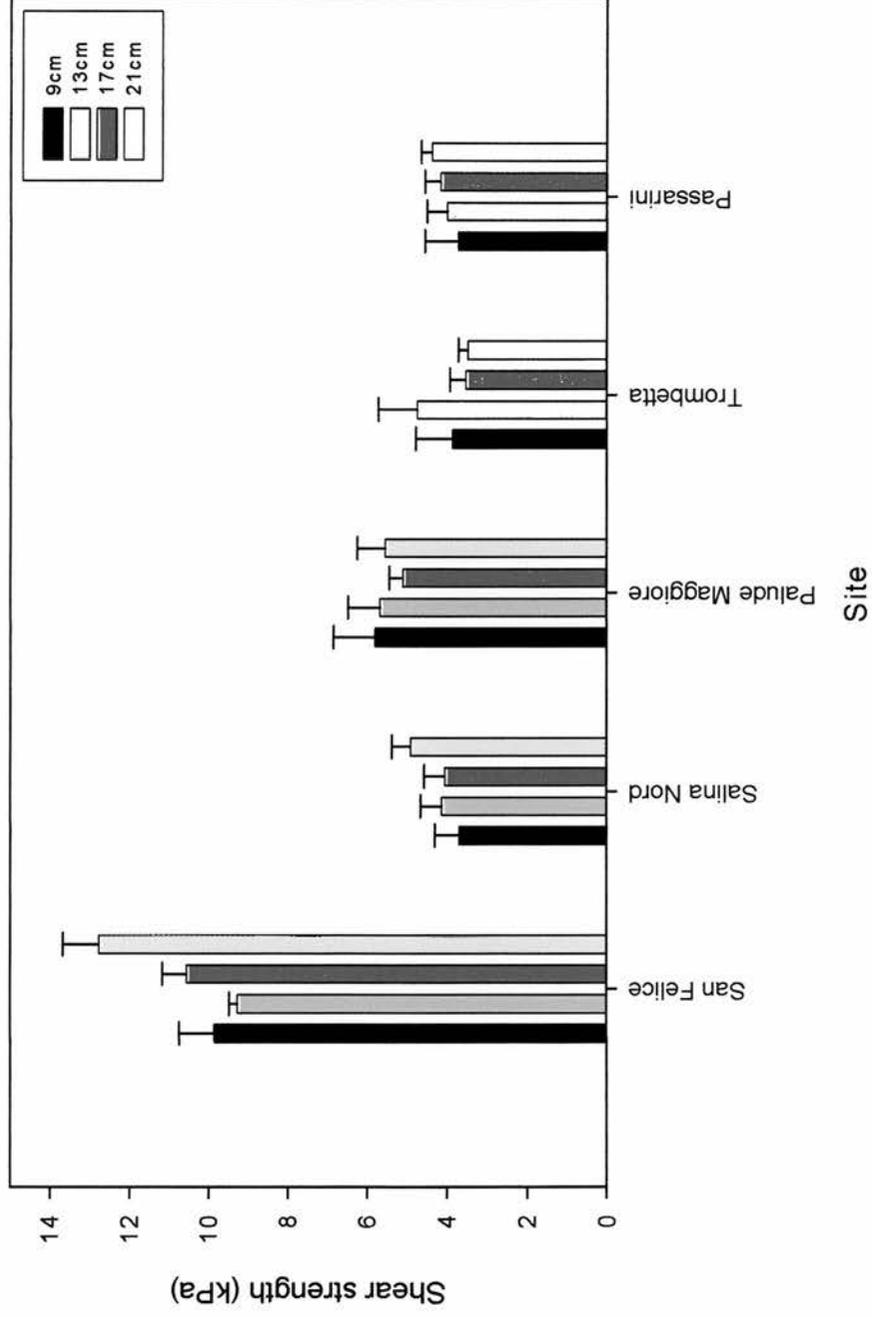


Figure 6.18: Shear strength (kPa) values at varying depths (9cm, 13cm, 17cm, and 21cm) at sites sampled during the July 2003 survey. Mean  $\pm$  s.e., n = 25.

	San Felice	Salina Nord	Palude Maggiore	Trombetta	Passarini
Colloidal-S carbohydrate (ppm G.E)	2752.71 (165.97) n = 27	3261.14 (409.74) n = 26	2863.74 (299.50) n = 26	5033.32 (473.12) n = 27	7062.19 (686.71) n = 26
Organic content (%)	11.80 (0.34) n = 27	8.46 (0.49) n = 26	11.40 (0.51) n = 27	16.98 (0.71) n = 27	19.58 (0.39) n = 26
Dry Bulk density (gcm <sup>-1</sup> )	0.63 (0.03) n = 26	0.76 (0.06) n = 26	0.53 (0.03) n = 26	0.33 (0.02) n = 27	0.26 (0.01) n = 26
Chlorophyll a content (mgm <sup>-2</sup> )	51.31 (5.65) n = 26	88.49 (13.86) n = 26	213.16 (24.15) n = 26	86.88 (12.14) n = 26	43.94 (6.24) n = 26
Critical shear stress (Nm <sup>-2</sup> )	115.68 (35.26) n = 9	3559.18 (990.61) n = 7	218.66 (67.18) n = 5	1572.99 (1081.88) n = 7	4138.92 (1011.77) n = 7

Table 6.5: Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll  $a$ , and critical shear stress, from surface salt marsh sediments collected during July 2003.

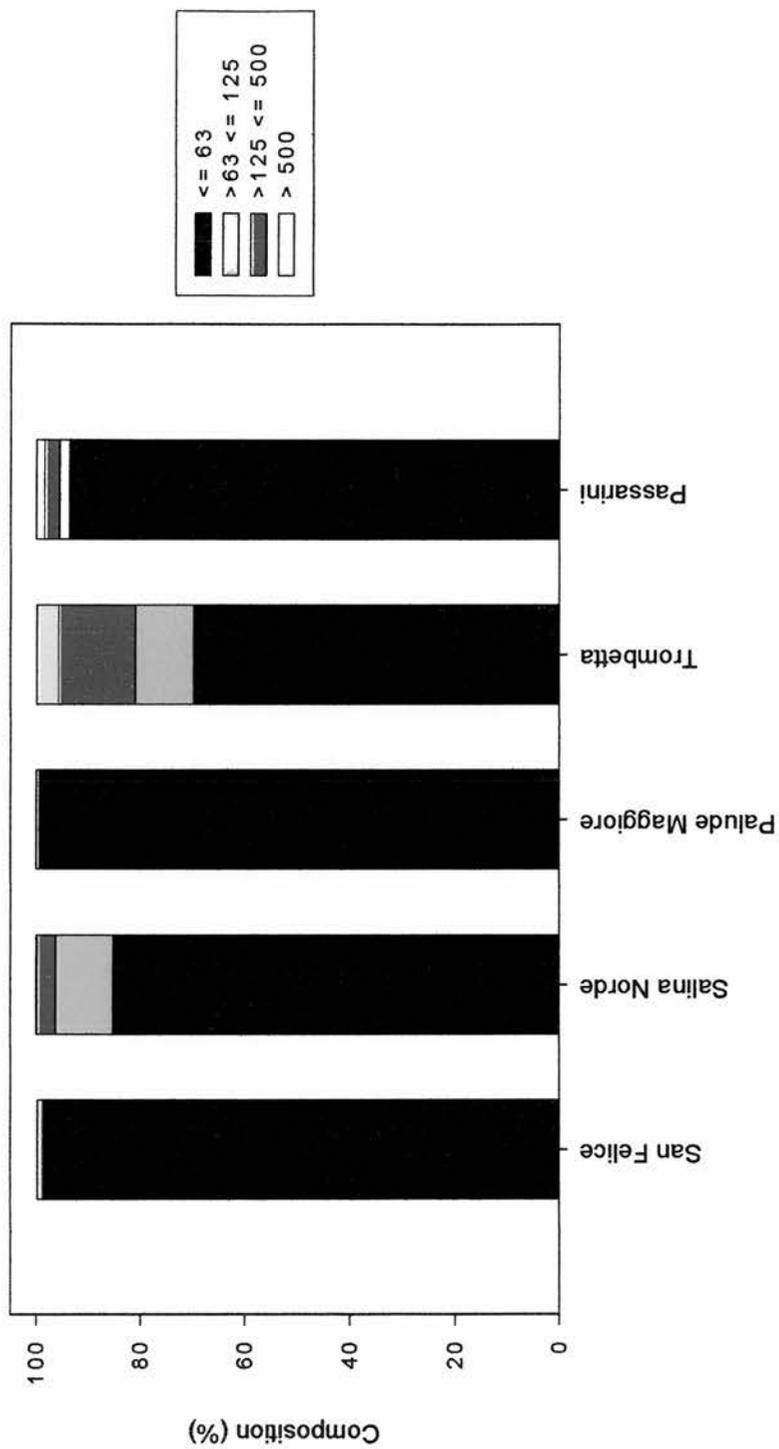


Figure 6.19: Percentage of grain sizes found at each site during the July 2003 survey. The majority of sediment at all sites was within the  $\leq 63\mu\text{m}$  range.

### 6.3.2.2 Relationship between variables

Correlations carried out between variables measured indicated that dry bulk density and colloidal-S carbohydrate content were negatively correlated ( $r_s = -0.629$ ;  $p < 0.001$ ), organic content and chlorophyll *a* content were negatively correlated ( $r_s = -0.496$ ;  $p = 0.002$ ), and organic content and dry bulk density were negatively correlated ( $r_s = -0.596$ ;  $p < 0.001$ ), organic content and colloidal-S carbohydrate were positively correlated ( $r_s = 0.512$ ;  $p = 0.002$ ), and organic content and critical shear stress were negatively correlated ( $r_s = -0.336$ ;  $p = 0.048$ ). Significant relationships between the variables are described (Figure 6.20). Principle components analysis ordination indicates the surface sediments at San Felice, Palude Maggiore and Salina Norde were most influenced by dry bulk density. San Felice and Passarini were least influenced by chlorophyll *a* content. Passarini was influenced by colloidal-S carbohydrate and organic carbon content. Principle components 1 and 2 together account for 79% of the total sample variability (Figure 6.21).

### 6.3.2.3 Microphytobenthic assemblages

Examination of microphytobenthic assemblages present within the sediments (Table 6.3) showed variation in composition between sites (Figure 6.22). These variations in assemblage composition were most obvious between Passarini and San Felice, which exhibited an ANOSIM R values of 0.999. The diatom species most responsible for the dissimilarities between assemblage composition were *Mastogloia* sp, *Amphora rhombica* and *Navicula cryptocephala*. Trombetta and Passarini had the most similar assemblages, (ANOSIM R value = 0.525). A significant difference was observed between

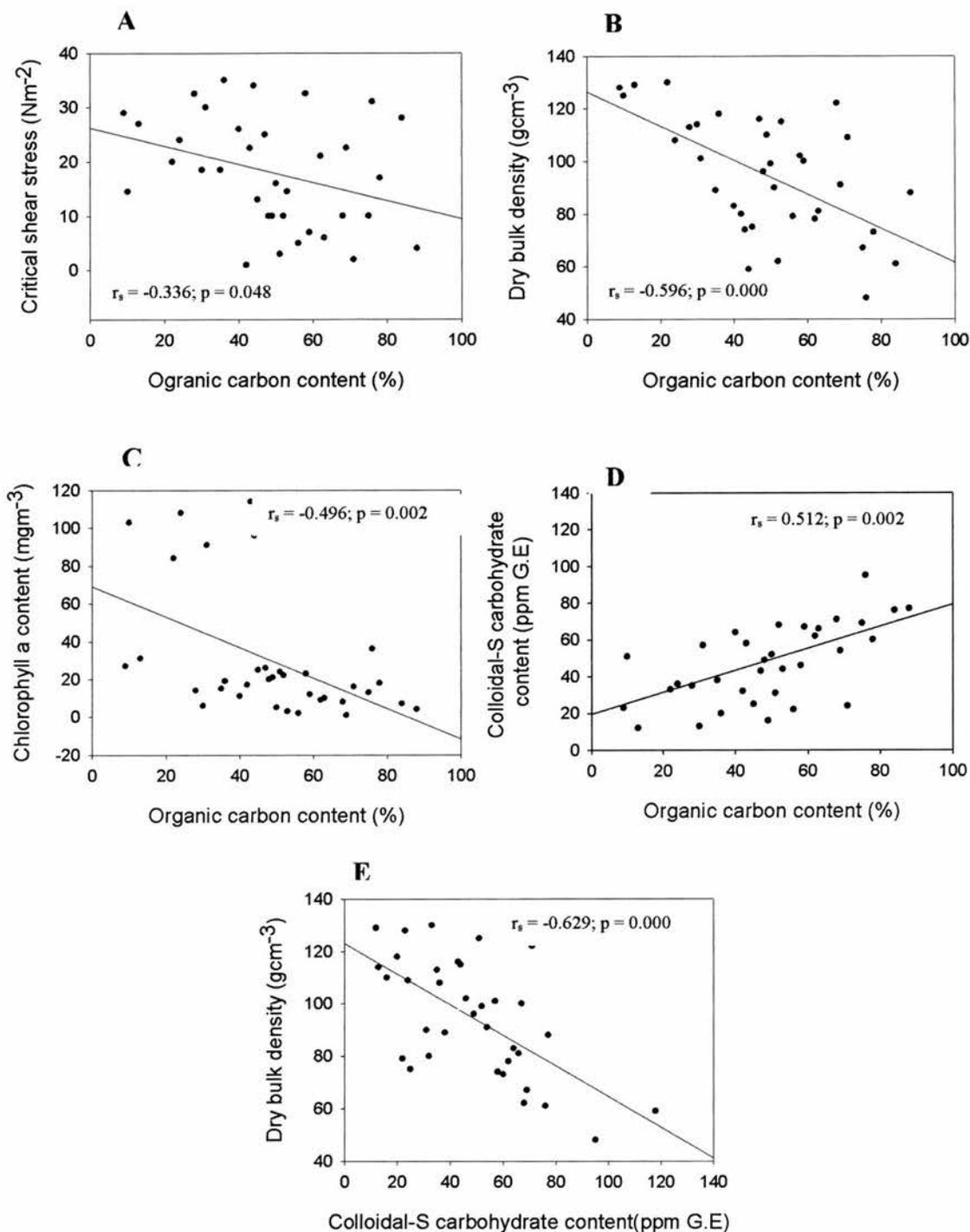


Figure 6.20: The relationship between parameters measured during the July 2003 survey. A) Critical shear stress and organic carbon content, B) dry bulk density and organic carbon content, C) chlorophyll a content and organic carbon content, D) colloidal-S carbohydrate content and organic carbon content, and E) dry bulk density and colloidal-S carbohydrate content.

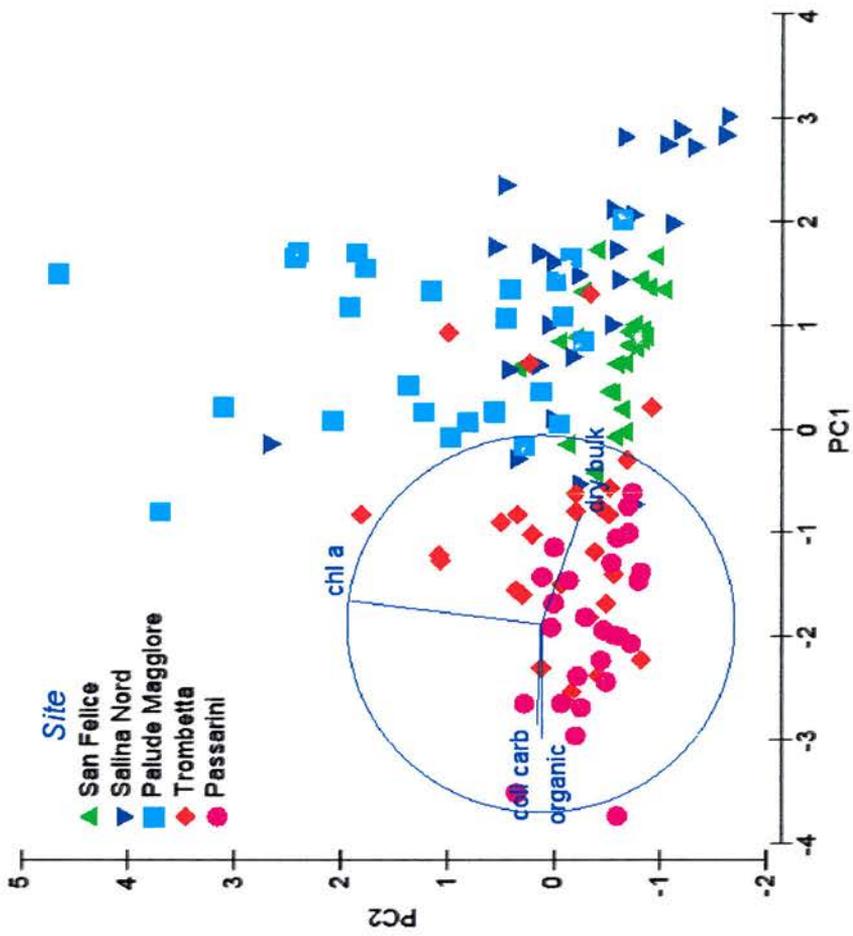


Figure 6.21: Principle components ordination indicates the surface sediments at San Felice, Palude Maggiore and Salina Nord were most influenced by dry bulk density. San Felice and Passarini were least influenced by chlorophyll  $a$  content. Passarini was influenced by colloidal-S carbohydrate and organic carbon content. Principle components 1 and 2 together account for 79% of the total sample variability.

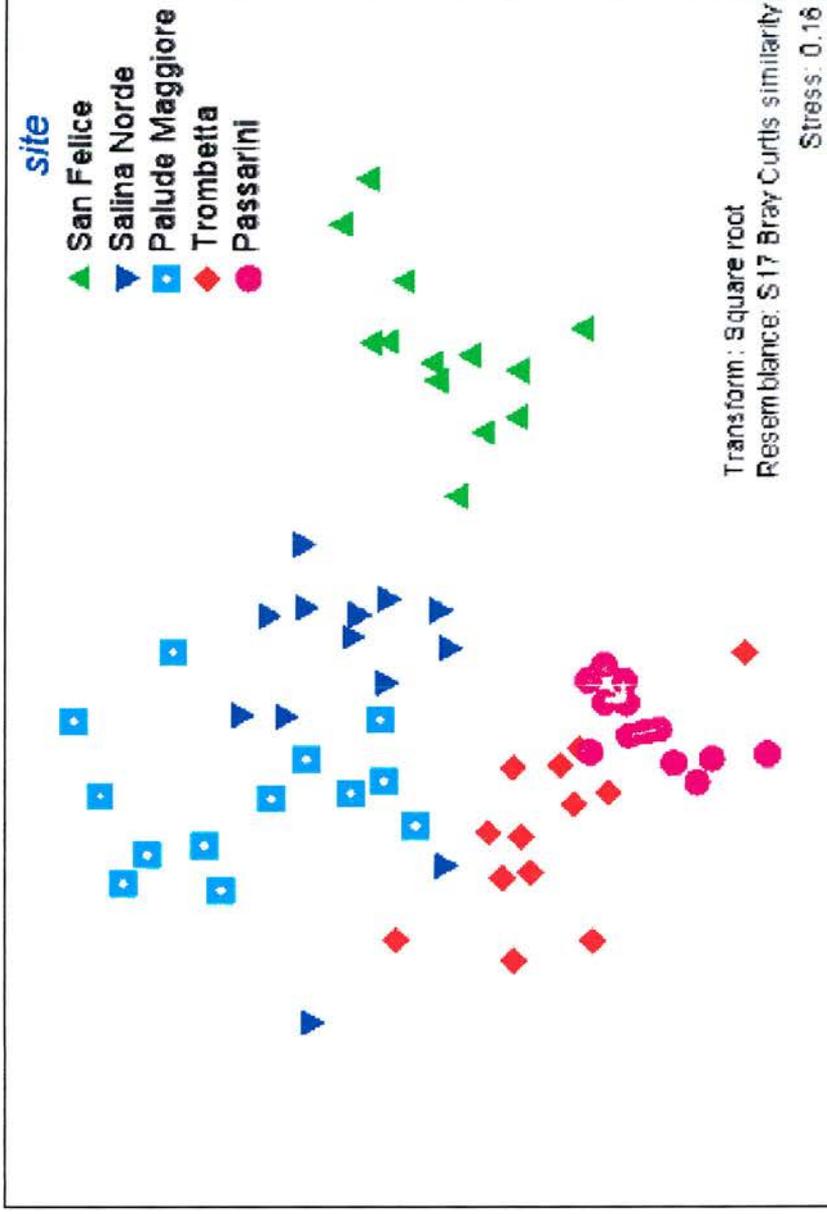


Figure 6.22: Multi-dimensional scaling plots of the microphytobenthic community assemblages present at study sites during the July 2003 survey.

sites during the July 2003 survey ( $H = 15.67$ ;  $d.f = 4$ ;  $p = 0.004$ ). Assemblage diversity values (Shannon  $H'$ ) ranged from 2.5892 at San Felice, to 2.91 at Passarini. Low-temperature scanning electron micrographs confirmed the presence of a diatomaceous biofilm and the associated presence of EPS. The dominant surface species tended to be naviculoid species, however, cyanobacterial biofilms were also observed to be present in high numbers (Figure 6.23).

### 6.3.3 February 2004

#### 6.3.3.1 Sediment variables

The organic content, colloidal-S carbohydrate content, dry bulk density, sediment stability, shear strength, sediment grain size and chlorophyll *a* were examined in the surface of the salt marsh sediments (Figure 6.24-6.30). Where a significant difference was found within individual sites during the survey in February, 2004 this is indicated in Table 6.6.

Significant variation of organic content was seen at all sites studied ( $H = 92.34$ ;  $d.f = 4$ ;  $p < 0.001$ ) except Trombetta and Passarini ( $W = 597.0$ ;  $p = 0.094$ ) (Figure 6.24). A significant difference in colloidal-S carbohydrate content was observed between all sites ( $H = 73.65$ ;  $d.f = 4$ ;  $p < 0.001$ ), except Salina Norde and San Felice ( $W = 665.0$ ;  $p = 0.6671$ ) (Figure 6.25). A significant difference in dry bulk density was observed at all sites ( $H = 93.34$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 6.26). A significant difference between sites was observed in chlorophyll *a* content ( $F = 51.25$ ;  $p < 0.001$ ) for all sites bar two: Trombetta and Palude Maggiore ( $W = 628.0$ ;  $p = 0.667$ ), and Trombetta and San Felice ( $W = 756.0$ ;  $p = 0.073$ ) (Figure 6.27). A significant difference between sites was

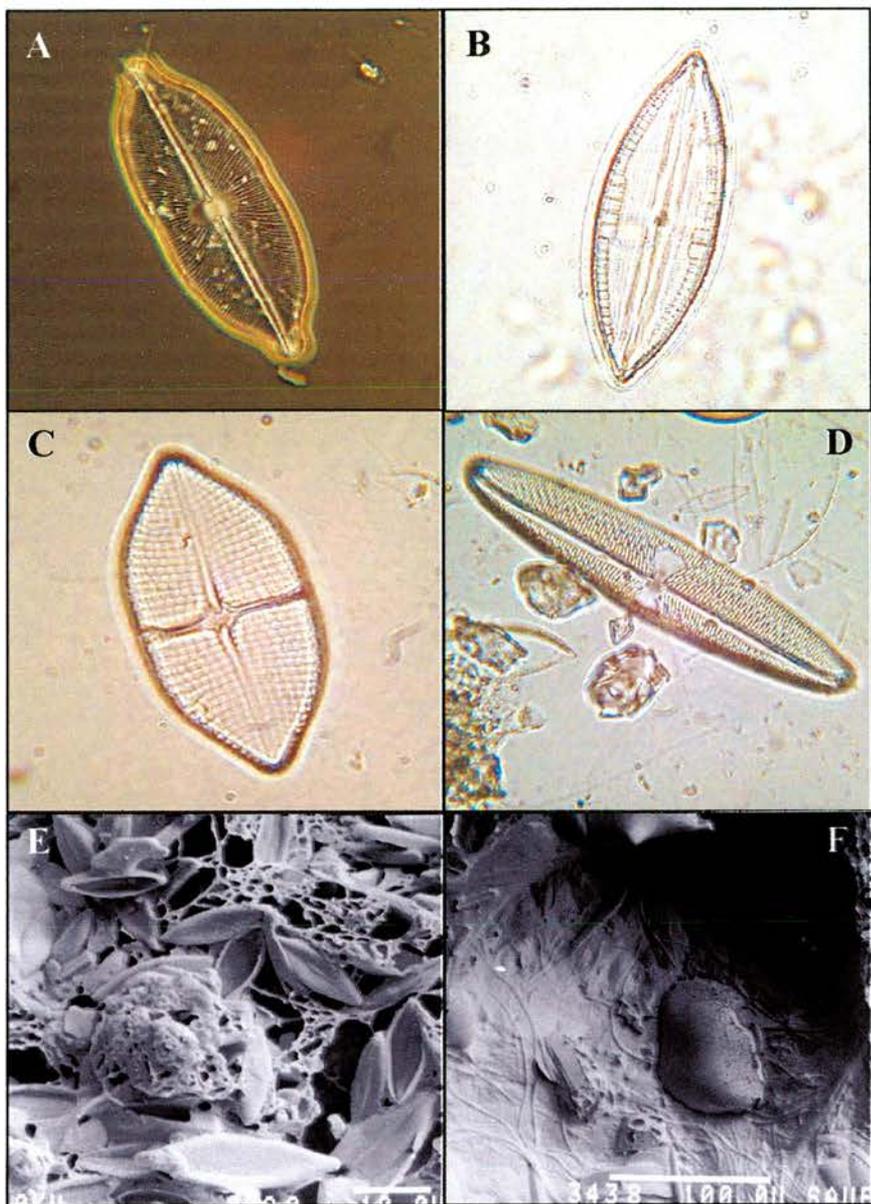


Fig 6.23: Cyanobacteria and diatoms are the most dominant forms of microphytobenthos found within salt marsh sediments. Examples of diatomaceous species found within the sediments studied during the July 2003 survey include *Petroneis latissima* (A), *Mastogloia* sp (B), *Tryblionella* sp(C), and *Stauroneis* sp (D). These episammic cells migrate through the surface sediments and the movement is aided by the release of extra cellular polymeric substances (EPS) from the raphe structure in the silica frustule, and can be seen to occur as strands and sheets amongst the cells (E) under low temperature scanning electron microscopy. Cyanobacteria filaments (F) can be seen in low temperature scanning electron micrographs providing evidence for the structural support provided by cyanobacteria in salt marsh sediments.

