SPATIAL VARIABILITY IN INTERTIDAL MACROFAUNAL AND MICROBIAL COMMUNITIES AND THEIR SEDIMENTARY ENVIRONMENTS

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THIS THESIS IS DEDICATED

TO MY FATHER PROFESSOR MOHAMMAD TUFAIL

AND MY LATE MOTHER SARWARI TUFAIL

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ABSTRACT SUMMARY

The objectives of my thesis were to study levels of abundances and their spatial heterogeneity in macrofaunal and microbial communities living in sediments on an intertidal muddy sand beach at Ardmore bay, Clyde Estuary, Scotland (55° 28'N, 4° 49'W). The macrofaunal communities were studied by a field survey, and the microbial communities by nutrient enriched cores in the laboratory. The rationale for the two approaches is given in the introduction. The results were statistically analysed by analyses of variance, Student's t tests, F ratios, correlation analyses and Chi square tests, as appropriate.

MACROFAUNAL COMMUNITIES

Spatial heterogeneity and abundance of infaunal benthic communities and their sedimentary environments were studied at two intertidal sites at Ardmore bay in summer.

The high tide site (HT) was a low energy depositional environment dominated by patches of algal mats (Enteromorpha sp.) (diameter c. 0.75m to 2.5m) and bare areas of sediment with no algal mats - termed algal and nonalgal areas respectively. The low tide site (LT) was a higher energy erosional environment dominated by large sand waves with distinct peaks and troughs (wavelength c. 25m).

An initial survey was followed by a detailed 50m transect survey, both done on all four areas - algal and nonalgal areas at the high tide site and peaks and troughs of the sand waves at the low tide site. The 50m transects were sampled at 1m intervals. Sediment shear strength and redox potential, and water table were measured. Percent algal cover was measured at high tide site.

Sediment cores were taken for macrofaunal abundances. Arenicola marina was counted by faecal casts.

The species in order of decreasing abundance were, * = species common to both sites.

High tide site:

Fabricia sabella, Corophium volutator, *Pygospio elegans, *Nereis diversicolor, Hydrobia neglecta, *Macoma balthica and *Arenicola marina

Low tide site:

*Pygospio elegans, Bathyporeia guilliamsoniana, *Nereis diversicolor, *Macoma balthica and *Arenicola marina

I defined the following scales of spatial heterogeneity in macrofaunal abundances and sediment parameters: micro-scale $\leq$ 1m, meso-scale $>$ 1m to $\leq$ 50m and macro-scale $>$ 50m.

The high tide and low tide sites were significantly different sedimentary environments on a macro-scale and there were also clear meso-scale differences between the algal and nonalgal areas at the high tide site and the peaks and troughs of the sand waves at the low tide site.

The sediment at the high tide areas was finer than the low tide areas and sediment parameters were very different between the four areas emphasising the different sedimentary environments. Algal areas contained finer sediment than nonalgal areas and had a higher shear strength and lower redox potential. Trough sediment was more widely distributed between particle sizes (less well sorted) than peak sediment and had a lower shear strength.

Species abundance and spatial variability in abundance showed highly significant differences between the two sites - macro-scale, and between the two areas at each site - meso-scale. For example, A. marina was more abundant and its abundance less variable at the low tide site than at the high tide site and species diversity

indices were higher in the troughs than in the peaks at the low tide site.

Significant correlations were established between species abundances, species abundances and sedimentary parameters, and the sedimentary parameters. For example, there were more significant correlations at the low tide site than at the high tide site. At the high tide site A. marina and C. volutator were negatively correlated with percent algal cover, and at the low tide site B. guilliamsoniana and N. diversicolor were negatively correlated with shear strength.

Two methods were developed to distinguish between macro-, meso-, and micro-scale heterogeneity in the transect survey. One used variances from analyses of variance, the other used differenced data at progressively greater distances apart along the transect (1m, 5m, 10m, 20m, 30m, and 40m). They showed a number of effects including the greater meso-scale and micro-scale variability in redox potential at the high tide site than at the low tide site, and the greater differenced data for M. balthica and N. diversicolor at the high tide site.

In the discussion I review some of the huge literature on sediment properties affecting macrobenthic infaunal communities and relate this to my results under the following topics: sediment properties, scales of spatial heterogeneity, algal mats and sand waves, correlations and species diversity.

MICROBIAL COMMUNITIES

Abundance and spatial heterogeneity of microbial communities on sand grains from the low tide area at Ardmore bay were studied in nutrient enriched sediment columns incubated for 25 days in the laboratory. Columns were maintained under 17h light/7h dark (L) and total dark (D) regimes. Photosynthetic (M) and heterotrophic (B) media were used in both regimes. Mean particle size was 195 μm.

Sediments incubated in the light (ML, BL) simulated intertidal and inshore surface sediments. Sediments incubated in the dark (MD, BD) simulated subsurface sediments in the same environments and also surface sediments which are below the euphotic zone. Sediments enriched with photosynthetic medium (ML, MD) simulated sediments where inorganic nutrients in soil run-off occurs from the land. Sediments enriched with heterotrophic medium (BL, BD) simulated sediments with a higher organic content like those near sewage outlets. Control columns (C) contained formalin.

A detailed description of the microbial communities on the sand grains in the different media is presented with scanning electron microscope photographs. Monospecific and mixed species colonies of a wide range of microorganisms were noted. More growth occurred on subangular (sharp) sand grains than on subrounded (smooth) sand grains.

I defined the following scales of spatial variability in microbial abundances: Micro-scale variability on each individual sand grain (not investigated through lack of time), meso-scale variability between sand grains in the same medium, and macro-scale variability between different media.

There were considerable differences in the microbial communities and their spatial variability between sand grains in the same medium - meso-scale, and between sand grains in different media - macro-scale. These reflect the different media used, and hence the different sedimentary environments being simulated.

Large populations of photosynthetic microorganisms (diatoms, blue-green algae) developed in the ML columns including a Thraustochytrid fungus. The most abundant was the blue-green alga Schizothrix sp.. A wide range and high abundance of heterotrophic bacteria (rods and cocci) developed in the BL and BD columns. These were only described morphologically. No biochemical identification of bacterial species was done.

Meso-scale and macro-scale differences occurred in the variability of species abundances, including the high meso-scale variability of the Schizothrix sp. in the ML medium and the large macro-scale difference between the high variability of cocci in the BL medium and their low variability in the BD medium.

This short *abstract summary* is presented because the University of Glasgow requires a summary of 250 to 1000 words at the beginning of the Ph.D. thesis. A *full summary* is presented after the discussion.

INTRODUCTION

"To the natural philosopher, the descriptive poet, the painter, the sculptor, and indeed every earnest observer, the power most important to cultivate, and at the same time, hardest to acquire, is that of seeing what is before him."

(Marsh, 1874)

INTRODUCTION

Variations in abundance of organisms in space and time (spatial and temporal heterogeneity) can occur to different degrees (extreme patchiness or uniformity) (Cushing & Tungate, 1963; McIntyre, 1969; Holligan, 1978) and can be on different scales (μm to km, days to years) (Haury et al., 1978; Radach & Mann, 1981). These variations are of great importance in the community structure of macrofauna, meiofauna and microorganisms (ZoBell, 1946a; Levinton, 1972; Sieburth, 1975; Woodin, 1976; Holm, 1978; Peterson, 1979; Connell & Sousa, 1983; Ducklow, 1984; Valiela, 1984; Wethey, 1984; Meadows & Tait, 1985; Reise, 1985, 1987; Wildish, 1985; Tyler, 1988; Gooday & Turley, 1990; Angel, 1991), and as a result there is a considerable literature on the subject. The aim of the research presented in this thesis was to investigate some aspects of these variations in intertidal benthic communities of macrofauna and microorganisms living in sediments.

Almost all temperate climate populations of benthic marine organisms show temporal heterogeneity often as seasonal cycles of abundance, and in a similar way spatial heterogeneity in the form of patchiness in benthic community structure and the sedimentary environment has been documented by many authors. These are considered below. Small-scale spatial heterogeneity of the sort that I have investigated at Ardmore bay, Clyde Estuary, in macrofauna under field conditions and in microorganisms from the same environment under laboratory conditions, has received less attention although there are a number of important analyses in this field (c.f. Orth, 1977; Reise, 1977; Rades-Rohkohl et al., 1978; Eckman, 1979; Maurer et al., 1979; Nickels et al., 1981; Wilson, 1981; DeFlaun & Mayer, 1983; Olafsson & Persson, 1986).

1. Temporal heterogeneity in benthic communities

Temporal heterogeneity of macrofaunal benthic communities has been widely investigated in the intertidal zone (Heydemann, 1979; Maurer et al., 1979; Valiela, 1984; Saenger et al., 1988) in subtidal coastal communities (Blegvad, 1925; Raymont, 1949; Naylor, 1962; Fager, 1968; Green & Hobson, 1970; Parker, 1975; Reise, 1977; Buchannan et al., 1978; Davis & van Blaricom, 1978; Maurer et al., 1979; Josefson, 1981; Saenger et al., 1988) and in the deep-sea (Gage et al., 1980; Tyler, 1988). Although time did not permit me to study the temporal heterogeneity of the species abundance and sedimentary parameters at Ardmore, I feel it necessary to stress its importance since there is a considerable literature on it and because one example of it - seasonality - is particularly important in temperate climates.

Meiofaunal and microbial populations in sediments also show temporal heterogeneity often in the form of seasonal variations (Matthews, 1964; Muus, 1967; Barnett, 1968; McIntyre, 1969; Skoolmun & Gerlach, 1971; Harris, 1972; McIntyre & Murison, 1973; Warwick, 1977; Coull & Bell, 1979; Colijin & Dijkema, 1981; Giere & Pfannkuche, 1982; DeFlaun & Mayer, 1983; Heip et al., 1985; Christensen & Sorensen, 1986; Bebout et al., 1987). At Whitstable, Kent for example (Perkins, 1974, p 236 fig. 9.7), the meiofauna shows a seasonal maximum in summer which is closely related to temperature. The maximum consists of a few species that are dominant while the remaining species occur only intermittently and are less abundant. As another example, DeFlaun & Mayer (1983) have shown seasonal changes in microbial populations in the intertidal zone. Here, benthic microalgae and bacteria showed marked seasonal changes, but the effects were inverse. Bacterial numbers were high in summer while the microalgal numbers were high in winter (loc. cit. p 880).

These and other studies on a wide variety of benthic marine ecosystems show that temporal heterogeneity in benthic communities of macrofauna, meiofauna and microorganisms, particularly seasonality, is of great importance. A study of temporal heterogeneity should therefore be an integral part of any future survey work at Ardmore, preferably to be conducted over a number of years. This would then provide a much needed long term time-series for detailed analysis which would complement the studies on spatial heterogeneity presented in this thesis.

2. Spatial heterogeneity in benthic communities and sedimentary environments

Spatial heterogeneity is found both in pelagic and benthic populations and the scales on which it can occur vary from microns to kilometres (Bainbridge, 1952; Cushing & Tungate, 1963; Clutter, 1969; Wiebe, 1970; Maul, et al., 1974; Walsh et al., 1977; Haury et al., 1978; Anderson & Meadows, 1978; Radach & Mann, 1981; Wimpenny, 1982; Balch et al., 1983; Connell & Sousa, 1983; Ducklow, 1984; Nicholson et al., 1987).

In the pelagic ecosystem, phytoplankton and zooplankton patches occur at horizontal distances of 10^{-1}m and 10^{5}m to 10^{8}m respectively (Bainbridge, 1953; Valiela, 1984; Boney, 1989). These patches can be caused by social (Kamamura, 1974) or reproductive behaviour (Clutter, 1969), and there are many examples.

Spatial distribution and heterogeneity of benthic macrofaunal, meiofaunal and microbial communities have been widely investigated, often in relation to sediment parameters (Allen, 1899; Allen & Todd, 1900, 1902; Ford, 1923; Steven, 1930; Stephen, 1933; Pirrie & Moore, 1932; ZoBell & Anderson, 1936; Pearse et al., 1942; Holme, 1949, 1953, 1961; Round, 1965, 1968; Sanders, 1968; Riznyk, 1973; Vanderborght & Billen, 1975; Hummon & Hummon, 1977; Warwick & Davies, 1977; McCall, 1978; Weise & Rheinheimer, 1978; Eckman, 1979; Farke et al., 1979; Gage et al., 1980; Warwick & Uncles,

1980; Findlay, 1981; Nickels et al., 1981; Cammen, 1982; Valiela, 1984; Reise, 1987; Dobbs & Guckert, 1988; Downing & Rath, 1988; Blanchard, 1990; Schaffner, 1990; Warwick & Clark, 1991). It can occur in the vertical or horizontal plane depending on the ecosystem (Castenholz, 1963; Jumars & Eckman, 1983; Plante et al., 1986; Schaffner, 1990) and sometimes on very small scales, particulary in microbial communities. For example Jorgensen (1977), Anderson and Meadows (1978) and Paerl (1985) all describe differences in microbial communities on a scale of millimetres to microns in which they term microniches, microenvironments and microzones respectively, and the structure of marine microbial mats on a micron scale has received considerable attention (Doemel & Brock, 1977; Jorgensen et al., 1979; Jorgensen et al., 1983; Nicholson et al., 1987; Pierson et al. 1987).

Spatial heterogeneity in the abundance of benthic organisms is affected by a very large number of factors. For macrofauna and meiofauna these include sediment properties (Longbottom, 1970; Ward, 1975; Giere, 1977; Warwick & Davies, 1977; McCall, 1978; Creutzberg et al., 1984; Gray et al., 1985; Savidge & Taghon, 1988), the presence of algal mats such as those present towards high tide at my sampling site, Ardmore Bay, Clyde Estuary (Perkins & Abbott, 1972; Howes et al., 1981; Hull, 1987), availability of food (organic matter and nutrients) (Beukema et al., 1977; Heydemann, 1979; Findlay, 1981; Decho & Castenholz, 1986; Ritz et al., 1989), predation (Reise, 1977; Peterson, 1979; Zwarts & Esselink, 1989) competition (Seed & Boaden, 1977; Witte & Wilde, 1979; Jensen & Kristensen, 1990), reproductive activity (Thornson, 1966; Farke et al., 1979; Jensen, 1985), salinity (McLusky, 1971), oxygen concentrations (Giere, 1977), moisture content (Watling, 1988; Harrison & Wass, 1965), tidal stress (Warwick & Uncles, 1980), biogenic structures (Eckman, 1979; Findlay, 1981), larval dispersal (Sheltema, 1977; Tyler, 1977), interactions with other plants and animals (Woodin, 1974; Reise, 1977, 1983; Wurzin, 1977; Wilson, 1981; Olafsson & Persson, 1986; Pennings, 1991), and

pollutants (Sanders, 1978). Some of these factors are discussed in more detail in relation to my own work, in the discussion (pp. 188, 201). Similar factors affect spatial heterogeneity in the abundance of microorganisms but they have received less attention (Wormald & Stirling, 1979; Cox & Bazin, 1980; Nickels et al., 1981; Weise & Rheinheimer, 1978; Hennig et al., 1983; Nygaard et al., 1988).

Spatial heterogeneity also occurs in sedimentary environments in the form of changes in particle size and distribution and in the topography of the sediment surface (Allen, 1899; Ford, 1923; Stephen, 1929; Pirrie & Moore, 1932; Smith, 1932, fig. 1 p 251; Dorjes et al., 1969; Krumbein, 1971; Reineck & Singh, 1980; Anderson et al., 1981; Selley, 1982; Allen, 1985; Bird, 1984; Sleath, 1984; Collinson & Thompson, 1989). Some of these phenomena such as ripples, sand waves and flat beds are well known in the sedimentological literature (Sundborg, 1956; Allen, 1968, 1973, 1978; Belderson et al., 1972; D'Olier, 1979; Dyer, 1979; Reineck & Singh, 1980; Kidd & Roberts, 1982; Gardner & Kidd, 1983; Siever, 1988; Collinson & Thompson, 1989). This heterogeneity is produced by water movement in the form of waves, tides and water currents and their effects on sediment erosion, transport and deposition (Hjulstrom, 1939; Sundborg, 1956; Terwindt, 1967; Visher, 1969; Allen, 1970; Swift et al., 1972; Sundby, 1974; Visher & Howard, 1974; Buller & McManus, 1975; Reineck & Singh, 1980; Sleath, 1984). It is also produced on a local scale by biological activity (Crozier, 1918; Dapples, 1942; Rhoads & Stanley, 1965; Gordon, 1966; Rhoads, 1967, 1974; Dillon & Zimmerman, 1970; Goldring & Seilacher, 1971; Rhoads & Young, 1971; Schafer, 1972; Gray, 1974; Howard & Frey, 1975; Cadee, 1976; Myers, 1977; Buchanan et al., 1978).

Spatial heterogeneity in sediments can cover a wide range of scales. Small scale heterogeneity of the order of microns to centimetres is often more noticeable in vertical profiles than horizontally, and geotechnical and geochemical properties such as shear strength, redox potential, organic carbon

and nitrogen, sulphide, can all change rapidly with increasing sediment depth (Moore, 1931, fig. 9, p 349; Hargrave & Nielsen, 1977; Vosjan & Olanczuk-Neyman, 1977; Anderson & Meadows, 1978; Pearson & Stanley, 1979; Anderson et al., 1981; Howes et al., 1981; Lyle, 1983; Boynton & Kemp, 1985; Jorgensen & Revsbech, 1985; Meadows & Tait, 1985; Seitzinger & Nixon, 1985; Wilson et al., 1985; Downing & Rath, 1988; Siever, 1988; Thode-Andersen & Jorgensen, 1989; Chester, 1990; Schimmelman et al., 1990). Micro-ripples at the sediment surface are a good example of physical heterogeneity at scales of 1 to 10cm (Allen, 1968; Hogue & Miller, 1981; Klein, 1985). On a larger scale of metres to kilometres sediment properties and granulometry are well known to change significantly in the intertidal zone and subtidally on the continental shelf and slope (Bruce, 1928b, fig. 1 p 557; Evans, 1965; Hargrave & Nielsen, 1977; Stanley & Taylor, 1977; Tyler & Banner, 1977; Stanley & Wear, 1978; Pearson & Eleftheriou, 1981; Stanley et al., 1981). Other examples of heterogeneity at this scale include the mega-ripples on sand banks at the mouth of the Brahmaputra River (Coleman, 1969), mega-ripples on North Sea tidal flats (Reineck & Singh, 1980, p. 42; Reise, 1985), the large sand waves towards low tide at my sampling site, Ardmore Bay, the Clyde Estuary, mud volcanoes in the Caspian Sea associated with oil and gas deposits (Newton et al., 1980) and sea bed pock marks probably associated with water or gas release in the Aegean Sea and North Sea (Newton et al., 1980; Hovland & Gudmestad, 1984).

3. Clyde Estuary and the study site (Ardmore bay)

My study site at Ardmore bay (Plate 1) is in the Clyde Estuary, Scotland which together with the Firth of Clyde make up the Clyde Sea Area (Jardine, 1986) (Figure 1). The Firth of Clyde is usually taken as starting at Gourock, just west of Greenock, and extending west and then south to Girvin, Ailsa Craig, and the lower end of the Mull of Kintyre. The Clyde

Plate 1. Ardmore bay. General view.

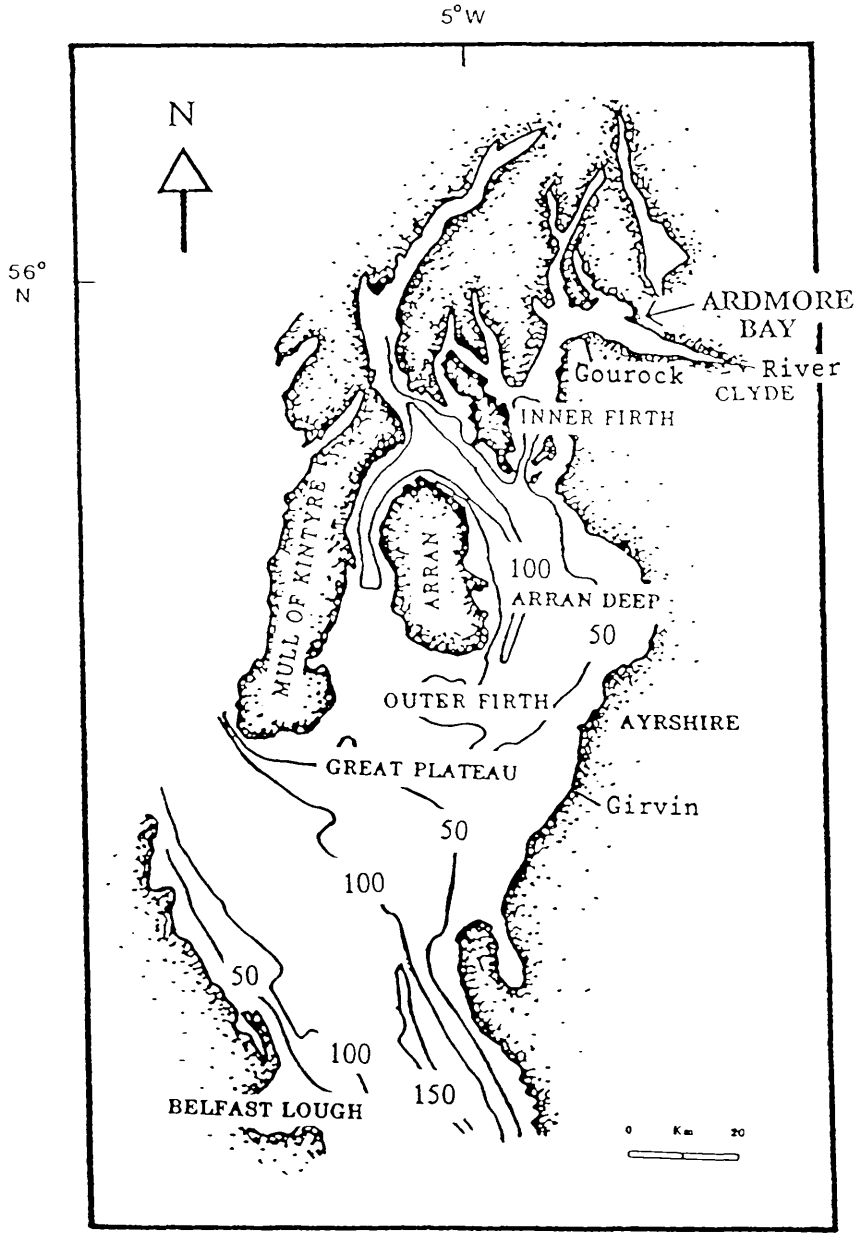


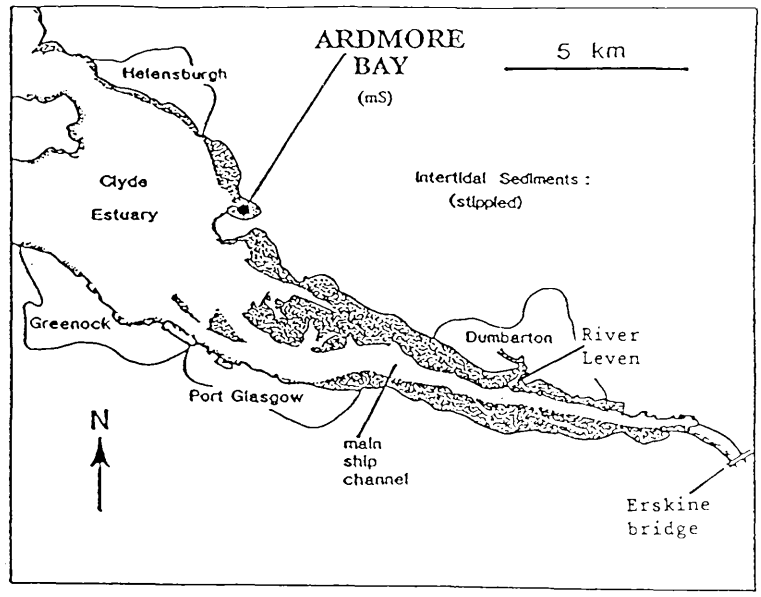
Figure 1 . Clyde Sea Area showing the Inner and Outer Firths and the Great Plateau in relation to the Clyde Estuary and Ardmore bay. Depth contours are in metres.

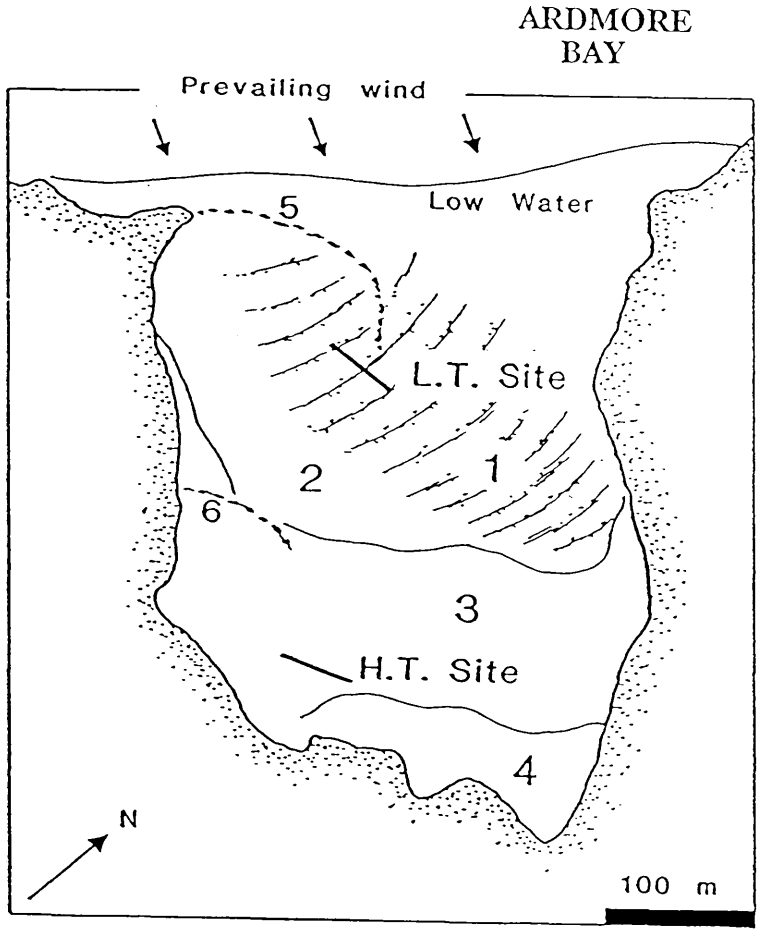
Estuary begins at the tidal weir just past Stockwell Bridge (Riddell, 1979; Gibb, 1983). This point is the furthest limit to which salt water penetrates at extreme high tide and low river-flow. From here the estuary extends 22 miles downstream (westwards) to Gourock where the salinity reaches $35\%_0$. At Ardmore Bay which is towards the seaward end of the estuary the salinity ranges from $18\%_0$ in winter to $33\%_0$ in summer although run-off from the land is often as low as $1\text{-}5\%_0$. At Greenock (which is the closest port to Ardmore) the mean neap tide range is 1.9m and the mean spring tide range 3.0m. The estuary is a partially-mixed type 2b one: where there is appreciable stratification, net flow reverses at depth, and both advection and diffusion contribute to the upstream salt flux (Hansen & Rattray, 1966; Schubel, 1984).

The distribution of sediments in the Clyde Estuary and Sea Area has been described in an excellent paper by Deegan et al. (1973) and Figure 2 (upper diagram) shows a map of the inner Clyde Estuary with intertidal sediment stippled. This map also shows my intertidal sampling site at Ardmore, which contains muddy sand.

Using Folk's (1974) classification, Deegan et al. (1973) record three main sedimentary facies (types) in the Clyde Estuary and Sea Area that are closely related to water depth. The coarse littoral facies contains clean sands and sediments containing gravel. Most of the particles in these sediments are coarser than 62.5 μm. The facies extends from high water to about 40m depth. The transitional facies has a wide range of grain size, and according to Deegan et al (1973) has a somewhat limited distribution. Personal observations suggest that it is fairly widely distributed in the Clyde Estuary. Most of the intertidal sediments belong to this facies and it is the sediment present in the intertidal zone at Ardmore. The deep silty clay facies is usually found only in the deeper parts of the Clyde, but in terms of area is the most common facies. Deegan et al. (1973) state that the coarse littoral facies contains the most diverse fauna (highest number of species), the transitional facies is intermediate, and the silty clay facies contains the least diverse fauna.

Figure 2 . Upper diagram: Inner Clyde Estuary, Scotland, showing intertidal sediments (stippled) and the location of the sampling site at Ardmore bay (mS - muddy sand). Lower diagram: Ardmore bay showing the two sampling sites. 1: area of sand waves; 2: area of bare sand; 3: area of algal mats interspersed with muddy sand and boulders; 5, 6: two rows of boulders. The two black lines show the position of the 50m transects at the high tide (H.T.) and low tide (L.T.) sites. 4: as in 3 but without boulders.


ARDMORE
BAY
(mS)
5 km
Helensburgh
Clyde
Estuary
Intertidal Sediments :
(stippled)
Greenock
Dumbarton
River
Leven
Port Glasgow
N
main
ship
channel
Erskine
bridge


ARDMORE
BAY
Prevailing wind
5
Low Water
L.T. Site
2
1
6
3
H.T. Site
4
N
100 m

The distribution and abundance of the benthic flora and fauna of the Clyde Estuary and the Firth of Clyde have been studied extensively, and the literature extends well back into the nineteenth century (Grieve, 1863; Grieve & Robertson, 1869; Walker-Arnott, 1869; Herdman, 1880; Henderson, 1886; Robertson, 1892a, b; Scott, 1900; Stephenson, 1911a, b; Chumley, 1918; Renouf, 1920; Watkin, 1942). However most of the early work, although thorough, consists only of distributional records. The most recent detailed compilation of information is given by Stobie et al. (1976) and by a number of authors in a Royal Society of Edinburgh Symposium on the Environment of the Estuary and the Firth of Clyde held in Glasgow in 1985 (Atkinson, 1986; Barnett & Watson, 1986; Eleftheriou et al., 1986; Norton, 1986; Pearson et al., 1986). The benthic fauna and flora of sediments in the Clyde estuary range from impoverished communities in the upper parts to very diverse ones in the outer estuary. In the upper reaches of the estuary immediately below Erskine Bridge they are relatively sparse in numbers and species, mainly because of the low salinities there, but also probably because of pollution. Downstream of this area there are very large populations of the polychaetes Nereis diversicolor and Manayunkia aestuarina, the oligochaete Tubifex costatus and the amphipod Corophium volutator. Although the number of organisms is high there is a low diversity with only these four species being present to a significant extent. According to Stobie et al. (1976) this community extends downstream to about 2.5 to 3km west of the mouth of the River Leven. Westward of this point the diversity of the benthic communities in sediments increases and includes the polychaetes Arenicola marina, Fabricia sabella, Pygospio elegans, and the molluscs Hydrobia ulvae (H. neglecta?), Mytilus edulis, Macoma balthica and Cerastoderma edule. Common intertidal seaweeds also become more abundant especially on small boulders (Enteromorpha sp., Ulva sp., Ascophyllum nodosum, Fucus serratus, Fucus vesiculosus, and Pelvetia canaliculata). Ardmore bay is 10km downstream of the River Leven, and so falls clearly into

this area.

The sampling area I chose to work on was the intertidal muddy sand beach at Ardmore bay in the Clyde Estuary, Scotland (55^{o} 28' N, 4^{o} 49' W; Nat. Grid NS 320 792) (Figures 1, 2; Plate 1). Ardmore bay has highly contrasting features at the high tide and low tide sites and the intertidal muddy sand beach is divided into a number of visually distinct areas. The high tide (HT) area is covered by algal mats (Enteromorpha sp.) of 1 to $5m^2$ (meso-scale) that are interspersed with bare sediment (Plate 2). Here parts of the bare sediment remain covered with water after the tide has receded. The mats die down in winter, but are recognisable throughout the year and maintain their approximate position and size. The high tide area is sheltered by the surrounding land and is a relatively low energy depositional sedimentary environment. Between the low and high tide areas there is a flat featureless zone on the left hand side (west) of the bay.

Towards the low tide site (LT), sand waves are present that have a wavelength of about 25m and which are at right angles to the prevailing winds (Figure 2, lower diagram, Plate 3). 1 to 3cm of water remains in the centre of their troughs after the tide recedes and so the centres are not usually exposed to the air. These sand waves are almost certainly maintained by the prevailing winds acting on the water while the tide covers the beach, and they persist in size and position throughout the year. This is a higher energy erosional area of the beach, and receives more wave action than the high tide area described above. The main areas of the beach, in particular the sand waves at the low tide site and the algal mats at the high tide site, have been permanent features of the beach at Ardmore for at least 10 years.

Note: Throughout this thesis the terms high tide (HT) and low tide (LT) mean the high tide site and the low tide site respectively.

Plate 2. Ardmore bay. High tide site showing algal mats.

Plate 3. Ardmore bay. Low tide site showing peaks (bare sediment) and troughs (with water) of the sand waves.

4. Rationale of work presented in the thesis

The overall objectives of my work have been to study benthic macrofaunal and microbial communities and their spatial variability on different scales in sediments. The work has been conducted on the intertidal muddy sand beach at Ardmore Bay and in the laboratory. It has consisted of two contrasting approaches, a field survey of the macrofaunal communities and sediment parameters and a laboratory study of the microbial communities. In both parts the work has involved describing the constituent species and abundance, analysing spatial variability in abundance, and considering the possible environmental causes of this spatial variability.

Benthic infaunal communities contain a very wide size range of organisms from macrofauna through meiofauna to microorganisms, whose abundances are likely to vary on different scales of magnitude. I chose to work on the two size classes of benthos representing either end of the spectrum - macrofauna and microorganisms. They are dealt with separately in the two sections of the thesis. I have defined the scales of magnitude for the macrofauna and microorganisms differently mainly because of their size difference. However, the choice of scales is inevitably subjective and will reflect the interests and views of the investigator, particularly when laboratory studies are extrapolated to the field as is the case in my microbial work. The topic has received attention by a number of authors in both terrestrial and aquatic ecosystems (Castenholz, 1963; Mader, 1963; Round, 1968; McCormack & Wilding, 1969; Beckett & Webster, 1971; Anderson & Meadows, 1978; Eckman, 1979; Maurer et al., 1979; Findlay, 1981; Allen & Starr, 1982; Ducklow, 1984; Wimpenny et al., 1984; Paerl, 1985; Seitzinger & Nixon, 1985; Plante et al., 1986; Baillie, 1987; Remillard et al., 1987; Yoder et al., 1987; Groffman & Tiedje, 1989; Schimel et al., 1989; Smith & Brumsickle, 1989; Thode-Andersen & Jorgensen, 1989; Tufail et al., 1989; Schaffner, 1990).

I define the spatial scales for macrofauna and microorganisms in my thesis as follows:

Macrofauna: micro-scale $\leq$ 1m

meso-scale > 1 - $\leq$ 50m

macro-scale > 50m

Microorganisms: micro-scale $\leq$ 1mm

meso-scale > 1mm - $\leq$ 10cm

macro-scale > 10cm

4.1. Macrofaunal communities - field survey

I investigated the macrofaunal communities and their spatial variability by an ecological survey of two contrasting sites on the shore at Ardmore. The first site was the high tide area referred to above, which was dominated by Enteromorpha sp. algal mats (Plate 2), and the second the low tide area which was dominated by the large sand waves (Plate 3). The work consisted of an initial survey followed by a more detailed transect survey. In the initial survey, observations were taken of infaunal abundance and sediment parameters in the algal and nonalgal areas at high tide and the peaks and troughs of the large sand waves at low tide. In the more detailed transect survey, a 50m transect was established across the algal and nonalgal areas of sediment in the high tide area, and another across the peaks and troughs of the sand waves in the low tide area and particular attention was paid to spatial variability. Samples and measurements were then taken at 1m intervals along both transects.

The details of the two sampling areas of the bay and the species and sedimentary parameters measured in the initial survey and in the transect survey are described in full in the material and methods of section 1.

4.2. Microbial communities - laboratory study

I considered two different ways in which sedimentary microbial communities and their spatial variability at Ardmore could be studied. One was an ecological approach similar to that of the macrofauna, in which 1 metre transects would be established in contrasting sedimentary environments on the shore and sampled every 1cm. The other was a laboratory approach in which columns consisting of cores of sediment obtained from the intertidal zone at Ardmore would be set up and maintained under controlled conditions that mimiced different inshore sedimentary environments.

I chose the laboratory approach for several reasons. Firstly, to complete an ecological survey of microbial communities and spatial variability using transects would not have been possible with the time available to me. Secondly, natural microbial communities and some aspects of their spatial variability in the intertidal zone in the Clyde Estuary have been already described in classic ecological work by Meadows & Anderson (1966, 1968) and Anderson & Meadows (1969, 1978). Thirdly, the column method involving laboratory incubations of sediment cores and slurries has been successfully used by many microbial ecologists to study a wide range of different aquatic environments (Winogradsky, 1949; Ardakani et al., 1973; Ramm & Bella, 1974; Paerl, 1975; Uydess & Vishniac, 1976; Rades-Rohkohl et al., 1978; Wormald & Stirling, 1979; Cox & Bazin, 1980; Harrison & Harrison, 1980; Landry et al., 1980; Nickels et al., 1981; Anderson & Ineson, 1982; DeFlaun & Mayer, 1983; Hennig et al., 1983; Pringle & Bowers, 1984; Wilson & Noonan, 1984; Alongi, 1985; Jorgensen & Revsbech, 1985; Seitzinger & Nixon, 1985; Christensen & Sorensen, 1986; Bebout et al., 1987; Smith & Klug, 1987; Thode-Anderson & Jorgensen, 1989; King, 1990; Pfarl et al., 1990). The principle involves collecting sedimentary material from the field, and then incubating it under carefully controlled conditions that mimic different field environments.

Suitably chosen microbiological media are often used to enrich the sediment, thus encouraging the growth of specific groups of microorganisms; this was the approach that I used.

I set up columns consisting of sediment cores, enriched them with two types of microbial media one to stimulate photosynthetic microbial growth (e.g. diatoms, blue-green algae) and one to stimulate heterotrophic microbial growth (e.g. heterotrophic bacteria) and incubated them in the light and in the dark for 25 days. Individual sand grains were then examined by scanning electron microscopy to assess microbial species, their abundance and their spatial variability. No work on sediment properties was done. The details are given in the materials and methods of the microbial section of my thesis.

The two contrasting approaches that I have used, an ecological one with the macrofauna and a laboratory experimental one with the microorganisms, have advantages and disadvantages. It is for example more difficult to make statements about causes and effects from ecological survey work, while laboratory studies inevitably suffer from being to some extent artificial. However the contrasting approaches that I have adopted with the two sizes of organisms has proved to be a rewarding one, and has provided new information on community structure and its variability at different spatial scales. Having completed the work, I regard the most innovative part of the first section (macrofauna) as being the analysis of spatial variability in community structure, and of the second section (microorganisms) as being the description of the different microbial communities that develop under enrichment conditions. Both parts have led to publications (Tufail, 1985, 1987; Tufail et al., 1989).

MATERIALS AND METHODS

"How can we be sure, it may be asked, that it is the correct technique? The proof of the pudding is in the eating, and the first and most convincing test of the system is that it works."

(Huxley, 1943)

MATERIALS AND METHODS

MACROFAUNAL COMMUINITIES

The high tide (HT) and low tide (LT) areas of the intertidal zone at Ardmore bay referred to in the introduction (p 20) are distinctly different sedimentary environments (Plates 2 and 3). The high tide area has algal mats interspersed with bare sediment and the low tide area has large sand waves with well defined peaks and troughs. This provided an ideal opportunity for comparing differences in species abundances and sediment parameters, and their spatial variability, in the two types of environments at high tide (algal mat and nonalgal mat areas) and the two types of environments at low tide (peaks and troughs).

I therefore carried out an initial survey to investigate the differences in species abundances and sediment parameters between the algal and nonalgal sediment at the high tide and between the peak and trough areas at the low tide sites. This formed part 1 of the results. In part 2 of the results, I studied the differences in species abundances and sediment parameters, their spatial variability and correlations by examining 50 contiguous 1m quadrats along two 50 metre transects, one at high tide and one at low tide (Figure 2 lower diagram). The field work for both parts was carried out during summer.

1. Initial Survey

The initial survey was carried out on the high tide and low tide sites to compare differences between the algal and nonalgal areas at high tide and between the peak and trough areas at low tide. The initial survey was conducted in 2 parts, both of which were done on each of the four areas (HT: algal, nonalgal; LT: peak, trough) (Figure 3).

In the first part I measured species abundances and the sediment parameters shear strength, water content, permeability, particle size, redox potential (Eh), and pH (horizontal measurements) (Figure 3). In the second part I studied vertical profiles of shear strength, water content, redox potential and pH (vertical profiles) (Figure 3).

Note: the results of the two parts are described under three headings in the results section: 1.1 Abundances of species, 1.2 sediment parameters measured in surface sediment, and 1.3 vertical profiles of sediment parameters. The first two of these come from part one of the methods, and the third from part two.

1.1. Horizontal Measurements (Figure 3)

I used a 0.25 m^2 quadrat which was laid on the sediment surface, and readings of Eh, pH and shear strength were taken within this area. At the high tide site one quadrat was placed on the sediment surface so that part of it covered an algal area and part of it covered an area without algal cover (Plate 4).

At the low tide site one quadrat was placed on a peak and one on a trough. In this way it was possible to compare differences in Eh, pH and shear strength between the 2 contrasting areas at the high tide and at the low tide sites. Replicate readings of redox potential - (Eh), pH and shear strength were taken within the quadrats. The points at which the readings were taken were defined by string guidelines within the quadrats (Figure 4, Plate 4). These procedures provided the following number of replicate readings for redox

Figure 3 . Initial survey. Flow diagram showing the sampling methods used and measurements taken for the species abundances and sediment parameters in the algal and nonalgal areas at the high tide site (HT), and in the peak and trough areas at the low tide site (LT).

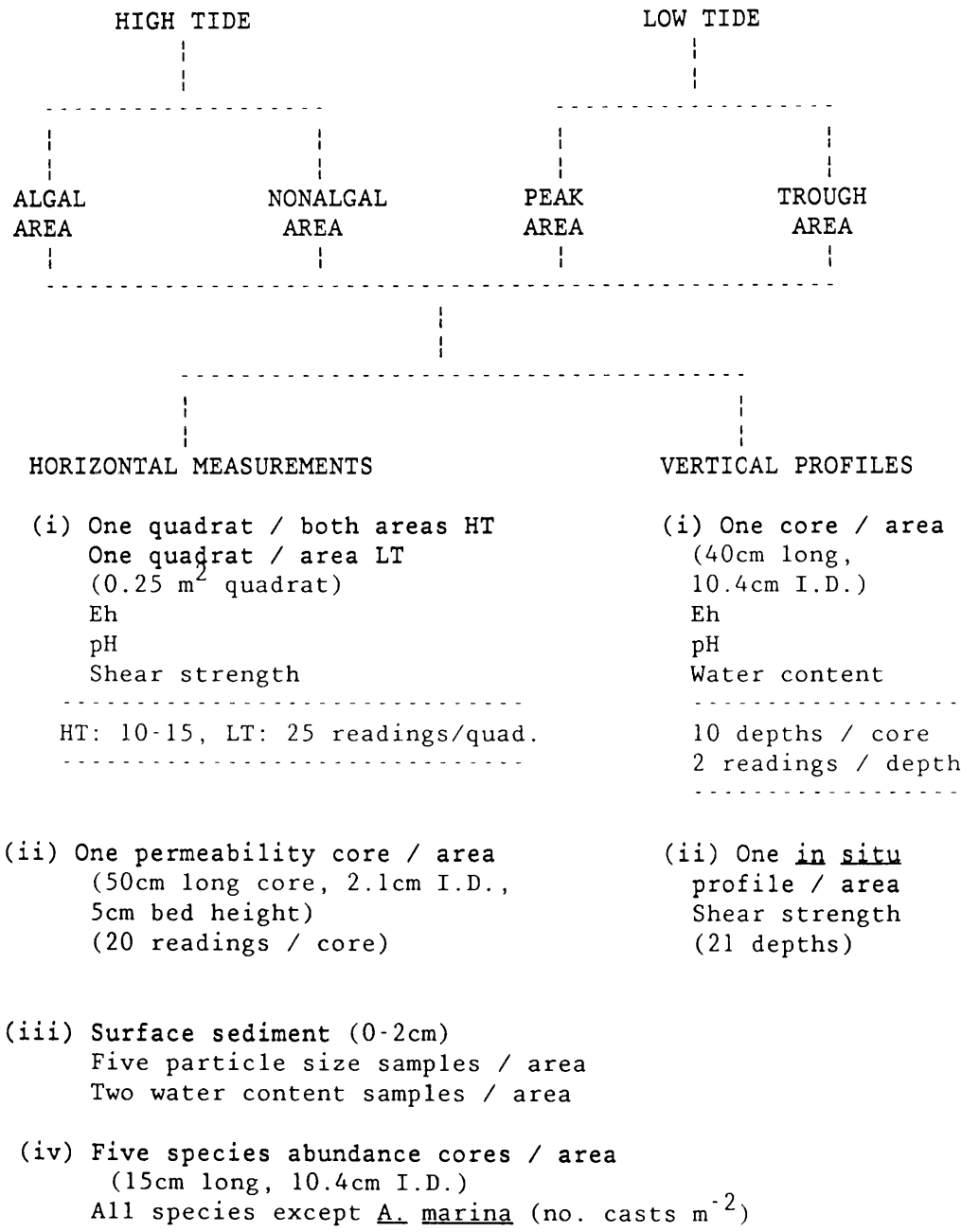


Plate 4. Ardmore bay. Initial survey. High tide. $0.25m^2$ quadrat covering algal and nonalgal mat area. (String used for precise sampling points for measuring shear strength, redox potential - Eh and pH).

Plate 5. Ardmore bay. Low tide site sediment on the peak of a sand wave showing Arenicola marina casts.

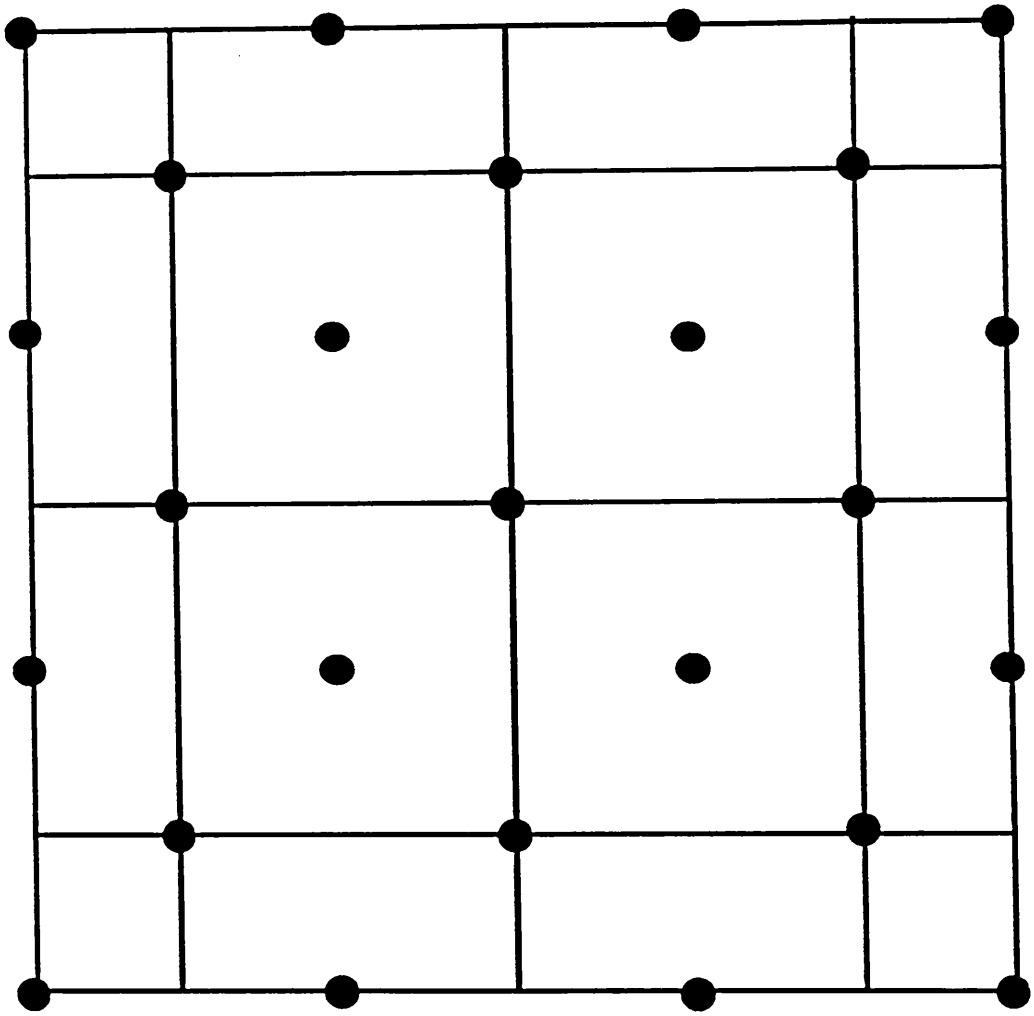


Figure 4 . Position of points (black dots) within the $0.25m^2$ quadrat where measurements of redox potential, pH and shear strength* were taken at high tide and low tide sites.