Shear strength	Trombetta	Passarini	Palude Maggiore	Salina Nord
Passarini	0.531			
Palude Maggiore	/	/		
Salina Nord	0.403	1.000	/	
San Felice	<b>0.012</b>	<b>0.012</b>	/	0.060
Critical shear stress	Trombetta	Passarini	Palude Maggiore	Salina Nord
Passarini	0.764			
Palude Maggiore	<b>0.000</b>	<b>0.001</b>		
Salina Nord	<b>0.000</b>	<b>0.001</b>	0.703	
San Felice	<b>0.000</b>	<b>0.001</b>	0.840	0.678
Chlorophyll a content	Trombetta	Passarini	Palude Maggiore	Salina Nord
Passarini	<b>0.001</b>			
Palude Maggiore	0.667	<b>0.000</b>		
Salina Nord	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	
San Felice	0.073	<b>0.013</b>	<b>0.023</b>	<b>0.000</b>
Organic carbon content	Trombetta	Passarini	Palude Maggiore	Salina Nord
Passarini	0.094			
Palude Maggiore	<b>0.007</b>	<b>0.000</b>		
Salina Nord	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	
San Felice	<b>0.000</b>	<b>0.000</b>	<b>0.013</b>	<b>0.000</b>
Dry bulk density	Trombetta	Passarini	Palude Maggiore	Salina Nord
Passarini	<b>0.003</b>			
Palude Maggiore	<b>0.000</b>	<b>0.000</b>		
Salina Nord	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	
San Felice	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
Colloidal carbohydrate content	Trombetta	Passarini	Palude Maggiore	Salina Nord
Passarini	<b>0.010</b>			
Palude Maggiore	<b>0.004</b>	<b>0.000</b>		
Salina Nord	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	
San Felice	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.667

Table 6.6: Descriptive statistics carried out to compare between sites studied. Mann-Whitney tests were used to determine significant differences ( $p < 0.050$ ), which are indicated in bold.

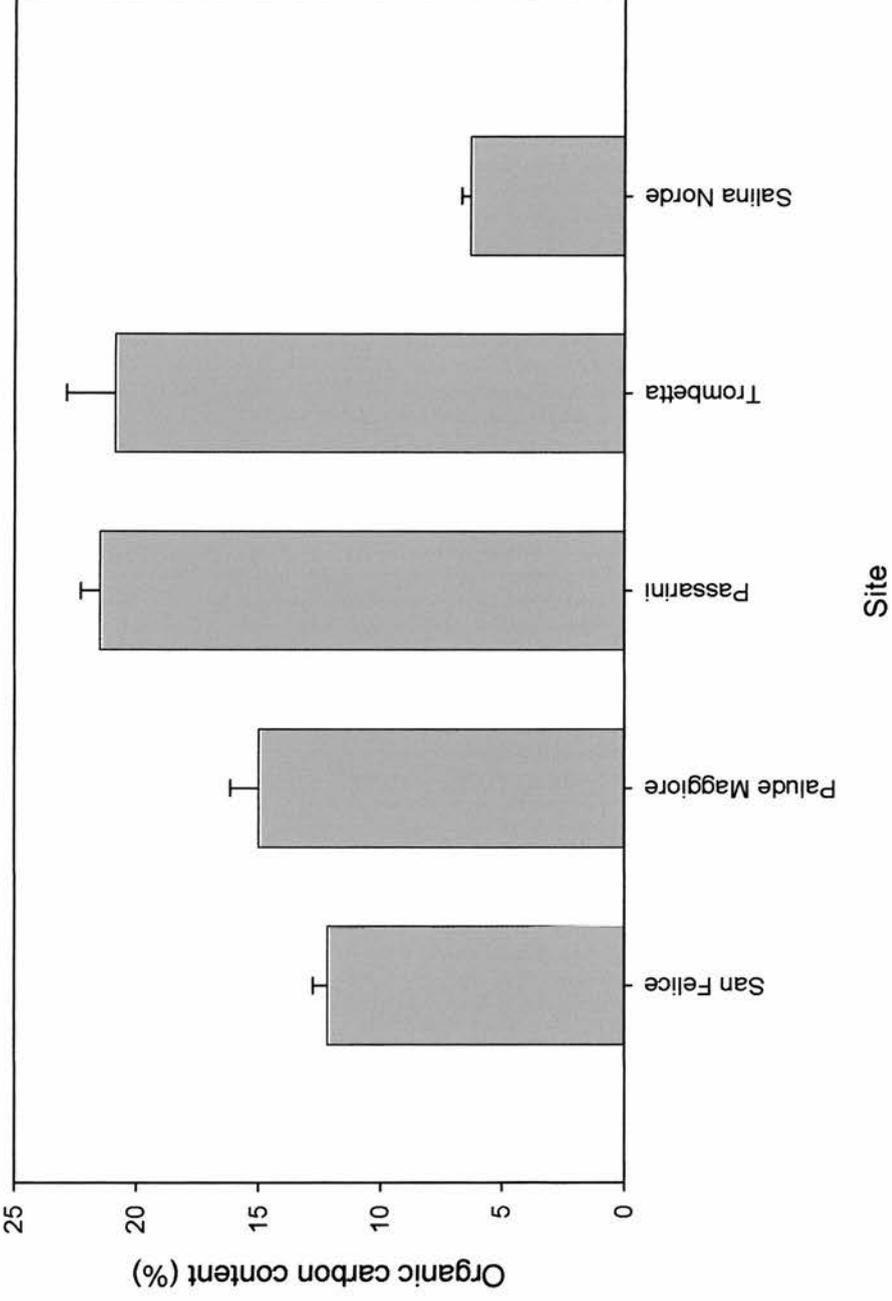


Figure 6.24: Organic carbon content (%) for samples taken during the February 2004 survey. Mean  $\pm$  s.e, n = 26-27.

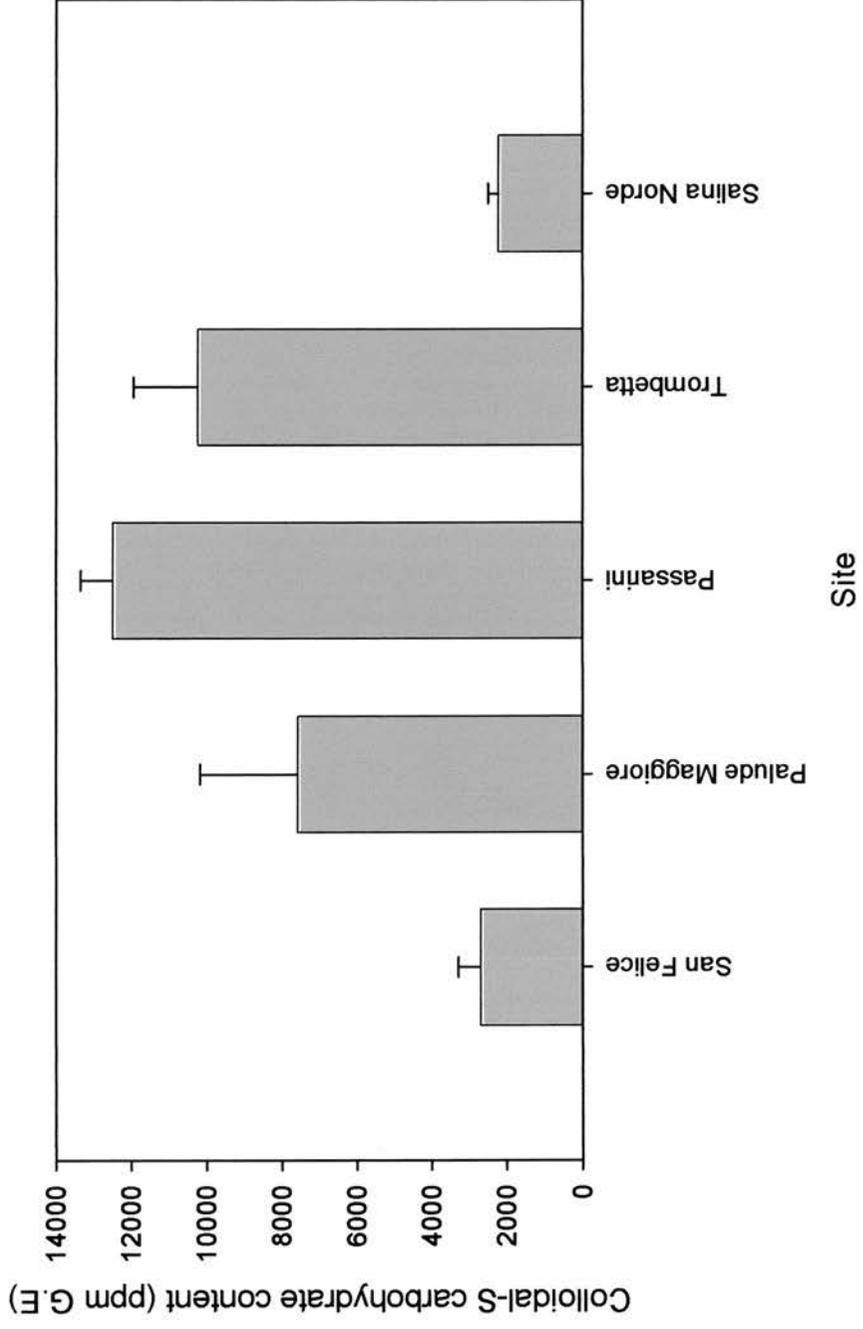


Figure 6.25: Colloidal-S carbohydrate content (ppm G.E) for samples taken during the February 2004 survey. Mean  $\pm$  s.e., n = 26-27.

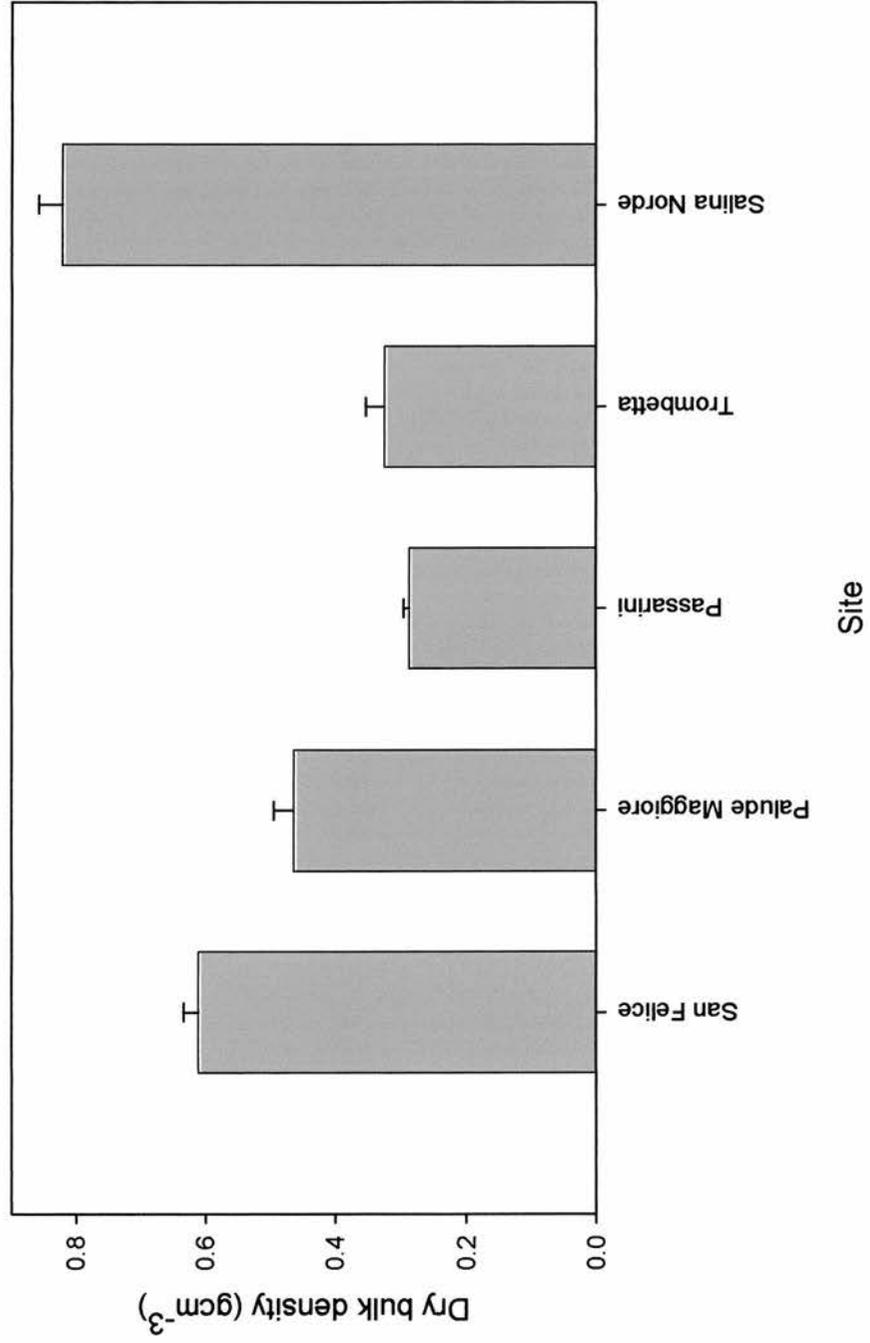


Figure 6.26: Dry bulk density (gcm<sup>-3</sup>) for samples taken during the February 2004 survey. Mean  $\pm$  s.e, n = 25-27.

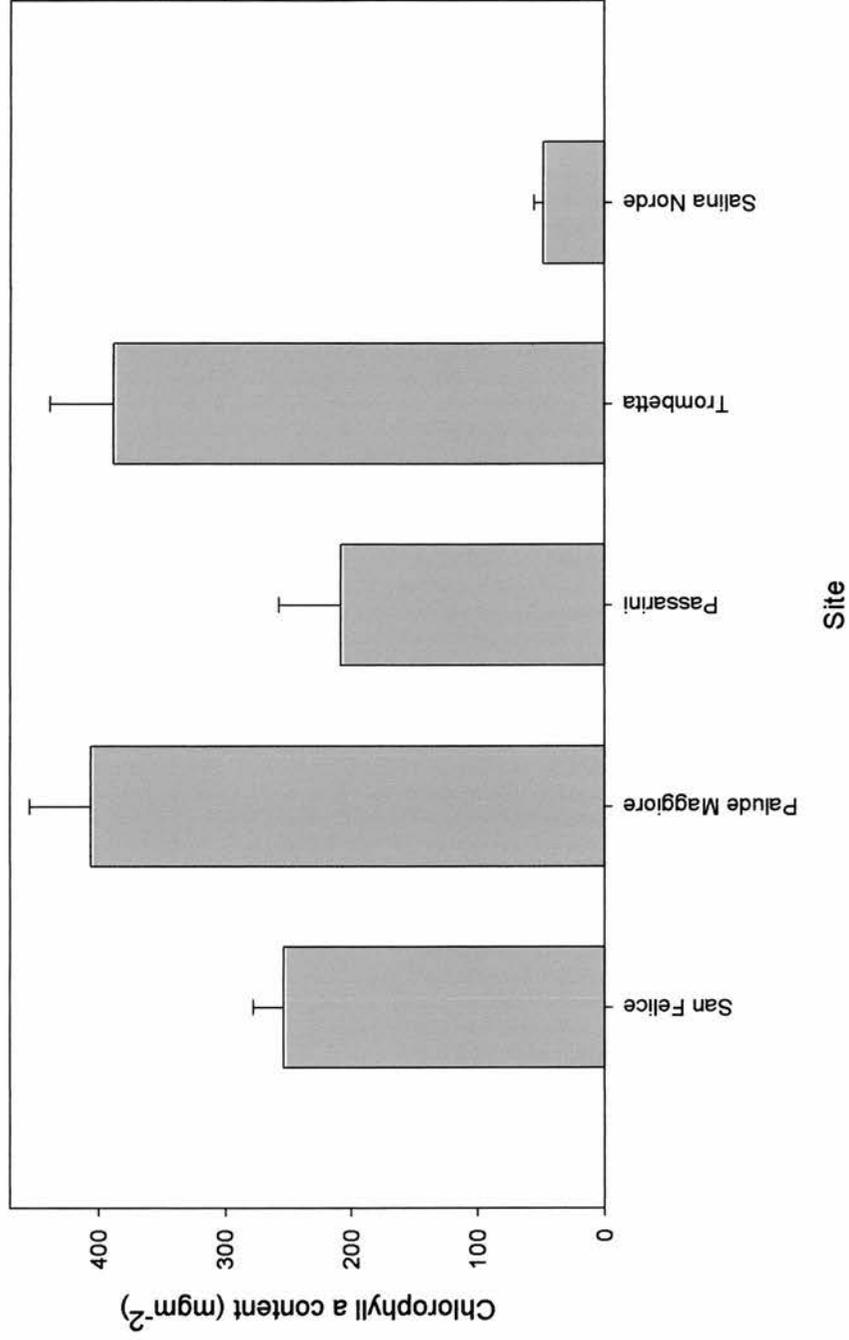


Figure 6.27: Chlorophyll *a* content (mgm<sup>-2</sup>) for samples taken during the February 2004 survey. Mean  $\pm$  s.e, n = 23-26.

observed in critical shear stress ( $H = 30.56$ ;  $d.f = 4$ ;  $p < 0.001$ ) (Figure 6.28). All sites were significantly different to Passarini and Trombetta, but when compared, these two sites did not have significantly different critical shear stresses ( $W = 343.0$ ;  $p = 0.7636$ ). At a depth of 9cm significant differences were observed in sediment shear strength ( $H = 9.83$ ;  $d.f = 3$ ;  $p = 0.020$ ) (due to missing data no results were available from Palude Maggiore). Only two sites showed statistically different shear strength values, these being Trombetta and San Felice ( $W = 15.0$ ;  $p = 0.012$ ), and Passarini and San Felice ( $W = 15.0$ ;  $p = 0.012$ ) (Figure 6.29). The significant differences shown in all parameters measured, indicates significant variations of sediment stabilisation, and indicators of microbial biogenic stabilisation of the sites within the lagoon (Table 6.7). Sediment at Trombetta was entirely composed of grains  $< 63\mu\text{m}$  in diameter. At least 86% of the sediment at Salina Norde and San Felice was composed of  $<63\mu\text{m}$  grain size, however only 77% of sediment sampled from Palude Maggiore and 61% of sediment from Passarini contained sediment of  $<63\mu\text{m}$  grain size diameter (Figure 6.30).

#### 6.3.3.2 Relationship between variables

Correlations carried out between parameters measured indicated that dry bulk density and chlorophyll *a* content were negatively correlated ( $r_s = -0.235$ ;  $p = 0.036$ ), organic content and colloidal-S carbohydrate content were positively correlated ( $r_s = 0.751$ ;  $p < 0.001$ ), organic content and dry bulk density were negatively correlated ( $r_s = -0.579$ ;  $p < 0.001$ ), dry bulk density and colloidal-S carbohydrate were negatively correlated ( $r_s = -0.486$ ;  $p < 0.001$ ), and dry bulk density and critical shear stress were negatively correlated ( $r_s = -0.249$ ;  $p =$

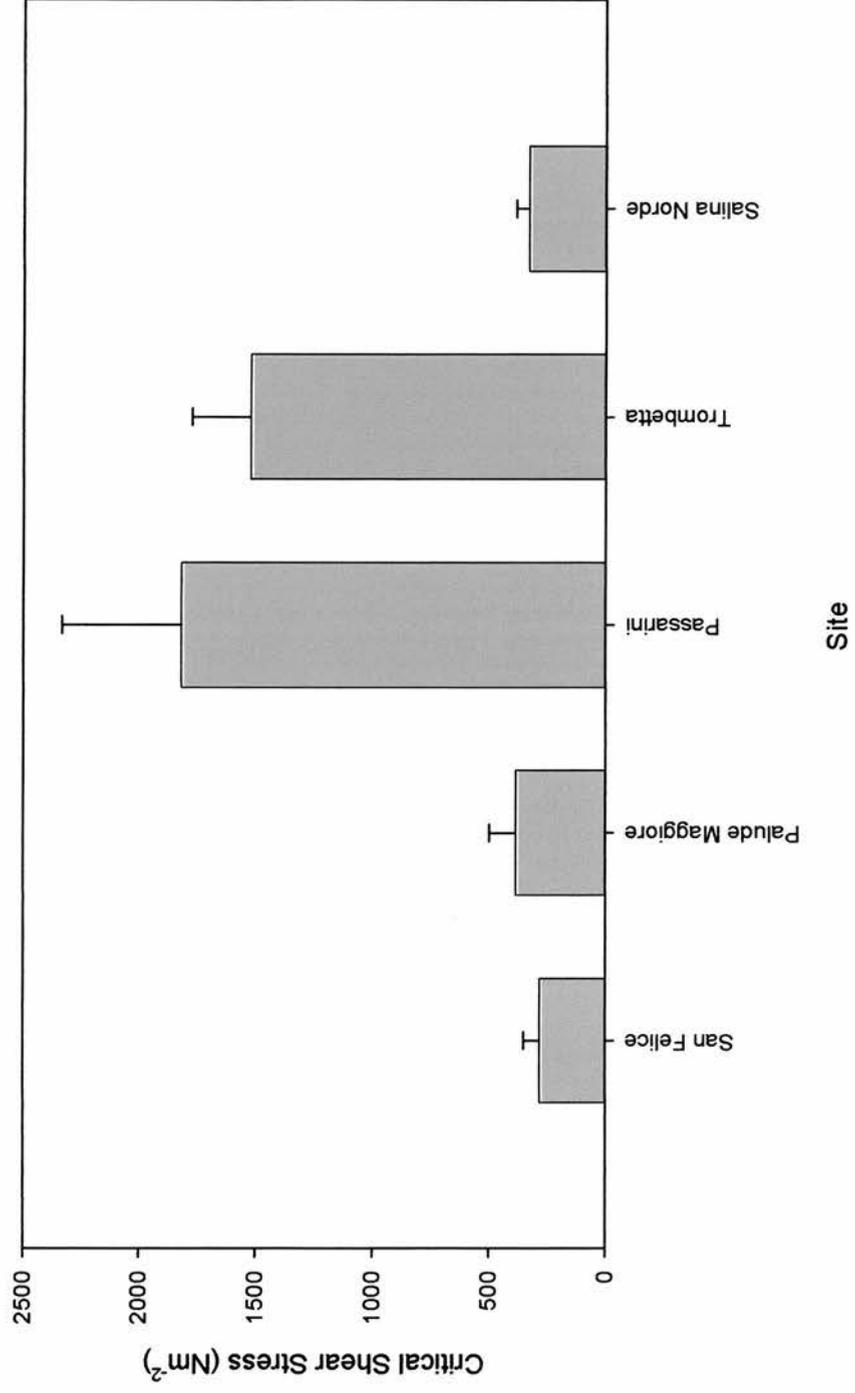


Figure 6.28: Critical shear stress (Nm<sup>-2</sup>) for samples taken during the February 2004 survey. Mean  $\pm$  s.e, n = 11-18.

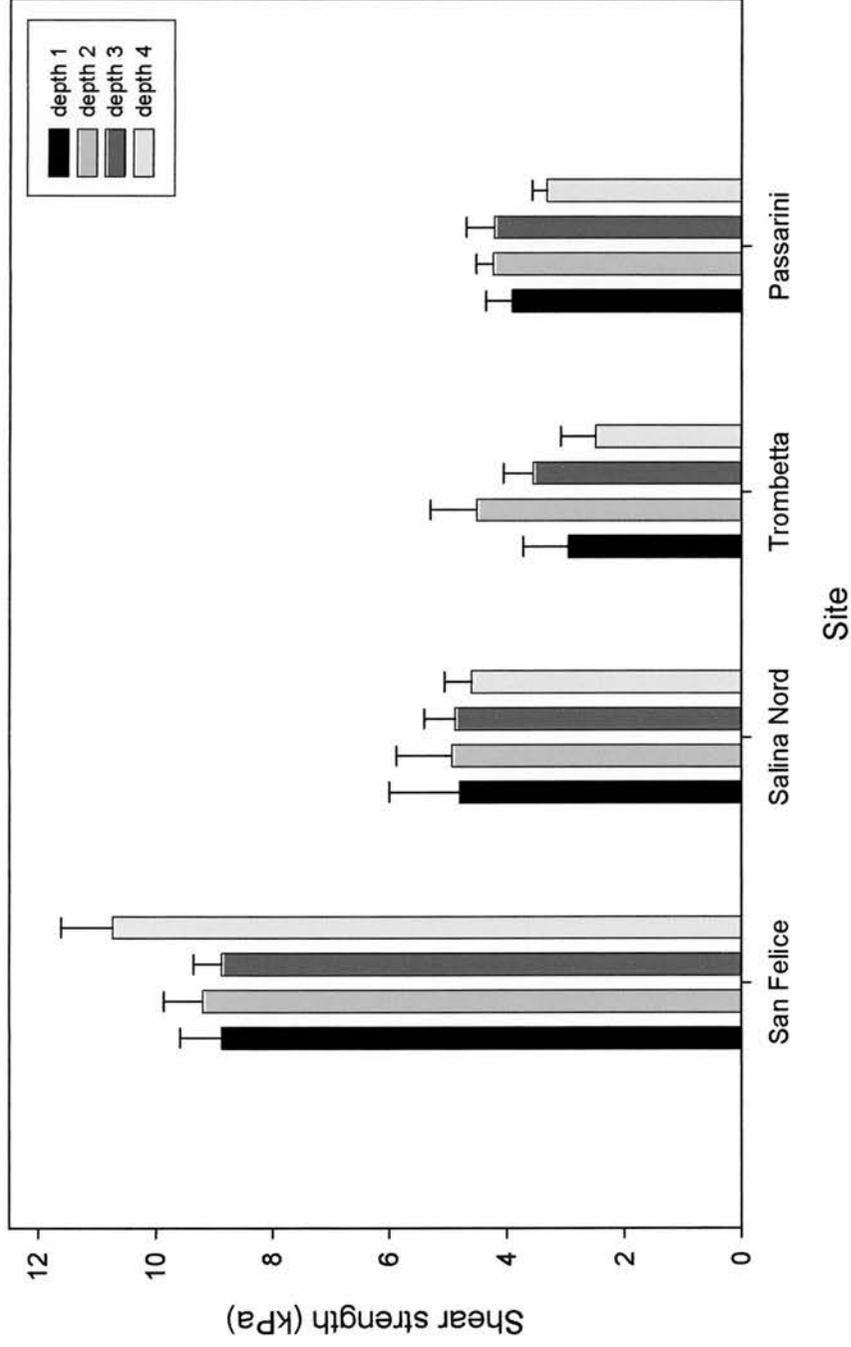


Figure 6.29: Shear strength (kPa) values at varying depths (9cm, 13cm, 17cm, and 21cm) at sites sampled during the February 2004 survey. Mean  $\pm$  s.e, n = 25.