* The formula used to calculate sediment shear strength was as follows:

$$S = \frac{k \times Q}{h^2} \times 9.81 \quad kN.m^{-2}$$

k = a constant depending on the angle of the cone used, for example the 60^{o} cone used in this study had k = 0.225

Q = weight of cone (g)

h = depth of penetration (mm) of cone into the sediment

potential, pH and shear strength at the high and low tide sites.

	High tide site		Low tide site	
	Algal	Nonalgal	Peak	Trough
Redox potential	13	10	25	25
pH	13	10	25	25
Shear strength	10	15	25	25
	one quadrat		one quadrat	one quadrat

The electrodes used for measuring Eh were the standard platinum, metal electrode 1213 400 series and a calomel reference electrode 1370 210 series and for measuring pH was a combination pH electrode 1118 series (Kent Industrial Measurements, Ltd., England) connected to a CORNING pH meter model 120. A correction factor of +249 mV was applied to each Eh reading (ZoBell, 1946b). A Geonor falling cone apparatus (Geonor ROA, Oslo, Norway) (Hansbo, 1957) was used for measuring shear strength.

Two surface sediment samples were also taken within the quadrats for water content and five for particle size, from each of the algal, nonalgal and peak and trough areas.

Water content was obtained as follows. Wet sediment (c 1-2 g) was weighed and then left to dry in a 60°C oven for 24 h. The dry sediment was transferred to a desiccator to cool and then the dry weight of the sediment taken. The percent water content was calculated using the wet and dry weights of the sediment ((wet weight - dry weight)x100/dry weight; BS 1377, 1975; Smith, 1981).

Particle size was determined by the dry sieving technique (BS 1377, 1975; Buchanan, 1984). Samples were oven dried at 60°C for 24 hrs and 10 g of the dried sediment shaken continuously for 0.5 h through a set of sieves on a mechanical sieve shaker (Endecotts Octagon 200 Variable Amplitude Test Sieve Shaker). The sediment in each sieve was then transferred into a

preweighed plastic dish and weighed. The sieve sizes used were 0ϕ (1mm), +1ϕ (500 μm), +2ϕ (250 μm), +3ϕ (125 μm), +4ϕ (63 μm), and the receiver, where $\phi = -\log_2$ (mm). The equivalent midpoints were taken as -0.5ϕ (1410 μm), +0.5ϕ (710 μm), +1.5ϕ (351 μm), +2.5ϕ (177 μm), +3.5ϕ (88 μm), and +4.5ϕ (44 μm). The coarsest (-0.5ϕ, 1410 μm) and the finest (+4.5ϕ, 44 μm) midpoints were obtained by assuming an extra sieve (-1ϕ, 2000 μm) above the coarsest one used, and taking the pan as equivalent to an extra sieve (+5ϕ, 31.5 μm) below the finest sieve, respectively. This is normal practice (Lindholm, 1987). Particle size statistics from sieve analyses (mean, sorting, skewness, kurtosis) can be obtained graphically or algebraically (Krumbein & Pettijohn, 1938; Briggs, 1977; Folk, 1974; Buchanan, 1984; Lindholm, 1987). The algebraic method (i.e. moment measures) is considered to be more accurate (Swan et al., 1979, p.498; Lindholm, 1987, p. 172). Details are given in Folk (1974, p. 45-46) and Lindholm (1987, p. 168-169). I used the algebraic method, for which a computer programme was available. I entered the sediment weights from each sieve into the computer programme to calculate the mean particle size, sorting coefficient, skewness and kurtosis of each sample in phi (ϕ) units

Four mini-cores of surface sediment were taken for permeability measurements one from each of the four areas (algal, nonalgal at high tide site; peak and trough at low tide site). Each core provided 20 readings of permeability. The cores were taken and permeability was measured as follows. A glass core of ID 2.1 cm and 50 cm long was pushed vertically into the sediment until a sediment bed height of 5 cm was reached. The surrounding sediment was dug out and the core was carefully lifted whilst one hand was held at the bottom of the core to stop the sediment from falling out. The lower end of the core was then carefully covered with a square piece of fine nylon mesh followed by an outer fine grid stainless steel mesh. This method ensures that sediment is retained in the core when permeability measurements are taken. Seawater collected on site was used to fill the core to a height of 41 cm above the

sediment core. Permeability was measured by the falling head permeameter technique (Smith, 1981) by noting the time (sec.) taken for the water level to drop 1 cm. The water level was then topped up, and in this way 20 replicate readings were taken for the algal/nonalgal and the peak/trough cores. These data were used to calculate the permeability coefficient k($mm.s^{-1}$) for the 4 cores.

The abundance of all species except A. marina were measured by taking 5 replicate sediment cores of 10.4 cm diameter and 15 cm depth. The abundance of A. marina was measured by counting casts using the 0.25 m^2 quadrat and expressing these as number of individuals m^{-2}. There is a 1:1 relationship between casts and animals on this shore - see below. The cores were brought to the laboratory and the animals were separated by wet sieving (500 μm). Light was used for separating the species. The detailed method is given on pg.39

1.2. Vertical Measurements (Figure 3)

I collected one sediment core (10.4 cm diam., 40 cm length) from each of the algal and nonalgal areas at high tide and peak and trough areas at low tide (4 cores in all). The cores were taken using a PVC tube split longitudinally into two halves and then taped together. Redox potential (Eh), pH and water content were measured at depths of 0, 2.5, 5, 10, 15, 20, 25, 30, 35, and 40 cm after splitting the core using a scalpel to cut through the tape. Two replicate readings were taken for Eh, pH and water content at each depth. The methods and equipment used for these parameters were exactly the same as explained above. One shear strength profile was measured in each of the four areas. The shear strength profile was measured by a Pilcon hand vane tester (using a 19 mm diameter and 25mm long vane) (Serota & Jangle, 1972; Mooney, 1974; BS 1377, 1975) at depth intervals of 5 cm starting from the surface down to 100 cm. At each depth a peak reading of the shear strength (initial reading at each

depth) was followed by a residual reading of the shear strength (second reading at each depth - disturbed by initial reading). This is standard practice (Lambe & Whitman, 1979, pp. 144, 302, 312; Capper & Cassie, 1976, p. 80).

2. Transect Survey

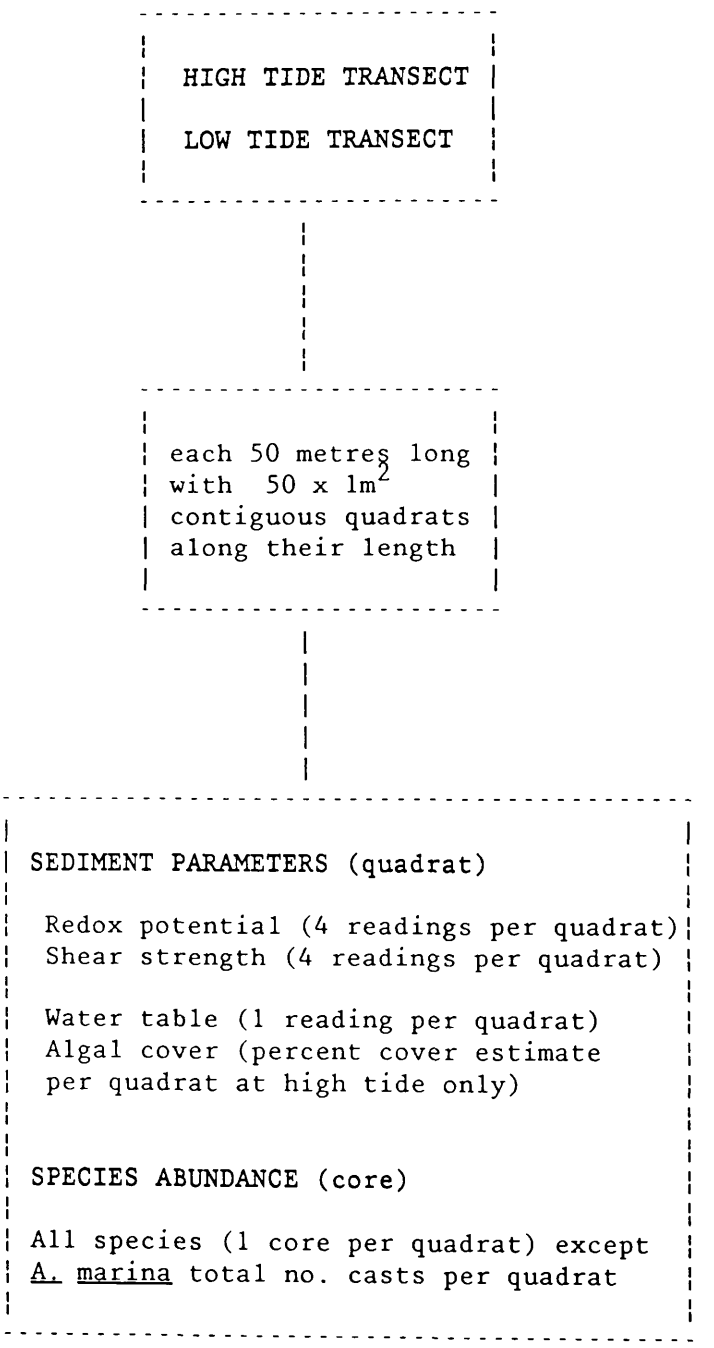
Two 50 m transects were established, one at the high tide area and one at the low tide area (Figure 2 lower diagram). Wooden pegs were pushed into the sediment at 10 m intervals along each transect as reference points. The transect at the high tide site crossed a number of algal mats and areas of bare sediment, and the transect at the low tide site was at right angles to the sand waves.

At each transect the sampling procedure was the same. This ensured that the high and low tide data were comparable. Measurements were taken at 1 m intervals along each transect using a 1 m^2 metal quadrat (Figure 5). The following procedure was adopted for measuring the levels of the species abundances, sediment parameters, algal cover, and the water table.

2.1. Animal abundances

Animal abundances in each quadrat were measured in two ways (Figure 5). Arenicola marina abundance was measured by counting numbers of casts in each quadrat, since it had been established from previous work on this shore that the number of casts and animals are linearly related 1:1 (Girling, 1984) (Plate 5). Other studies have shown a similar relationship (Holme, 1949; Longbottom, 1970; Cadee, 1976; Evans, 1977). Casts of coil diameter 1-2 mm were classed as juvenile, and of 2.5-4.0 mm as adult. There was always a clear distinction between these two sizes of cast at the time of the survey. The abundances of the remaining species were measured by taking one core in each quadrat. The PVC corer had an internal diameter of 10.4 cm and was 15 cm

Figure 5. Transect study. Flow diagram showing the sampling methods used and measurements taken for the species abundance and sediment parameters along the high tide and low tide transects.



long. The sediment core obtained with it was 10.4 cm in diameter and about 13 cm long. Previous tests had shown that this diameter and depth of core gave suitable samples and was deep enough to sample all the animals - excluding A. marina.

Each sediment core was transferred from the corer to a prelabelled polybag on site. In the laboratory sediment was sieved through a 500 μm sieve using seawater. The sieving was done carefully so that animals were not damaged. Each sediment core was sieved in small portions at a time. The animals were then transferred into a flat plastic tray by pouring clean seawater onto the sieve from its reverse side.

The cores with algal mats were treated as follows. The algae on the surface of the core was washed on a 2 mm sieve. The filtrate from the 2 mm sieve was sieved through a 1 mm sieve to separate the finer algae. The algae retained on the 2 mm and 1 mm sieves were transferred into a bowl of seawater, and gently mixed. This ensured that the animals in the algae emerged. The algae were removed and the animals remaining in the seawater were pipetted into smaller containers. The filtrate from the 1 mm sieve and the remaining sediment from the core was sieved as above.

The trays containing the live animals in seawater were placed on a bench and illuminated from one end for a minimum of 12 hours. This method separated photopositive from photonegative species and has been used for many years (Murphy, 1962; Lewis, 1968; Segal, 1970). In this study N. diversicolor, P. elegans, and F. sabella were photonegative, C. volutator was photopositive, and M. balthica, H. neglecta, and B. guilliamsoniana were relatively unaffected. The technique is particularly effective for extracting the tube-dwelling smaller species such as F. sabella and P. elegans which leave their tubes and move away from the light source.

The animals were removed from the trays with a glass pipette. A Pasteur pipette was used for the smaller species such as P. elegans and a slightly larger bore pipette for the larger species such as B. guilliamsoniana. If

counting was not done on the same day then the containers were transferred to 10^{o} C. The slow moving animals such as P. elegans and F. sabella were counted live and then preserved in 20% alcohol. Fast swimmers such as B. guillimsoniana and C. volutator were first preserved in 20% alcohol and then counted. The number of individuals for each species was converted to $No.m^{-2}$. Species identification was based on Fauvel (1923, 1927), Muus, 1963; Nicol (1967), McMillan (1968), Newell (1970), Schafer (1972), Perkins (1974), Campbell (1982), Lincoln (1979), and Barrett and Yonge (1980).

2.2. Sediment parameters

Four readings of shear strength and four of redox potential were taken within each quadrat (Figure 5). Shear strength (Hansbo, 1957) was measured with the cone penetrometer and redox potential was measured with standard redox potential electrodes as described above. The shear strength readings were taken at the surface of the sediment, and the redox potential readings at a depth of 0.25 to 0.5 cm - the minimum depth of penetration of the electrodes.

2.3. Estimation of algal cover and relation to species abundance and sediment parameters at high tide

Algal mats at high tide, and their relationships to the abundance of species and sediment parameters were assessed by three methods (Table 1).

(i) Abundance of A. marina vs algal/nonalgal areas. The percentage algal cover of each 1 m^2 quadrat was obtained from drawings on squared graph paper made on site. If the cover was more than 70 % it was taken as an algal mat quadrat (20 quadrats). Quadrats with 70 % to 30 % algal cover were excluded from the analysis (19 quadrats). If the cover was less than 30% it was taken as a nonalgal quadrat (11 quadrats). This gave counts of A. marina casts in 20

Table 1. Measurement of algal cover at high tide in relation to species abundance and sediment parameters. Number of observations. Methods (i), (ii), and (iii) are explained in the materials and methods of the macrofaunal communities (section 2.3).

Method of estimating algal cover:	% algal cover	
Method (i): 1 m^2 quadrats		
A. marina	100% - 70% (A)	20 quadrats
	(70% - 30%)	(19 quadrats excluded)
	30% - 0% (NA)	11 quadrats

Methods of estimating algal cover:	Present (A) / absent (NA)	
Method (ii) : cores		
All species except A. marina	A	28 cores
	NA	22 cores
Method (iii): 1 m^2 quadrats		
Shear strength	A	77 readings
	NA	123 readings
Redox potential Eh	A	98 readings
	NA	102 readings

algal quadrats and 11 non algal quadrats.

(ii) Abundance of other species vs algal/nonalgal areas. Species abundance was measured by coring, the surface of the core was then recorded as either algal mat present (28 algal cores) or algal mat absent (22 nonalgal cores).

(iii) Levels of sediment parameters vs algal/nonalgal areas. Each of the four readings of Eh and of shear strength in each quadrat was recorded as algal or nonalgal depending on whether the reading was in an algal or nonalgal part of the quadrat. This gave 77 algal and 123 nonalgal readings of shear strength and 98 algal and 102 nonalgal readings of Eh.

The three methods led to no observable inconsistencies in the analysis of the data.

2.4. Estimation of Peak and Trough quadrats at low tide

Like the high tide transect which was divided into algal and nonalgal quadrats, the sand waves along the low tide transect were classified into peak and trough quadrats based on the water table values (Figure 6). The 50 m transect at low tide had one complete peak in the centre and two half peaks at each end. The peaks were separated by two complete troughs (Plate 3). Six quadrats were chosen from the top of the middle peak and three and four from the tops of the two outer peaks respectively. Similarly six and seven quadrats were selected from the two troughs respectively. The quadrats located on the immediate slope separating the peak and trough were not selected due to the slope effect. In total 13 peak and 13 trough quadrats were used in the analysis. The height of the sediment above the water table ranged from 10.50 to 18.80 cm for the peak quadrats and 0.00 to -2.00 cm for the trough quadrats (i.e. the trough quadrats were at or below the water table, and hence were covered by water - see below).

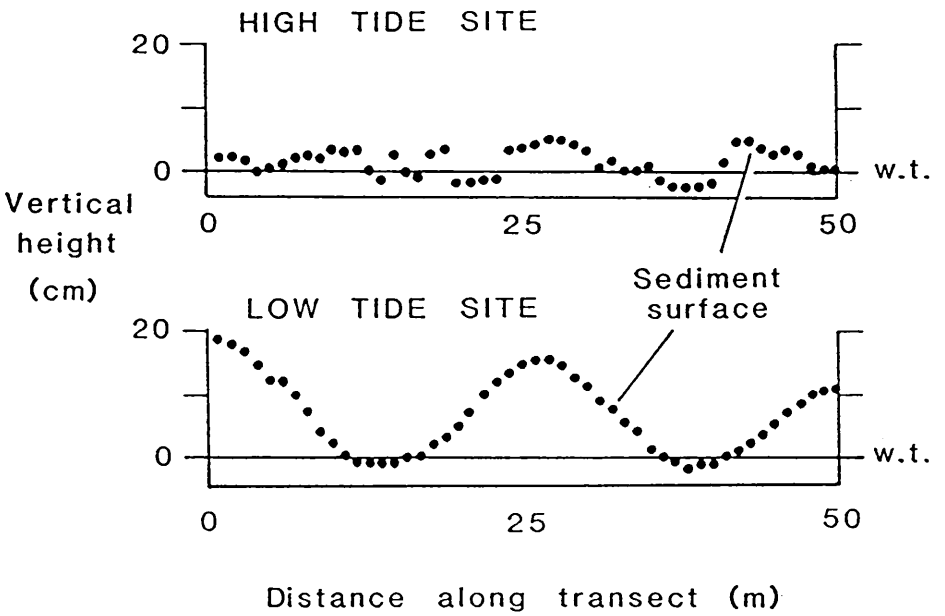


Figure 6.

Sediment profiles and the level of the water table (w.t.) along the High tide and Low tide transects.

2.5. Water table

The water table is defined as the height at which water stands in an open borehole below the ground level (Lee et al., 1983). The depth of the water table below the sediment surface along the 2 transects was measured by digging a hole in each quadrat, allowing the hole to fill with water until it reached an equilibrium position, and then measuring the distance between the the sediment surface and the water surface (Figure 6). If the water was above the sediment surface this distance was recorded as a negative value, if the water was below the sediment surface the distance was recorded as a positive value.

2.6. Data Analyses

The data obtained from the species abundances and sediment parameters were statistically analysed by one way analysis of variance, Student's t tests, correlation analyses, F ratio tests, and Chi square tests.

Before I applied parametric statistical tests to the data (Students t, analysis of variance (anova), correlation analyses), I transformed the data to normalise it using ln(i.e. $\log_e$) (Scheffe, 1959; Fisher & Yates, 1963; Snedecor & Cochran, 1967; Gregory, 1968; Winer, 1971; Sokal & Rohlf, 1981; Underwood, 1981). I tried other transformations (square root, $\log_{10}$) but the ln transformation was the best.

Note: It is important not to confuse the F ratios conducted on the untransformed data with the F ratios that were an integral part of the one way analysis of variance on ln transformed data. Both types of F ratios were used to assess spatial variability but in different ways (Tables 6, 10, 11, 14 to 18).

There were a number of zeros in the original data. The logarithm of zero does not exist, therefore I added a constant to the original data before applying the ln transformation. These constants were as follows:

(i) +0.01 All species except M. balthica, mean shear strength, s.d. shear strength, and s.d. redox potential.

(ii) +5 M. balthica, Shannon Wiener and Simpson's diversity indices, and water table.

(iii) +230 mean redox potential - initial survey.

+110 mean redox potential - transect survey.

A constant was not added to the remaining data because there were no zero values. The percent algal cover values were divided by 100 and an arcsine transformation was done on these. When Student's t tests were applied, the variances of the two populations being compared were assumed to be unequal (Bailey, 1981). This meant that the degrees of freedom, which are calculated on a formula that depends on the variances of the two populations, varied from comparison to comparison (Ryan et al., 1976, pp. 140-142; Bailey, 1981, pp. 49-51).

In the transect survey, I compared spatial variability between the abundances of pairs of species along the transects using the F ratio (ratio of bigger variance to smaller variance). This was done on untransformed data because the ln transformation is specifically designed to remove differences in variances. I took expert statistical advice on this before hand.

Except when otherwise specified, the probability scale for the statistical analyses used throughout my thesis are as follows.

* $0.05>P>0.01$
** $0.01>P>0.001$
*** $P<0.001$

Two diversity indices, the Shannon Wiener index and Simpson's index, were calculated for each 1 m^2 quadrat. The Shannon Wiener diversity index was taken as

$$-\sum (n_i/N \ (\ln(n_i/N)))$$

and Simpson's index as

$$1 - \sum ((n_i/N)^2)$$

where n_i = number of individuals in the i^{th} species; N = the total number of individuals in all the species (Pielou, 1977; May, 1981). I wrote a computer program to calculate the Shannon Wiener and Simpson's diversity indices (see Appendix 1, computer program: flow diagram, listing, and example of a run).

Lastly, it is important to note that I have used the phrases spatial variability and spatial heterogeneity synonymously throughout the thesis.

MICROBIAL COMMUNITIES

Sediment (0-2 cm) was collected from low tide at Ardmore, Clyde Estuary, Scotland (Nat. Grid NS 320 792) (Figure 2 upper and lower). It was sieved through a 500 μm sieve using 0.45 μm membrane filtered seawater and then gently mixed. A small portion was preserved in 2.5% glutaraldehyde in artificial seawater and stored at 4°C as a control for scanning electron microscopy (SEM). Mean particle size was 195 μm.

Ten 50 cm long glass columns (I.D. 2.9 cm) were prepared by covering their lower ends with nylon and stainless steel mesh and then sterilised. Sediment was added to the columns by allowing it to settle through sterile seawater until a core height of 5 cm was obtained. Each column was gently lowered into a 500 ml glass measuring cylinder containing medium. The level of the medium was adjusted in the cylinder until it was 10 cm above the sediment surface. Four of the columns were filled with photosynthetic medium (M), four with heterotrophic medium (B), and two with control medium (C). Two of each of the four photosynthetic and bacterial medium columns were covered with a double layer of silver foil and termed dark columns (D). The remainder were termed light columns (L). This resulted in a total of 10 columns : two photosynthetic medium columns incubated in the light (ML), two photosynthetic medium columns incubated in the dark (MD), two heterotrophic medium columns incubated in the light (BL), two heterotrophic medium columns incubated in the dark (BD), and two control media columns (C).

The light columns were maintained at 20°C under simulated natural light for 25 days in a 17h light/7h dark photoperiod. Media were changed

every two days by lifting the column and letting it drain, emptying the measuring cylinder, and refilling with sterilized medium to the previous level.

The photosynthetic medium was a modification of the Medium M12 (Asher & Spalding, 1982) and contained 50 ml soil extract, 2 g $NaNO_3$ and 0.014 g $Na_2HPO_4.2H_2O$ made up to 1 litre with artificial seawater. The bacterial medium contained 5 g bacteriological peptone (Oxiod L37) (Cruickshank el al., 1975) and 0.1 g $FePO_4 . 2H_2O$ made up to 1 litre with artificial seawater. The control medium contained 25 ml of 40% formaldehyde completed to 70 ml with distilled water made up to 1 litre with 82% ASW. The final salinity of the seawater in all media was 75% ($26\%_o$). Media were autoclaved and filtered through sterile Whatman No. 1 filter paper before use.

After twenty five days the sediment was removed from the columns. Sediment from the surface was taken for examining microbial types and estimating their abundance. Sediment from the columns was prepared for SEM by preserving in 2.5% glutaraldehyde in artificial seawater at 4^oC. The control sediment preserved initially and the sediment preserved after twenty five days were rinsed four times with membrane filtered seawater and transferred to sodium cacodylate buffer (pH 7.6). They were post-fixed in 4% osmium tetroxide for one hour, rinsed four times in distilled water, dehydrated in an ascending series of acetone, and critical point dried from anhydrous analar acetone. Sand grains from the samples were then mounted on aluminium stubs. The stubs were gold coated to a thickness of c. 20 nm and examined by SEM. For each microbial species SEM photomicrographs of five randomly chosen sand grains per treatment were examined and cell counts taken. These counts were converted to number of cells mm^{-2} sand grain surface. Thraustochytrid sporangia were counted on 20 sand grains and their average dimensions were measured. Detailed description of microbial cells and distribution were made by SEM.

RESULTS

"To be sure, it might be said that the fact that science cannot describe *everything* just doesn't matter - that what alone counts for descriptive completeness is that it can describe *anything*. But the question still remains, can it describe anything completely? After all, the complete description of any one thing runs off into endless detail. A clear lesson emerges. Descriptive completeness of detail at the factual level must be recognized to be in principle impossible."