	Trombetta	Passarini	Palude Maggiore	Salina Nord	San Felice
Colloidal carbohydrate (ppm G.E)	10231.30 (1694.30) n = 26	12495.41 (841.39) n = 26	7581.17 (2593.07) n = 26	2217.04 (273.96) n = 27	2711.18 (582.71) n = 26
Organic content (%)	20.88 (1.96) n = 26	21.50 (0.77) n = 26	15.01 (1.16) n = 26	6.30 (0.36) n = 27	12.18 (0.59) n = 26
Dry Bulk density (gcm <sup>-1</sup> )	0.33 (0.03) n = 27	0.29 (0.01) n = 26	0.47 (0.03) n = 27	0.82 (0.04) n = 25	0.61 (0.02) n = 25
Chlorophyll a content (mgm <sup>-2</sup> )	388.36 (50.30) n = 26	208.17 (49.01) n = 26	406.41 (48.40) n = 23	48.29 (7.36) n = 25	253.92 (24.10) n = 25
Critical shear stress (Nm <sup>-2</sup> )	1520.31 (250.66) n = 18	1816.60 (515.62) n = 18	385.92 (113.58) n = 18	329.89 (55.31) n = 15	281.81 (69.68) n = 11

Table 6.7: Mean ( $\pm$  SE) values for measurements of colloidal-S carbohydrate, organic carbon, dry bulk density, chlorophyll a, and critical shear stress, from surface salt marsh sediments collected during February 2004.

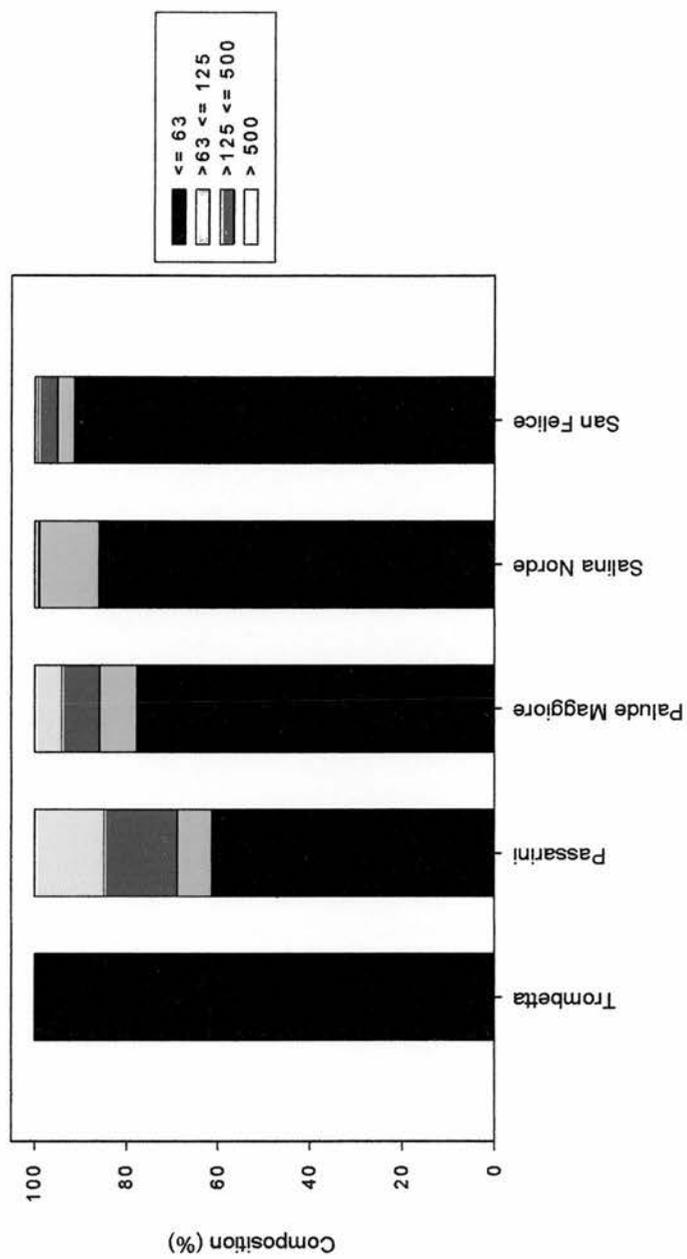


Figure 6.30: Percentage of grain sizes found at each site during the February 2004 survey. The majority of sediment at all sites was within the  $\leq 63\mu\text{m}$  range.

0.026). Significant relationships between the variables are described (Figure 6.31). Principle components ordination indicates the surface sediments at all sites were most influenced by colloidal carbohydrate and organic carbon content. Principle components 1 and 2 together account for 85% of the total sample variability (Figure 6.32).

#### 6.3.3.3 Microphytobenthic assemblages

Examination of microphytobenthic assemblages present within the sediments (Table 6.3) showed variation in composition between sites (Figure 6.33). These variations in assemblage composition were most obvious between Passarini and Salina Nord (ANOSIM R value = 0.944) and Passarini and San Felice (ANOSIM R values = 0.902). The diatom species most responsible for the dissimilarities between assemblage composition were *Navicula cryptocephala*, *Diploneis crabro*, *Pleurosigma* sp, and *Amphora ovalis*. Trombetta and Passarini had the most similar assemblages, (ANOSIM R value = 0.314). A significant difference was observed between sites during the July 2003 survey ( $H = 26.25$ ; d.f = 4;  $p < 0.001$ ). Assemblage diversity values (Shannon  $H'$ ) ranged from 1.7601 at Salina Norde, to 2.7221 at Passarini. The presence of mixed diatom assemblages was determined from low temperature scanning electron micrographs, along with high quantities of EPS forming sheet like plates between cells (Figure 6.34).

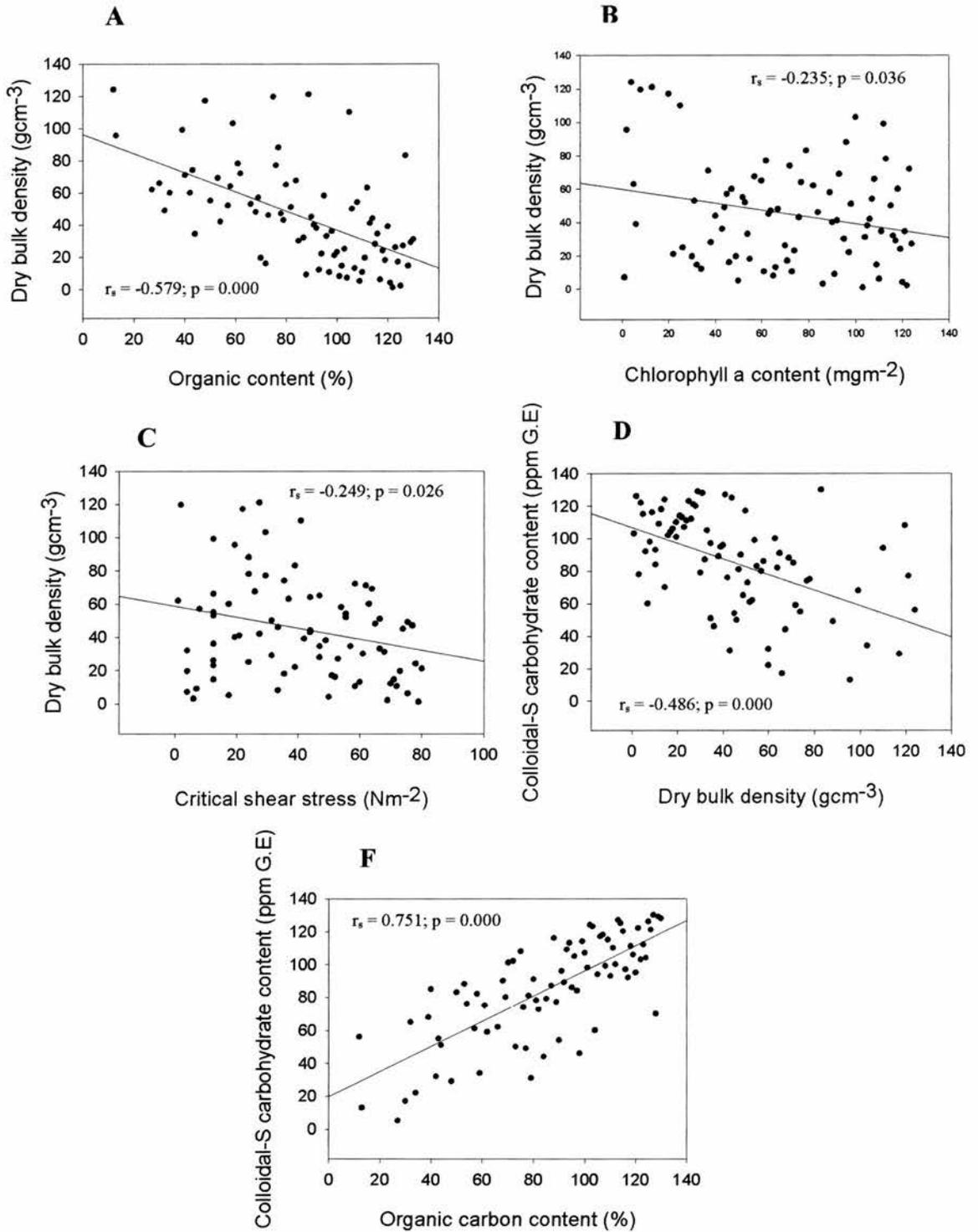


Figure 6.31: The relationship between parameters measured during the February 2004 survey. A) dry bulk density and organic carbon content, B) dry bulk density and chlorophyll a content, C) dry bulk density and critical shear stress, D) colloidal-S carbohydrate content and dry bulk density, E) colloidal-S carbohydrate content and organic carbon content.

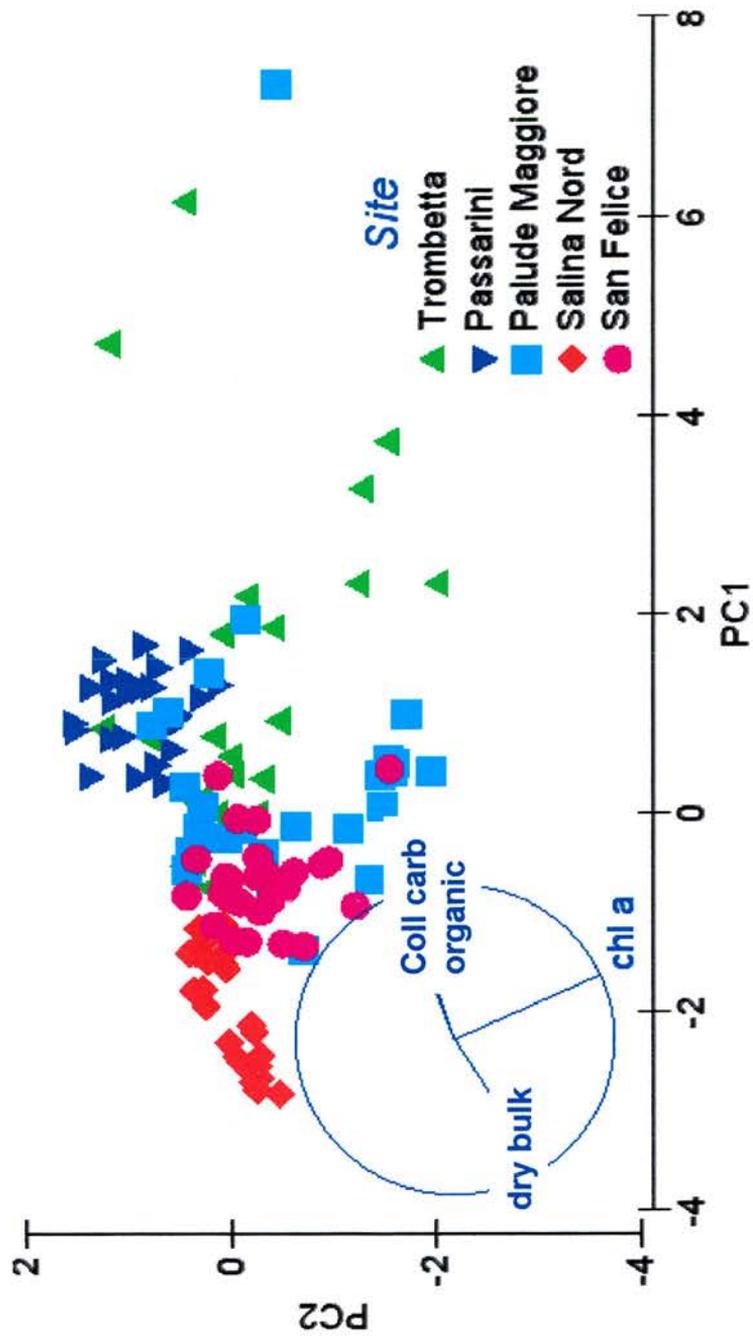


Figure 6.32: Principle components ordination indicates the surface sediments at all site were most influenced by colloidal carbohydrate and organic carbon content. Principle components 1 and 2 together account for 85% of the total sample variability.

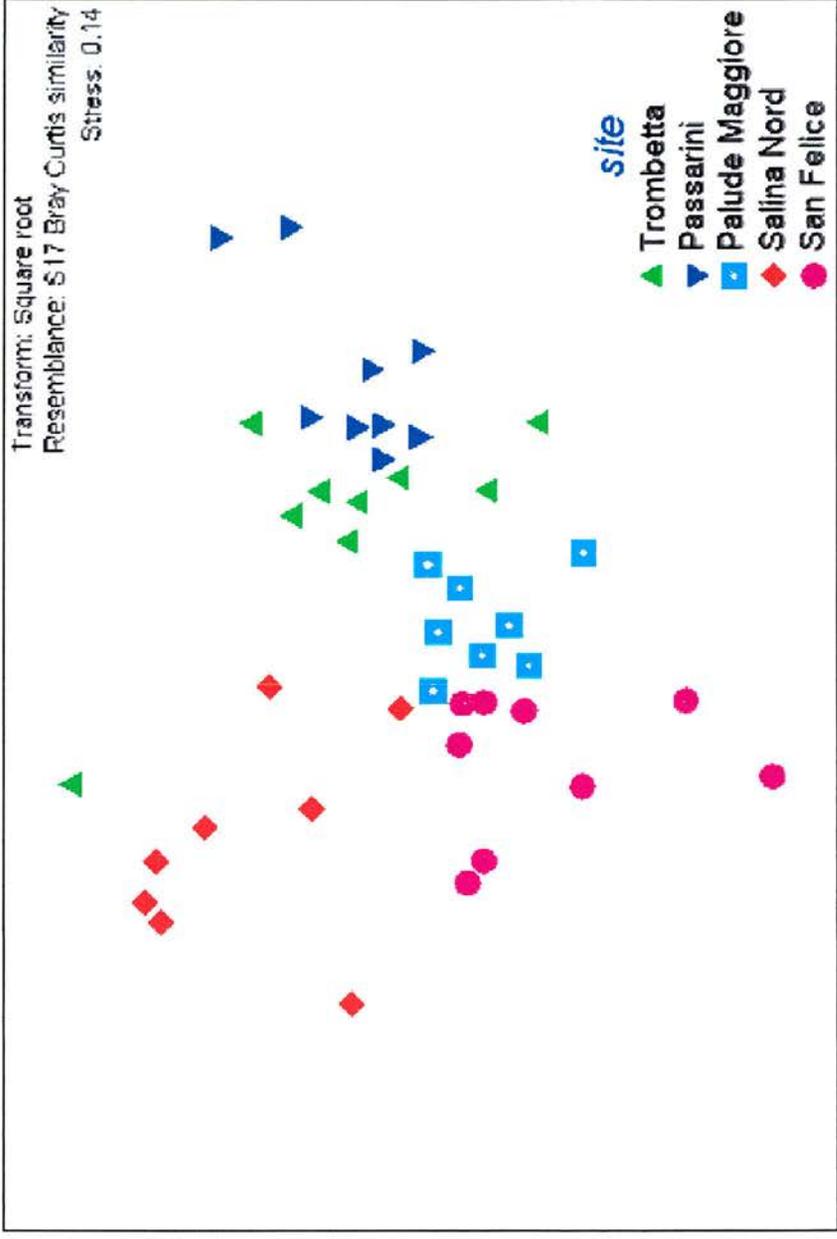


Figure 6.33: Multi-dimensional scaling plots of the microphytobenthic community assemblages present at study sites during the February 2004 survey.

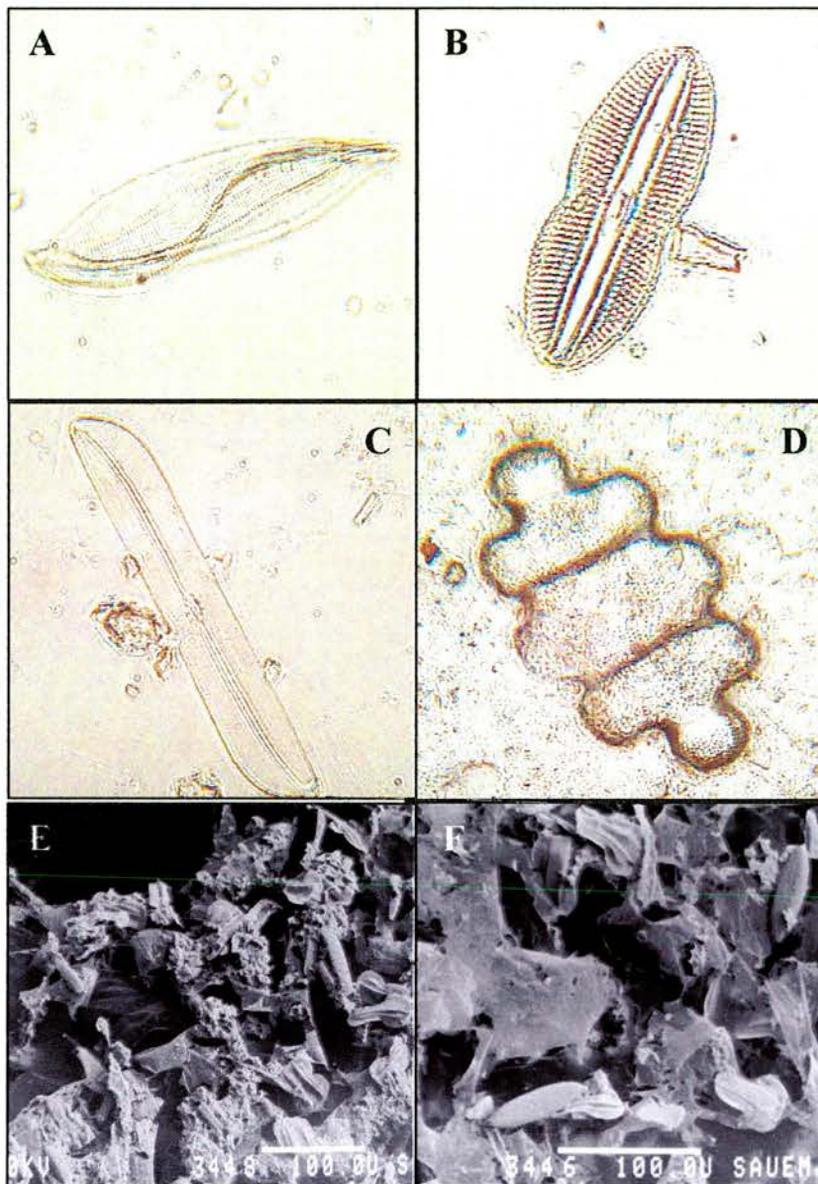


Fig 6.34: Diatoms are the most dominant forms of microphytobenthos found within salt marsh sediments. Examples of diatomaceous species found within the sediments studied during the February 2004 survey include *Amphiprora paludosa* (A), *Diploneis crabro* (B), *Gyrosigma eximium* (C), and *Terpsinoe americana* (D). Extra cellular polymeric substances (EPS) are exuded from the raphe structure during locomotion, and can be seen to occur as strands and sheets amongst the cells (E, F) under low temperature scanning electron microscopy.

#### 6.3.4 Changes in measured variables over time

Significant differences in colloidal-S carbohydrate content were observed between the three years studied at San Felice ( $H = 23.80$ ;  $d.f = 2$ ;  $p < 0.001$ ), Palude Maggiore ( $H = 21.77$ ;  $d.f = 2$ ;  $p < 0.001$ ), Passarini ( $H = 76.65$ ;  $d.f = 2$ ;  $p < 0.001$ ), and Trombetta ( $H = 53.56$ ;  $d.f = 2$ ;  $p < 0.001$ ). There was no significant difference in colloidal-S carbohydrate content observed over the three years at Salina Nord ( $H = 3.54$ ;  $d.f = 2$ ;  $p = 0.170$ ). At San Felice, Passarini, and Trombetta colloidal-S carbohydrate content within the sediment was significantly different during each of the three years sampling period. At Palude Maggiore colloidal-S carbohydrate content within sediment collected during 2003 was not significantly different to that collected during 2002, however significant differences were observed between 2004 and the previous two years.

Significant differences in organic carbon content were observed over the three years studied at San Felice ( $H = 48.69$ ;  $d.f = 2$ ;  $p < 0.001$ ), Palude Maggiore ( $H = 12.58$ ;  $d.f = 2$ ;  $p = 0.002$ ), Passarini ( $H = 22.40$ ;  $d.f = 2$ ;  $p < 0.001$ ), and Salina Nord ( $H = 16.91$ ;  $d.f = 2$ ;  $p = 0.000$ ). There was no significant difference in organic carbon content observed over the three years at Trombetta ( $H = 1.36$ ;  $d.f = 2$ ;  $p = 0.506$ ).

Significant differences in dry bulk density were observed between the three years studied at all sites sampled; San Felice ( $H = 81.23$ ;  $d.f = 2$ ;  $p < 0.001$ ), Palude Maggiore ( $H = 12.76$ ;  $d.f = 2$ ;  $p = 0.002$ ), Passarini ( $H = 7.40$ ;  $d.f = 2$ ;  $p = 0.025$ ), Salina Nord ( $H = 51.36$ ;  $d.f = 2$ ;  $p < 0.001$ ), and Trombetta ( $H=23.35$ ;  $d.f = 2$ ;  $p < 0.001$ ).

Significant differences in chlorophyll *a* content were observed between the three years studied at all sites sampled; San Felice ( $H = 57.90$ ;  $d.f = 2$ ;  $p <$

0.001), Palude Maggiore ( $H = 56.72$ ;  $d.f = 2$ ;  $p < 0.001$ ), Passarini ( $H = 32.04$ ;  $d.f = 2$ ;  $p = 0.000$ ), Salina Nord ( $H = 21.96$ ;  $d.f = 2$ ;  $p < 0.001$ ), and Trombetta ( $H=44.63$ ;  $d.f = 2$ ;  $p < 0.001$ ).

Critical shear stress differed significantly over the three years at San Felice ( $H = 30.16$ ;  $d.f = 2$ ;  $p < 0.001$ ), Palude Maggiore ( $H = 11.99$ ;  $d.f = 2$ ;  $p = 0.002$ ), and Salina Nord ( $H = 10.30$ ;  $d.f = 2$ ;  $p = 0.006$ ). Critical shear stress of the salt marsh sediments did not change significantly at Passarini ( $H = 0.34$ ;  $d.f = 2$ ;  $p = 0.843$ ) or Trombetta ( $H = 1.23$ ;  $d.f = 2$ ;  $p = 0.540$ ). The shear stress results obtained throughout the study exhibited three stages to the erosion process occurring within the salt marsh sediments (Figure 6.35). Three stages in the erosion process were apparent, linked to the stratified microbial layer, changing with depth (Figure 6.36). The surface layer was formed by a dense microbial assemblage, visible to the naked eye at most sites, composed of cyanobacterial and diatomaceous species. The second layer was an oxygenated layer composed of bacterial species capable of carrying out non oxygenic photosynthesis. Beneath the second layer was the anaerobic layer, dominated by anaerobic sulphate reducing species. The second and third layers described were eroded by greater pressures than those required to erode the first layer. However this does not necessarily represent the pressure required to erode the sediment at this depth, it is simply a result of the incremental increase in pressure from the CSM and the increasing distance of the layer from the jet.

Sediment shear strength was only tested during 2003 and 2004, and during these sampling periods no change in shear strength at the sediment surface (9cm depth) was observed at any of the sites.

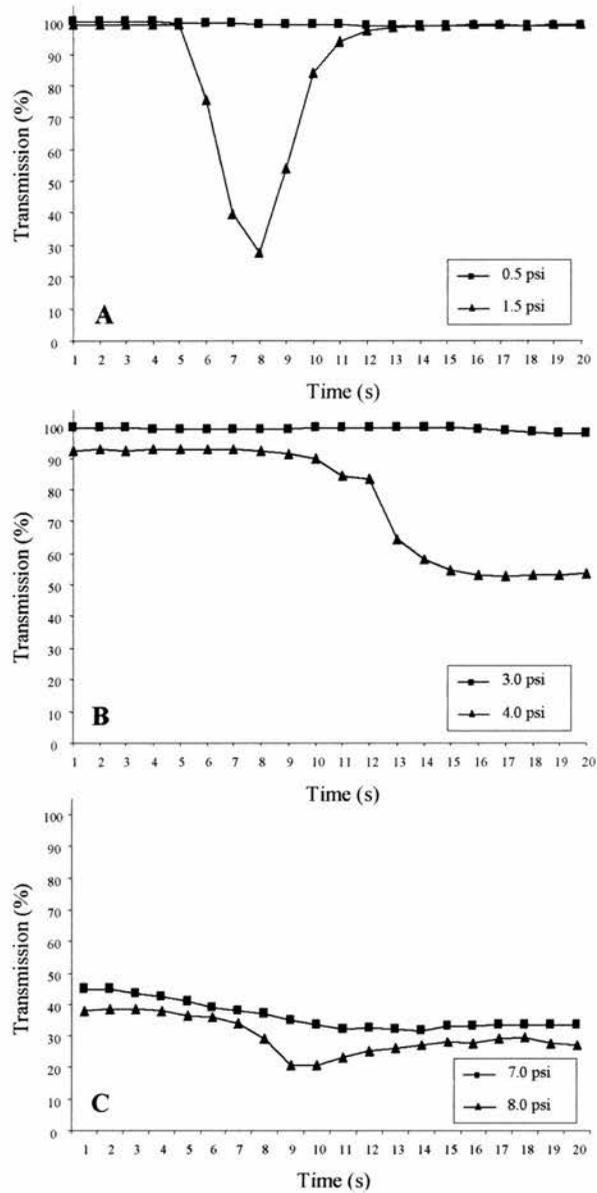


Figure 6.35: Erosion profiles created from data obtained using the cohesive strength meter described three main erosion stages. These erosion stages correspond to three observed stratified microbial layers, which will be described in more detail in Figure 6.34. The initial layer is dominated by a dense microphytobenthic biofilm containing loose surface flocs which are relatively easily eroded (A). Once erosion of this first layer occurs the erosive jet is prevented from causing further erosion by a second layer of photosynthetic assemblages (B), until the critical erosive pressure is reached, at which point a third less stable anaerobic layer is exposed (C).

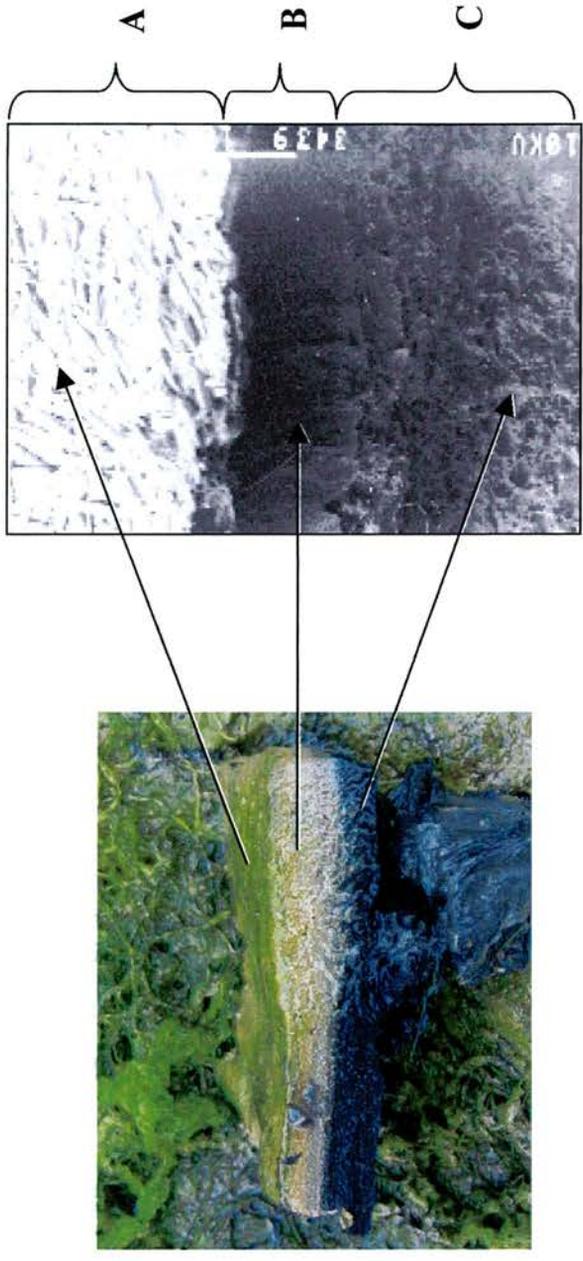


Figure 6.36: The shear stress results obtained throughout the study exhibited three steps to the erosion process, and can be described in terms of a stratified microbial layer, changing with depth. The first layer (A) is formed by a dense covering of microbial assemblages which could be seen with the naked eye at most sites formed by a combination of cyanobacterial and diatomaceous species. The second layer (B) is an oxygenated layer due to the activities of the migrating and photosynthetic assemblages, alongside the bacterial species capable of carrying out non oxygenic photosynthesis. The third layer (C) is the anaerobic layer, dominated by anaerobic sulphate reducing species.

## 6.4 Discussion

### 6.4.1 The Venice salt marsh as a biogenic system.

The results gained from analysis of the samples collected indicated the varied and diverse nature of the sites studied within the Venice Lagoon, in terms of both physical properties (dry bulk density, grain size, and critical shear stress), and biological properties (chlorophyll *a* content, organic content, colloidal-S carbohydrate content, and microphytobenthic assemblage occurrence). Whilst few patterns were observed amongst the variables, the relatively high cohesion of the system compared to other systems subjected to biogenic stabilisation was of interest.

The sampling was carried out to investigate the relationship between microbial assemblages present within the marsh sediments and the stability of the sediments. Small sediment samples were collected over an area of 8 x 8m. However, the surface of the salt marsh system proved to be very heterogeneous (Figure 6.37) with spatial variation ranging from m to cm, so any correlations or relationships were masked by huge variations within the data set.

### 6.4.2 Microphytobenthic influences in salt marsh systems

The study of flow dynamics (Shi *et al* 1995, 1996, Ziebis 1996) and the colonization of macrophytes (Maynard 2001, Sherwood *et al* 2000 and references within) and microphytobenthos (Aspden *et al* 2004b, Mason *et al* 2003, Paterson and Hagerthey 2001, Zong and Horton 1998, and Underwood 1997) in salt marsh systems are relatively well documented in literature. For diatom rich assemblages a linear relationship between chlorophyll *a* and



Figure 6.37: The salt marsh vegetation was heterogeneous with spatial variation ranging from scales of metres (A) to cm (B).

colloidal-S carbohydrate content has been observed in previous studies (Underwood and Paterson 1993). This relationship was not detected during the present study, however, the assemblages present within the salt marshes of the Venice Lagoon were mixed assemblages containing cyanobacteria as well as diatomaceous species and this may explain the lack of correlation.

The results gained during this study determined that distinct microphytobenthic community assemblages were present at each site studied over the three study periods (Figure 3.11, 3.22, 3.33). This may be a result of variations in periods of exposure or salinity at the different sites. Zong and Horton (1998) determined a strong zonation pattern of diatom taxa from mudflat through to high salt marsh, due to frequency and duration of tidal inundation. Various species of diatoms are adapted to different light and temperature conditions and as such migrate vertically in sediments at different rates and in response to varying conditions (Consalvey *et al* 2004). This may explain variations found in the community assemblages determined at the sites studied. Microphytobenthic assemblages have been found to vary according to sediment grain size (Zong and Horton 1998). However, sediment size was determined to be of secondary importance, and tended to control the composition of the assemblage as oppose to the distribution of certain species. Underwood (1994) determined that no single measured variable could explain the distribution of diatoms species in the study, and proposed that the differences observed in species composition and diversity was due to the gradients of environmental stress and disturbance between upper and lower shores. During the course of the present study no relationship between grain size and the diatom assemblage

composition was observed, nor could any single measured variable be singled out as being most influential upon the salt marsh sediments.

#### 6.4.3 The stability of salt marsh sediments

The shear stress results obtained throughout the study exhibited three steps to the erosion process occurring within the salt marsh sediments (Figure 6.36) related to a stratified microbial layer, changing with depth. The dense covering of microbial assemblages which could be seen with the naked eye at most sites, formed by a combination of cyanobacterial and diatomaceous species. These dense mats form the first barrier of defence for surface sediments against erosion. By forming a network of filaments the cyanobacteria can trap and retain sediment within the matrix structure, forming a stabilised layer of fine sediment on the surface of the marsh. A similar phenomenon can be observed in stands of filamentous algae (Scoffin 1970, Airoidi *et al* 1996, Airoidi and Virgillio 1998) (Chapter 3) and cyanobacterial assemblages (Stoltz *et al* 2001) (Chapter 7). The grain size results obtained show that the particles within the marsh sediments are mostly  $<63\mu\text{m}$ , and as a result once trapped within the filaments the sediment particles are also retained due to cohesion by EPS associated with the microbial assemblages. The matrix of cyanobacterial filaments forms a filter in which the sediment grains are trapped. The large surface area: volume ratio increases the inter-particle cohesion due to electrostatic forces creating a stable and somewhat rubbery surface layer. This stable layer of sediment was observed to be highly spatially variable, but no single variable could be attributed to the stability of the sediments. The second layer is an oxygenated layer due to the activities of the migrating and photosynthetic assemblages, alongside bacterial species capable of

carrying out non oxygenic photosynthesis. Depending on the environmental conditions the cyanobacteria and diatoms will migrate at different times, each optimising the potential for photosynthesis. This results in a change in surface assemblage, and possibly of stability. Beneath this boundary layer is a layer of sediment with low critical shear stress. This anaerobic layer, dominated by anaerobic sulphate reducing species had a very low critical shear stress, suggesting the importance of microphytobenthic assemblages in the stability of salt marsh sediments.

## **6.5 Conclusions**

Stabilisation of the salt marsh sediments during this study was highly variable within and between sites (Figure 6.7, 6.17, 6.28). However, the grain size distribution across the sites was constant removing the possibility that this variable was the cause of the variation. Thus the variation between sites and within sites may have more in keeping with the biological nature of the sediment and hence the inherent spatial variability of biological assemblages. The microbial assemblages showed distinctive clusters on the multi dimensional scaling plots, suggesting that each site had specific species compositions. Future studies should also determine the extent to which the assemblages were composed of cyanobacterial species, as the data collected during this study suggests that these species play an integral role in the functioning and ecogeomorphology of salt marsh systems.

The data suggests that dry bulk density appears to influence the salt marsh sediments more than the other measured parameters, however the stability

of the salt marsh could not be related to any individual measured parameter, which is concurrent to findings of Underwood (1994), and this poses an interesting discussion point. Either the system is too variable to predict with our current knowledge or a more holistic approach might be required, including the nature of the higher salt marsh plants present at each site. Sampling protocols were established to be in keeping with the TIDE programme, with the objective to retrieve *in situ* data for the ground truthing of remote sensing data (Silvestri *et al* 2002). In retrospect these objectives may be mutually exclusive. The spatial scale required for remote sensing ground truthing is usually at the 1m scale. However, extreme spatial variability of the Venice system (Figures 6.3-7 and 6.37) suggests that for studies of the type described above, for the purpose of determining a relationship between MPB and stability, a smaller scale study with greater replication needed to be carried out. If a relationship between the microphytobenthos, stability, and the higher plants can be established remote sensing ground truthing may be a successful method of data collection, nevertheless, much more work needs to be carried out in order to establish whether this kind of relationship indeed exists.

## **6.6 Publication**

Work from this study has been published in *The Ecogeomorphology of Tidal Marshes*.

See Aspden, R.J., Vardy, S., and Paterson, D.M. (2004). Salt Marsh Microbial Ecology: Microbes, Benthic Mats and Sediments Movement. *The Ecogeomorphology of Tidal Marshes : Coastal and Estuarine Studies Series* (AGU). Editors – Fagherazzi, S., Marani, M., and Blum, L.K.

## **CHAPTER 7**

**THE INFLUENCE OF LIGHT AND TIME ON THE  
BIOSTABILISATION OF SEDIMENT BY MODERN  
MARINE STROMATOLITES.**

## **Chapter Seven – Abstract**

The relative capabilities of the stromatolite surface to retain grains deposited by natural wave action, and the ability of damaged stromatolite material to regenerate was determined using the cohesive strength meter (CSM). Samples were selected from various sites containing stromatolites of differing growth stages.

Ooid particles were found to be effectively retained on the stromatolite surface within a period of 24h. The critical time period required for grain retention was determined to be less than 10h. Grain retention was dependent on the type of mat, and the light conditions the stromatolite material was subjected to. Stromatolite samples maintained in the light treatments showed greater retention capacity than those maintained in the dark treatments. Diatom species present on the surface of the samples were observed to trap and bind ooid particles within the surface structure of the stromatolites.

Stromatolite material exhibited an ability to biostabilise relatively quickly after major disturbance. This biostabilisation was significantly higher in material maintained in natural conditions compared to samples maintained in darkness. Low-temperature scanning electron microscopy revealed that samples maintained in disparate light regimes supported different microphytobenthic assemblages at the surface of the samples.

## 7.1 Introduction

### 7.1.1 Stromatolite formation

Despite the fact stromatolites have been present in marine systems for 3.5 billion years (Schopf 1983), the biomechanical processes involved in the formation and structure are little understood. Whilst the existence of these ancient structures provide evidence for the role of prokaryotes in the trapping and binding of sediments, and the lithification of microbial biofilms; the modern equivalents provide an excellent opportunity to research the processes involved in stromatolite formation in further detail. Stromatolite formation is strongly dependent on the ability of associated microbial assemblages to trap and bind sediment grains into the structure of the stromatolite, whilst preventing the erosion of captured sediment particles due to the wave action and currents acting upon and around the stromatolites. Stromatolites are created by the lithification of microphytobenthic and bacterial mats combined with periods of sediment accretion (Walter 1976, Reid *et al* 1995), and the initial processes in the formation are similar to those exhibited by filamentous algae, turfs, and microphytobenthic mats. These structures are capable of accumulating sediment particles through a combination of physical entrapment within the filaments, and binding of the sediment particles by exopolymers produced by the microbial community present (Scoffin 1970, Stewart 1983, Kendrick 1991, Airoidi 1996). Stoltz *et al* (2001) described three sedimentary process involved in the formation of stromatolite structures; the trapping of carbonate ooid grains, the lithification process and formation of the micritic layer, and the fusion of ooid grains. These processes are seen to underpin the three growth stages of stromatolite formation

described during a two year study of the stromatolite systems in Exuma Sound, Bahamas, by Reid *et al* (2000) (Figure 7.1). In this study each growth stage was found to be dominated by different microbial communities, suggesting the importance of biogenic influences in the formation of stromatolite structures, in what has commonly been thought of as a dominantly physical process. Type I mats were reported (Reid *et al* 2000) to form during periods of sediment accretion. The filamentous cyanobacteria *Schizothrix* sp found within this mat type was observed to migrate vertically to the surface of the stromatolite, trapping and binding ooid particles with its sheathed filaments as it moved. Type II mats are typified by the development of micrite on the surface of the stromatolite structure. This lithification process occurs during short periods of no/low sedimentation, during which anaerobic and aerobic bacterial activity is high, promoting the precipitation of aragonite, which in turn leads to the calcification of the biofilm. Whilst *Schizothrix* sp can be found in high densities beneath the biofilm, it is not present in high quantities within the biofilm itself. Instead the biofilm is dense with exopolymers, which drape over the stromatolite surface bridging the gaps between the particles. Also within the exopolymers are aragonite crystals, often found associated with dense populations of bacteria. Type III mats form during longer periods without significant sediment accretion, and are densely populated by the endolithic coccoid cyanobacteria *Solentia* sp., which bores through the grains often causing fusion between ooid grains. Carbonate precipitation is promoted by the microboring of *Solentia* sp and so infilling of the bore holes by calcium carbonate precipitate occurs (MacIntyre *et al* 2000). Ooid grains fuse together when a bore hole crosses from one ooid into

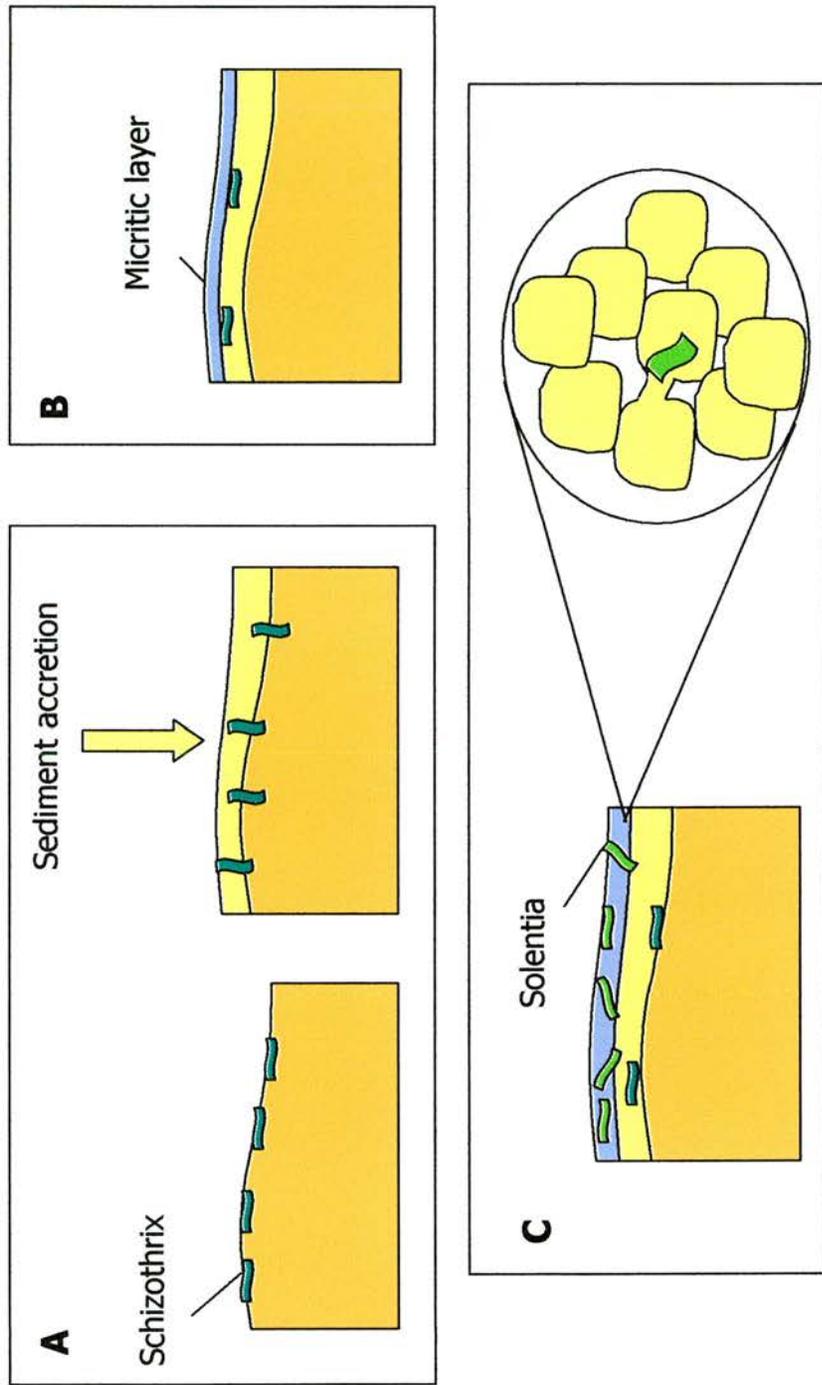


Fig 7.1: During stromatolite formation in Exuma Cay three growth stages of stromatolite formation have been observed (Reid *et al* 2000). (A) Type I mats form during periods of sediment accretion. The filamentous cyanobacteria *Schizothrix* sp was found within this mat type and observed to migrate vertically to the surface of the stromatolite binding ooid particles with filament sheaths as it moved. (B) Type II mats show the development of micrite. This lithification process occurs during short periods of no/low sedimentation, during which anaerobic and aerobic bacterial activity is high, promoting the precipitation of aragonite, which in turn leads to the calcification of the biofilm. (C) Type III mats form during longer periods of limited sediment accretion, and are densely populated by the coccooid cyanobacteria *Solentia* sp. which bores through the grains often causing fusion at points where the grains are in contact. *Schizothrix* sp. is also still present beneath the biofilm in small numbers.

another at a point of contact. This fusion increases the stability of the surface ooids. *Schizothrix* sp. is also still present beneath the biofilm in small numbers.

### 7.1.2 Stromatolite history

Stromatolites declined at the beginning of the Phanerozoic period (Awramik, 1971), coinciding with the evolution of invertebrates. The newly evolved invertebrates added extra demands on the stromatolite systems including bioturbation and grazing pressure. This may have reduced stromatolite formation to areas where invertebrates could not compete, such as the hypersaline pools at Shark Bay, Australia, however unusually the stromatolites forming in Exuma Cay, Bahamas, occur in normal marine conditions. Riding *et al* (1991) suggests that the early cementation of the type I layers may be a strategy developed to prevent bioturbation by invertebrates, however the continued occurrence of stromatolites and lack of invertebrates may be due to the high shear stress, resulting from the significant hydrodynamic forcing in the area.

Other studies have suggested growth stages to be dependent on physical factors such as sedimentation rates, and position of the stromatolites within the reef with respect to movement of dune structures (MacIntyre *et al* 1996, Golubic and Browne 1996). Sedimentation rates in areas of stromatolite formation have an important role in the structure and formation of the stromatolite assemblages. The microbial assemblages present in stromatolites have been shown to adapt to varying sedimentation rates, thereby creating the three stromatolite types described by Reid *et al* (2000). For example, *Schizothrix* sp does not become abundant until sedimentation rates decrease or become negligible.

Calcification of the type I mats (*Schizothrix* sp layers) is inhibited by the presence of the *Schizothrix* sp filament sheaths (EPS) (Kawaguchi and Decho 2002). This inhibition is due to a combination of factors surrounding the presence of EPS. Whilst *Schizothrix* sp is present, during periods of sedimentation, anaerobic sulphur-metabolising bacteria responsible for the calcification process are absent (Visscher *et al* 1998, 2000). These bacteria need the stable surface provided by the type I mats, but cannot colonise until the *Schizothrix* sp is out competed during periods of low sedimentation. Another factor preventing the calcification process may be the acidic proteins and acidic polysaccharides present in EPS. These compounds bind to the  $\text{Ca}^{2+}$  ions preventing calcium carbonate precipitation (Kawaguchi and Decho 2002).

Previous studies of the formation of stromatolites have concentrated on the cyanobacterial species present largely responsible for the autochthonous production within stromatolite systems. However, although there is little literature available on the subject, it is becoming apparent that some of these roles may also be undertaken by diatomaceous species. Diatoms date back to the early Jurassic period and although they are a relatively recent development of the eukaryotes, it is fair to assume that they have been associated with stromatolite systems since their emergence. 420 species of diatoms have been identified from recent material associated with stromatolites in the Bahamas (Winsborough 2000 and references within) and it has been noted that these species have a key role to play in the trapping and binding of freshly deposited sediment, due to their growth form (stalked and branching) and the copious production of EPS (Awramik and Riding 1988, Paterson and Black 2000, Underwood and Paterson 2003).

Whilst stromatolites are now recognised as structures formed through a combination of biotic and abiotic factors, very little information is available detailing the stabilisation of the structures, and the mechanisms involved in the formation and structure. The following studies were designed to examine aspects of biostabilisation and particle capture by stromatolite assemblages.

During this research the following hypotheses were tested in order to investigate the biogenic aspects of stromatolite systems:

- Ooid capture and retention of ooids is greater within stromatolites when subjected to a light period
- Ooid capture and retention of ooids is greater within stromatolites containing diatoms.
- The stabilisation of stromatolite material after major disturbance occurs most rapidly when exposed to a light period.

## **7.2 Materials and Methods**

### **7.2.1 Ooid retention**

Stromatolite sections were selected and carefully removed from their *in situ* position, minimising damage to the donor stromatolite. The samples were removed from three sites of varying growth stages: site 1 (mats with diatomaceous covering; site 2 (type I mats with diatoms); site 12 (type II mat, micritic mats with few diatoms). These excised sections were introduced to an outdoor running seawater system (max water temperature = 37.9°C, min water temperature = 29.1°C) and allowed to acclimatize for 12 h. The light treatments

were subject to natural light conditions (min = -1.77; max = 4.45 log-lumen m<sup>-2</sup>), whilst no light was detectable in the dark treatments. Once the samples had reacclimatized, clean ooids (no organic matter) were sprinkled onto the surface of the stromatolite samples and left for a period of 10 h. The relative retention of the ooids was determined using the CSM system (Paterson 1989, Tolhurst *et al* 1999), reconfigured without the standard optical sense head (Figure 7.2).

The pressure required to achieve four stages of erosion was recorded:

- Stage one: surface grain movement.
- Stage two: underlying surface becoming visible.
- Stage three: General clearance of underlying surface, individual grains remaining.
- Stage four: Total clearance of all grains from the surface.

The jet was maintained at a 45° angle and the distance of the nozzle was set at 3cm from the stromatolite surface, throughout the experiments, to ensure all samples were treated to the same hydrodynamic forcing. Minimums of 5 replicates were prepared. On each of the replicates three different areas of the surface were tested to ensure that small scale patchiness and variability were not having an effect. Control tests were carried out by exposing the clean ooids to the erosive pulses of the CSM immediately after the ooids had been deposited on the stromatolite surface.

Sections of each type of mat were placed in a vial and stored at -80°C until low temperature scanning electron microscopy could be carried out to investigate the fine detail of the surface structure.

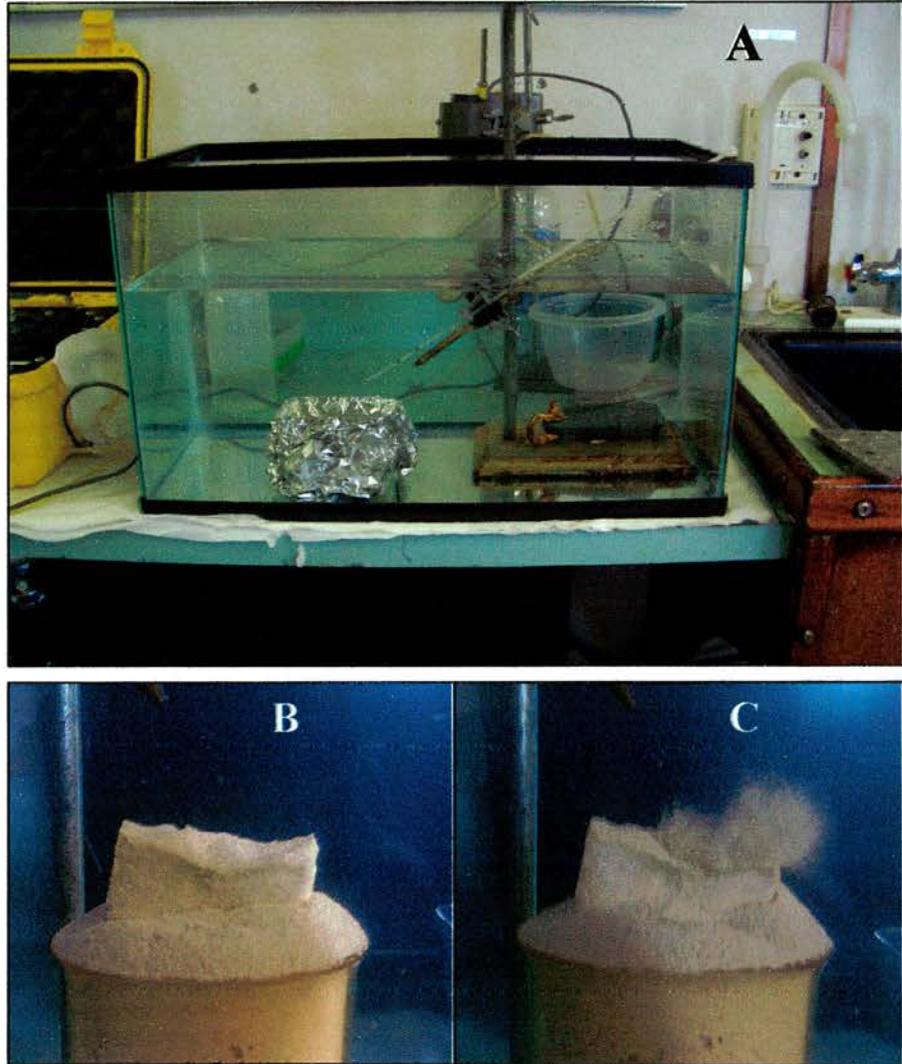


Figure 7.2 - Grain retention experiments using the CSM jet system. A - The jet aperture is shown on the top left of the image. Pulses of increasing water pressure are directed at the grain surface until grain motion is detected during grain retention experiments. B - Before a pulse is triggered. C - The disturbance of grains by a jet pulse.

Time series experiments were carried out to determine the time required for optimum binding activity to occur. Samples were collected from sites 2 and 12, and prepared as previously described. Ooid retention was determined using the same experimental set up as previously described; retention was tested at 0, 12, 36h periods (an additional measurement taken at 48h from the site 12 samples).

Sections of stromatolite were also removed from each area in order to determine the grain sizes retained within the natural structure. Sediment traps were placed in the areas the samples were taken from in order to determine the nature and mass of suspended sediment in the water column, the source for stromatolite accumulation.