(Rescher, 1984)

RESULTS

MACROFAUNAL COMMUNITIES

The intertidal bay at Ardmore contains a fairly diverse range of flora and fauna considering its estuarine position. This is because the bay has a number of different habitats : muddy sand in the main part of the bay, shingle, boulders and rock surfaces at each side, and a salt marsh at the upper closed end. Although I have not attempted to identify all the animals and plants in the bay, the following are the more commonly occurring ones.

MACROFAUNA

Polychaeta:

Arenicola marina
Eulalia viridis
Fabricia sabella
Lanice conchilega
Manayunkia aestuarina
Nephthys hombergii
Nereis diversicolor
Phyllodoce maculata
Pygospio elegans
Scoloplos armiger

Bivalvia:

Macoma balthica
Mytilus edulis

Gastropoda:

Hydrobia neglecta
Littorina littoralis
Littorina littorea

Crustacea:

Bathyporeia guilliamsoniana
Carcinus maenus
Chthalmus montagui
Corophium volutator
Gammarus sp.
Ligia oceanica
Orchestia sp.
Semibalanus balanoides

MACROALGAE

Chlorophyceae:

Enteromorpha sp.
Ulva sp.

Phaeophyceae:

Ascophyllum nodosum
Fucus serratus
Fucus vesiculosus
Pelvetia canaliculata

Rhodophyceae:

Chondrus crispus
Polysiphonia lanosa

The macro-faunal species that were present at the high and low tide sites at which the initial survey and transect survey were conducted were in order of decreasing abundance:

High tide	Low tide
F. sabella	*P. elegans
C. volutator	*B. guilliamsoniana
*P. elegans	*N. diversicolor
*N. diversicolor	*M. balthica
H. neglecta	*A. marina
*M. balthica	
*A. marina	

Four of the species were present at both high and low tide sites (*). These were A. marina, M. balthica, N. diversicolor, and P. elegans. Three species were found only at the high tide site - Corophium volutator, F. sabella and Hydrobia neglecta, and one was found only at the low tide site - Bathyporeia guilliamsoniana.

The overall objectives of the ecological work in this part of my thesis were to study the abundances of benthic infaunal macrofauna and their spatial variability in relation to the high and low tide sedimentary environments at Ardmore, these latter being the algal and nonalgal areas at high tide and the peaks and troughs of the sand waves at low tide. I did this by conducting the initial survey followed by the more detailed transect survey described in the materials and methods. In this context, it is important to note that the spatial variability (heterogeneity) of the abundances of the species and of the sediment parameters was not measured in the initial survey, nor were correlations calculated between species abundances and between sedimentary parameters. These form major parts of the main transect survey section.

The initial survey should be regarded as preliminary work setting the scene. It allowed me to identify the species present and assess their abundances, and to test out sedimentary techniques and obtain an idea of the

different sedimentary environments in the two high tide and two low tide areas. The results of the initial survey are presented first, followed by the results of the transect survey.

1. Initial survey

The results of the initial survey are divided into three parts.

1.1. Abundance of species (Figure 3 - horizontal measurements).

1.2. Sediment parameters measured in surface sediment (Figure 3 - horizontal measurements).

1.3. Vertical profiles of sediment parameters (Figure 3 - vertical measurements).

1.1. Abundance of species

The means and standard deviations of the abundances of the species found in the algal and nonalgal areas at high tide and the peak and trough areas at low tide and their comparisons by Student's t tests are given in tables 2 and 3. The values of the sediment parameters in the algal and nonalgal areas at high tide and the peak and trough areas at low tide are shown in tables 4 and 5.

The results of these comparisons were surprising. At high tide, although the abundances of A. marina, H. neglecta and C. volutator were higher in the nonalgal than in the algal areas and those of F. sabella, M. balthica, N. diversicolor and P. elegans were higher in the algal areas, only one of these differences was statistically significant. This was the higher abundance of juvenile A. marina in the nonalgal when compared with the algal area.

The same effect was true of the abundances at low tide. A. marina and P. elegans were more abundant in the peak areas and B. guilliamsoniana, M. balthica, and N. diversicolor were more abundant in the trough areas

Table 2 . Abundance of species (No. m^{-2}) in algal (A) and nonalgal (NA) areas at high tide site (untransformed data).
Student's t compares data between algal and nonalgal areas (ln transformed data).
!! present at high tide and low tide sites; ! present only at high tide.
+ve t: algal mean > nonalgal mean
-ve t: algal mean < nonalgal mean

Species		mean	s.d.	n	Student's t	d.f.	P
!!Arenicola marina							
	A	10.8	13.1	5			
Total					-2.75	4	0.1>P>0.05
	NA	152	107	5			
	A	5.7	12.2	5			
Adults					-2.40	4	0.1>P>0.05
	NA	13.6	13.7	5			
	A	5.03	5.51	5			
Juveniles					-2.71	5	0.05>P>0.02*
	NA	138	116	5			
	A	871	1882	5			
!Corophium volutator					-1.43	7	0.2>P>0.1
	NA	2166	2162	5			
	A	1907	1813	5			
!Fabricia sabella					1.53	4	0.2>P>0.1
	NA	1342	1641	5			
	A	588	432	5			
!Hydrobia neglecta					-0.39	6	0.8>P>0.7
	NA	612	305	5			
	A	188	244	5			
!!Macoma balthica					0.13	7	P>0.9
	NA	118	118	5			
	A	400	404	5			
!!Nereis diversicolor					0.61	4	0.6>P>0.5
	NA	188	105	5			
	A	1365	1323	5			
!!Pygospio elegans					0.51	4	0.7>P>0.5
	NA	777	1149	5			

Table 3 . Abundance of species (No. m^{-2}) in peak (P) and trough (T) areas at low tide site (untransformed data).
Student's t compares data between peak and trough areas (ln transformed data).
!! present at high tide and low tide sites; ! present only at low tide.
+ve t: peak mean > trough mean
-ve t: peak mean < trough mean

Species		mean	s.d.	n	Student's t	d.f.	P
!!*Arenicola marina*							
Total	P	55.8	20.7	5	4.58	7	0.01>P>0.001**
	T	20.83	5.90	5			
Adults	P	15.08	3.55	5	-0.55	6	P>0.9
	T	17.72	7.25	5			
Juveniles	P	40.7	22.4	5	2.95	4	0.05>P>0.02*
	T	3.11	2.88	5			
!*Bathyporeia guilliamsoniana*	P	71	105	5	-2.95	4	0.05>P>0.02*
	T	1412	1546	5			
!!*Macoma balthica*	P	23.5	52.6	5	-2.35	7	0.1>P>0.05
	T	165	105	5			
!!*Nereis diversicolor*	P	235	186	5	-1.40	4	0.3>P>0.2
	T	636	214	5			
!!*Pygospio elegans*	P	7745	4572	5	2.42	5	0.1>P>0.05
	T	3437	894	5			

although only two of these differences were significant (A. marina, B. guilliamsoniana) (Table 3).

The relative lack of significant differences in the abundances of the species between the algal and nonalgal areas at high tide and between the peak and trough areas at low tide when compared with the results of the transect survey was at first sight surprising because the differences in abundances were often obvious by digging and casual observation. However a careful consideration of the number of replicates in the initial survey (n=5 for algal, nonalgal, peak and trough areas) with the number of replicates in the transect survey (algal: n=20; nonalgal: n=11 for A. marina only; algal: n=28; nonalgal: n=22; for other species except A. marina; peak: n=13; trough: n=13; for all species) suggested that the reason was lack of replication in the initial survey. There were no contradictions in the differences in mean abundances between the initial and transect survey apart from the lack of significances of the Student's t tests in the initial survey. For those species whose means were significantly different in both surveys, the direction of the differences were the same (A. marina: P>T; B. guilliamsoniana: T>P). For those species whose means were significantly different in the transect survey but which were not significantly different in the initial survey, the direction of the difference were also the same (A. marina: NA>A; C. volutator: NA>A; M. balthica: T>P; N. diversicolor: T>P).

1.2. Sediment parameters in surface sediment

The sedimentary parameters I measured in the four areas and their comparisons by Student's t tests are shown in Tables 4 and 5. In contrast to the differences in abundances of the species, most of the differences in the levels of the sedimentary parameters between the algal and nonalgal areas and between the peak and trough areas were statistically significant, thus indicating the different nature of the sedimentary environments in the four areas.

Table 4 . Levels of sediment parameters in algal (A) and nonalgal (NA) areas at high tide site (untransformed data).
Student's t compares data between algal and nonalgal areas (ln transformed data).
+ve t: algal mean > nonalgal mean
-ve t: algal mean < nonalgal mean

Sediment parameters		mean	s.d.	n	Student's t	d.f.	P
Particle size parameters (ϕ units)							
Mean diameter (ϕ)	A	2.680	0.02799	5	4.73	7	0.01>P>0.001**
	NA	2.587	0.03367	5			
Sorting (ϕ) coefficient	A	0.5953	0.03121	5	-1.39	6	0.3>P>0.2
	NA	0.6174	0.01681	5			
Skewness (ϕ)	A	-0.2834	0.1255	5	-0.12	6	P>0.9
	NA	-0.2754	0.07847	5			
Kurtosis (ϕ)	A	3.127	0.7488	5	2.15	7	0.1>P>0.05
	NA	2.227	0.5631	5			
Particle size fractions with midpoint (% weights)							
Midpoint							
-0.5 ϕ 1410 μm	A	0.3341	0.2210	5	0.594	7	0.6>P>0.5
	NA	0.2589	0.1770	5			
+0.5 ϕ 710 μm	A	0.8292	0.1450	5	-2.175	5	0.1>P>0.05
	NA	1.178	0.3280	5			
+1.5 ϕ 351 μm	A	5.557	0.4790	5	-8.126	5	P<0.001***
	NA	9.840	1.080	5			
+2.5 ϕ 177 μm	A	67.44	2.48	5	0.156	4	0.9>P>0.8
	NA	67.26	0.463	5			
+3.5 ϕ 88 μm	A	25.48	2.41	5	3.246	7	0.02>P>0.01*
	NA	21.25	1.64	5			
+4.5 ϕ 44 μm	A	0.3643	0.119	5	2.570	5	0.1>P>0.05
	NA	0.2167	0.0471	5			

contd:

Table 4 contd.

Sediment parameters		mean	s.d.	n	Student's t	d.f.	P
Shear strength ($kN.m^{-2}$)	A	4.71	2.89	10	3.02	14	$0.01>P>0.001^{**}$
	NA	2.302	0.835	15			
% Water content	A	27.94	0.1838	2	5.14	1	$0.2>P>0.1$
	NA	26.02	0.4808	2			
Permeability ($K\ mm.s^{-1}$)	A	0.4329	0.00302	20	20.62	30	$P<0.001^{***}$
	NA	0.02973	0.00123	20			
Redox potential (mV)	A	+7.000	110	13	-3.49	12	$0.01>P>0.001^{**}$
	NA	+270.8	38.3	10			
pH	A	7.01	0.0899	13	1.37	14	$0.2>P>0.1$
	NA	6.94	0.138	10			

Table 5 . Levels of sediment parameters in peak (P) and trough (T) areas at low tide site (untransformed data).
Student's t compares data between peaks and troughs (ln transformed data).
+ve t: peak mean > trough mean
-ve t: peak mean < trough mean

Sediment parameters		mean	s.d.	n	Student's t	d.f.	P
Particle size parameters (ϕ units)							
Mean diameter (ϕ)	P	2.416	0.03059	5	4.02	7	$0.0>P>0.001^{**}$
	T	2.348	0.02235	5			
Sorting (ϕ) coefficient	P	0.4326	0.05697	5	-5.69	5	$0.01>P>0.001^{**}$
	T	0.5890	0.02296	5			
Skewness (ϕ)	P	-0.6177	0.2600	5	1.34	5	0.3>P>0.2
	T	-0.7891	0.1171	5			
Kurtosis (ϕ)	P	5.928	2.354	5	0.75	5	0.5>P>0.4
	T	5.098	0.8025	5			
Particle size fractions with midpoint (% weights)							
Midpoint							
-0.5 ϕ 1410 μm	P	0.1882	0.313	5	-3.336	7	$0.02>P>0.01^{*}$
	T	0.7658	0.228	5			
+0.5 ϕ 710 μm	P	0.6547	0.478	5	-7.375	6	$P<0.001^{***}$
	T	2.522	0.303	5			
+1.5 ϕ 351 μm	P	10.96	2.30	5	-2.668	5	$0.05>P>0.02^{*}$
	T	13.96	1.04	5			
+2.5 ϕ 177 μm	P	83.76	2.42	5	5.243	7	$0.01>P>0.001^{**}$
	T	76.68	1.80	5			
+3.5 ϕ 88 μm	P	4.428	0.734	5	-2.155	5	0.1>P>0.05
	T	6.046	1.51	5			
+4.5 ϕ 44 μm	P	0.01344	0.00449	5	-1.442	4	0.3>P>0.2
	T	0.02516	0.0176	5			

contd:

Table 5 contd.

Sediment parameters		mean	s.d.	n	Student's t	d.f.	P
Shear strength ($kN.m^{-2}$)	P	31.90	29.10	25	19.31	47	$P<0.001^{***}$
	T	0.727	0.544	25			
% Water content	P	31.48	1.011	2	0.56	1	$0.5>P>0.4$
	T	30.89	1.110	2			
Permeability ($K\ mm.s^{-1}$)	P	0.1432	0.00837	20	22.80	37	$P<0.001^{***}$
	T	0.09707	0.00483	20			
Redox potential (mV)	P	+350.8	13.80	25	8.25	25	$P<0.001^{***}$
	T	+225.2	65.60	25			
pH	P	7.37	0.248	25	-7.62	43	$P<0.001^{***}$
	T	7.85	0.188	25			

1.2.1. Particle size

The phi means, sorting coefficients, skewnesses, and kurtoses of the five particle size samples I took from each of the four areas are given in tables 4 and 5. They have all been quoted in phi values, as this is the unit in the computer programme I used, and it is not possible to convert standard deviations in phi units into standard deviations in microns (Pierce & Graus, 1981, p. 1349; Lindholm, 1987, p. 167).

At high tide (Table 4), the mean particle size was finer in the algal area than in the nonalgal area when compared by Student's t, although the sorting coefficients, skewnesses and kurtoses were the same in both areas (Table 5). At low tide, the mean particle size was finer and had a smaller sorting coefficient in the peak area than in the trough area. There was no difference in skewness or kurtosis between the peak and trough areas. After taking statistical advice I was informed that the application of Student's t tests in these cases may not have been strictly correct, particularly when comparing means of means. In fact this whole area is a very difficult one (Pierce & Graus, 1981; Ehrlich, 1983) and to quote Lindholm (1987 p. 175) "there is widespread despair regarding statistical parameters of grain-size".

I was then advised to analyse the data in a different way as follows (Tables 4, 5, lower half). I calculated the means and standard deviations of the percentage weights on each of the six sieves for each area (algal, nonalgal - Table 4; peak, trough - Table 5), and then compared the algal and nonalgal and the peak and trough means for each sieve by Student's t. An arcsine transformation is often used when comparing widely different percentages (Sokal & Rohlf, 1981). This was not required for my data because the percentages being compared were similar.

The results were very interesting and I am informed are entirely valid statistically. The algal/nonalgal comparisons (Table 4) showed that the algal sediment contained significantly more finer sediment in the +3.5 ϕ

size range than did the nonalgal sediment, but significantly less coarser material in the +1.5 ϕ size range. These significant effects presumably reflect the trapping action of the algal mats and resultant retention of finer particles.

The peak/trough comparisons (Table 5) showed a different effect. Here in the modal particle size (+2.5 ϕ) there was a significantly greater % weight of sediment in the peaks than in the troughs, while in all the other particle sizes (coarser: -0.5ϕ, +0.5ϕ, +1.5ϕ, finer: +3.5ϕ, +4.5ϕ), the troughs contained a significantly greater % weight of sediment. The sediment from the troughs was more widely distributed between the different particle sizes, and hence less well sorted, than the sediment from the peaks. This means that greater sorting takes place on the peaks of the sand waves than in the troughs, which is to be expected because the effects of wave action are likely to be greater there.

Student's t comparisons were then made between the high tide and low tide by comparing the particle sizes (percent weights; table not presented in thesis) of algal and nonalgal sediments at high tide with the peak and trough sediments at low tide. In the coarser particle sizes of +2.5 ϕ midpoint and greater, 10 out of the 16 comparisons between high and low tide data were statistically significant, and in all of these the high tide areas had less sediment by weight than the low tide sediment. In the finer particles of +3.5ϕ midpoint and +4.5 ϕ midpoint, all the 8 comparisons between high and low tide data were significant and in all of them the high tide sediment had more sediment by weight than the low tide sediment. These comparisons, therefore, show conclusively that the high tide areas had predominantly finer sediments than the low tide areas, thus indicating that the high tide areas were in a lower energy sedimentary environment and the low tide areas were in a higher energy environment.

1.2.2. Permeability

The results of the permeability measurements are given in Tables 4 and 5.

The permeability of the algal area was significantly higher than that of the nonalgal area, probably because the strands of algae in the sediment produced a more open and hence more permeable structure. The permeability of the peak area was significantly higher than the permeability of the trough area, probably because the sediment in the peaks was better sorted than in the troughs (smaller sorting coefficient) - see above.

1.2.3. Redox potential and pH

The redox potential (Eh) was significantly lower in the algal area than in the nonalgal area at high tide, and in the trough area than in the peak area at low tide (Table 4, 5, Figure 7). This may have been caused at high tide by decaying algal strands just below the sediment surface and at low tide by more detrital material in the troughs. Associated with this, the pH was higher in the algal area than in the nonalgal area and in the troughs than in the peaks, although only the latter difference was statistically significant.

1.2.4. Shear strength

At high tide, shear strength was significantly higher in the algal than in the nonalgal area. This might have been caused by the algal mat inhibiting penetration of the cone and possibly also by microbial extracellular polymeric materials produced just below the sediment surface during algal decay binding the sediment particles together.

At low tide shear strength was significantly higher in the peaks than in the troughs. This was probably because the sediment was better drained there - the water table was well below the surface of the sediment, and possibly because the peak sediment was better sorted.

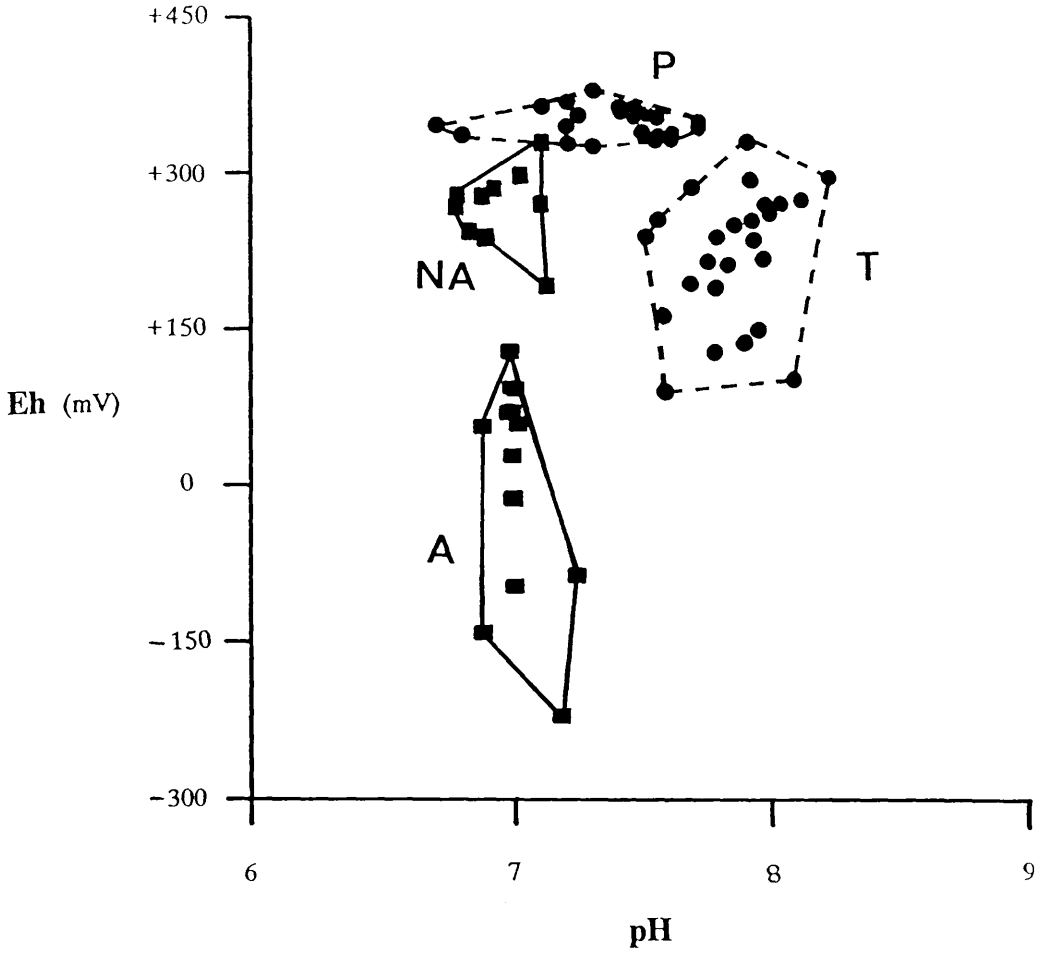


Figure 7. Eh - pH diagram. High tide and low tide sites.
High tide: algal mat (A), nonalgal mat (NA).
Low tide: peak (P), trough (T).

The results of the redox potential and shear strength differences between the algal and nonalgal areas at high tide and the peak and trough areas at low tide are borne out by the more detailed analyses along the transects in the transect survey.

There were no differences in the water content of the algal and nonalgal areas or of the peak and trough areas.

1.3. Vertical profiles of shear strength, water content, redox potential and pH at the high and low tide sites

Figure 8 shows the peak shear strength and residual shear strength profiles in the algal and nonalgal areas at high tide and in the peak and trough areas at low tide. In general the peak shear strength and residual shear strength increased with depth, the former increasing more rapidly than the latter. At high tide the peak shear strength increased more slowly in the algal area than in the nonalgal area. At low tide the peak shear strength increased slightly more quickly in the peak area than in the trough area. The rate of increase of the residual shear strength with depth did not differ markedly between the four sites.

Figure 9 shows the percent water content profiles in the algal and nonalgal areas at high tide and in the peak and trough areas at low tide. These profiles show similar trends in water content. They are high at the sediment surface falling to lower values at c 25 or 30cm sediment depth then rising again. The only exception to this general trend is that one of the two peak profiles at low tide shows a rapid drop from the surface to 5cm depth and then a peculiar dome-shaped curve.

Figure 10 shows the vertical profiles of redox potential (Eh) for the four areas. The profiles for the four areas were different from each other. The redox potential profiles in the algal area at high tide were low and did not fluctuate greatly with depth. In the nonalgal area the surface sediment had a

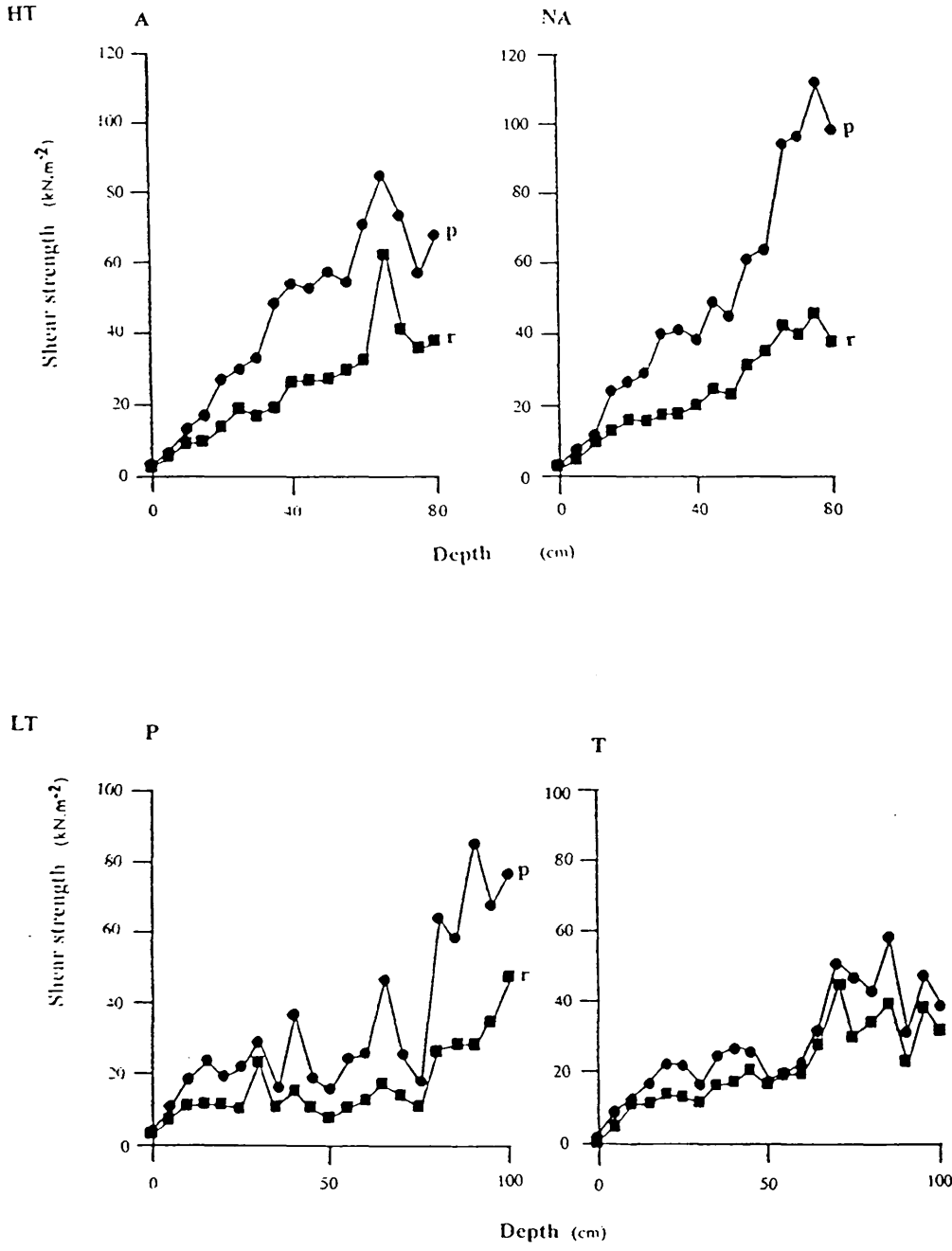


Figure 8. Shear strength ($kN.m^{-2}$) depth profile in sediment. Top: High tide (HT) site, algal (A) and nonalgal (NA) areas. Lower: Low tide (LT) site, peak (P) and trough (T) areas, p=peak and r=residual readings.