#### 7.2.2 Reconstitution of stromatolite material

Stromatolite material was carefully chosen and removed from two sites (site 1 and site 10) avoiding any permanent damage to the donor stromatolite. The chosen material was broken down into individual ooid particles and any large fragments were removed by passing the material through a 1mm sieve. The material from each site was placed in 14 replicate trays; 7 placed in a natural light set, and 7 in darkness. 7 control samples (beach ooids) were placed along side the natural light treatments. All experimental treatments were placed in an outdoor, running seawater set up (max water temperature = 37.9°C, min water temperature = 29.1°C) and left to reacclimatize for 12h, after which an initial measurement was made with the CSM (normal configuration) (Figure 7.3). The test was repeated every two days until the experiment ended 204 h later.



Figure 7.3: Reconstitution experiments. A- incubation tray used during the experiments; B- after each measurement was taken the erosional imprint could be seen on the sediment surface. Care was taken not to test the same area twice.

During each measurement four stages of erosion were recorded:

1. Incipient erosion (10% reduction in transmission)
2. Significant surface erosion (20% reduction in transmission)
3. Erosion of underlying material (50% reduction in transmission)
4. General erosion (90% reduction in transmission).

Sections of each type of mat were placed in a vial at the end of the experiment and stored at  $-80^{\circ}\text{C}$  until low temperature scanning electron microscopy could be carried out to investigate the fine detail of the surface structure.

### 7.2.3 Statistics used

Due to the type of data collected by the CSM it was not possible to use parametric tests. Although the data are normal, they are discrete and do not have equal variances; therefore more conservative non-parametric tests with lower power were used. For data sets with 1 factor to be tested the Mann-Whitney U statistical test was used, and for tests with 2 or more factors the Kruskal-Wallis test was used (Dytham, 2003). Statistics were tested within a 95% confidence limit.

## 7.3 Results

### 7.3.1 Ooid retention

Control experiments were cleared by a pulse of 0.3 psi or less, suggesting little evidence for ooid retention due to the cohesiveness of the ooid particles themselves. A highly significant difference in the retention of ooids to the stromatolite surface was observed when light, dark and control treatments were studied ( $H = 33.08.05$ ,  $df = 2$ ,  $p = 0.000$ ). Stromatolite surfaces maintained under dark and light treatment conditions were observed to retain ooid grains more effectively over a 10 h period than the control treatments (dark treatments:  $W = 345.0$ ,  $p = 0.00$ ; light treatments:  $W = 345.0$ ,  $p = 0.000$ ) (Figure 7.4, Table 7.1). Stromatolite samples maintained in light treatments exhibited a significantly higher grain retention capacity than the samples maintained in darkness ( $w = 165.0$ ,  $p = 0.005$ ). After a 10 h period the maximum pressure of 60 psi was often not enough to remove all particles from the surface of the stromatolite section.

Samples taken from site 1 appeared to have a 'fluffy' surface layer unlike the relatively smooth surface material from sites 2 and 12. When viewed under a stereo microscope it became apparent that this layer consisted of at least three species of stalked and chain forming diatoms, dominated by a species of *Actinella* sp (Figure 7.5 and 7.6).

Previous experiments indicated that the extent of grain retention was time dependent, and so this was further investigated, and it was determined that grain retention did not vary significantly after a further 12 hour period (Figure 7.7).

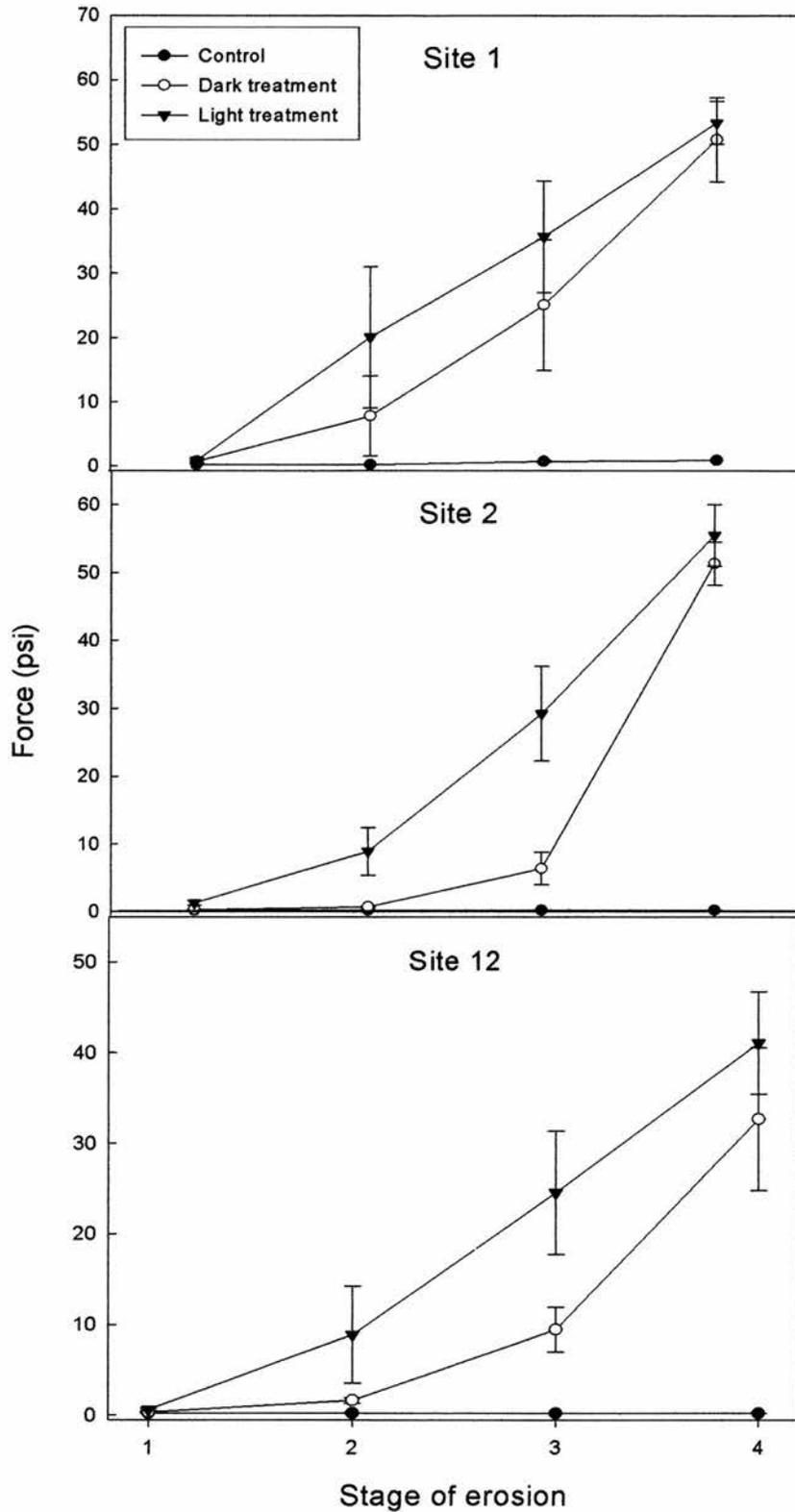


Figure 7.4: Particle retention under varying light conditions. Samples were maintained in light or dark conditions over a 10h period. The force required to erode ooids held within the surface layers of the stromatolite increased over 10h and greatest effects were seen after light treatments. Stages of erosion are as follows: 1) surface grain movement; 2) underlying surface becoming visible; 3) general clearance of underlying surface, individual grains remaining; 4) total clearance.

Site	1			2			12		
	Light	Dark	Control	Light	Dark	Control	Light	Dark	Control
Number of samples	20	20	12	20	20	20	20	20	20
Mean force required (psi)	21.085	27.510	0.500	14.678	23.732	0.208	11.017	18.779	0.202
Minimum force required (psi)	0.200	0.200	0.200	0.200	0.230	0.200	0.200	0.330	0.200
Maximum force required (psi)	60.000	60.000	0.900	58.000	60.000	0.230	60.000	60.000	0.230
( $\pm$ S.E)	5.421	5.539	0.095	4.972	5.241	0.003	3.531	4.273	0.001

Table 7.1: Mean  $\pm$  SE and range of jet pulses (psi) required to overcome grain retention on stromatolite surface.

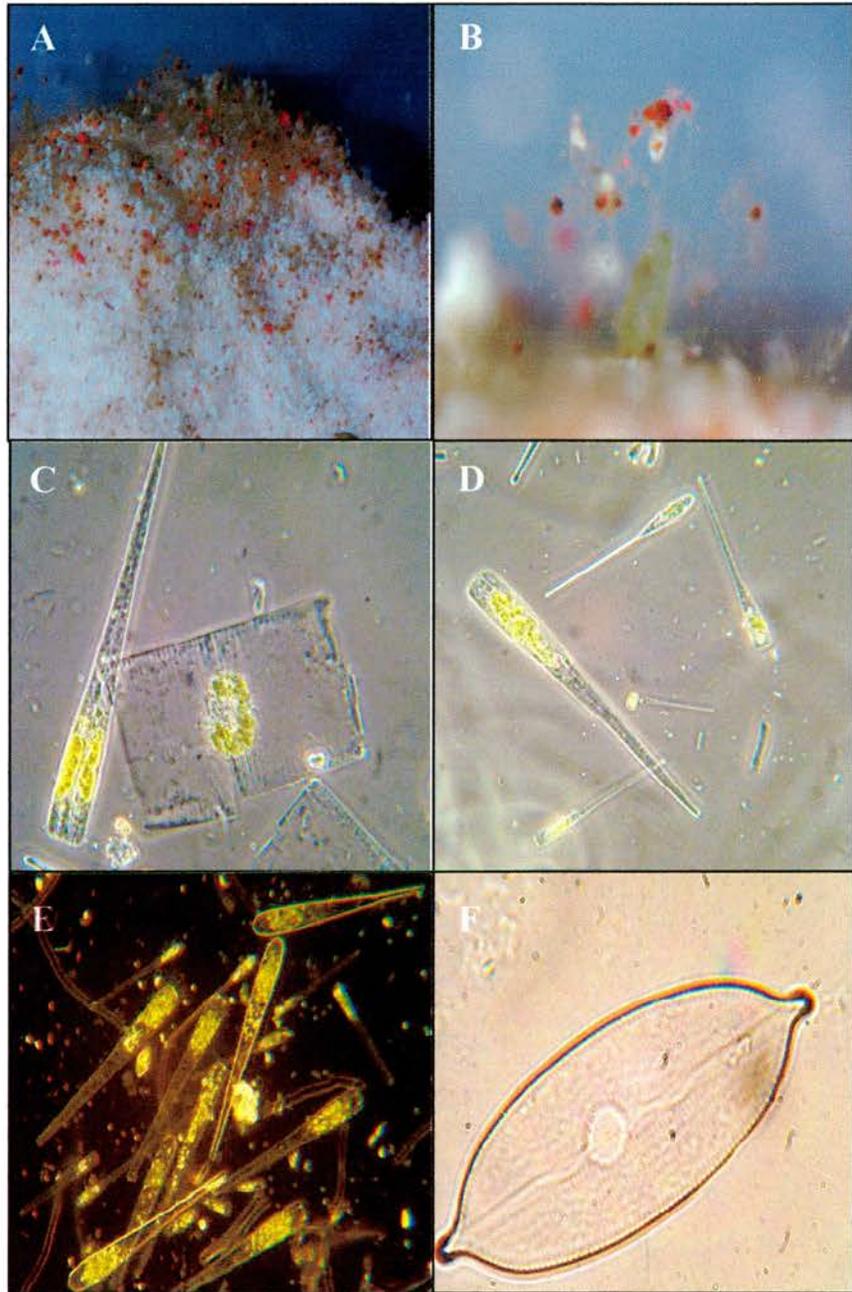


Figure 7.5– Diatoms present at site 1. Stereomicroscopy was used to show dyed ooid particles (red) (A) held within the stalks of the diatoms present (B) (Photos courtesy of P Reid). Compound microscopy allowed the fine detail of stalked and chain forming diatoms (C-E) present to be studied. Although the majority of diatoms present within the stromatolite material were chain forming or stalked, motile species were also present. The dominant species of motile diatoms was *Navicula menaiana* (F).

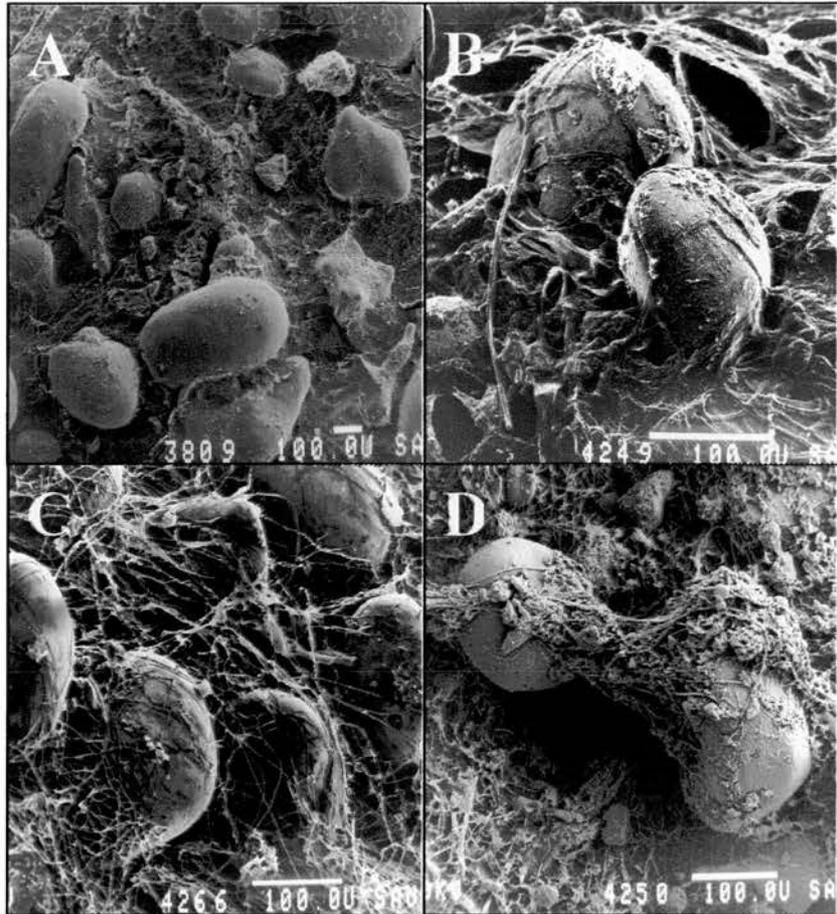


Figure 7.6 – Low-temperature scanning electron microscopy exhibited the absence of microphytobenthic assemblages (A) within samples subjected to dark conditions. Ooids within samples subjected to normal light conditions were observed to be trapped within cyanobacterial filaments (B & C) and mucilage produced by the cyanobacterial and diatomaceous assemblages present. Organic content was high and microphytobenthic assemblages denser at site 12 (D) when compared to other sites.

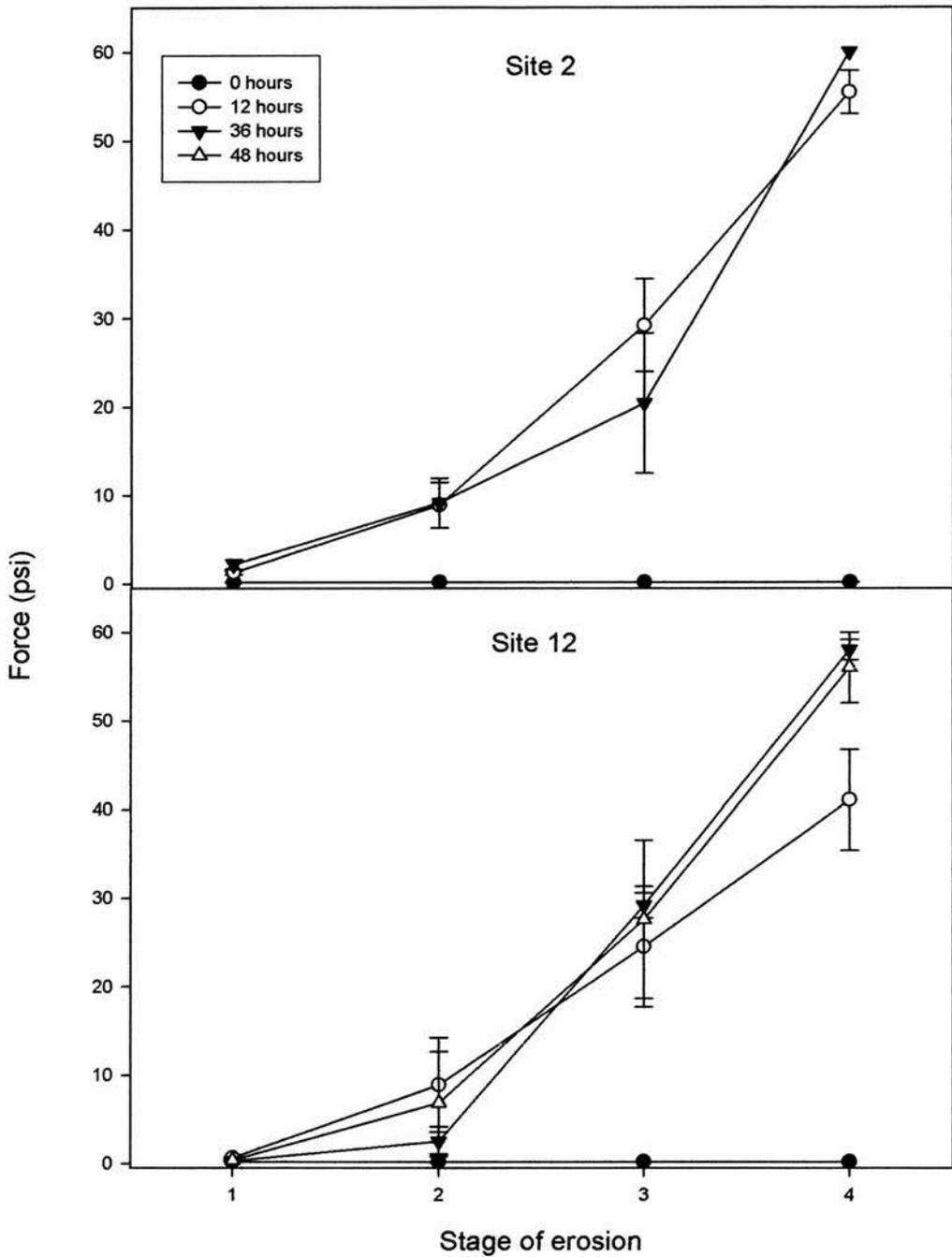


Figure 7.7: Time series showing retention of ooids over time. Samples were maintained in light conditions of a normal night/day cycle. Stages of erosion are as follows: 1) surface grain movement; 2) underlying surface becoming visible; 3) general clearance of underlying surface, individual grains remaining; 4) total clearance.

### 7.3.2 Reconstitution of stromatolite material

No significant change in the stability of the control sediment was seen throughout the experimental period ( $W = 38.0$ ,  $p = 0.9348$ ). Samples maintained under natural light cycles, from both sites, exhibited rapid sediment stabilisation over the course of the experiment. The stabilisation of reconstituted material subjected to the light treatment increased significantly over the 156 hours (site 1:  $w = 28$ ,  $p = 0.003$ ; site 10:  $w = 21$ ,  $p = 0.003$ ) (Figure 7.8 and 7.9, Table 7.2). Stabilisation of samples under the light treatments was significantly higher than stabilisation within the dark treatments for the samples taken from both sites 1 and 10 (site 1:  $W = 631.0$ ;  $p = 0.009$ ; site 10:  $W = 541.0$ ;  $p = 0.000$ ) (Figure 7.8 and 7.9, Table 7.2).

Examination of the surface structure of site 2 material maintained in dark conditions showed limited microphytobenthic growth, and ooids were loosely packed. (Figure 7.6A). Examination of the surface structure of site 2 material maintained in light conditions provided evidence of higher quantities of cyanobacterial and diatomaceous species than the dark treatments. Ooids appeared to be more densely packed within the sample and were observed trapped within cyanobacterial filaments (Figure 7.6B & C).

The surface structure of site 12 material exhibited the presence of greater cyanobacterial biomass than the other sites. Organic matter was also present in high quantities held within the diatomaceous, cyanobacterial and associated polymer matrix (Figure 7.6D).

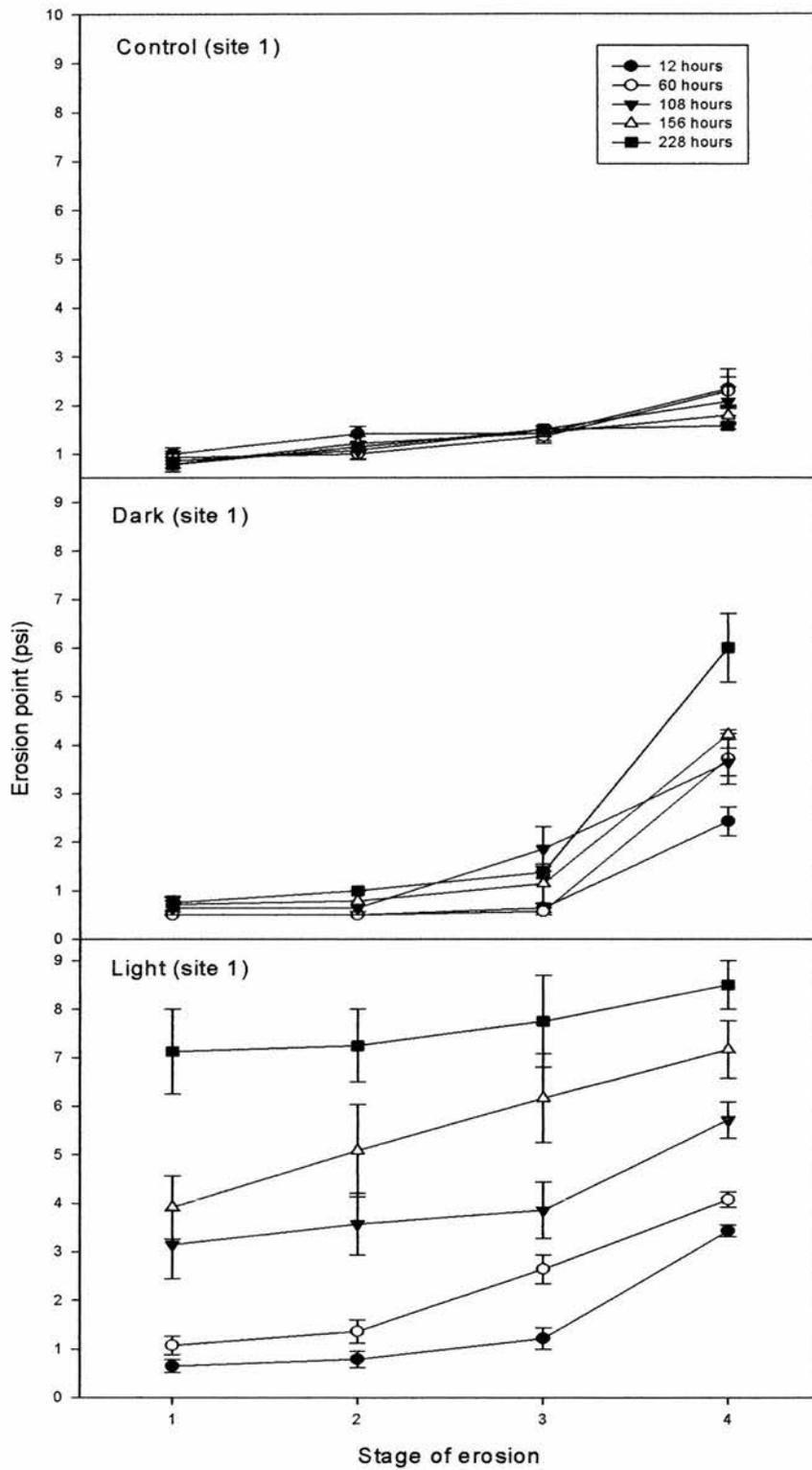


Figure 7.8: Stability of reconstituted stromatolite material from site 1. Samples were maintained in conditions of natural light and total darkness. Stability was measured at 12, 60, 108, 156 and 228 hours. Stages of erosion are as follows: 1) surface grain movement; 2) underlying surface becoming visible; 3) general clearance of underlying surface, individual grains remaining; 4) total clearance.

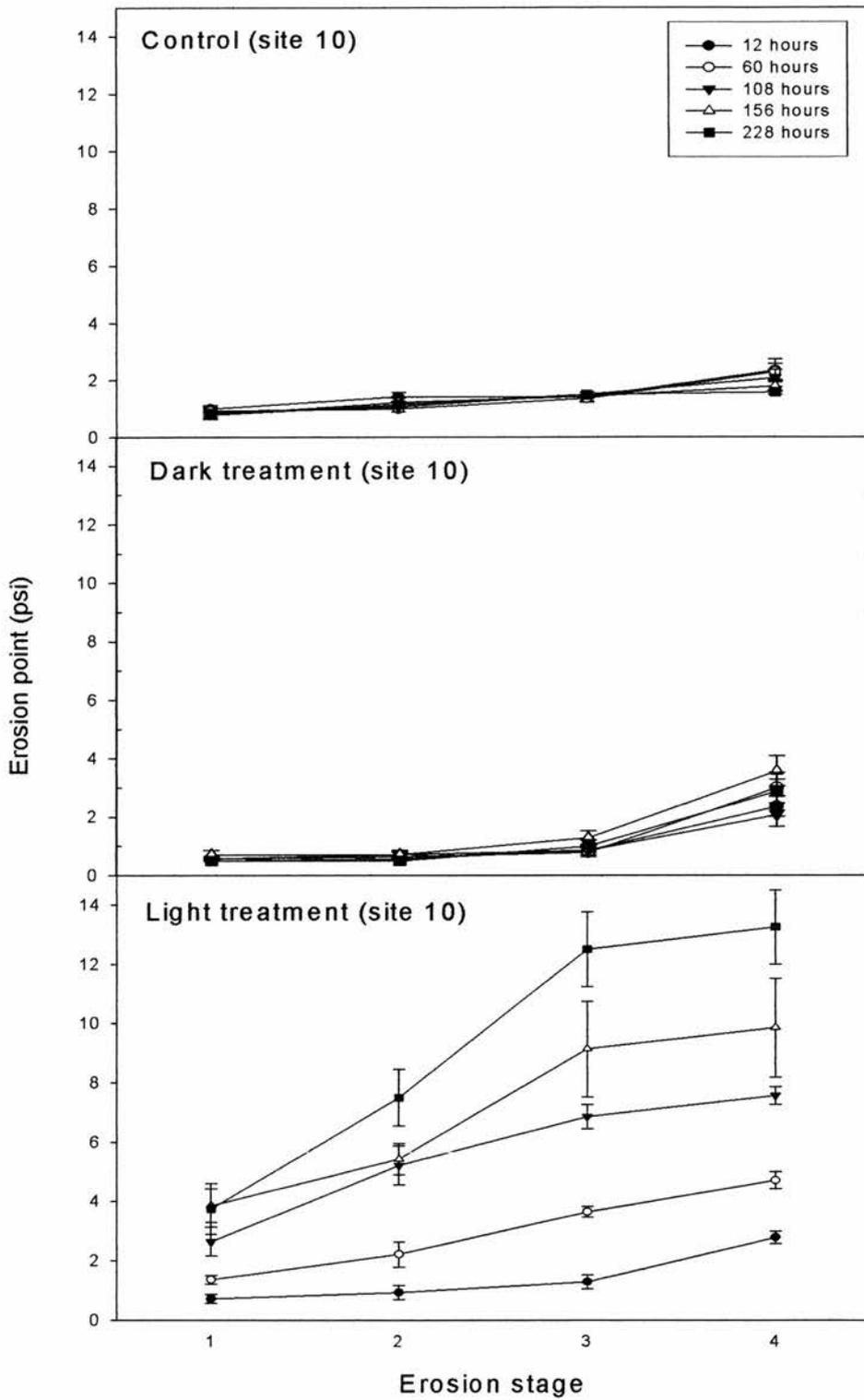


Figure 7.9: Stability of reconstituted stromatolite material from site 10. Samples were maintained in conditions of natural light and total darkness. Stability was measured at 12, 60, 108, 156 and 228 hours. Stages of erosion are as follows: 1) surface grain movement; 2) underlying surface becoming visible; 3) general clearance of underlying surface, individual grains remaining; 4) total clearance

		Site									
		1					10				
Hours	Treatment	Number of samples	Mean force required (psi)	Minimum force required (psi)	Maximum force required (psi)	(±S.E)	Number of samples	Mean force required (psi)	Minimum force required (psi)	Maximum force required (psi)	(±S.E)
12	Light	7	3.20	2.50	5.00	0.34	6	2.83	2.00	3.50	0.23
	Dark	7	1.80	1.50	2.50	0.15	7	1.50	1.50	1.50	0.00
	Control	7	5.86	3.00	12.00	1.38	7	5.86	3.00	12.00	1.38
60	Light	7	4.70	4.00	5.00	0.15	7	5.71	5.00	7.00	0.29
	Dark	7	4.40	3.00	6.00	0.37	7	3.50	3.00	4.50	0.19
	Control	7	2.20	1.50	2.50	0.15	7	2.21	1.50	2.50	0.15
108	Light	7	6.86	2.00	9.00	0.88	7	8.86	8.00	10.00	0.26
	Dark	7	5.07	4.50	8.00	0.49	7	4.00	3.00	5.00	0.27
	Control	7	3.93	3.50	4.50	0.13	7	3.93	3.50	4.00	0.13
156	Light	6	8.00	6.00	10.00	0.63	7	11.00	8.00	18.00	1.48
	Dark	7	4.79	4.00	6.00	0.26	7	5.36	2.50	9.00	0.81
	Control	6	3.58	2.50	4.00	0.22	6	3.58	2.50	4.00	0.22

Table 7.2: Mean ± SE and range of jet pulses (psi) required to cause erosion of the reconstituted stromatolite surface. Measurements taken at 12, 60, 108, and 156 hours.

### 7.3.3 Grain size

Grain size analysis was completed for material caught in sediment traps inside and outside the reef, and ooids retained within the structure of the stromatolite itself. The grain size caught inside the reef was not significantly different from the sediment caught outside the reef. However, grain size within the structure of the stromatolites was significantly different from the grain size caught in the traps both inside and outside the reef ( $p < 0.05$ ) (Figure 7.10).

## 7.4 Discussion

The formation of stromatolites is highly dependent on sediment accretion rates and associated microbial assemblages that trap and bind sediment particles that fall upon the surface of the structures. This ability to retain sediment particles promotes the growth of stromatolites despite ambient hydrodynamic forces acting upon them.

### 7.4.1 Ooid retention

Control experiments carried out suggested that ooid particles themselves exhibit little or no cohesiveness towards other ooid particles. This strengthens the argument that any increase in retention of ooids or increase in surface strength of the stromatolite is due to biotic influences acting within the stromatolite structure.

Ooid retention was observed to be greater in the light treatment studies than in the dark treatment studies. This highlights the importance of a light cycle for the retention of ooids into the stromatolite formation in all three types of

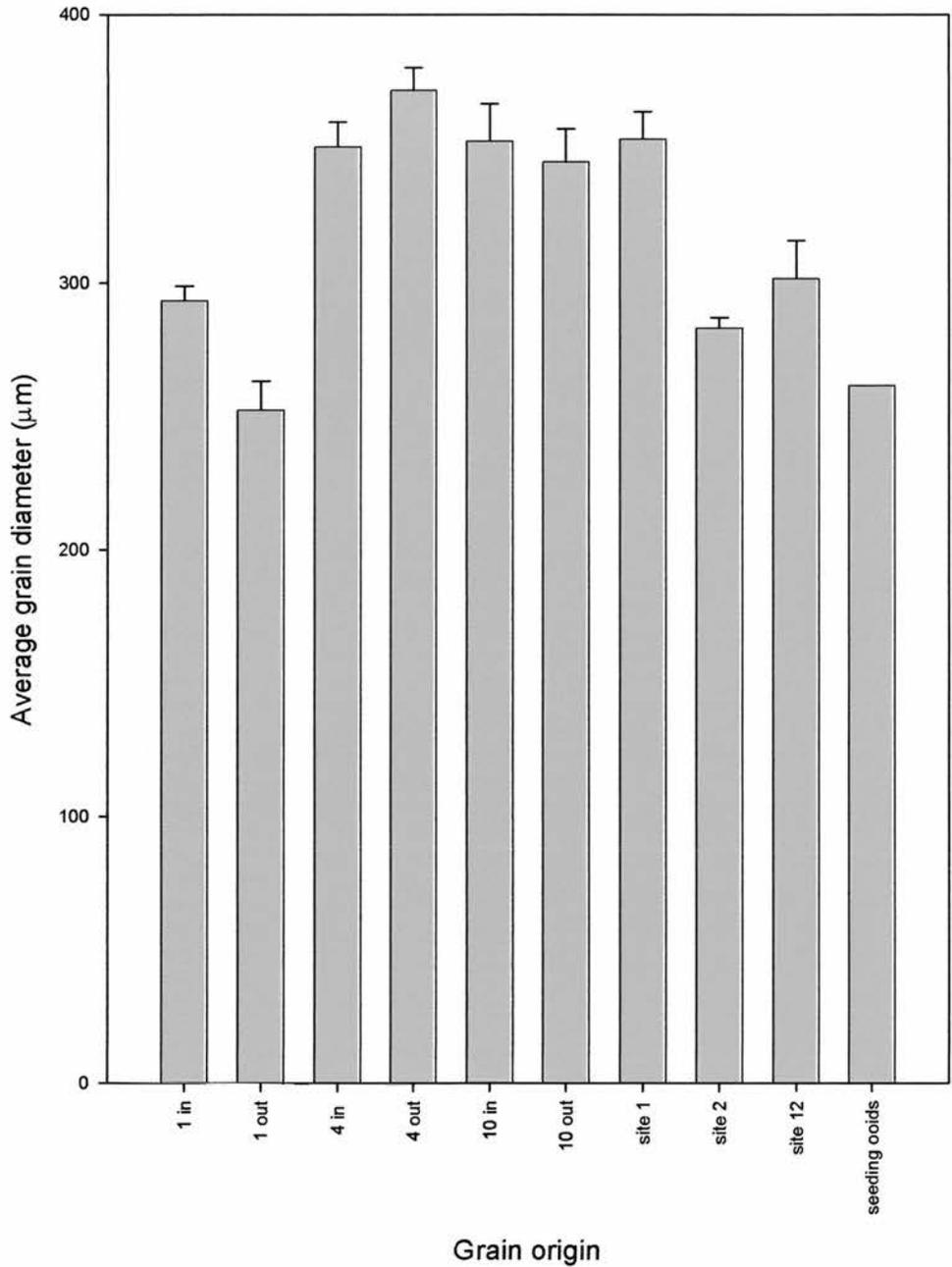


Figure 7.10: Grain size analysis carried out of ooids caught in the sediment traps at sites 1, 4, and 10 within (in) and outside (out) the reef (data courtesy of RIBS). Grain size analysis was also determined for ooids retained within the structure of stromatolites from sites 1, 2 and 12, along with analysis of the control ooids.

stromatolite. This conclusion is strengthened by work carried out by Consalvey and Dijkman (2003), demonstrating that photosynthetic efficiency recovered rapidly on exposure to light after a period of burial.

Stromatolites at site 1 were characterised by an orange 'fluffy' layer, which was identified as diatomaceous. There were at least three species of stalked and chain-forming diatoms present, believed to be partly responsible for the retention of ooids due to the capacity of the stalks to trap the ooid particles and of the associated EPS to bind the ooid particles within the structure (Figure 7.5). EPS is produced and deposited within the grains during migration by motile diatoms or is deposited as stalks, tubes, and filaments by sessile forms (Underwood *et al* 1995, Underwood and Paterson, 2003 Decho, 1990, 2003). Deposited EPS causes a cohesive effect on the sediment grains it surrounds, thereby increasing the critical erosion velocity required to cause erosion of the surface sediments (Tolhurst *et al* 1999). Although the present study suggests that diatoms play an integral role in the trapping and binding of deposited sediments leading to the formation of stromatolite structures, previous studies suggest that cyanobacteria has a far more effective stabilising role. Cyanobacterial biofilms were found to be more resistant to erosion than diatomaceous biofilms (Stal 2003). However it is suggested (Yallop *et al* 1994) that this is probably due to the presence of trichomes within the cyanobacterial mat as opposed to the presence of EPS alone.

Whilst the ooids are retained during the trapping process, this may not be a part of the stromatolite formation, as the ooids are not becoming part of the stromatolite structure itself as a type I stromatolite. Golubic and Browne (1996) observed an increase in diatom diversity during tidal exposure of the

stromatolite. In this situation the diatoms out compete the *Schizothrix* sp due to the lack of sediment burial. High sedimentation rates have been found to maintain the community of *Schizothrix* sp but as soon as the accretion rates decrease the benthic community becomes more diverse including diatoms, coccoid cyanobacteria and foraminifera (Seong-Joo *et al* 2000). Whilst it appears the presence of diatoms within the microphytobenthic mats on the stromatolite surface is affected by sedimentation rates, it is also possible that this may be linked to light levels. Studies by Grover, 1997 and Consalvey *et al*, 2004 and references within) have shown gradients in lights levels have caused variations in assemblage structure. Optimum light levels for different species of cyanobacteria and diatoms are wide ranging, and whilst cyanobacteria tend to be shade adapted organisms (Stal 1995), diatoms are often found to be positioned above cyanobacterial layers in sediment samples (Underwood and Kromkamp 1999). High rates of sedimentation will not only cause diatom abundance to decrease because of physical abrasion and burial, but also due to the lack of light caused by the deposition of sediment. This decrease in diatom abundance will give the cyanobacterial species, adapted to thrive in lower light levels, an opportunity to out compete the diatoms, thereby allowing the creation of a type I stromatolite.

The time series experiments showed that ooids could be effectively retained on the stromatolite surface within 12 h. 60 psi was often not enough to remove all particles from the surface of the stromatolite section, suggesting that the critical time period for efficient retention of ooids was less than 12 h. Grain retention did not vary significantly after a 12 hour period, however it was noted that limited retention occurred at 6 hours, suggesting that a period of 6-12 hours

is necessary for the ooids to be retained in the stromatolite structure. This could be due to the lack of a dark period and it would be beneficial to the study of stromatolite formation for further experiments to be carried out to determine the critical time period required for optimum retention to occur, and whether the retention of ooids is dependent on a diel cycle.

#### 7.4.2 Reconstitution of stromatolite material

As found in the retention experiments, control treatments showed no significant variation in surface erodibility suggesting negligible occurrence of cohesiveness amongst clean ooids (no organics present).

The results obtained from the reconstitution experiments suggest that light is an essential component for the biostabilisation of stromatolite material as neither the control nor dark treatments showed any variation in stability over the experimental time period. The stability of the stromatolite material subjected to the light treatment, from both sites 1 and 10, increased significantly over the experimental time period. The requirement for a light period in the biostabilisation suggests that initial stabilisation of stromatolite surface layers is carried out by autotrophic organisms, such as cyanobacteria and diatoms (Winsborough 2000, and Reid *et al* 2000). This is supported by previous studies (Reid *et al* 2000; Kawaguchi and Decho 2002 and Decho *et al* 2005) suggesting that the initial stage of stromatolite formation is carried out by the cyanobacteria *Schizothrix* sp. Personal observations also provided evidence of various stalked and chain forming diatoms present within the stromatolites surface communities at site 1 (Figure 6.7, and 6.8). The reconstitution of material from sites 1 and 10 were not found to be statistically different, suggesting the original presence of

different microbes in the two sites had no effect on the reconstitution of the material. Whilst the experiment does not replicate the processes that occur for the formation of natural stromatolites, it does give an indication of the ability of the structures to recover following a disturbance event, and demonstrates the capacity of the microbial assemblages present within the systems to biostabilise the material found naturally.

#### 7.4.3 Grain size analysis

The size of sediment grains inside and outside the reef did not show any significant variation suggesting that the reef did not have any effect on the size of sediment grains being transported towards the beach from outside the reef. However, the sediment grains caught by the sediment traps was significantly different from the sediment grains found retained within the structure of the stromatolite, suggesting a system of selective filtration. The presence of different sized ooids within the stromatolite compared to those outside the structures may be due to the size of the spaces between cyanobacterial, and other microphytobenthic filaments present. These filaments may act as a filter allowing certain sized particles into the structure. Unlike the algal turf in chapter three, in this case the grain size within the stromatolite structure is larger than the grain size found outside the structure. This may be due to the high energy system in which they occur resulting in the deposition of larger grain sizes, and the maintained suspension of smaller grain sizes. The larger ooids may become trapped more effectively as any microturbulence amongst the stromatolites and surrounding reef may cause the suspension of smaller particles. The presence of EPS, produced by microphytobenthos, has been shown to promote the physical

stabilisation of microbial cells, which in turn provide a matrix in which the ooids become trapped. The EPS also forms a cohesive network to which ooids become attached (Kawaguchi and Decho, 2002, Decho *et al* 2005).

## 7.5 Conclusion

This study shows that stromatolitic assemblages can rapidly self-organise into a biostabilising structure, the efficiency of which is partly determined by environmental variables such as light. Whilst the processes described have been induced by mechanical disruption and are not identical to those occurring in natural systems, they demonstrate the biostabilising abilities of the microbial systems occurring within the stromatolites. The formation of ancient stromatolites outdate the presence of diatoms in history, suggesting the occurrence of diatoms in modern stromatolitic analogues are by no means integral or necessary to the formation of the structures. However, diatoms play an important initial role in modern stromatolite formation by trapping ooids on the surface layers in preparation for the lithification process by cyanobacterial biofilms during periods of low sedimentation. The results obtained can help to determine the mechanisms behind natural mat formation, and the abilities of these structures to survive a hydrodynamically extreme environment.

Living stromatolites provide a modern analogue for one of Earth's earliest ecosystems, and due to the development of new functional groups (such as grazers and bioturbators) (Riding *et al* 1991, Stal 2000), and climate change (such as sea level rise and sea temperature increase) (IPCC, 2001), they are now

very rare ecosystems. The biogeochemical processes performed by the microbial assemblages present within stromatolite systems have significant effects on the functioning of the ecosystem. Although prokaryotic assemblages were responsible for the formation of ancient stromatolites, the modern analogues, whilst some are still dominated by prokaryotic assemblages, are mostly made up with mixed assemblages of prokaryotic and eukaryotic assemblages. These mixed assemblage systems can be compared in terms of ecosystem functioning to other mixed assemblage biostabilising systems such as tidal flats and salt marshes, in which significant research has been carried out and has shown the increasing importance of these ecosystems to the survival of coastal areas. The functional capacity of all these systems, and the value of the ecosystem must be considered before any management plans are created and implemented. The work carried out in this study has highlighted the organisational capacity of stromatolites and as such has provided an insight into the ecosystem engineering capabilities of these systems. For this reason the continued research in this area is essential.

## **CHAPTER EIGHT**

### **GENERAL DISCUSSION**

## **Chapter 8: General Discussion**

The coastal areas studied throughout this thesis are some of the most productive natural ecosystems on Earth despite the harsh conditions in which they occur (Costanza 1997). Physical forces acting upon each of these systems may be very similar, however it is the combination of these forces and the biological activity within the sediments that shapes the environment forming very different systems with similar functional roles.. Therefore it is important that in order to fully understand the complexities of coastal dynamics within these environments researchers from many different disciplines must collaborate in order to obtain a holistic and accurate interpretation of the processes occurring (Barker 2005, Christie 2005 Convention on Biological Diversity (CBD), 2000). Throughout the present studies a multidisciplinary approach has been taken to collect a wide selection of variables in order to provide a comprehensive and unique examination of biogenic mediation of coastal systems.

### **8.1 Spatial scale of studies**

Recent advances in sampling techniques have allowed coastal systems to be studied on increasingly diverse spatial scales, from remote sensing, to microelectrodes. Whilst coastal systems have significance on a large spatial scale with regards conservation and socioeconomics, examining systems on a microscale, in order to understand the processes occurring within the systems as a whole, is equally important as has been emphasised during these studies. For example, low-temperature scanning electron microscopy allows the qualitative

examination of the sediment surface structure at a microscale (Paterson 1995) with minimum disruption to the structural integrity of the sample. This ability has proved invaluable in interpreting the results of both laboratory and field analysis, enabling researchers to observe the 'real' system, as it is in situ. This is often overlooked during laboratory studies and the effects of removing material from the natural environment may often lead to results that are not necessarily relevant to natural conditions. Whilst these experiments are important and valuable in their own right, especially when studying single variables, the value of data such as that obtained by techniques such as low-temperature scanning electron microscopy in representing the natural system is still invaluable. For example, in studies of *Rhodothamniella* sp (Chapter 3) the filaments of the turf could be observed to physically trap the grains within a structural matrix. A similar strategy was observed for cyanobacterial assemblages (Chapters 6 and 7) where trichomes wound amongst and around the grains trapping them within the surface layers creating a stabilised layer of sediment. At a slightly larger scale (cm), the cohesive strength meter, contact cores and cryolandars measure sediment variables which highlight the biogenic patchiness of coastal sediments (Chapters 5 and 6). On basin scale (km) the use of remote sensing (Silvestri *et al* 2002) allows the examination of a large region of surface sediments. Remote sensing requires ground truthing and whilst remote sensing itself was not used during any of the studies contained here, it was with the requirements for remote sensing ground truthing that data was collected describing the Eden Estuary and the Venice Lagoon salt marshes (Chapters 5 and 6). Remote sensing for depositional habitats is still in the early stages of development, and whilst the potential for this technique is huge, there are still many ground truth

measurements to be carried out in order to establish if relationships between the microphytobenthic assemblages and sediment dynamics do exist, and this must initially be established at a much smaller scale.

A major problem to be addressed is the migratory behaviour of microphytobenthos (Consalvey *et al* 2004). The biomass at the sediment surface can vary relatively quickly (ie during the period of tidal exposure), and this may have major implications for large scale remote sensing surveys carried out over a matter of hours. Therefore any ground truth measurements being made in order to relate back to remote sensing images must take into consideration migratory induced spatial heterogeneity at the surface. This migratory behaviour may result in the patchiness of biofilm at the sediment surface and any ecosystem models created as a result of measurements taken during large scale surveys must allow for this migratory behaviour.

## **8.2 Biogenic mediation**

Whilst the habitats studied in this thesis differ in structure and function, one common link among them all is the presence of microphytobenthic assemblages. Microphytobenthic assemblages not only serve as primary producers in the ecosystem but also provide a number of other ecosystem services (Chapin *et al* 1997) including the stabilisation of cohesive sediment. The ability of microphytobenthic assemblages to mediate the sediment dynamics of coastal systems (Holland *et al* 1974, Grant *et al* 1986, Hoagland *et al* 1993, Yallop 1994, Sutherland 1996) has been a common theme throughout the habitats studied. However, the type of assemblage appears to control the type of mediation that occurs. Paterson (1994) divided the mechanisms of biogenic

stabilisation into 5 different categories: flow effects, network effects, boundary layer effects, cohesive effects and matrix effects. It is unlikely that these effects would ever occur individually, and indeed these effects could all be observed throughout the studies carried out (Table 8.1). Flow, network and boundary layer effects were observed for *Rhodothamniella* sp (Chapter 3) in addition to the retention of sediment within the turf structure. The growth strategy of the turf promoted the retention of sediment by trapping the grains within the filaments (Sousa *et al* 1981, Seapy and Littler 1982, Stewart 1983) which was exaggerated by the presence of diatoms within the filaments exuding EPS, thereby forming a canopy layer and “hydrodynamic boundary” surface. This hydraulically smooth surface promotes skimming flow over the turf structure, therefore increasing the stability of the entire structure, preventing erosion of the turf from the rock substratum.

The stabilisation of fine cohesive sediments illustrated the cohesive and matrix effects (Chapters 4, 5 and 6) due to the production of cohesive biofilms by microphytobenthic assemblages and the associated production of EPS. The formation of a cohesive biofilm will also lead to the influence of boundary layer effects due to the reduction in roughness, promoting smooth flow and reduced shear stress. Network, cohesive and matrix effects were observed to occur in stromatolite samples (Chapter 7) due to the presence of cyanobacterial filaments. Thus, the work here supports the observations of Paterson (1994) but emphasises that all of the systems studied show evidence of several mechanisms of biomediation.

Site	Site features	Dominant stress upon the system	Importance of site	Dominant mechanisms of biostabilisation	Biogenic mediators studied
Sandy beach with rocky outcrops, Scotland (Chapter 3)	Exposed bay, high wave energy, tidal currents.	Wave stress, desiccation and salinity fluctuations upon exposure.	Coastal protection, recreation, and feeding grounds for wildfowl and macrofauna.	Flow, network, boundary, and cohesive effects.	<i>Rhodohammiella</i> sp. and associated diatom assemblage.
Sub-tidal lagoon sediments, Venice (Chapter 4)	Sheltered lagoon basin, tidal influence.	Low soil oxygenation, variable light levels.	Fisheries, industry and recreational importance.	Flow, cohesive and matrix effects.	Microphytobenthic assemblages.
Intertidal mud flats, Scotland (Chapter 5)	Sheltered bay, tidal currents.	Desiccation, salinity fluctuations upon exposure.	Coastal protection, industry and feeding ground for wild fowl.	Boundary layer, cohesive and matrix effects.	Microphytobenthic assemblages.
Salt marsh, Venice (Chapter 6)	Sheltered lagoon basin, tidal influence.	Low soil oxygenation, high salinity.	High faunal and floral diversity, coastal protection, feeding and breeding ground for wild fowl.	Flow, network, boundary layer, cohesive and matrix effects.	Microphytobenthic assemblages, and higher vascular plants.
Stromatolite systems, Bahamas (Chapter 7)	Exposed shoreline, high wave energy.	Wave stress, desiccation and salinity fluctuations upon exposure.	Modern equivalents of ancient stromatolite structures, one of few existing in normal marine salinities.	Flow, network and cohesive effects.	Microphytobenthic assemblages, dominated by cyanobacteria.

Table 8.1: Comparative attributes of systems studied throughout this thesis.

### 8.3 Sediment partitioning

The trapping and retention of sediments is an efficient method evolved by filamentous turfs and biofilms to promote stabilisation in what are highly dynamic and physically stressful environments (Hay 1981, Airoidi *et al* 1996, Airoidi and Virgillio 1998). Filamentous structures appear to modify the flow promoting the deposition of sediments (Scoffin 1970). However, due to the hydrodynamically smooth flow observed during experimental scenarios (Chapter 3), I suggest that the variation in sand grain sizes held within filamentous structures is not only due to the transportation of different grain sizes, but also induced by the size of the interstices within the filaments. The grain sizes found within the stromatolite structures (Chapter 7) and turf matrix (Chapter 3) varied from those found in the surrounding sediments, suggesting a system of selective filtration. The presence of different sized grains within the structures compared to those found in the surrounding sediments may be due to the size of the spaces between cyanobacterial, and other microphytobenthic filaments present. These filaments may act as a filter allowing certain sized particles into the structure. The grains found within the turf structure were smaller than those found in the surrounding sediments, however the grain size within the stromatolite structure was larger than the grain size found outside the structure. This suggests that the grain capture mechanisms are quite selective and not based on hydrodynamics even under the high energy in which the stromatolites occur. The larger ooids may become trapped more effectively as any microturbulence amongst the stromatolites and surrounding reef may cause the suspension of smaller particles. The presence of the turf did not induce turbulent flow, and so we can presume that any significant variations in sediment retention were not flow related,

suggesting the turf selectively filters sediment during transport of grains. As well as considering the effects the organisms have on the sediments, it must be considered that the grain size and sediment dynamics may control the spatial distribution, species diversity and abundance of benthic diatoms due to the sediment types and sizes of sediment particles present (Paterson and Hagerthy 2001, Saburova et al 1995). Whilst no relationship between diatom diversity and grain size was observed during any of the studies carried out during this thesis, such relationships have been observed in past literature (Paterson and Hagerthy 2001, Cahoon et al 1999, Sabbe and Vyverman 1991), but it is actually the space available between the grains that is the important factor. Intermediate interstitial grain sizes tend to host a higher diversity of diatom species than small or large interstitial spaces (Bergey 1999), and this may help to explain patterns observed in chapter 5 where the grain size at site A was mostly composed of grains  $>125\leq 500\mu\text{m}$ , in comparison with the sediment at Site B which was mostly composed of  $\leq 63\mu\text{m}$  grains. This variation in grain size at the two sites may account for the fact that microbial assemblage compositions were most similar at site A top and mid shores, and exhibited large differences in assemblage composition when compared to site B.

#### **8.4 Coastal ecosystems as biogenic systems**

Past studies have exhibited strong relationships between colloidal carbohydrate concentrations and chlorophyll *a* content of sediments (Underwood and Smith 1998, Underwood *et al* 1995), allowing certain assumptions and predictions to be made regarding the relative stability of intertidal sediments.

During the studies of subtidal sediment in the Venice Lagoon (Chapter 4) strong relationships were observed between the presence of microphytobenthic biofilms and sediment stability. Regular harvesting destroyed the structural integrity of the sediment bed and increased the potential for resuspension. However, the data produced suggests that if the surface sediments are not disturbed and left to establish healthy benthic diatom blooms and associated extracellular polymeric substances, the stability can increase dramatically. A crucial question for the management of the lagoon is the critical time between harvesting events at particular sites.

The data obtained in chapters 5 & 6 suggests no single variable measured during the Eden Estuary or Venice salt marsh studies could be used to predict sediment stability. This suggests that either the systems are too heterogeneous to predict with our current knowledge or a more holistic approach may be required, in order to determine useful data sets suitable to use in predictive models. Although this study goes some way to examining the roles of biogenic mediators in coastal systems, by no means have all the variables involved in the functioning of the system been considered and this work should continue, particularly given the current legislative pressure of the EU and the potential of a new Marine Bill covering the coastal zone in England and Wales.