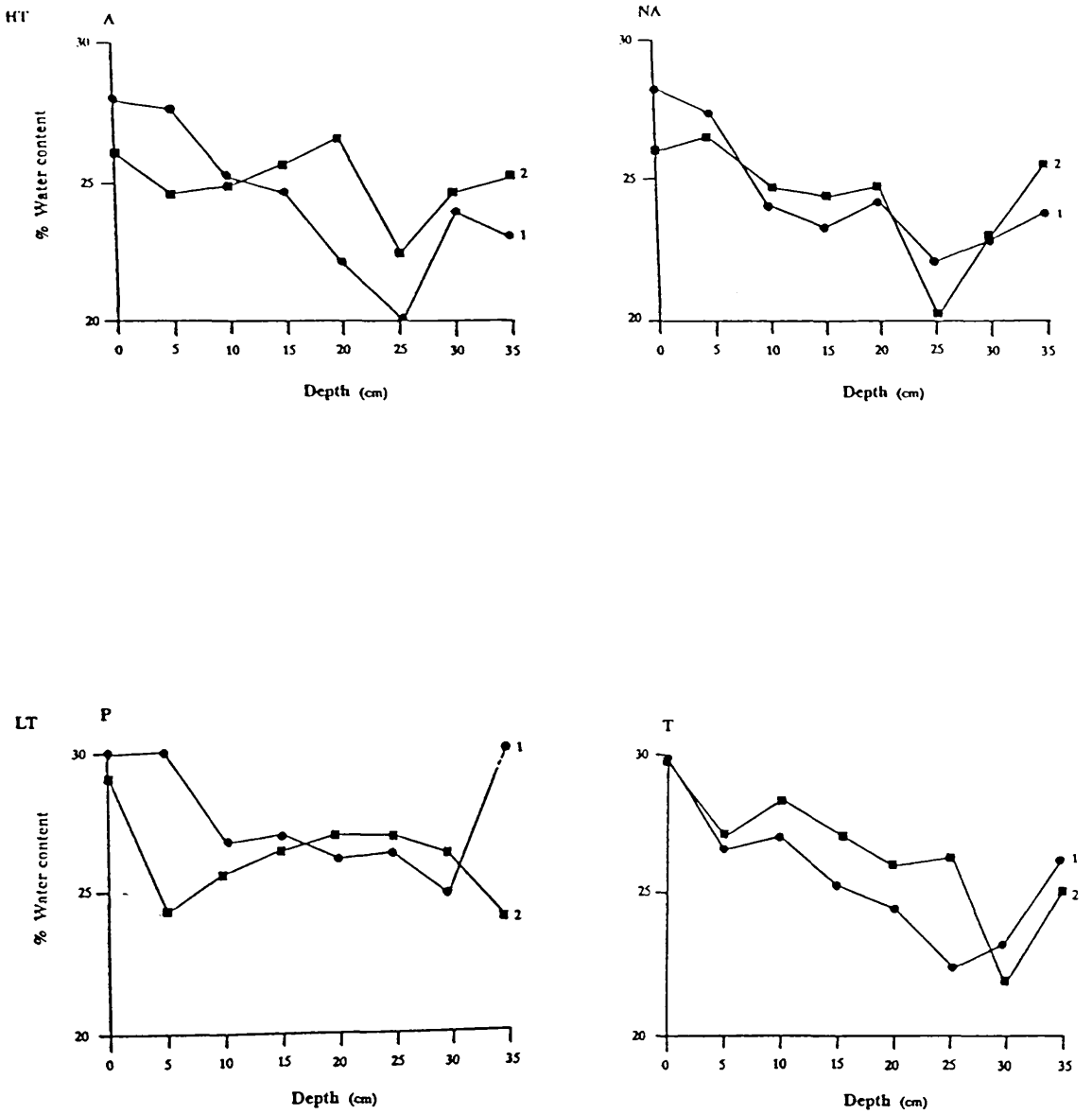


Figure 9. Percent water content depth profile in sediment. Top: High tide (HT) site, algal (A) and nonalgal (NA) areas. Lower: Low tide (LT) site, peak (P) and trough (T) areas. Replicates 1 and 2.

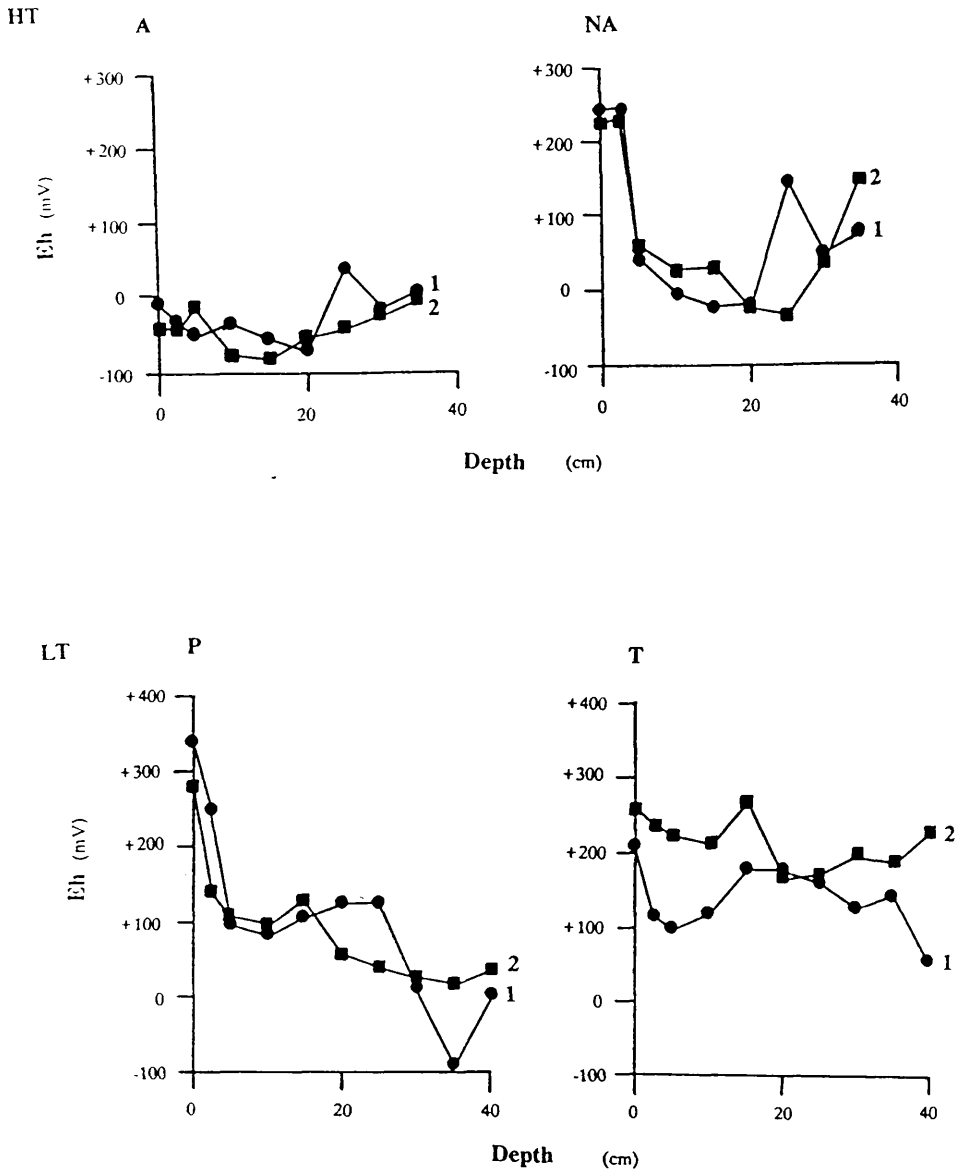


Figure 10. Redox-potential Eh (mV) depth profile in sediment. Top: High tide (HT) site, algal (A) and nonalgal (NA) areas. Lower: Low tide (LT) site, peak (P) and trough (T) areas. Replicates 1 and 2.

high redox potential which dropped very rapidly and increased again more slowly. The redox potential profile in the peak area at low tide showed a high redox potential at the surface of the sediment which decreased with depth. The redox potential profile in the trough area had a slightly lower Eh at the sediment surface and showed a very slight decrease with depth.

Figure 11 shows the vertical profiles of pH for the four areas. There is very little change with depth, except for an anomaly between 30-35cm in one of the replicates in the peak area at low tide.

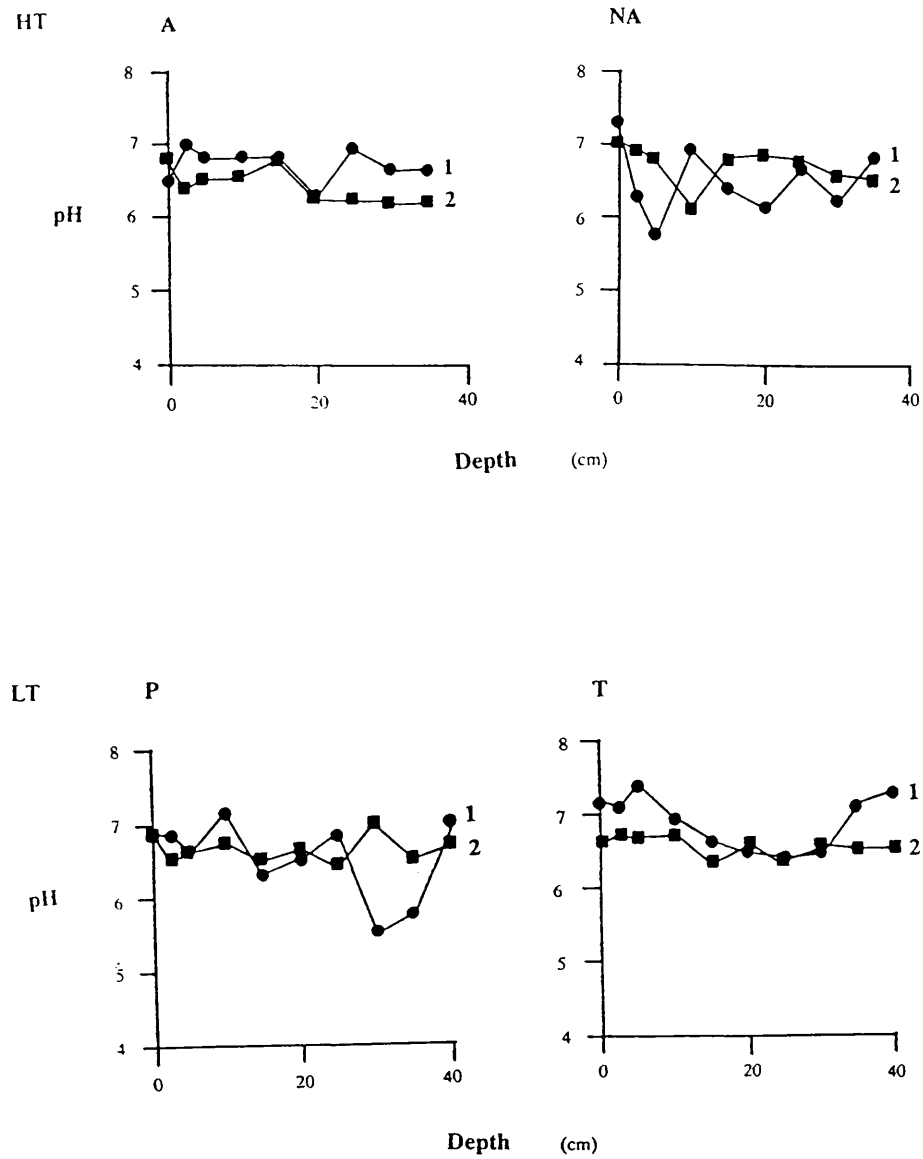


Figure 11. pH depth profile in sediment.
Top: High tide (HT) site, algal (A), nonalgal (NA) areas.
Lower: Low tide (LT) site, peak (P), trough (T) areas.
Replicates 1 and 2.

2. Transect survey

The aim of the initial survey was to broadly define the sediment parameters and species abundance for the two areas at high tide and the two areas at low tide. This then allowed me to design the detailed transect study to assess mean values of and spatial variability (heterogeneity) in the species abundances and sediment parameters, to test statistical correlations between species abundances and between sediment parameters, and to measure diversity by two diversity indices and its spatial variability.

It became clear during the planning of the transect work that a considerable amount of work would be generated during sampling each $1m^2$ quadrat along the two 50m transects and by the subsequent analysis in the laboratory. I therefore gave careful thought to the maximum work load I could handle. After considerable discussion with my supervisor and other colleagues, I decided that in each quadrat I would be able to measure the abundances of all species that had been identified and counted in the initial survey, and to measure shear strength, redox potential (Eh) and the water table. Because of time constraints it was not possible to measure particle size and pH, or to take any vertical profiles of sedimentary parameters in the quadrats. These were therefore excluded from the transect survey.

The results of the transect survey were divided into three parts:

2.1. Mean species abundance, diversity indices, and sediment parameters and their spatial heterogeneity.

2.2. Correlations between species abundance, sediment parameters, algal cover and water table.

2.3. Two additional methods of assessing spatial heterogeneity.

The three parts describe the results of a number of different analyses that have been used on the transect data comparing means and variability (analyses of variance, Student's t test, F ratios, correlation analyses, χ^2 tests, and a differencing technique). In order to simplify the understanding of the way these different analyses have been used in the three parts I have constructed a flow diagram for each part in turn (Figures 12, 13, 14, 15.1, 15.2). These diagrams require careful study. They are constructed to help the reader to distinguish between macro-, meso-, and micro-scale effects and to distinguish between comparisons of means (e.g. by Student's t tests; Figure 12) and comparisons of spatial heterogeneity or variability (e.g. by F ratio tests on the variances of the means Figure 12 and on variances obtained from analyses of variance Figures 14, 15.1, 15.2) and comparisons of correlation coefficients (Chi square tests Figure 13).

2.1. Mean species abundance, diversity indices, and sediment parameters and their heterogeneity

This part is divided into 4 subdivisions comparing the species abundance, the diversity indices, and the sediment parameters as follows:

(2.1.1.) macro-scale differences between the high and low tide sites.

(2.1.2.) meso-scale differences along the high tide transect and along the low tide transect.

(2.1.3.) meso-scale differences between algal and nonalgal areas on the high tide transect.

(2.1.4.) meso-scale differences between peak and trough areas on the low tide transect.

Reference should be made to Figure 12 for a full understanding of the methods of analyses used in sections 2.1.1. to 2.1.4.

Figure 12 . Flow diagram showing the different analyses used for macro-scale and meso-scale comparisons of species abundances and sediment parameters for the high tide (HT) and low tide (LT) transects. Numbers refer to sections in the Results of macrofaunal communities.

Note: * means that sediment parameters are not compared because redox potential and shear strength are two entirely different parameters, while species abundances have the same units and are therefore compared.

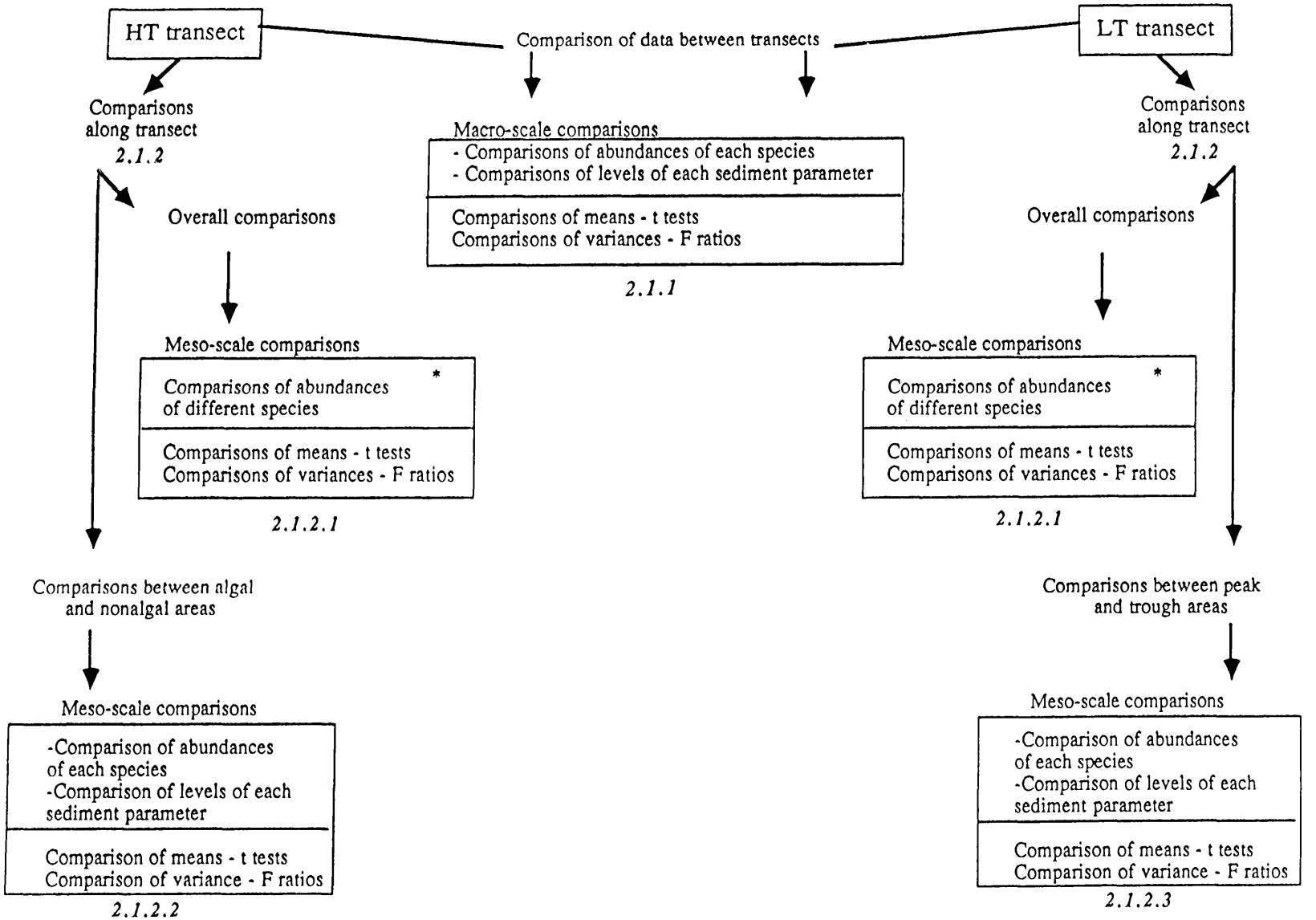

HT transect
Comparison of data between transects
LT transect
Comparisons along transect
2.1.2
Macro-scale comparisons
- Comparisons of abundances of each species
- Comparisons of levels of each sediment parameter
Comparisons of means - t tests
Comparisons of variances - F ratios
2.1.1
Comparisons along transect
2.1.2
Overall comparisons
Overall comparisons
Meso-scale comparisons
Comparisons of abundances of different species *
Comparisons of means - t tests
Comparisons of variances - F ratios
2.1.2.1
Meso-scale comparisons
Comparisons of abundances of different species *
Comparisons of means - t tests
Comparisons of variances - F ratios
2.1.2.1
Comparisons between algal and nonalgal areas
Comparisons between peak and trough areas
Meso-scale comparisons
-Comparison of abundances of each species
-Comparison of levels of each sediment parameter
Comparison of means - t tests
Comparison of variance - F ratios
2.1.2.2
Meso-scale comparisons
-Comparison of abundances of each species
-Comparison of levels of each sediment parameter
Comparison of means - t tests
Comparison of variance - F ratios
2.1.2.3

Figure 13 . Flow diagram showing how correlation analyses were applied to the species abundance and sediment parameter data to give macro-scale and meso-scale comparisons for the high tide (HT) and low tide (LT) transects. Numbers refer to the sections in the Results of macrofaunal communities.

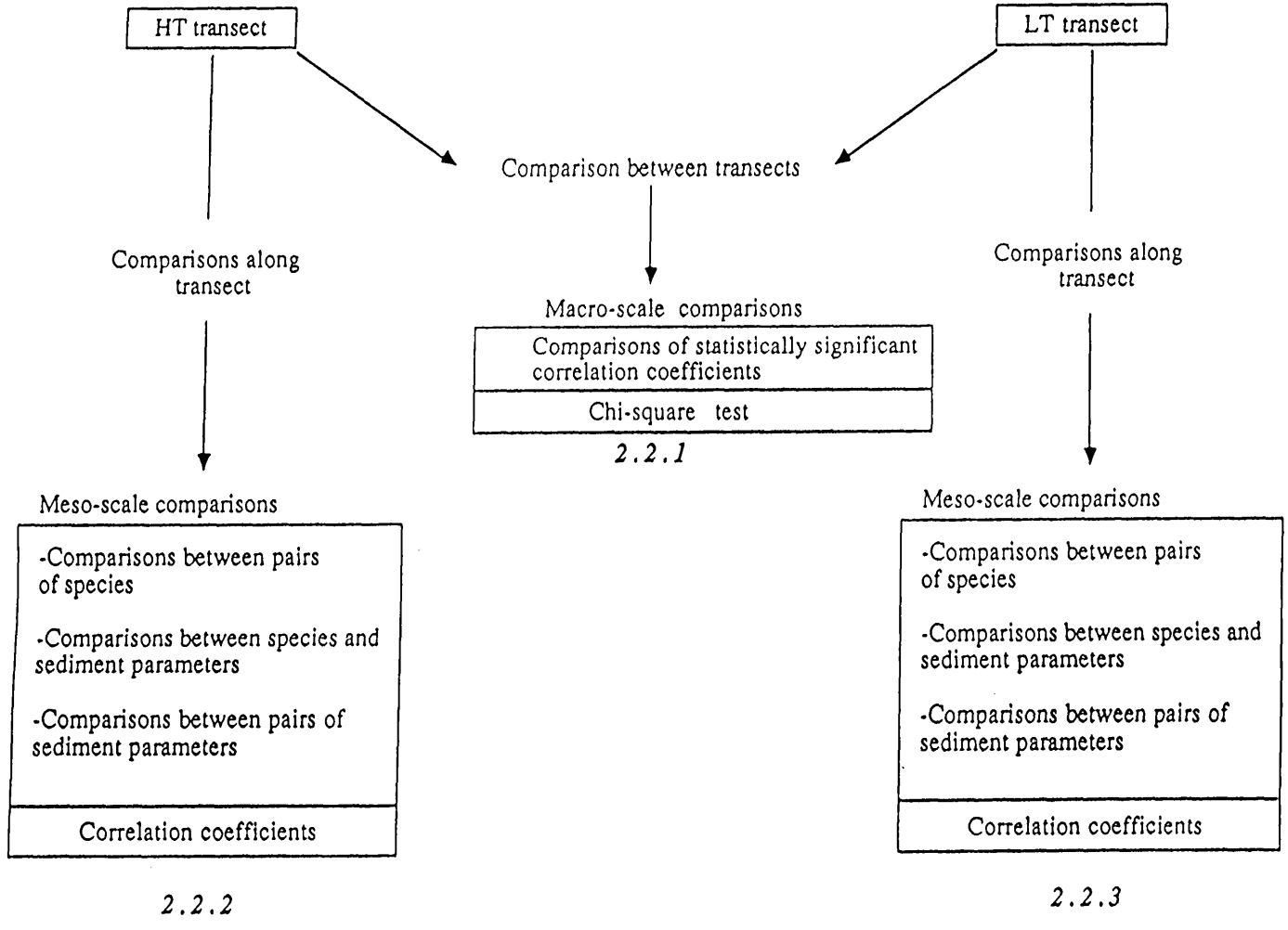

HT transect
LT transect
Comparison between transects
Comparisons along transect
Comparisons along transect
Macro-scale comparisons
Comparisons of statistically significant correlation coefficients
Chi-square test
2.2.1
Meso-scale comparisons
-Comparisons between pairs of species
-Comparisons between species and sediment parameters
-Comparisons between pairs of sediment parameters
Correlation coefficients
2.2.2
Meso-scale comparisons
-Comparisons between pairs of species
-Comparisons between species and sediment parameters
-Comparisons between pairs of sediment parameters
Correlation coefficients
2.2.3

Figure 14. Flow diagram showing method of calculating meso- and micro-scale in shear strength and redox potential using one way analysis of variance.

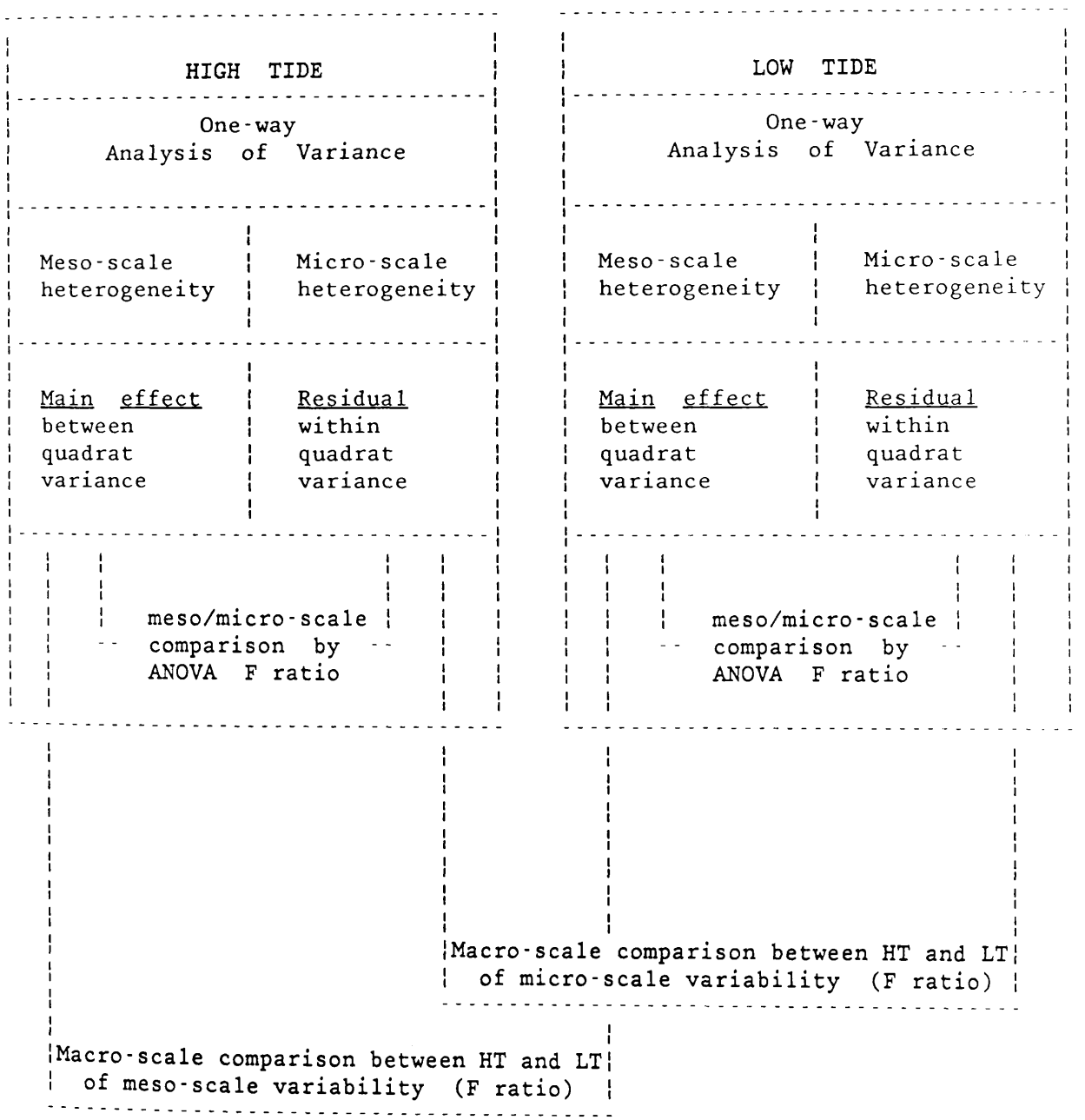
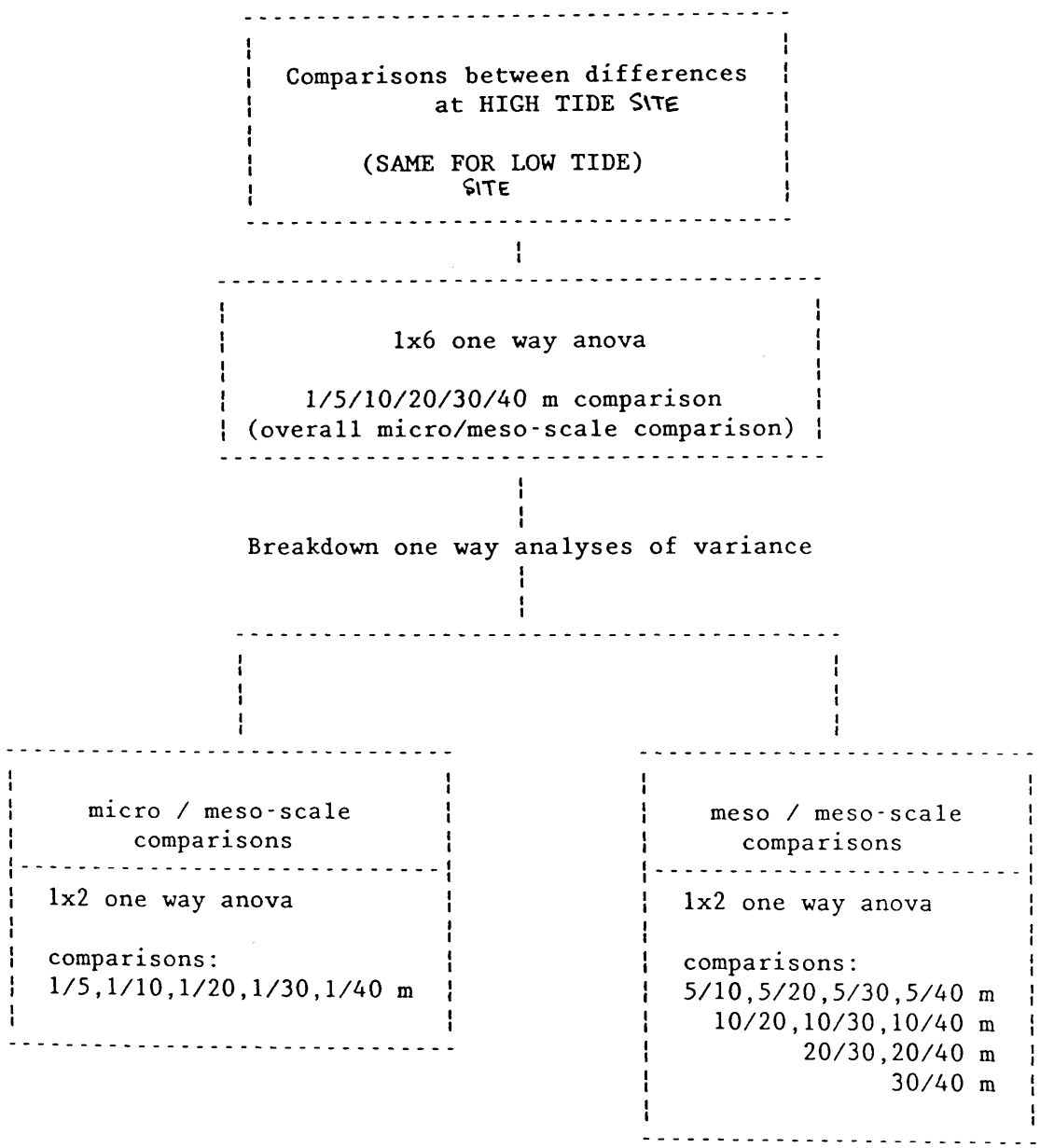
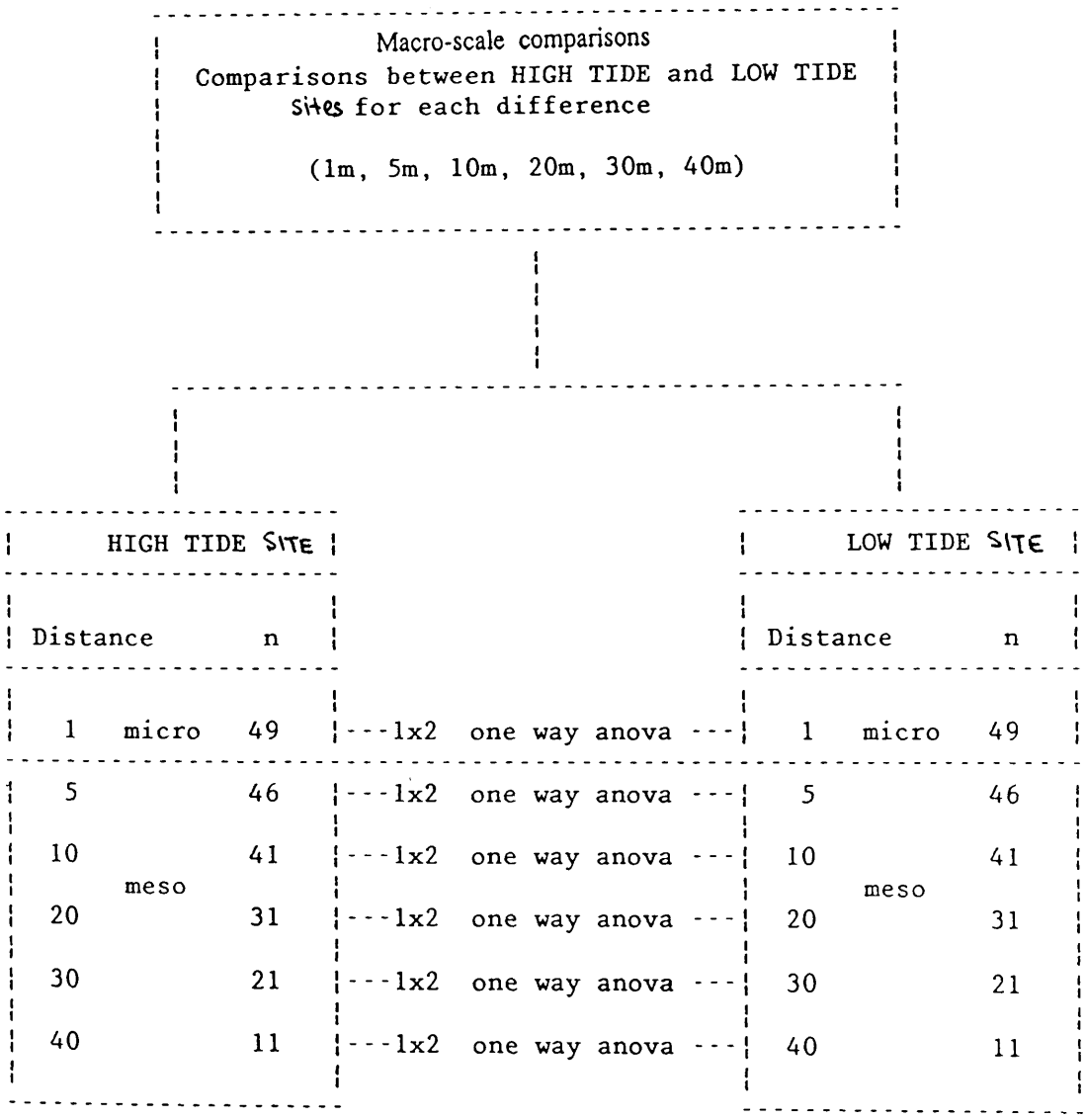


Figure 15.1 . Flow diagram showing comparisons between meso- and micro-scale differences at high tide and low tide site.
Micro-scale ≤ 1m : 1m differences
Meso-scale > 1m, <50m : 5, 10, 20, 30 and 40m differences.



Applied to: Species abundances, Shannon Wiener diversity index and sediment parameters.

Figure 15.2. Flow diagram showing comparisons between high tide and low tide sites for each difference.



Applied to: Species abundances, Shannon Wiener diversity index and sediment parameters.

2.1.1. Macro-scale differences in species abundances, diversity indices and sediment parameters between the high and low tide sites

The data are given in Appendix 2 Tables 1 to 9. The means and standard deviations of species abundances, diversity indices, and sediment parameters at high and low tide are given in Table 6. These values were calculated from the data obtained in the $\frac{1}{4}m^2$ quadrats on the cores along the 2 transects.

Macro-scale comparisons between the high and low tide data were then conducted by Student's t tests on the ln transformed data and by F ratios on the untransformed data. The Student's t tests compare between means, and the F ratios assess relative variability between the two populations being compared (Table 6). The high tide/low tide site comparisons were done on the abundances of the 4 species common to the high and low tide transects, the diversity indices at high and low tide and the sediment parameters at high and low tide.

The results of the t-tests show that there was no difference in the mean abundance of M. balthica and N. diversicolor, however A. marina and P. elegans were more abundant at low tide. The means of both diversity indices were higher at high tide than at low tide, there was no significant difference in the mean shear strength between high and low tide, but the mean redox potential was lower at high tide.

There were important differences in variability of the untransformed data between the high and low tide (significant F ratios). The abundance of three of the four species (A. marina, M. balthica, N. diversicolor) was more variable at high than at low tide in other words the variances for these species were significantly greater at high tide than at low tide. In contrast the abundance of P. elegans was more variable at low tide. Both diversity indices were less variable at high tide but this was only significant for Simpson's diversity index. The variation

Table 6 . Abundance of species (no. m^{-2}), value of diversity indices, and levels of sediment parameters at the high tide (HT) and low tide (LT) sites (untransformed data).

(i) Student's t comparing means of ln transformed data.
(ii) F ratio comparing variances of untransformed data between high and low tide sites.

TABLE 6.

Species		mean	s.d.	Comparison of HT and LT (i) Student's t (ii) F ratio	d.f.	P
Arenicola marina	HT	36.72	71.89	(i) 5.00	51	$P<0.001^{***}$
	LT	41.97	20.59	(ii) 12.19	49, 49	$P<0.001^{***}$
Macoma balthica	HT	131.8	228.9	(i) 1.72	93	$0.1>P>0.05$
	LT	47.10	78.82	(ii) 8.434	49, 49	$P<0.001^{***}$
Nereis diversicolor	HT	967.4	1298	(i) 0.93	86	$0.4>P>0.3$
	LT	388.4	246.3	(ii) 27.77	49, 49	$P<0.001^{***}$
Pygospio elegans	HT	1215	1344	(i) 5.74	52	$P<0.001^{***}$
	LT	5982	4224	(ii) 9.760	49, 49	$P<0.001^{***}$
Corophium volutator	HT	2556	3387			
Fabricia sabella	HT	5240	9398			
Hydrobia neglecta	HT	595.4	479.8			
Bathyporeia guilliamsoniana	LT	1116	1664			
Diversity Indices						
Shannon Wiener	HT	1.059	0.2810	(i) 8.90	95	$P<0.001^{***}$
	LT	0.5268	0.3141	(ii) 1.250	49, 49	$0.25>P>0.1$
Simpson	HT	0.5633	0.1373	(i) 8.51	86	$P<0.001^{***}$
	LT	0.2778	0.1930	(ii) 1.976	49, 49	$0.01>P>0.005^{**}$
Sediment Parameters						
Shear strength ($kN.m^{-2}$)	HT	6.997	5.99	(i) 0.26	98	$0.8>P>0.7$
	LT	6.742	3.07	(ii) 3.807	49, 49	$P<0.001^{***}$
Redox potential (mV)	HT	+69.30	72.1	(i) 12.93	56	$P<0.001^{***}$
	LT	+261.0	39.5	(ii) 3.332	49, 49	$P<0.001^{***}$

in the two sediment parameters was significantly greater at high tide than at low tide.

Table 6 gives A. marina data for which juveniles and adults have been combined. The separate abundances of juvenile and adult A. marina with their statistical analyses are given in Table 7. Two sets of statistical comparisons were made on these data. The first compared high tide with low tide abundances. There were significantly more adults at low tide site than at high tide site (t tests), but greater variability at high tide (F ratio). The second compared adult with juvenile abundances. There were significantly more juveniles than adults at high tide (t tests). The juvenile abundances were more variable than the adults at both sites (F ratios).

2.1.2. Meso-scale differences in species abundances, and sediment parameters, along the high tide transect and along the low tide transect

The meso-scale changes in abundance of species, sediment parameters and algal cover along the high and low tide transects are shown in Figures 16 to 26. There were considerable differences in the abundances of the species, in the diversity indices, and in the sediment parameters along both transects. In many cases these differences were related at high tide to the algal mats and at the low tide to the sand waves, both of which have a major modifying effect on their local environment. I first statistically analyse the differences between the species abundances on the transect at the high tide site and then on the transect at the low tide site. These analyses which are presented in 2.1.2.1., take no account of any differences between the algal and nonalgal areas at high tide and the peaks and troughs at low tide, since they are concerned only with the overall means and standard deviations of the species along the two transects. I then analyse the data in more detail by considering differences between the algal and nonalgal areas at high tide (2.1.2.2.), and between the peaks and troughs at low tide (2.1.2.3.).

Table 7. *Arenicola marina* adult and juvenile (No. casts m^{-2}) at high and low tide sites.

(i) Student's t comparing means of ln transformed data,
(ii) F ratio comparing variances of untransformed data.

	Adults mean ± s.d.	Juveniles mean ± s.d.
High tide	5.530 ± 7.866	31.19 ± 71.55
Low tide	16.71 ± 4.825	25.26 ± 22.47

	(i) Student's t (ii) F ratio	d.f.	P
Comparison between HT and LT			
Adults	(i) 9.54	55	$P<0.001^{***}$
	(ii) 2.658	49, 49	$P<0.001^{***}$
Juveniles	(i) 3.00	83	$0.01>P>0.001^{**}$
	(ii) 10.14	49, 49	$P<0.001^{***}$
Comparison between adults and juveniles			
High tide	(i) 2.25	85	$0.05>P>0.02^{*}$
	(ii) 82.74	49, 49	$P<0.001^{***}$
Low tide	(i) 0.30	55	$0.80>P>0.70$
	(ii) 21.69	49, 49	$P<0.001^{***}$

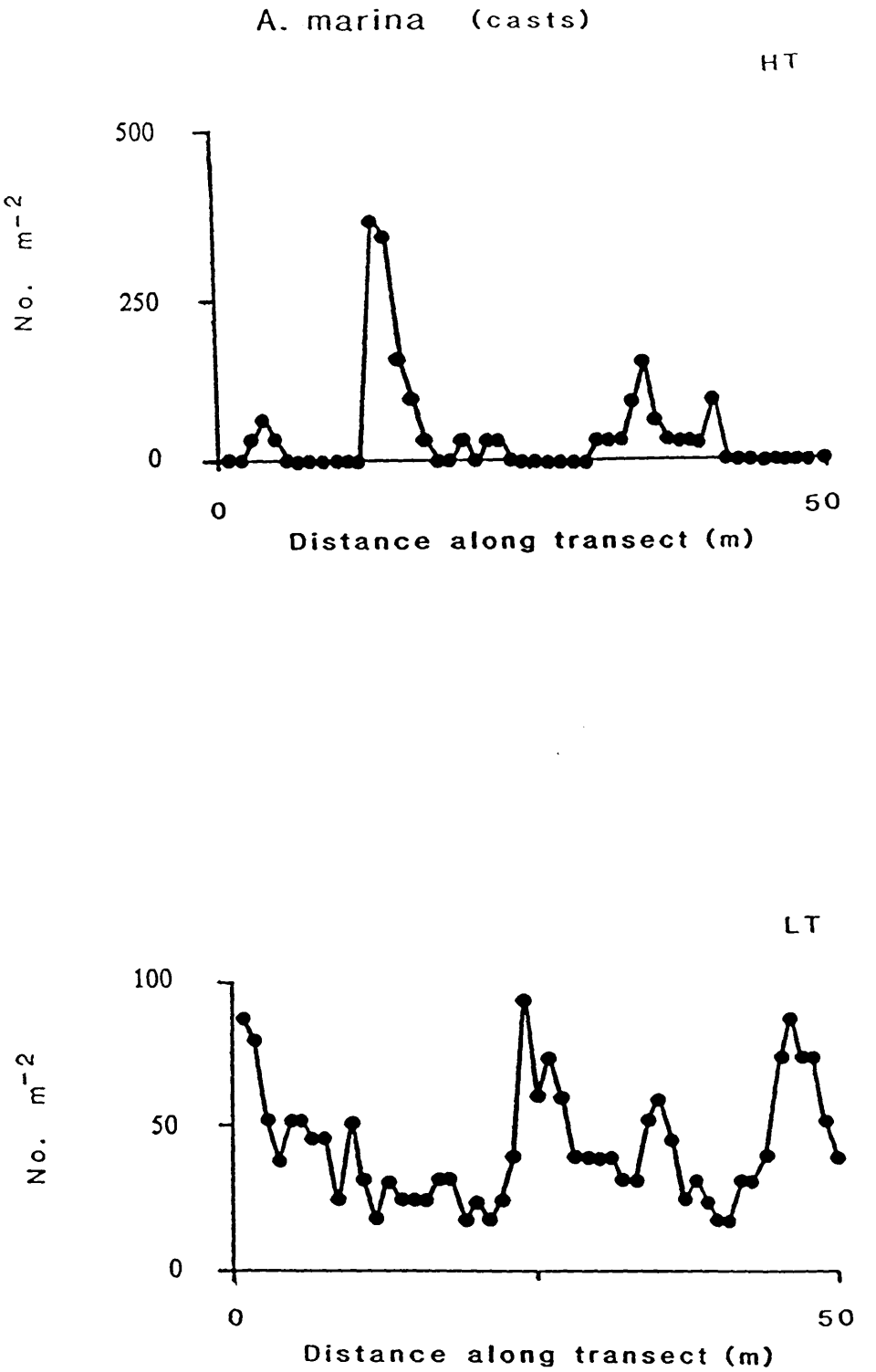


Figure 16.

Arenicola marina casts (No. m^{-2}).

Upper graph : High Tide (HT) 50 m transect.
Lower graph : Low tide (LT) 50 m transect.