## **8.5 Critique of methodologies**

### **8.5.1 Assemblage analysis**

In order to carry out accurate diatom taxonomy and observe the fine detail of the frustules, samples were oxidised and the protoplast destroyed during

the process of acid cleaning. Therefore no accurate measure of determining whether the cells counted were from live samples was available. Due to the possibility of transportation of valves from other areas by wind and wave action, or the inclusion of fossilised cells, there is a chance that there may be an error involved in the cell counts collected. However, all microphytobenthic assemblage samples were collected due to the dependence of cells to actively migrate through two layers of lens tissue, of which the top is removed and kept for analysis. Therefore the error of counting non viable cells is minimised by the method of sample collection.

#### 8.5.2 Cohesive Strength Meter

The CSM was originally designed for the measurement of sediment stability of cohesive estuarine sediments. The relative stability of consolidated or armoured sediments (Tolhurst *et al* 2002) was beyond the power of the device. However, significant improvements have been made to the system over the past year, allowing very stable and consolidated sediments, such as those found in salt marsh systems, to be measured. This improvement refers to the recalibration of the CSM system and new description of the force exerted on the sediment surface by Vardy *et al* (2005 in press). Due to the fact this recalibration was determined part way through the completion of this thesis, only the data from chapter 6 is determined using the new calibration devised by Vardy *et al* (2005), and therefore this data set should not be compared to shear stress data reported in the others chapters.

## 8.6 Future work

### 8.6.1 Rocky intertidal studies

The ability of filamentous turfs to retain sediment has been shown during this study, however further research should be carried out in order to compare the retention capacities of other rocky intertidal macroflora and fauna, such as *Mytilus* sp beds. I suggest that whilst these species perform similar sediment retention roles within the habitat, the sediment size retained and therefore the microhabitat they provide will be very different. I also suggest that their presence will have very different impacts on the surrounding environments due to the topography effects on the flow dynamics, the functioning of these areas within the ecosystem as a whole will vary considerably.

### 8.6.2 Venice Lagoon studies

Studies should be carried out to determine the extent to which intertidal microphytobenthic assemblages are composed of cyanobacterial species. The data collected during the Venice Lagoon and stromatolite studies (chapter 6 and 7) suggests that these species play an integral role in the functioning and ecogeomorphology of salt marsh and stromatolite systems. Pigment analysis could be carried out to enable zeoxanthin:chlorophyll *a* ratios to be determined, therefore indicating the cyanobacterial biomass within the surface sediments.

In order to determine the effects of clam harvesting on subtidal lagoon sediments future studies should include more representative control sites by allowing the establishment of areas protected from seabed disturbance by clam harvesting for varying periods of time, allowing them to revert to a natural disturbance frequency, based on episodic storm and flow events.

Due to the high site specificity of the microbial assemblages found within the salt marsh sediments, I feel further work should be carried out to investigate the relationship of microphytobenthos with zonation of vascular salt marsh fauna. The preliminary data collected during chapter 6 studies (data not shown) suggests that these relationships may exhibit strong patterns of zonation, as was observed by Zong and Horton (1998), and Underwood (1997). If these patterns truly exist within the salt marsh sediments in the Venice Lagoon this may be an integral step towards the effective use of remote sensing to model and predict sediment dynamics, as the classification of higher plants is already well established (Silvestri *et al* 2002 and references within).

#### 8.6.3 Eden Estuary studies

Future work to be carried out should involve a more detailed analysis of the microphytobenthic assemblages present within intertidal mud flat sediments. Relationships between these assemblages and measured variables should be clarified in order to provide detailed and accurate data for the use of validation of comprehensive dynamical models, allowing the future prediction of the overall system behaviour. This could be carried out by CANOCO analysis in order to explain variation of species composition with respect to environmental variables measured.

#### 8.6.4 Stromatolite studies

Stromatolites have been shown to be capable of rapid biostabilisation. However, each stage appears to be controlled by assemblages of varying composition. In order to understand these systems and the services they

provide, the roles of each of these groups must be examined in detail, and in isolation.

## 8.7 Summary

- The presence of filamentous turf structures on rocky outcrops promotes the retention sediment, which in turn reduces mass erosion events.
- Frequent harvesting of clams in the Venice Lagoon prevents the establishment of microphytobenthic communities, thereby preventing biostabilisation and reducing the stability of surface sediments within the Lagoon. The frequency of sediment disturbance is of great importance with respect to time to allow establishment of benthic biotic communities, which can aid sediment stability.
- Stability of intertidal mud flats appears to be dependent on two factors: the sediment grain size and chlorophyll *a* content within the sediments, however this is highly site dependent, and the use of proxy parameters for the prediction of sediment dynamics is not possible.
- Stabilisation of the salt marsh sediments is highly variable and variation in variables measured is highly site specific. Whilst the microbial assemblages provide vital ecosystem services no single variable can be used to predict sediment dynamics within the system.
- Diatoms play an important initial role in modern stromatolite formation by trapping ooids on the surface layers in preparation for the lithification process by cyanobacterial biofilms during periods of low sedimentation. Stromatolitic assemblages can rapidly self-organise into a biostabilising

structure, the efficiency of which is partly determined by environmental variables such as light.

## **8.8 Conclusions**

The biogenic mediation of sediments had previously been studied by examining the effects of single species. This thesis has provided a multidisciplinary approach to determine which variables are responsible for shaping the environment on a site specific basis. The data retrieved strongly suggests that for predictive models to be successful, the examination of systems must incorporate a holistic approach, as it is rare that single biological or physical factors act independently of each other, and that many of the relationships observed are highly site specific.

## **CHAPTER NINE**

### **REFERENCES**

## Chapter 9: Reference List

- Adam, P. (2002) Saltmarshes in a time of change. *Environmental Conservation* **29**: 39-61.
- Adey, W.H., and Goertemiller, T. (1987). Coral reef algal turfs: master producers in nutrient poor seas. *Phycologia*. **26** (3): 374-386.
- Admiraal, W. (1984). The ecology of estuarine sediment-inhabiting diatoms. *Progress in Phycological Research* **3**: 269-322.
- Airoldi, L. (1998). Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology*. **79** (8): 2759-2770.
- Airoldi, L. (2000). Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. *Marine Ecology Progress Series*. **195**: 81-92.
- Airoldi, L., Rindi, F., and Cinelli, F. (1995). Structure, seasonal dynamics and reproductive phenology of a filamentous turf assemblage on a sediment influenced, rocky subtidal shore. *Botanica Marina*. **38**: 227-237.
- Airoldi, L., and Cinelli, F. (1996). Early patterns of recovery of filamentous algal turf on a rocky subtidal shore (Mediterranean Sea). *S. It. E. Atti*. **17**: 341-344.
- Airoldi, L., Fabiano, M., and Cinelli, F. (1996). Sediment deposition and movement over a turf assemblage in a shallow rocky coastal area of the Ligurian Sea. *Marine Ecology Progress Series*. **133**: 241-251.
- Airoldi, L. and Cinelli, F. (1997). Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. *Journal of Experimental Marine Biology and Ecology* **215**: 269-288.
- Airoldi, L. and Virgilio, M. (1998). Responses of turf-forming algae to spatial variations in the deposition of sediments. *Marine Ecology Progress Series*. **165**: 271-282.
- Allen, J.R.L. (1992). Principles of physical sedimentology. *Chapman and Hall*.
- Amos, C.L., Brylinsky, M., Sutherland, T.F., O'Brien, D., Lee, S., and Cramp, A. (1998) The stability of a mudflat in the Humber estuary, south Yorkshire, UK. In: *Sedimentary processes in the intertidal zone* Black, K.S., Paterson, D.M., and Cramp, A. (Eds.) Geological Society, London, Special Publications, **139**: 25-43.
- Aspden, R.J., Vardy, S., Perkins, R.G., Davidson, I.R., Bates, R., and Paterson, D.M. (2004a). The effects of clam fishing on the properties of surface sediments in the lagoon of Venice, Italy. *Hydrology and Earth Systems Sciences* **8**(2):160-169.

- Aspden, R.J., Vardy, S., and Paterson, D.M. (2004b) Salt Marsh Microbial Ecology: Microbes, Benthic Mats and Sediments Movement. In *The Ecogeomorphology of Tidal Marshes*. Coastal and Estuarine Studies Series (AGU). Fagherazzi, S., Marani, M., and Blum, L.K. (Eds.).
- Aspden, R.J., and Paterson, D.M. (2005). Sediment partitioning and ecosystem engineering by the red alga, *Rhodothamniella* sp. *Marine Ecology Progress Series* (submitted).
- Austen, I., Andersen, T.J., and Edolvang, K. (1999) The influence of benthic diatoms and invertebrates on the erodability of an intertidal mudflat, the Danish Wadden Sea. *Estuarine, Coastal and Shelf Science* **49**: 99-111.
- Auster, P.J. (1998) A conceptual model of the impacts of harvesting gear on the integrity of fish habitats. *Conservation Biology* **12** (6): 1523-1739.
- Awramik, S.M. (1971) Precambrian columnar stromatolite diversity: reflection of metazoan appearance. *Science* **174**: 825-827.
- Awramik, S.M., and Riding, R. (1988) Role of Algal Eukaryotes in Subtidal Columnar Stromatolite Formation. *Proceedings of the National Academy of Sciences of the United States of America*. **85** (5): 1327-1329.
- Barker, A. (2005) Capacity building for sustainability: towards community development in coastal Scotland. *Journal of Environmental Management*. **75**: 11-19.
- Barranguet, C., Kromkamp, J., and Peene, J. (1998) Factors controlling primary production and photosynthetic characteristics of intertidal microphytobenthos. *Marine Ecology Progress Series*. **173**: 117-126.
- Barranguet, C., and Kromkamp, J., (2000). Estimating primary production rates from photosynthetic electron transport in estuarine microphytobenthos. *Marine Ecology Progress Series*. **204**: 39-54.
- Barber, H.G., and Haworth, E.Y. (1981) A guide to the morphology of the diatom frustule. *Freshwater Biological Association, Scientific Publication No.44*.
- Bell, R.G., T.M. Hume, T.J. Dolphin, M.O. Green and Walters, R.A. (1997) Characterisation of physical environmental factors on an intertidal sandflat, Mankau harbour, New Zealand. *Journal of Experimental Marine Biology and Ecology* **216**: 11-31.
- Bergey, E. (1999) Crevices as refugia for stream diatoms: effects of crevice size on abraded substrates. *Limnology and Oceanography* **44**: 1522-1529.

- Black, K. S., Paterson, D.M. (1997). Measurement of the Erosion Potential of Cohesive, Marine Sediments: a Review of Current in Situ Technology. *Journal of Marine Environmental Engineering* **4**: 43-84.
- Black, K.S., T.J. Tolhurst, D.M. Paterson, and S.E. Hagerthey. 2002. Working with natural cohesive sediments. *Journal of Hydraulic Engineering. Forum*: 2-8.
- Blanchard, G., and Guarini, J.M. (1996) Studying the role of mud temperature on the hourly variation of the photosynthetic capacity of microphytobenthos in intertidal areas. *Ecology* **319**: 1153-1158.
- Blanchard, G.F., Sauriau, P.G., Cariou-Le Gall, V., Gouleau, D., Garet, M.J., and Olivier, F. (1997). Kinetics of tidal resuspension of microbiota: testing the effects of sediment cohesiveness and bioturbation using flume experiments. *Marine Ecology Progress Series*. **151**: 17-25.
- Blanchard, G.F, Paterson, D.M., Stal, L., Richard, P., Galois, R., Huet, V., Kelly, J., Honeywill, C., de Brouwer, J., Dyer, K., Christie, M.C., and Seguignes, M. (2000) The effect of geomorphological structures on potential biostabilisation by microphytobenthos on intertidal mudflats. *Continental Shelf Research* **20**: 1243-1256.
- Blanchard, G. F., Bouhet, S.B., and Guarini, J.M. (2002). Properties of the dynamics of intertidal microphytobenthic biomass. *Journal of Marine Biological Association* **82 (6)**: 1027-1028.
- Brotas, V., and Plant-Cuny, M.R. (1998) Spatial and temporal patterns of microphytobenthic taxa of estuarine tidal flats in the Tagus Estuary (Portugal) using pigment analysis by HPLC. *Marine Ecology Progress Series*. **171**: 43-57.
- Brown, E., Colling, A., Park, D., Phillips, J., Rothery, D., Wright, J. (1999). *Waves, Tides and Shallow-Water Processes*, Second Edn. Butterworth-Heinemann.
- Cahoon, L.B., Nearhoof, J.E., and Tilton, C.L. (1999) Sediment grain size effect on benthic microalgal biomass in shallow aquatic ecosystems. *Estuaries* **22**: 735-741.
- Carey, D. A. (1983). Particle Resuspension in the Benthic Boundary Layer Induced by Flow Around Polychete Tubes. *Canadian Journal of Fisheries and Aquatic Science* **40**, 301-308.
- Chapin, F.S., Schulze, E.D., and Mooney, H.A. (1997) Biodiversity and ecosystem processes. *Tree*. **7**:107-108.
- Chenu, C. (1993) Clay polysaccharide or sand polysaccharide associations as models for the interface between microorganisms and soil – water related properties and microstructure. *Geoderma* **56**:143-156.

- Chenu, C., and Jaunet, A.M. (1992) Cryoscanning electron-microscopy of microbial extracellular polysaccharides and their association with minerals. *Scanning* **14**: 360-364.
- Christie, P. (2005) Is integrated coastal management sustainable? *Ocean and Coastal Management*. **48**: 208-232.
- Cohn, S.A., and Disparti, N.C. (1994) Environmental factors influencing diatom cell motility. *Journal of Phycology* **30**: 818-828.
- Cohn, S.A., Spurck, T.P., and Picket-Heaps, J.D. (1999) High-energy irradiation at the leading tip of moving diatoms causes rapid change of cell direction. *Diatom Research* **14**: 193-206.
- Collie, J.S., Hall, S.J., Kaiser, M.J., and Poiner, I.R., (2000). A quantitative analysis of harvesting impacts on shelf-sea benthos. *Journal of Animal Ecology* **69** (5): 785-798.
- Connell, J.H. (1978) Diversity in tropical rainforests and coral reefs. *Science* **199**: 1302-1310.
- Consalvey, M.C., Tolhurst, T.J., and Paterson, D.M. (2001). Intertidal biofilm recovery after a simulated *in situ* disturbance event. *Coastal Zone Topics*. **5**: 71-75.
- Consalvey, M.C. (2002) *The structure and function of microphytobenthic biofilms*. PhD Thesis, University of St Andrews.
- Consalvey, M., and Dijkman, N. (2003). R. V. Walton Smith, Highborne Cay, *RIBS Research Cruise Report*, November.
- Conslavey, M., and Paterson, D.M. and Underwood, G.J.C. (2004) The ups and downs of life in a benthic biofilm: Migration of benthic diatoms. *Diatom Research* **19** (2), 181-202.
- Costanza, R., d'Arge, R., de Groot, R., Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and van den Belt, M. The value of the World's ecosystem services and natural capital. *Nature* **387**: 253-260.
- D'Antonio, C.M. (1986) Role of sand in the domination of hard substrata by the intertidal alga *Rhodomela larix*. *Marine Ecology Progress Series*. **27**: 263-275.
- Dade, W. B., Davis, J.D., Nichols, P.D., Nowell, A.R.M., Thistle, D., Trexler, M.B., and White, D.C. (1990). Effects of bacteria exopolymer adhesion on the entrainment of sand. *Geomicrobiology Journal* **8**, 1-16.

- Daly, M.A., and Mathieson A.C., (1977) The effects of sand movement on intertidal seaweeds and selected invertebrates at bound rock, New Hampshire, USA. *Marine Biology*. **43**:45-55.
- Daniel, G.F., Chamberlain, A.H.L., and Jones, E.B.G. (1987). Cytochemical and electron microscopical observations of the adhesive materials of marine fouling diatoms. *British Phycology Journal* **22**: 101-118.
- Davidson, N.C., and Buck, A.L. (1997). *An inventory of UK estuaries*. Vol 1. Introduction and methodology. Joint Nature Conservation Committee. Vol. 1 of 7.
- Day Jr, J.W., Rybczyk, J., Scarton, F., Rismondo, A., Are, D., and Cecconi, G. (1999) Soil accretionary dynamics, sea-level rise and the survival of wetlands in Venice Lagoon: A field and modelling approach. *Estuarine, Coastal and Shelf Science*. **49**: 607-628.
- de Brouwer, J.F.C., Bjelic, S., de Deckere, E.M.G.T. and Stal, L.J. (2000) Interplay between biology and sedimentology on a mudflat (Biezelingsche Ham, Westerschelde, The Netherlands). *Continental Shelf Research* **20**: 1159-1177.
- de Jonge, V. N. (2000). Importance of Temporal and Spatial Scales in Applying Biological and Physical Process Knowledge in Coastal Management, an Example for the Ems Estuary. *Continental Shelf Research* **20**, 1655-1686.
- de Jonge, V.N., and Colijn, F. (1994) Dynamics of microphytobenthic biomass in the Ems Estuary. *Marine Ecology Progress Series* **104**: 185-196.
- Decho, A. W., Kawaguchi, T., Allison, M.A., Louchard, E.M., Reid, R.P., Stephens, F.C., Voss, K.J., Wheatcroft, R.A., Taylor, B.B. (1990). Microbial exopolymer secretions in ocean environments. Their role(s) in food webs and marine processes. *Oceanogr. Mar. Ann. Rev.* **28**, 73-153.
- Decho, A. W., Kawaguchi, T., Allison, M.A., Louchard, E.M., Reid, R.P., Stephens, F.C., Voss, K.J., Wheatcroft, R.A., Taylor, B.B. (2003). Sediment properties influencing upwelling spectral reflectance signatures: The "biofilm gel effect." *Limnology and Oceanography* **48**, 431-443.
- Decho, A.W., Visscher, P.T., Reid, R.P. (2005) Production and cycling of natural microbial exopolymers (EPS) within a marine stromatolite. *Palaeogeography, Palaeoclimatology, Palaeoecology* **219**:71-86.
- Defew, E. C., Tolhurst, T.J., Paterson, D.M. (2002). Site-specific features influence sediment stability of intertidal flats. *Hydrology and Earth Systems Sciences* **6**, 971-982.
- Delgado, M., de Jonge, V.N., and Peletier, H. (1991) Experiments on resuspension of natural microphytobenthos populations. *Marine Biology* **108**: 321-328.

- Denny, M. W. (1988). *Biology and the Mechanics of the Wave Swept Environment*. Princeton University Press.
- Doody, J.P. (2000) *Coastal Conservation and Management*. Conservation Biology Series.
- Dubois, M., Giles, K.A., Hamilton, J.K., Rebers, P.A., and Smith, F. (1956) Colometric assay for the determination of sugars and related substances. *Analytical Chemistry*. **28**: 350-356.
- Dytham, C. (2003). *Choosing and using statistics*. Second Edition. Blackwell publishing.
- Eaton, J.W., and Moss, B. (1966) The estimation of numbers and pigment contents in epipelagic algal populations. *Limnology and Oceanography* **11**: 584-595.
- Eckman, J. E., Nowell, A.R.M., Jumars, P.A. (1981). Sediment Destabilisation by Animal Tubes. *Journal of Marine Research* **39**, 361-374.
- Eckman, J. E. (1985). Flow Disruption by an Animal-Tube Mimic Affects Sediment Bacterial Colonization. *Journal of Marine Research* **43**, 419-435.
- Edgar, L.A., and Pickett Heaps, J.D. (1983) Ultra structural-localisation of polysaccharides in the motile diatom *Navicula cuspidate*. *Protoplasma* **113**:10-22.
- Edgar, L.A., and Pickett Heaps, J.D. (1984) Diatom locomotion. *Progress in Phycology Research*. **3**: 47-88.
- Emmerson, M., Solan, M., Emes, C., Paterson, D.M., and Raffaelli, D. (2001). Idiosyncratic effects of species diversity on ecosystem function. *Nature*. **411**, 73-77.
- Facca, C., Sfriso, A., Socal, G. (2002a). Changes in abundance and composition of phytoplankton and microphytobenthos due to increased sediment fluxes in the Venice Lagoon Italy. *Estuarine, Coastal and Shelf Science* **54**, 773-792.
- Facca, C., Sfriso, A., Socal, G. (2002b). Temporal and spatial distribution of diatoms in the surface sediments of the Venice Lagoon. *Botanica Marina*. **45**: 170-183.
- Fager, E.W. (1964). Marine Sediments: Effects of a tube-building polychaete. *Science*. **143**, 356-359.
- Fletcher, C.A., Stevenson, J.R., Dearnaley, M.P. (2001) The beneficial use of muddy dredged material. DEFRA Report No. SR 579.

- Fleming, B.W., and Delafontaine, M.T. (2000) Mass physical properties of muddy intertidal sediments: some applications, misapplications and non applications. *Continental Shelf Research*. **20**: 1179-1197.
- Fonseca, M. S., and Fisher, J.S. (1986). A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. *Marine Ecology Progress Series* **29**, 15-22.
- Ford, R.B., Thrush, S.F., and Probert, P.K. (1999) Macrobenthic colonisation of disturbances on an intertidal sandflat: the influence of season and buried algae. *Marine Ecology Progress Series*. **191**: 163-174.
- Ford, R.B., and Honeywill, C., (2002). Grazing on intertidal microphytobenthos by macrofauna: is pheophorbide a useful marker? *Marine Ecology Progress Series*. **229**: 33-42.
- Frankel, L., and Mead, D.J. (1973). Mucilaginous matrix of some estuarine sands in Connecticut. *Sedimentary Petrology*. **43**: 1090-1095.
- Friedrichs, M., Graf, G., Springer, B. (2000). Skimming Flow Induced Over a Simulated Polychete Tube Lawn at Low Population Densities. *Marine Ecology Progress Series* **192**, 219-228.
- Gersonde, R., and Harwood, D.M. (1990) *Lower Cretaceous diatoms from ODP Leg 113 Site 693 (Weddell Sea) I. Vegetative cells*. In Barker, P.F. and Kennett, J.P. Proceedings of the ocean drilling programme results. Ocean Drilling Programme.
- Gibbs, R. J., Matthews, M.D., and Link, D.A. (1971). The relationship between sphere size and settling velocity. *Journal of Sedimentary Petrology* **41**, 7-18.
- Ginsburg, R.N., Lowenstam, H.A. (1958). The influence of marine bottom communities on the depositional environment of sediments. *Journal of Geology*. **66**: 310-318.
- Golubic, S., and Browne, K.M. (1996) *Schizothrix gebelinii* sp. Nova builds subtidal stromatolites, Lee Stocking Island. *Algological Studies* **83**: 273-290.
- Grant, W., D., Boyer, L.F., Sanford, L.P. (1982). The Effects of Bioturbation on the Initiation of Motion of Intertidal Sands. *Journal of Marine Research* **40**, 659-677.
- Grant, J., Mills, E.L., Hopper, C.M. (1986). A Chlorophyll Budget of the Sediment-Water Interface and the Effect of Stabilizing Biofilms on Particle Fluxes. *Ophelia* **26**, 207-219.

- Grant, J., and Gust, G. (1987) Prediction of coastal sediment stability from photopigment content of mats of purple sulphur bacteria. *Nature* **330**: 244-246.
- Gratiot, N., Mory, M., Auchère, D. (2000). An acoustic Doppler Velocimeter (ADV) for the Characterisation of Turbulence in Concentrated Fluid Mud. *Continental Shelf Research* **20**, 1551-1567.
- Grover, J.P. (1997). Resource competition. Chapman and Hall, London.
- Hartley, B. (1996). An Atlas of British Diatoms. Sims, P.A. (Ed.).
- Harwood, D.M. (1988) Upper Cretaceous and lower Palaeocene diatom and silicoflagellate biostratigraphy of Seymour Island, Eastern Antarctic Peninsula. *Geological Society of America* **169**: 55-129.
- Hauton, C., and Paterson, D.M. (2003). A novel shear vane used to determine the evolution of hydraulic dredge tracks in sub-tidal marine sediments. *Estuarine and Coastal Shelf Science* **56**: 1-8.
- Hay, M.E. (1981) The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* **62** (3): 739-750.
- Hay, S. I., Maitland, T.C., and Paterson, D.M. (1993). The speed of diatom migration through natural and artificial substrata. *Diatom Research* **8**, 371-384.
- Heip, C.H.R., Goosen, N.K., Herman, .M., Kromkamp, J., Middleburgh, J.J.J., and Stoetaert, K. (1995) Production and consumption of biological particles in temperate tidal estuaries. *Oceanography and Marine Biology Annual Reviews* **33**: 1-149.
- Hoagland, K. D., Rosowski, J. R., Gretz, M. R., Roemer, S. C. (1993). Diatom extracellular polymeric substances: function, fine structure, chemistry, and physiology. *Journal of Phycology* **29**, 537-566.
- Holland, A. F., Zingmark, R.G., Dean, J.M. (1974). Quantitative Evidence Concerning the Stabilization of Sediments by Marine Benthic Diatoms. *Marine Biology* **27**, 191-196.
- Honeywill, C. (2001) *In situ* analysis of the biomass and distribution of microphytobenthos. University of St Andrews. PhD Thesis.
- Honeywill, C., Paterson, D.M., and Hagerthy, S.E. (2002). Instant determination of microphytobenthic biomass using fluorescence. *European Journal of Phycology*. **37**, 1-8.
- Houghton, J.T., Meira, L.G.F., Bruce, J., Hoelsing, L., Callender, B.A., Haites, E.N., and Maskell, K. (1994) *Climate change: Radiative forcing of*

*climate change and an evaluation of the IPCC 1592 emission scenarios.*  
Cambridge University Press.