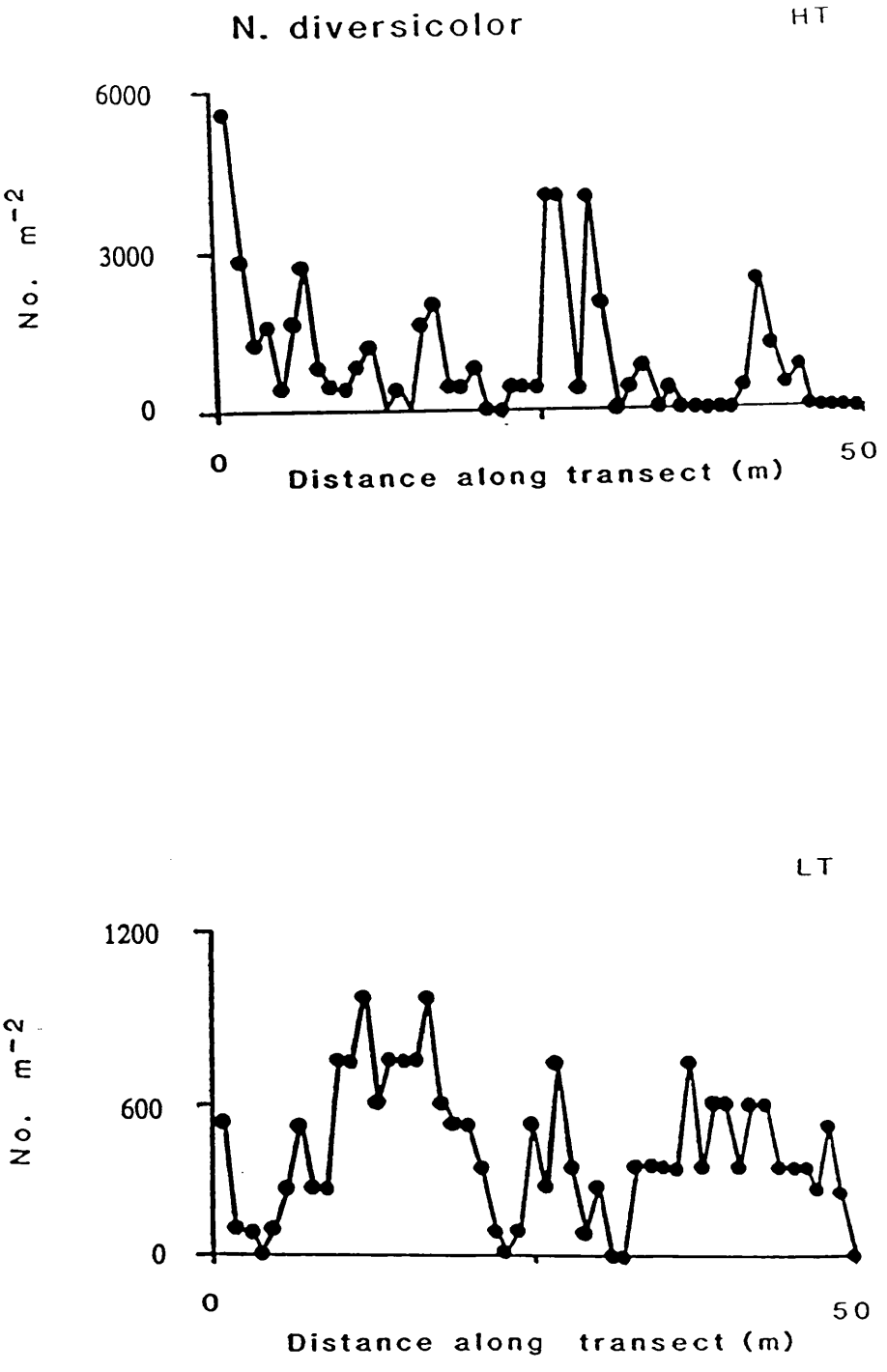


Figure 17.

Nereis diversicolor abundance (No. m^{-2}).

Upper graph : High Tide (HT) 50 m transect.
Lower graph : Low Tide (LT) 50 m transect.

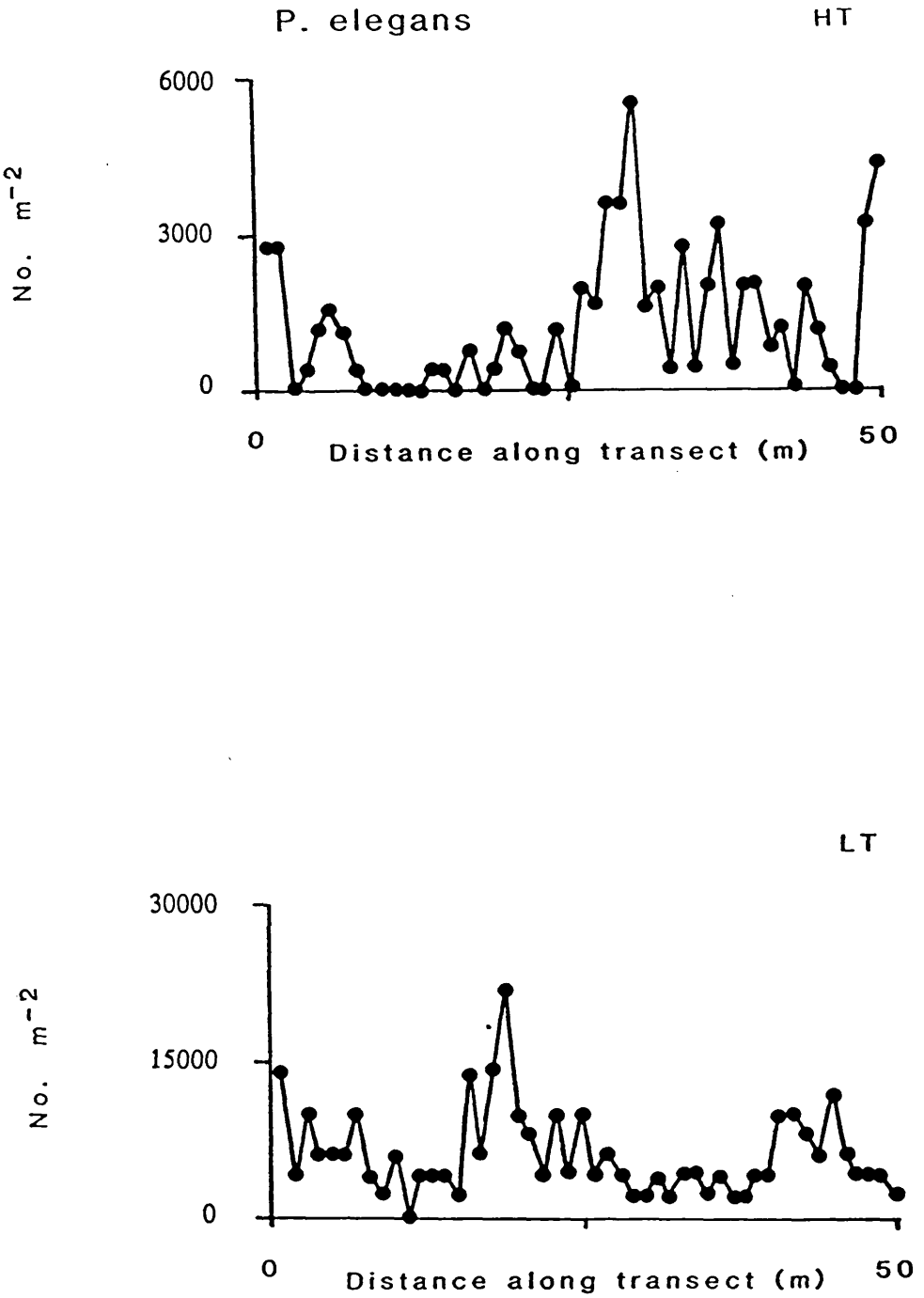
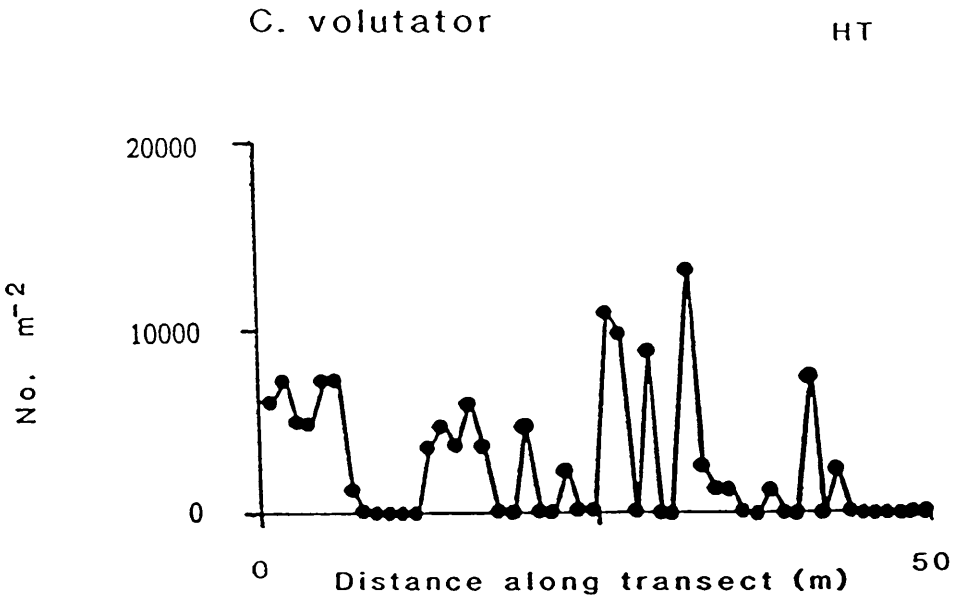


Figure 18.

Pygospio elegans abundance (No. m^{-2})

Upper graph : High Tide (HT) 50 m transect.
Lower graph : Low Tide (LT) 50 m transect.



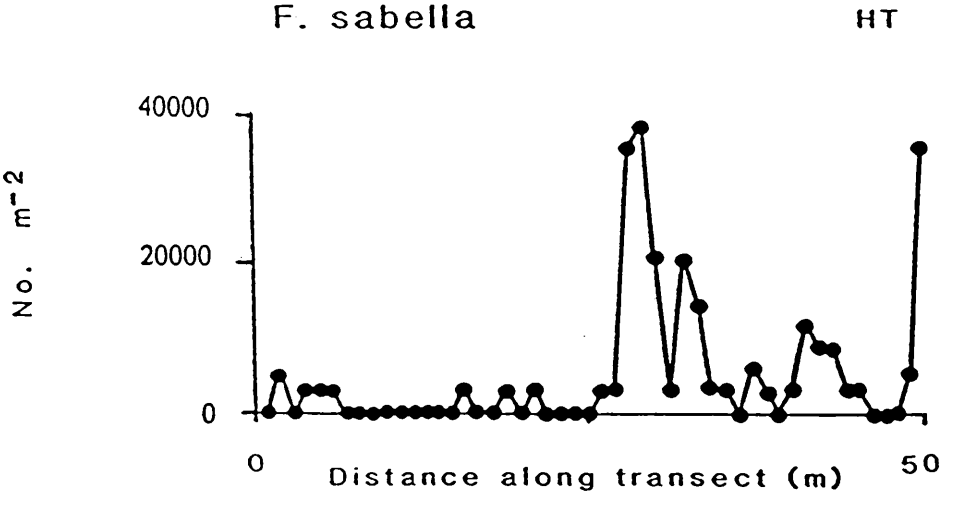


Figure 19.

Corophium volutator abundance (No. m^{-2}).
Upper graph : High Tide (HT) 50 m transect.

Fabricia sabella abundance (No. m^{-2}).
Lower graph : High Tide (HT) 50 m transect.

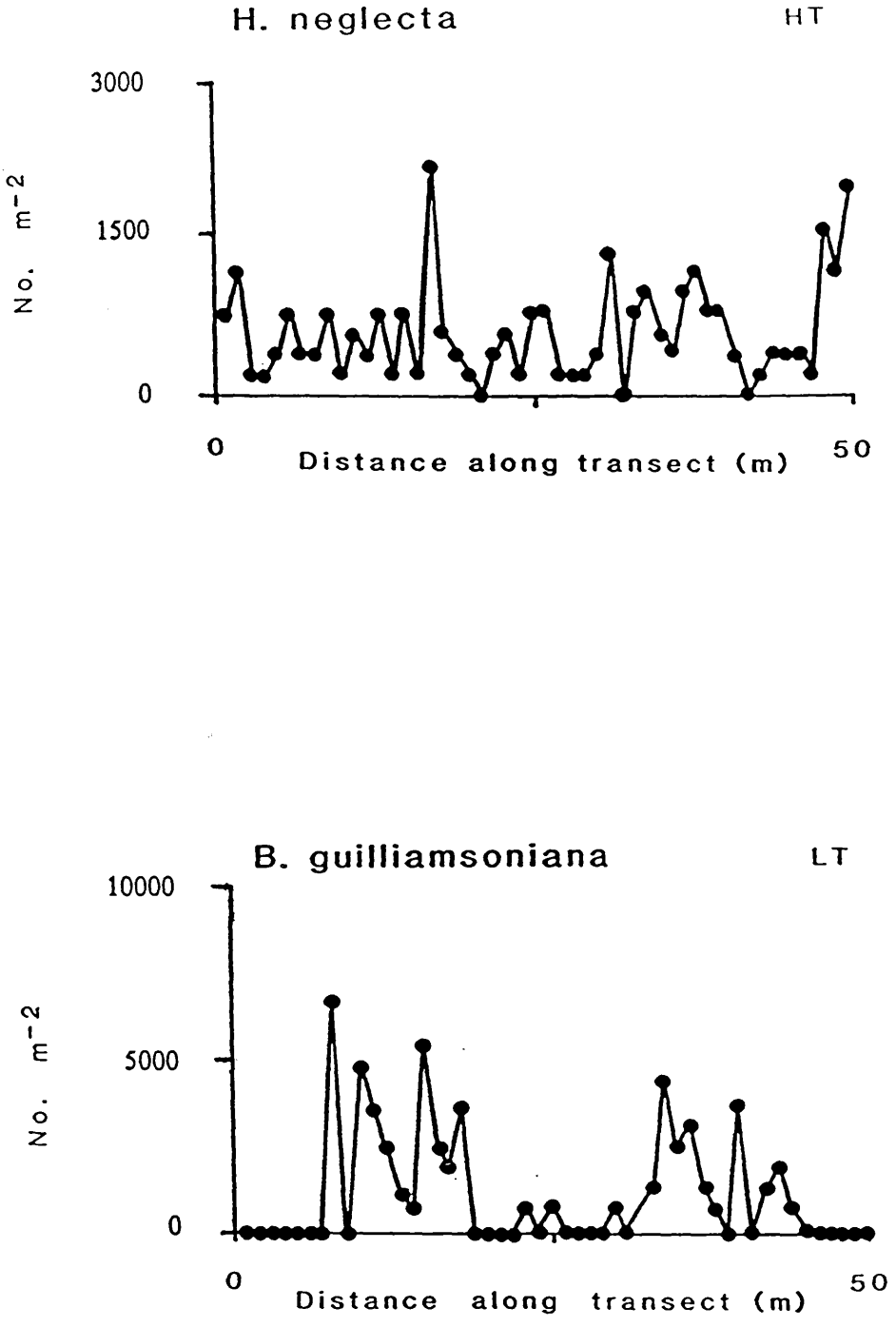


Figure 20.

Hydrobia neglecta abundance (No. m^{-2})
Upper graph : High Tide (HT) 50 m transect.

Bathyporeia guilliamsoniana abundance (No. m^{-2})
Lower graph : Low Tide (LT) 50 m transect.

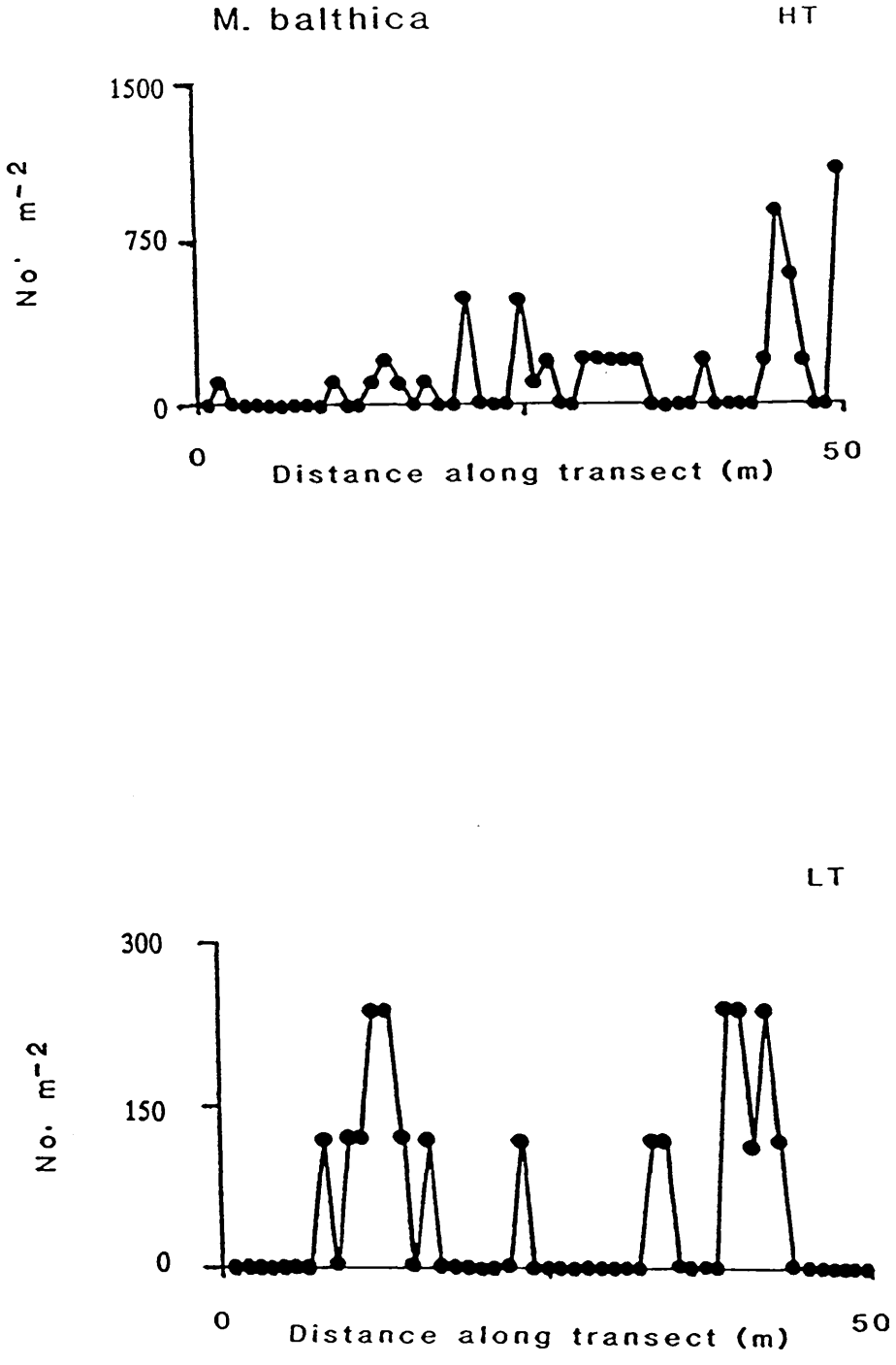


Figure 21.

Macoma balthica abundance (No. m^{-2}).

Upper graph : High Tide (HT) 50 m transect.
Lower graph : Low Tide (LT) 50 m transect.

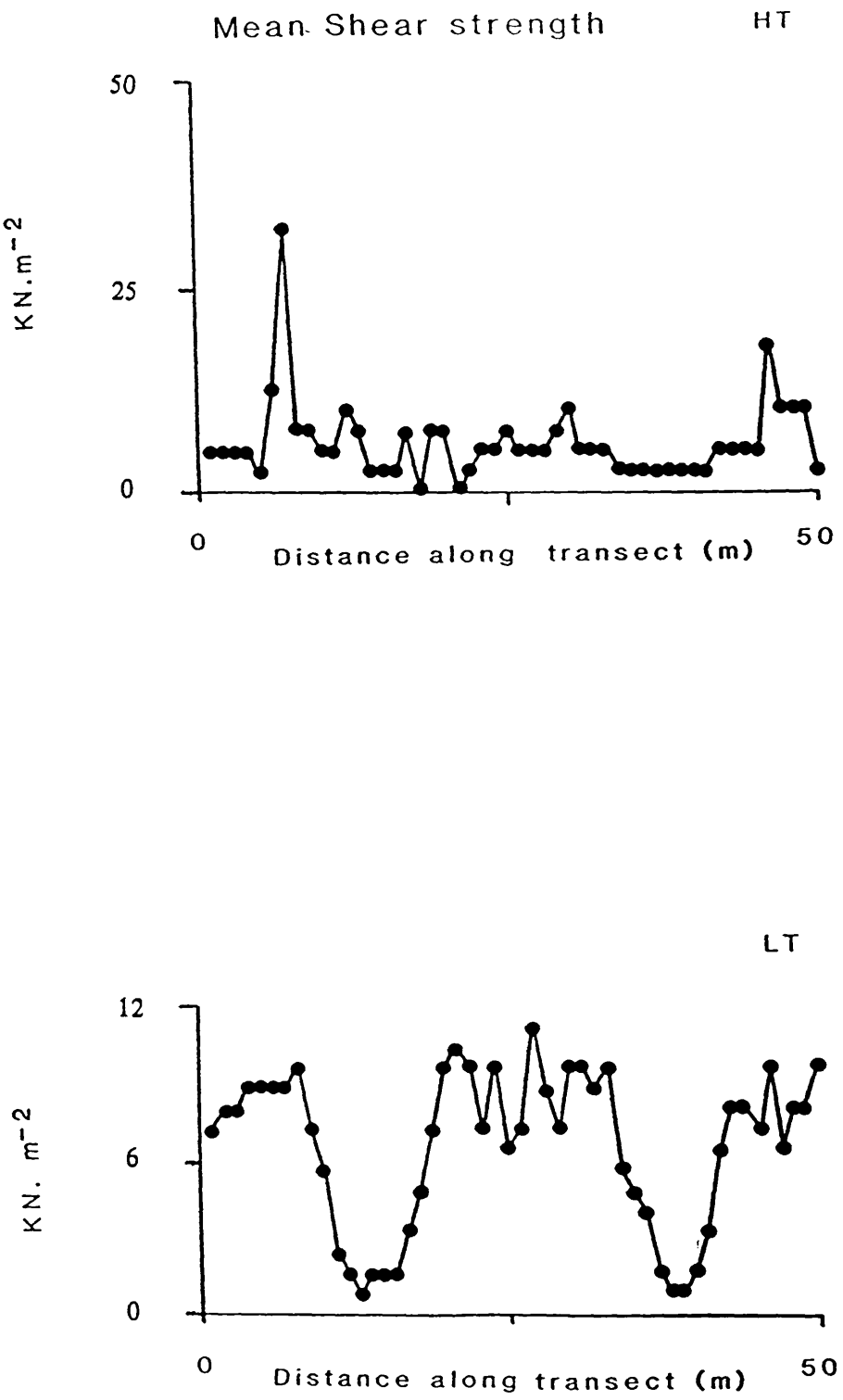


Figure 22.

Mean Shear Strength (kN. m^{-2}).

Upper graph : High Tide (HT) 50 m transect.
Lower graph : Low Tide (LT) 50 m transect.

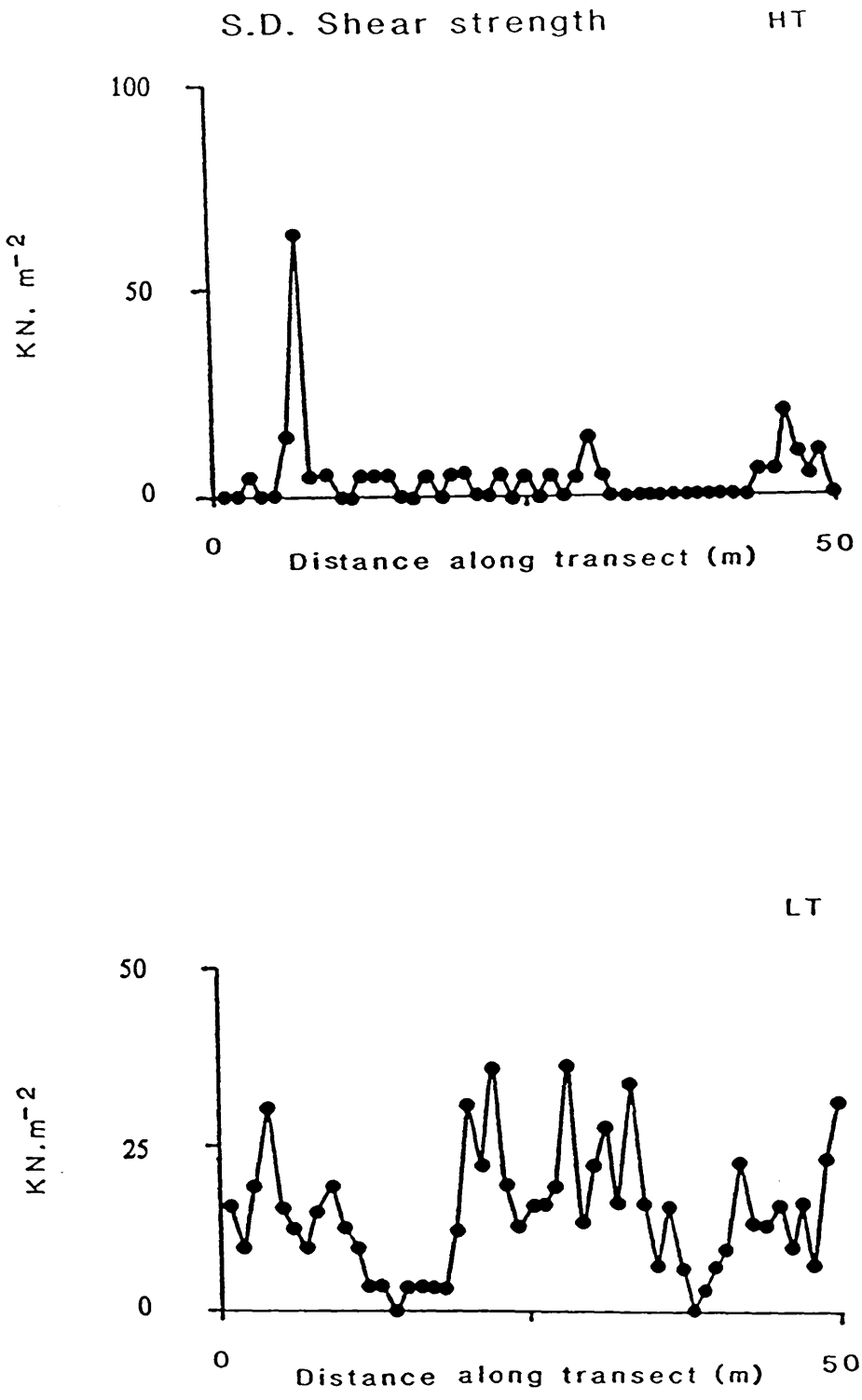


Figure 23.