- Huettel, M., Evamaria, W., Roy, K., and Roy, H. (2002). Seagrass – boundary flow interaction. *BIOFLOW workshop*, Yerseke.
- Hughes, R.G., and Paramor, O.A.L (2004). On the loss of saltmarshes in south-east England and methods for their restoration. *Journal of Applied Ecology*. **41**:440-448.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C., and Warr, K.J. (2001). Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series*. **213**, 127-142.
- Jones, G. (1994) Global warming, sea level change and the impacts on estuaries. *Marine Pollution Bulletin*. **28**: 7-14.
- IPPC (2001) Third Assessment Report: Climate change.
- Kaiser, M.J., Armstrong, P.J., Dare, P.J., and Flatt, R.P. (1998). Benthic communities associated with a heavily fished scallop ground. *Journal of the Marine Biological Association of the United Kingdom*. **78**: 1045-1059.
- Kawaguchi, T., and Decho, A.W. (2002) Isolation and biochemical characterization of extracellular polymeric secretions (EPS) from modern soft marine stromatolites (Bahamas) and its inhibitory effect on CaCO<sub>3</sub> precipitation. *Preparative Biochemistry and Biotechnology* **32**:51-63.
- Kendrick, G.A. (1991). Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion. *Journal of Experimental Marine Biology and Ecology* **147**: 47-63.
- Kennish, M.J. (Ed) (2000). In *Estuary restoration and maintenance: The national estuary programme*. CRC Press. Marine Science Series. 359pp.
- King, S. E., Lester, J.N. (1995). The Value of Salt Marsh Defence. *Marine Pollution Bulletin* **30**, 180-189.
- Kingston, M. B. (1999). Effect of light on vertical migration and photosynthesis of *Euglena proxima* (euglenophyta). *Journal of Phycology* **35**, 245-253.
- Kjerfve, B., Schettini, C.A.F., Knoppers, B., Lessa, G., and Ferreira, H.O. (1996). Hydrology and salt balance in a large hypersaline coastal lagoon: Lagoa de Araruama, Brazil. *Estuarine and Coastal Shelf Science* **42**(6): 701-725.
- Kromkamp, J., Barranguet, C. and Peene, J. (1998). Determination of microphytobenthos PSII quantum efficiency and photosynthetic activity

- by means of variable chlorophyll fluorescence. *Marine Ecology Progress Series* **162**:45-55.
- Littler, M.M., Martz, D.R., Littler, D.S. (1983). Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. *Marine Ecology Progress Series*. **11**: 129-139.
- Lubchenco, J., and Menge, B.A. (1978) Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* **48**: 67-94.
- Lucas, C.H., and Holligan, P.M. (1999). Nature and ecological implications of algal pigment diversity on the Molenplaat tidal flat (Westerschelde estuary, SW Netherlands). *Marine Ecology Progress Series*. **180**, 51-64.
- Macintyre, I. G., Reid, P., and Steneck, R.S. (1996). Growth history of stromatolites in a Holocene fringing reef, Stocking Island, Bahamas. *Journal of Sediment Research* **66**, 231-242.
- Macintyre, I. G., Prufert-Bebout, L., and Reid, P. (2000). The role of endolithic cyanobacteria in the formation of lithified laminae in Bahamian stromatolites. *Sedimentology* **47**, 915-921.
- Manzenrieder, H. (1983). Retardation of initial erosion under biological effects in sandy tidal flats. *Leichtweiss Inst Tech University Braunschweig*. 469-479.
- Mann, D.G. (1999) The species concept in diatoms. *Phycologia* **38**(6): 437-495.
- Mason, C.F., Underwood, G.J.C., Baker, N.R., Davey, P.A., Davidson, I., Hanlon, A., Long, S.P., Oxborough, K., Paterson, D.M., and Watson, A. (2003). The role of herbicides in the erosion of salt marshes in eastern England. *Environmental Pollution*. **122**: 41-49
- Maynard, C.E. (2003). Accelerating salt marsh formation on the Eden Estuary, Fife. *Coastal Zone Topics: Process, Ecology and Management*. **5: The estuaries and coasts of north-east Scotland**. (ECSA) Raffaelli, D., Solan, M., Paterson, D., Buck, A.L., and Pomfret, J.R (Eds.) **5**: 55-60.
- McQuaid, C., and Dower, K.M. (1990). Enhancement of habitat heterogeneity and species richness on rocky shores inundated by sand. *Oecologia*. **84**: 142-144.
- Medlin, L.K., Williams, D.M., and Sims, P.A. (1993) The evolution of diatoms (Bacillariophyta). I. Origin of the group and assessment of the morphology of its major divisions. *European Journal of Phycology* **28**: 261-275.

- Medlin, L.K., 2002. Why silica or better yet why not silica? Speculations as to why the diatoms utilise silica as their cell wall material. *Diatom Research*, **17**: 453-459.
- Miller, M.C., McCave, I.N., and Komar, P.D. (1977) Threshold of sediment motion under unidirectional currents. *Sedimentology*, **24**: 507-527.
- Muschenheim, D. K., Grant, J., and Mills, E.L (1986). Flumes for benthic ecologists: theory, construction and practice. *Marine Ecology - Progress Series* **28**, 185-196.
- Neu, T.R., (1994) Biofilms and microbial mats. In Krumbein, W.E., Paterson, D.M., and Stal, L.J. (Eds) *Biostabilisation of sediments*, Oldenburg.
- Neumann, A. C., Gebelin, C.D., Scoffin, T.P. (1970). The Composition, Structure, and Erodability of Subtidal Mats, Abaco, Bahamas. *Journal of Sedimentary Petrology* **40**, 274-297.
- Nowell, A. R. M., Jumars, P. A., and Eckman, J. E. (1981). Effects of Biological Activity on the Entrainment of Marine Sediments. *Marine Geology* **42**, 133-153.
- Orth, R.J. (1977). The importance of sediment stability in seagrass communities. *Ecology of Marine Benthos*. In: Coull, B.C. (Ed.). University of South Carolina Press, Columbia. pp 281-300.
- Orvain, F., Sauriau, P.G., Sygut, A., Joassard, L., and Le Hir, P. (2004) Interacting effects of *Hydrobia ulvae* bioturbation and microphytobenthos on the erodibility of mudflat sediments. *Marine Ecology-Progress Series*. **278**: 205-223.
- Orvain, F. (2005). A model of sediment transport under the influence of surface bioturbation: generalisation to the facultative suspension-feeder *Scrobicularia plana*. *Marine Ecology-Progress Series*. **286**: 43-56.
- Palmer, J.D., and Round, F.E. (1965) Persistent vertical-migration rhythms in benthic microflora. I. The effect of light and temperature on the rhythmic behaviour of *Euglena obtuse*. *Journal of the Marine Biological Association, UK* **45**: 567-582.
- Paramour, O. A. L., and Hughes, R.G. (2004). The effects of bioturbation and herbivory by the polychaete *Nereis diversicolor* on loss of salt marsh in south east England. *Journal of Applied Ecology* **41**, 449-463.
- Paterson, D.M. (1986) The migratory behaviour of diatom assemblages in a laboratory micro-ecosystem examined by low temperature scanning electron microscopy. *Diatom Research* **1**: 279-289.
- Paterson, D.M. (1988) The influence of epipellic diatoms on the erodability of an artificial sediment. *10<sup>th</sup> Diatom Symposium*.

- Paterson, D. M. (1989). Short-Term Changes in the Erodability of Intertidal Cohesive Sediments Related to the Migratory Behaviour of Epipellic Diatoms. *Limnology and Oceanography* **34**, 223-234.
- Paterson, D. M. (1995). Biogenic Structure of Early Sediment Fabric Visualized by Low-Temperature Scanning Electron Microscopy. *Journal of the Geological Society* **152**, 131-140.
- Paterson, D.M. (1997). Biological Mediation of Sediment Erodability: Ecology and Physical Dynamics. In Burt, N., Parker, R., and Watts, J., (Eds). *Cohesive Sediments*. John Wiley & Sons Ltd. pp 213-215.
- Paterson, D.M. (1994) Microbial mediation of sediment structure and behaviour. In: NATO ASI series **635 Microbial Mats**. Stal, L.J., Gaumethe, P. (Eds). Springer-Verlag, Berlin Heidelberg.
- Paterson, D.M., and Daborn, G.R. (1991). Sediment stabilisation by biological action: significance for coastal engineering. In: Peregrine, D.H., and Loveless, J.H., (Eds). *Developments in coastal engineering*. University of Bristol. 111-119.
- Paterson, D.M., Yallop, M.L., George, C. (1994) Spatial variability in sediment erodability on the island of Texel. In *Biostabilisation of Sediments*. Krumbein, W.E., Paterson, D.M., and Stal, L.J. (Eds), Oldenberg University press, Germany.
- Paterson, D. M., Wiltshire, K.H., Miles, A., Blackburn, J., Davidson, I., Yates, M.G., McGrorty, S., Eastwood, J.A. (1998). Microbiological Mediation of Spectral Reflectance from Intertidal Cohesive Sediments. *Limnology and Oceanography* **43**, 1207-1221.
- Paterson, D. M., and Black, K.S. (1999). Water Flow, Sediment Dynamics and Benthic Biology. *Advances in Ecological Research* **29**, 155-193.
- Paterson and Black. (2000). *Siliciclastic Intertidal Microbial Sediments*. Microbial Sediments, 76-83. Riding, R., and Awramik, S.M (Eds). Springer.
- Paterson, D.M., Tolhurst, T.J., Kelly, J.A., Honeywill, C., de Deckere, E.M.G.T., Huet, V., Shaylor, S.A., Black, K.S., de Brouwer, J., and Davidson, I. (2000) Variation in sediment properties, Skeffling mudflat, Humber estuary, UK. *Continental Shelf Research* **20**: 1373-1396.
- Paterson, D. M., and Hagerthy, S.E. (2001). Microphytobenthos in contrasting coastal ecosystems: biology and dynamics. 105-126. In Reise, K. (Ed), *Ecological Comparisons of sedimentary shores*. Ecological Studies 151, Springer-Verlag.

- Perkins, R.G., Underwood, G.J.C., Brotas, V., Jesus, B., Ribeiro, L. and Snow, G. (2001). *In situ* microphytobenthic primary production during low tide emersion in the Tagus estuary, Portugal: production rates, carbon partitioning and vertical migration. *Marine Ecology Progress Series* **223**, 101-112.
- Perkins, R. G., Oxborough, K., Hanlon, A.R.M., Underwood, G.J.C., and Baker, N.R. (2002). Can chlorophyll fluorescence be used to estimate the rate of photosynthetic electron transport within microphytobenthic biofilms. *Marine Ecology Progress Series* **228**, 47-56.
- Perkins, R. G., Honeywill, C., Consalvey, M., Austin, H.A., Tolhurst, T.J., and Paterson, D.M. (2003). Changes in microphytobenthic chlorophyll *a* and EPS resulting from sediment compaction due to de-watering: opposing patterns in concentration and content. *Continental Shelf Research* **23**, 575-586.
- Peterson, C.G., and Hoagland, K.D. (1990). Effects of wind-induced turbulence and algal mat development on epilithic diatom succession in a large reservoir. *Archive fur Hydrobiologie* **118** (1): 47-68.
- Pethick, J.S. (1993) Shoreline adjustments and coastal management: physical and biological processes under accelerated sea-level rise. *The Geographical Journal*. **159**: 162-168.
- Pethick, J. S. (1996). The Geomorphology of Mudflats in Nordstrom, K. F., Roman, C.T. (Ed), *Estuarine Shores: Evolution, Environments and Human Alterations*, John Wiley & Sons Ltd.
- Phelps, H.O. (1970). The friction coefficient fro shallow flows over simulated turf surface. *Water Resources Research* **6**: 1220-1226.
- Piazzini, L., and Cinelli, F. (2001). Distribution and dominance of two introduced turf-forming macroalgae on the coast of Tuscany, Italy, Northwestern Mediterranean Sea in relation to different habitats and sedimentation. *Botanica Marina*. **44**: 509-520.
- Pinckney, J., Piceno, Y., and Lovell, C.R. (1994) Short term changes in the vertical distribution of benthic algal biomass in intertidal muddy sediments. *Diatom Research* **9** (1): 143-153.
- Pilskaln, C.H., Churchill, J.H., and Mayer, L.M. (1998). Resuspension of sediment by bottom trawling in the gulf of maine and potential geochemical consequences. *Conservation Biology*. **12**, 1523-1739.
- Postma, H. (1967). *Sediment Transport and Sedimentation in the Estuarine Environment*.

- Poulsen, N.C., Spector, I., Spurck, T.P., Schultz, T.F., and Wetherbee, R. (1999) Diatom gliding is the result of an actin-myosin motility system. *Cell motility and the cytoskeleton*. **44**: 22-33.
- Ravera, O. (2000). The Lagoon of Venice: the result of both natural factors and human influence. *Journal of Limnology* **59**, 19-30.
- Reid, R.P., MacIntyre, I.G., Browne, K.M., Steneck, R.S., and Miller, T. (1995) Modern marine stromatolites in the Exuma Cays, Bahamas: Uncommonly common. *Facies* **33**: 1-18.
- Reid, R. P., Visscher, P.T., Decho, A.W., Stoltz, J.F., Bebout, B.M., Dupraz, C., MacIntyre, I.G., Paerl, H.W., Pinckney, .L., Prufert-Bebout, L., Steppe, T.F., and DesMarais, D.J. (2000). The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. *Nature* **406**, 989-992.
- Rhoads, D.C., McCall, P.L., and Yingst, J.Y. (1978). Production and disturbance on the estuarine seafloor. *American Scientist*. **66**, 577-586.
- Riding, R., Awramik, S.M., Winsborough, B.M., Griffen, K.M., and Dill, R.F. (1991) Bahamian giant stromatolites: microbial composition of surface mats. *Geological Magazine* **128**:227-234.
- Riethmüller, R., Hakvoort, J.H.M, Heineke, M., Heyman, K., Köhl, H., and Witte, G. (1998). Relating erosion shear stress to tidal flat surface colour. In: *Sedimentary processes in the intertidal zone*. Black, K.S., Paterson, D.M., and Cramp, A. (Eds.). Geological Society, London, Special Publications. **139**: 283-293.
- Riethmüller, R., Heineke, M., Köhl, H., and Keuker-Rüdiger, R. (2000). Chlorophyll *a* concentration as an index of sediment surface stabilisation by microphytobenthos. *Continental Shelf Research*. **20**: 1351-1372.
- Rijstenbil, J. W., Kamermans, p., and Nienhuis, P.H. (1996). Sinthesis Report, EUMAC.
- Roman, C. T., Garvine, R.W., Portnoy, J.W. (1995). Hydrologic Modelling as a Predictive Basis for Ecological Restoration of Salt Marshes. *Environmental Management* **19**, 559-566.
- Rosenberg, R., Nilsson, H.C., Gremare, A., and Amouroux, J-M. (2003) Effects of demersal trawling on marine sedimentary habitats analysed by sediment profile imagery. *Journal of Experimental Marine Biology and Ecology*. **285-286**: 465-477.
- Rossetto, L. (2000). <http://oregonstate.edu/dept/IIFET/2000/abstracts/rossetto>
- Round, F.E., Crawford, R.E., and Mann, D.G. (1990) The diatoms: biology and morphology of the genera. Cambridge University Press. Cambridge, Uk.

- Round, F.E., and Palmer, J.D. (1966) Persistent, vertical-migration rhythms in benthic microflora. *Journal of the Marine Biological Association U.K.* **46**: 191-214.
- Rowan, K.S. (1989). Chapter 3: Chlorophylls and derivatives. In: *Photosynthetic pigments of algae*. Cambridge University Press, Cambridge.
- RSPB (2000) <http://www.rspb.org.uk/countryside/habitats/coastal/index.asp>.
- Sabbe, K., and Vyverman, W. (1991) Distribution of benthic diatom assemblages in the Westerschelde (Zeeland, The Netherlands). *Belgium Journal of Botany*. **124**: 91-101.
- Saburova, M.A., Polikarpov, I.G. and Burkovsky, I.V. (1995) Spatial structure of an intertidal sandflat microphytobenthic community as related to different spatial scales. *Marine Ecology Progress Series*. **129**: 229-239.
- Sainsbury, K.J., Campbell, R.A., Lindholm, R., and Whitelaw, A.W. (1997). Experimental management of an Australian multispecies trawl fishery: examining the possibility of trawl induced habitat modification. In: *Global Trends: Fisheries Management. American Fisheries Society Symposium 20*. Pikitch, E.L., Huppert, D.D., and Sissenwine, M.P., (Eds). pp 107-112.
- Schopf, J. W. (1983). *Earth's Earliest Biosphere*. University Press.
- Schwinghamer, P., Gordon, D.C., Rowell, T.W., Prena, J., Mckeown, D.L., Sonnichsen, G., and Guign e, J.Y. (1998). Effects of experimental otter trawling on surficial sediment properties of a sandy-bottom ecosystem on the Grand Banks of Newfoundland. *Conservation Biology*. **12** (6): 1523-1739.
- Scoffin, T.P. (1970) The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Petrology*. **40**: 249-273.
- Seapy, R.R., and Littler, M.M. (1982). Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. *Marine Biology*. **71**: 87-96.
- Seong-Joo, L., Browne, K.M., Golubic, S. (2000) *On stromatolite lamination*. Microbial Sediments, 16-24. Riding, R., and Awramik, S.M (Eds). Springer.
- Ser dio, J., and Catarino, F. (1999) Fortnightly light and temperature variability in estuarine intertidal sediments and implications for microphytobenthic primary productivity. *Aquatic Ecology* **33**: 235-241.

- Sherwood, B.R., Gardiner, B.G., and Harris, T. (2000). *British Saltmarshes*. Linnean Society of London.
- Shi, Z., Pethick, J.S., Burd, F., and Murphy, B. (1996). Velocity profiles in a salt marsh canopy. *Geo-Marine Letters* **16**, 319-323.
- Shi, Z., Pethick, J.S., Pye, K. (1995). Flow structure in and above the various heights of a saltmarsh canopy: a laboratory flume study. *Journal of Coastal Research* **11**, 1204-1209.
- Silvestri, S., Marani, M., Settle, J., Benvenuto, F., and Marani, A. (2002). Saltmarsh vegetation radiometry. Data analysis and scaling. *Remote Sensing of Environment* **80**, 473-482.
- Silvestri, S., and Marani, M. (2004) Salt-marsh vegetation and morphology: modelling and remote sensing observations. In *The Ecogeomorphology of Tidal Marshes*. Coastal and Estuarine Studies Series (AGU). Fagherazzi, S., Marani, M., and Blum, L.K. (Eds.).
- Simonsen, R. (1974). The diatom plankton of the Indian Ocean expedition of R/V Meteor 1964-5. *Meteor Forsch-Ergebnisse Reihe D.*, **19**, 1-107.
- Smith, D.J. (1999) *Exopolymer production by epipelagic diatoms*. (PhD) Department of Biological and Chemical Sciences, University of Essex. 210 pages.
- Smith, D. J., and Underwood, J.C. (1998). Exopolymer Production by Intertidal Epipelagic Diatoms. *Limnology and Oceanography* **43**, 1578-1591.
- Sorokin, P.Yu., Sorokin, Yu.I., Zakuskina, O.Yu., and Ravagnan, G.-P., (2002). On the changing ecology of Venice lagoon. *Hydrobiologia*. **487**: 1-18.
- Sousa, W.P., Schroeter, S.C., and Gaines, S.D. (1981). Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. *Oecologia*. **48**: 297-307.
- Spencer, B.E., Kaiser, M.J., and Edwards, D. B. (1997). Ecological effects of intertidal Manila clam cultivation: observations at the end of the cultivation phase. *Journal of Applied Ecology*. **34** (2): 444-453.
- Spencer, B.E., Kaiser, M.J., and Edwards, D. B. (1998). Intertidal clam harvesting: benthic community change and recovery. *Aquaculture Research* **29**: 429-437.
- Stal, L.J. (1995). Tansley Review No. 84. Physiological ecology of cyanobacteria in microbial mats and other communities. *New Phytologist*. **131**: 1-32.

- Stal, L.J. (2000) Cyanobacterial mats and stromatolites. In *The ecology of cyanobacteria: Their diversity in time and space*. Whitton, B.A., and Potts, M., (Eds). Kluwer Academic Publishers.
- Stal, L.J. (2003). Microphytobenthos, the extracellular polymeric substances, and the morphogenesis of intertidal sediments. *Geomicrobiology Journal*. **20**: 463-478.
- Stewart, J.G. (1982). Anchor species and epiphytes in intertidal algal turf. *Pacific Science* **36** (1): 45-59.
- Stewart, J.G. (1983) Fluctuations in the quantity of sediments trapped among algal thalli on intertidal rock platforms in southern California. *Journal of Experimental Marine Ecology* **73**: 205-211.
- Stolz, J.F., Feinstein, T.N., Salsi, J., Visscher, P.T., and Reid, R.P. (2001) TEM analysis of microbial mediated sedimentation and lithification in modern marine stromatolites. *American Mineralogist* **86**:826-833.
- Sutherland, T.F. (1996) *Biostabilisation of estuarine sub-tidal sediments*. (PhD Thesis) Dalhousie University, Halifax, Nova Scotia.
- Sutherland, T. F., Amos, C.L., Grant, J. (1998). The Effect of Buoyant Biofilms on the Erodability of Sublittoral Sediments of a Temperate Microtidal Estuary. *Limnology and Oceanography* **43**, 225-235.
- Taylor, I.S., Paterson, D.M. (1998). Microspatial variation in carbohydrate concentrations with depth in the upper millimetres of intertidal cohesive sediments. *Estuarine Coastal Shelf Science*. **46**: 359-370.
- Tolhurst, T.J. (1999) Microbial mediation of intertidal sediment stability. PhD Thesis, University of St Andrews: 11.
- Tolhurst, T. J., Black, K. S., Shayler, S. A., Mather, S., Black, I., Baker, K., Paterson, D. M. (1999). Measuring the *in situ* Erosion Shear Stress of Intertidal Sediments with the Cohesive Strength Meter (CSM). *Estuarine, Coastal and Shelf Science*. **49**, 281-294.
- Tolomio, C., Moschin, E., Moro, I., and Andreoli, C. (1999). Phytoplankton de la Lagune de Venise I. Bassins nord et sud (Avril 198 - Mars 1989). *Vie at Milieu* **49**, 33-44.
- Underwood, G. J. C. (1994). Seasonal and spatial variation in epipellic diatom assemblages in the Severn Estuary. *Diatom Research* **9**, 451-472.
- Underwood, G. J. C. (1997). Microalgal Colonization in a Saltmarsh Restoration Scheme. *Estuarine, Coastal and Shelf Science* **44**, 471-481.

- Underwood, G. J. C., and Paterson, D.M. (1993). Seasonal Changes in Diatom Biomass, Sediment Stability and Biogenic Stabilization in the Severn Estuary. *Journal of Marine Biological Association* **73**.
- Underwood, G. J. C., Paterson, D.M., and Parkes, R.J. (1995). The Measurement of Microbial Carbohydrate Exopolymers from Intertidal Sediments. *Limnology and Oceanography* **40**, 1243-1253.
- Underwood, G. J. C., and Smith, D. J. (1998) Predicting epipellic diatom exopolymer concentration in intertidal sediments from sediment chlorophyll *a*. *Microbial Ecology* **35**: 116-125.
- Underwood, G. J. C., Kromkamp, J. (1999). Primary Production by Phytoplankton and Microphytobenthos in Estuaries. *Advances in Ecological Research* **29**, 93-141.
- Underwood, G. J. C., and Paterson, D.M. (2003). The importance of extracellular carbohydrate production by marine epipellic diatoms. *Advances in Botanical Research* **40**, 183-240.
- UKBAP, (2002). Action Plan for coastal salt marsh.  
<http://www.ukbap.org.uk/UKPlans.aspx?ID=33>
- Van der Werff, A., and Huls, H. (1976) Diatom Flora of the Netherlands. Otto Koeltz Science Publishers.
- van Eerdt, M.M. (1985). The Influence of Vegetation on Erosion and Accretion in Salt Marshes of the Oosterschelde, The Netherlands. *Vegetation* **62**: 367-373.
- Vardy, S., Saunders J.E., Tolhurst, T., Davies, P. and Paterson. D.M (In press, 2005). Calibration of the high pressure Cohesive Strength Meter. *Estuarine and Coastal Shelf Science*.
- Visscher, P. T., Reid, R.P., and Bebout, B.M., Hoefl, S.E., MaCintyre, I.G., and Thompson Jr, J.A. (1998). Formation of lithified micritic laminae in modern marine stromatolites (Bahamas): The role of sulfur cycling. *American Mineralogist* **83**: 1482-1493.
- Visscher, P.T., Reid, R.P., and Bebout, B.M. (2000) Microscale observations of sulfate reduction: Correlation of microbial activity with lithified micritic laminae in modern marine stromatolites. *Geology* **28**:919-922.
- Vogel, S. (1994). *Life in Moving Fluids : The Physical Biology of Flow.*, Second Edn. Princeton University Press.
- Walter, M.R. (1976). *Stromatolites: Developments in Sedimentology* 20. Walter, M.R. (Ed). Elsevier.

- Walter, M.R. (1983) In: *Earths earliest biosphere*. Schopf, J.W (Ed). 187-213. Princeton University Press.
- Warwick, R.M., Platt, H.M., Clarke, K.R., Agard, J., and Gobin, J. (1990). Analysis of macrobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. *Journal of Experimental Marine Biology and Ecology*. **138**: 119-142.
- Watling, L., and Norse, E.A. (1998). Disturbance of the seabed by mobile harvesting gear: A comparison to forest clear cutting. *Conservation Biology*. **12** (6): 1180-1197.
- Waugh, D. (1995) 2<sup>nd</sup> Ed. *Geography: An integrated approach*. Nelson.
- Widdows, J., Brinsley, M.D., and Elliot, M. (1998) Use of *in situ* flume to quantify particle flux (deposition rates and sediment erosion) for an intertidal mudflat in relation to changes in current velocity and benthic macrofauna. In *Sedimentary Processes in the Intertidal Zone* (Black, K.S., Paterson, D.M., and Cramp, A (Eds.)). Geological Society of London, Special publications, **139**: 85-97.
- Widdows, J., Brinsley, M. (2002). Impact of biotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. *Journal of Sea Research* **48**, 143-156.
- Widdows, J. Blauw, A., Heip, C.H.R., Herman, P.M.J., Lucas, C.H., Middelburg, J.J., Schmidt, S., Brinsley, M.D., Twisk, F., and Verbeek, H.. (2004). Role of physical and biological processes in sediment dynamics of a tidal flat in Westerschelde Estuary, SW Netherlands. *Marine Ecology-Progress Series*.**274**: 41-56 2004.
- Willows, R.I., Widdows, J., and Wood, R.G. (1998) Influence of an infaunal bivalve on the erosion of intertidal cohesive sediment: a flume and modelling study. *Limnology and Oceanography* **43**: 1332-1343.
- Wiltshire, K. H., Blackburn, J., Paterson, D.M. (1997). The Cryolander: A New Method for Fine-Scale *In Situ* Sampling of Intertidal Surface Sediments. *Journal of Sedimentary Research* **67**, 977-981.
- Wiltshire, K.H. (2000) Algae and associated pigments of intertidal sediments, new observations and methods. *Limnologica* **30**: 205-214.
- Winsborough, B. (2000) *Diatoms and benthic microbial carbonates*. Microbial Sediments, 76-83. Riding, R., and Awramik, S.M (Eds). Springer.
- Yallop, M. L., de Winder, B., Paterson, D.M., Stal, L.J. (1994). Comparative Structure, Primary Production and Biogenic Stabilisation of Cohesive and Non-Cohesive Marine Sediments Inhabited by Microphytobenthos. *Estuarine, Coastal and Shelf Science* **39**, 565-582.

- Zar, J.H. (1999) *Biostatistical Analysis*. Fourth Edition. Prentice-Hall Inc.
- Ziebis, W., Forster, S., Huettel, M., Jørgensen, B.B. (1996). Complex Burrows of the Mud Shrimp *Callinasa truncata* and their Geochemical Impact in thre Sea Bed. *Nature* **382**, 619-623.
- Zong, Y., and Horton, B.P. (1998) Diatom zones across intertidal flats and coastal saltmarshes in Britain. *Diatom Research*. **13**: 375-394.