Shear Strength (kN. m^{-2}). Standard deviation (S.D.)

Upper graph : High Tide (HT) 50 m transect.
Lower graph : Low Tide (LT) 50 m transect.

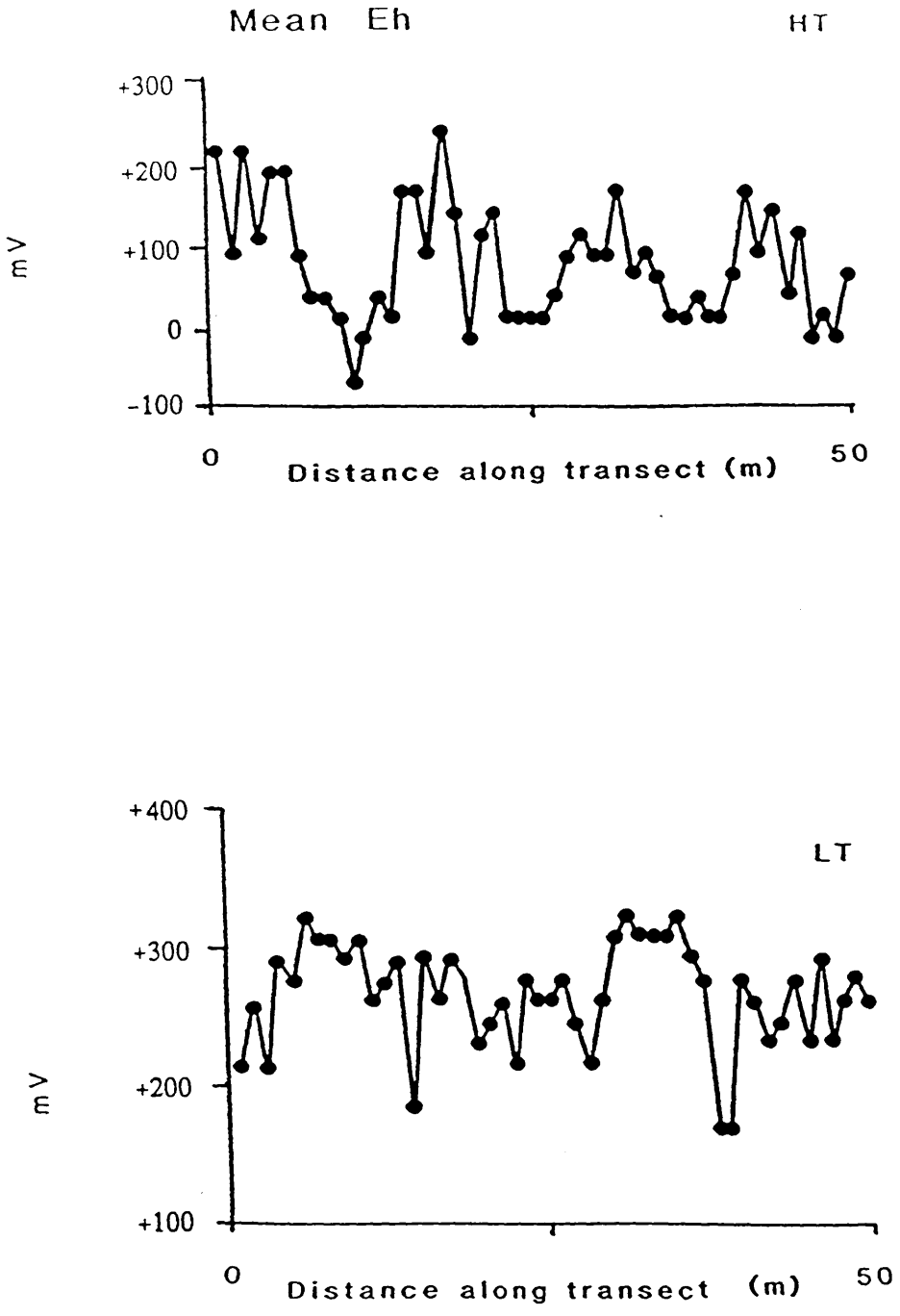


Figure 24.

Mean Redox Potential - Eh (mV)

Upper graph : High Tide (HT) 50 m transect.
Lower graph : Low Tide (LT) 50 m transect.

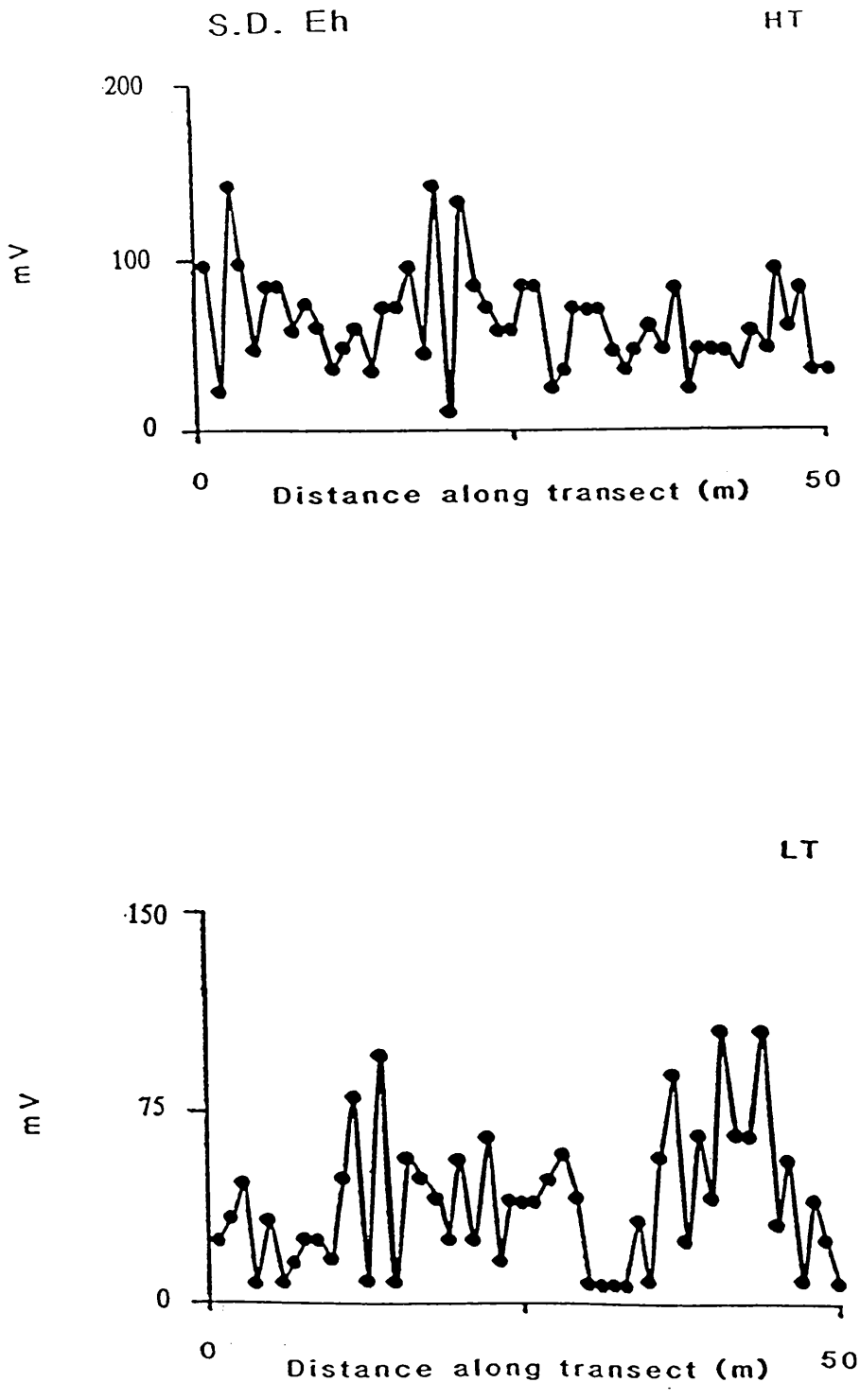


Figure 25.

Redox Potential - Eh (mV). Standard deviation (S.D.)

Upper graph : High Tide (HT) 50 m transect.
Lower graph : Low Tide (LT) 50 m transect.

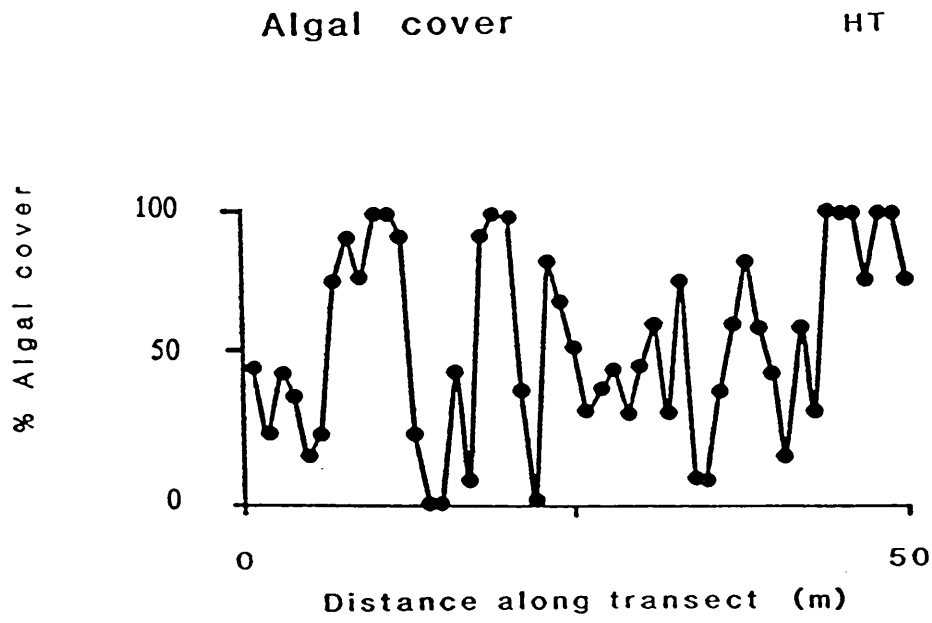


Figure 26. High tide (HT) site.

Percent algal cover along the 50 m transect.

2.1.2.1. Meso-scale differences between macrofaunal species abundances along the high tide transect and along the low tide transect

The results of the comparisons between species along the high tide transect and along the low tide transect by Student's t-tests and by F ratios are given in Tables 8 and 9.

High tide transect Table 8: At HT the abundance of F. sabella was highest and that of A. marina was lowest. The abundances of C. volutator, P. elegans, N. diversicolor, H. neglecta and M. balthica were intermediate. Nine out of the twenty one differences were statistically different so little importance can be attached to the observed differences. Five of these concerned comparisons of the abundance of A. marina with other species and three concerned M. balthica with other species.

The variance of the abundance of F. sabella was highest and that of A. marina was lowest. The variance of the abundance of M. balthica, N. diversicolor, P.elegans, C. volutator and H. neglecta were intermediate. Twenty out of the twenty one F ratios were significant and so the observed differences in the variances are very important. It is interesting that all the F ratios were significant in which the highest variance (F. sabella) and the lowest variance A. marina were compared with other variances.

Low tide transect Table 9: At LT the abundance of P. elegans was highest and that of A. marina lowest. The abundances of B. guilliamsoniana, N. diversicolor and M. balthica were intermediate. Seven out of the ten differences were statistically different. The three that were not statistically different were between B. guilliamsoniana and the species A. marina, M. balthica and N. diversicolor.

The variance of the abundance of P. elegans was highest, and that of A. marina was lowest. The variance of the abundance of M. balthica, N. diversicolor and B. guilliamsoniana were intermediate. All ten F ratios were

Table 8 . Abundance of species (no. m^{-2}) at the high tide (HT) site.

(i) Student's t comparing means of ln transformed data of pairs of species.

(ii) F ratio comparing variances of untransformed data of pairs of species.

TABLE B.

Tidal Level	Species	Mean	s.d.	(i) Student's t (ii) Fratio	d.f.	P
HT	A. marina	36.72	71.89	(i) -3.73	78	$P < 0.001^{***}$
	M. balthica	131.8	228.9	(ii) 10.14	49,49	$P < 0.001^{***}$
	A. marina	36.72	71.89	(i) -3.54	89	$P < 0.001^{***}$
	N. diversicolor	967.4	1298	(ii)325.9	49,49	$P < 0.001^{***}$
	A. marina	36.72	71.89	(i) -4.44	91	$P < 0.001^{***}$
	P. elegans	1215	1344	(ii)349.5	49,49	$P < 0.001^{***}$
	A. marina	36.72	71.89	(i) -1.89	77	$0.1 > P > 0.05$
	C. volutator	2556	3387	(ii)2219.7	49,49	$P < 0.001^{***}$
	A. marina	36.72	71.89	(i) -4.87	85	$P < 0.001^{***}$
	F. sabella	5240	9398	(ii)17089.7	49,49	$P < 0.001^{***}$
	A. marina	36.72	71.89	(i) -7.04	92	$P < 0.001^{***}$
	H. neglecta	595.4	479.8	(ii) 44.54	49,49	$P < 0.001^{***}$
	M. balthica	131.8	228.9	(i) 1.15	65	$0.3 > P > 0.2$
	N. diversicolor	967.4	1298	(ii) 32.16	49,49	$P < 0.001^{***}$
	M. balthica	131.8	228.9	(i) 2.10	67	$0.05 > P > 0.02^{*}$
	P. elegans	1215	1344	(ii) 34.48	49,49	$P < 0.001^{***}$
	M. balthica	131.8	228.9	(i) -0.24	59	$0.9 > P > 0.8$
	C. volutator	2556	3387	(ii)218.9	49,49	$P < 0.001^{***}$
	M. balthica	131.8	228.9	(i) 2.79	63	$0.01 > P > 0.001^{***}$
	F. sabella	5240	9398	(ii)1685.7	49,49	$P < 0.001^{***}$
	M. balthica	131.8	228.9	(i) 4.77	90	$P < 0.001^{***}$
	H. neglecta	595.4	479.8	(ii) 4.394	49,49	$P < 0.001^{***}$
	N. diversicolor	967.4	1298	(i) -0.67	97	$0.6 > P > 0.5$
	P. elegans	1215	1344	(ii) 1.072	49,49	$0.5 > P > 0.25$
	N. diversicolor	967.4	1298	(i) 0.97	92	$0.4 > P > 0.3$
	C. volutator	2556	3387	(ii) 6.809	49,49	$P < 0.001^{***}$
	N. diversicolor	967.4	1298	(i) -1.35	97	$0.2 > P > 0.1$
	F. sabella	5240	9398	(ii) 52.42	49,49	$P < 0.001^{***}$
	N. diversicolor	967.4	1298	(i) -1.83	77	$0.1 > P > 0.05$
	H. neglecta	595.4	479.8	(ii) 7.319	49.49	$P < 0.001^{***}$

CONTD:

TABLE 8 CONTD:

Tidal Level	Species	Mean	s.d.	(i) Student's t (ii) Fratio	d.f.	P
HT	P. elegans	1215	1344	(i) 1.57	90	0.2 > P < 0.1
	C. volutator	2556	3387	(ii) 6.351	49,49	P < 0.001***
	P. elegans	1215	1344	(i) -0.74	96	0.5 > P > 0.4
	F. sabella	5240	9398	(ii) 48.90	49,49	P < 0.001***
	P. elegans	1215	1344	(i) -1.06	79	0.3 > P > 0.2
	H. neglecta	595.4	479.8	(ii) 7.847	49,49	P < 0.001***
	C. volutator	2556	3387	(i) 2.13	95	0.05 > P > 0.02
	F. sabella	5240	9398	(ii) 7.699	49,49	P < 0.001***
	C. volutator	2556	3387	(i) -2.63	67	0.02 > P > 0.01*
	H. neglecta	595.4	479.8	(ii) 49.83	49,49	P < 0.002***
	F. sabella	5240	9398	(i) -0.09	73	P > 0.9
	H. neglecta	595.4	479.8	(ii)383.7	49,49	P < 0.001***

Table 9 . Abundance of species (no. m^{-2}) at the low tide (LT) site.

(i) Student's t comparing means of ln transformed data of pairs of species.

(ii) F ratio comparing variances of untransformed data of pairs of species.

TABLE 9.

Tidal Level	Species	Mean	s.d.	(i) Student's t (ii) Fratio	d.f.	P
LT	A. marina	41.97	20.59	(i) 4.19	57	$P < 0.001^{***}$
	M. balthica	47.10	78.82	(ii) 14.65	49,49	$P < 0.001^{***}$
	A. marina	41.97	20.59	(i) -2.68	51	$0.02 > P > 0.01^{*}$
	N. diversicolor	388.4	246.3	(ii)143.1	49,49	$P < 0.001^{***}$
	A marina	41.97	20.59	(i)-39.34	85	$P < 0.001^{***}$
	P. elegans	5982	4224	(ii)42085.8	49,49	$P < 0.001^{***}$
	A marina	41.97	20.59	(i) 0.49	49	$0.7 > P > 0.6$
	B. guilliamsoniana	1116	1664	(ii)6531.2	49,49	$P < 0.001^{***}$
	M. balthica	47.10	78.82	(i) 4.36	71	$P < 0.001^{***}$
	N. diversicolor	388.4	246.3	(ii) 9.765	49,49	$P < 0.001^{***}$
	M. balthica	47.10	78.82	(i) 23.52	68	$P < 0.001^{***}$
	P. elegans	5982	4224	(ii)2871.9	49,49	$P < 0.001^{***}$
	M. balthica	47.10	78.82	(i) 0.79	57	$0.5 > P > 0.4$
	B. guilliamsoniana	1116	1664	(ii)445.7	49,49	$P < 0.001^{***}$
	N. diversicolor	388.4	246.3	(i) -7.68	53	$P < 0.001^{***}$
	P. elegans	5982	4224	(ii)294.1	49,49	$P < 0.001^{***}$
	N. diversicolor	388.4	246.3	(i) 1.83	80	$0.1 > P > 0.05$
	B. guilliamsoniana	1116	1664	(ii) 45.64	49,49	$P < 0.001^{***}$
	P. elegans	5982	4224	(i) 6.86	50	$P < 0.001^{***}$
	B. guilliamsoniana	1116	1664	(ii) 6.444	49,49	$P < 0.001^{***}$

significant and so the observed differences in the variances are very important.

2.1.2.2. Meso-scale differences between algal and nonalgal areas

The meso-scale differences between the algal and nonalgal areas on the transect at the high tide site were analysed in detail as follows. The differences in the means were assessed by Student's t test on ln transformed data and variability by F ratio tests applied to the variances calculated from the untransformed data. Table 10 gives the means, standard deviations, Student's t test values and F ratios for the algal (A) and nonalgal (NA) areas along the high tide transect.

The t tests show that there were a few differences between the algal and nonalgal areas both in the means and in variability of the species abundances and sediment parameters. Two of the high tide species were significantly less abundant in the algal areas (A. marina and C. volutator). The remaining species did not show significant differences in abundances. There were no differences in the diversity indices between the algal and non-algal areas. Shear strength was significantly higher and redox potential significantly lower in the algal than in the nonalgal areas.

The F ratios show that the abundances of four of the species showed significantly more variability in the nonalgal than in the algal areas (A. marina, C. volutator, F.sabella, N. diversicolor), while the reverse was true for two of the species (H. neglecta and M. balthica). P. elegans showed no significant difference in variability between the algal and non-algal areas. There were no significant differences in the variability of the two diversity indices between the algal and nonalgal areas. Shear strength showed greater variability in the algal than in the nonalgal areas, on the other hand there was no difference in the variability of the redox potential.

Table 10 . Abundance of species (no. m^{-2}), values of diversity indices, and levels of sediment parameters in algal (A) and non-algal (NA) areas at the high tide site (untransformed data).

(i) Student's t comparing means of ln transformed data,
(ii) F ratio comparing variances of untransformed data between algal and non-algal areas.

TABLE 10.

Comparison of Algal and Nonalgal

Species		mean	s.d.	(i) Student's t (ii) F ratio	d.f.	P
Arenicola marina	A	7.482	10.77	(i) 5.21	28	$P<0.001^{***}$
	NA	115.9	122.0	(ii) 128.3	10, 19	$P<0.001^{***}$
Corophium volutator	A	605.3	1412	(i) 5.56	47	$P<0.001^{***}$
	NA	5039	3559	(ii) 6.353	21, 27	$P<0.001^{***}$
Fabricia sabella	A	3392	7548	(i) 0.80	45	0.5>P>0.4
	NA	7591	11069	(ii) 2.15	21, 27	$0.05>P>0.025^{*}$
Hydrobia neglecta	A	659.9	549.4	(i) 0.91	35	0.4>P>0.3
	NA	513.6	369.6	(ii) 2.210	27, 21	$0.05>P>0.025^{*}$
Macoma balthica	A	142.9	278.0	(i) 0.71	46	0.5>P>0.4
	NA	117.7	149.8	(ii) 3.444	27, 21	$0.005>P>0.001^{**}$
Nereis diversicolor	A	701.9	813.7	(i) 1.31	48	0.3>P>0.2
	NA	1305	1692	(ii) 4.324	21, 27	$P<0.001^{***}$
Pygospio elegans	A	1198	1431	(i) 2.02	41	0.1>P>0.05
	NA	1236	1256	(ii) 1.299	27, 21	0.5>P>0.25
Diversity Indices						
Shannon Wiener	A	1.066	0.1396	(i) 0.76	24	0.5>P>0.4
	NA	1.147	0.2762	(ii) 1.339	10, 19	0.5>P>0.25
Simpson	A	0.5749	0.1516	(i) 0.05	22	P>0.9
	NA	0.5773	0.1404	(ii) 1.166	10, 19	0.25>P>0.1
Sediment Parameters						
Shear strength ($kN.m^{-2}$)	A	11.90	16.40	(i) 2.61	29	$0.02>P>0.01^{*}$
	NA	4.112	1.960	(ii) 70.02	76, 122	$P<0.001^{***}$
Redox potential (mV)	A	+37.86	86.80	(i) 2.11	27	$0.05>P>0.02^{*}$
	NA	+99.50	90.50	(ii) 1.087	101, 97	0.5>P>0.25

2.1.2.3. Meso-scale differences between peak and trough areas

The meso-scale differences between the peak and trough areas on the transect at the low tide site were analysed as for the algal and nonalgal areas at high tide. The differences in the means were assessed by Student's t test on the ln transformed data and variability by F ratio tests applied to the variances calculated from the untransformed data. Table 11 gives the means, standard deviations, Student's t test values and F ratios for the peak (P) and trough (T) areas along the low tide transect.

The t tests show that there were a number of differences between the peak and trough areas in the means of the different species abundance, sediment parameters and diversity indices. Three of the low tide species were significantly less abundant in the peaks of the sand waves (B. guilliamsoniana and N. diversicolor), while M. balthica was totally absent from the peaks. A. marina was significantly more abundant in the peaks while P. elegans did not show significant differences in abundance between the peaks and troughs. Both the Shannon Wiener and the Simpson's diversity indices were significantly higher in the troughs than in the peaks. Shear strength was significantly higher in the peaks while the redox potential showed no difference between the peak and trough areas.

The F ratios showed that the mean abundance of A. marina was significantly more variable in the peaks while the abundance of B. guilliamsoniana was more variable in the troughs. N. diversicolor and P. elegans showed no significant difference in variability between the peaks and troughs. There were significant differences in the variability of the two diversity indices between the peaks and troughs with a higher variability in the troughs. The redox-potential showed significantly more variability in the troughs than in the peaks, while the shear strength showed no difference in variability between the peaks and troughs.

Table 11. Abundance of species (No. m^{-2}), values of diversity indices and levels of sediment parameters in peak (P) and trough (T) quadrats at low tide site (untransformed data)

(i) Student's t comparing means of ln transformed data,
(ii) F ratio comparing variances of untransformed data between peaks and troughs at low tide site.

TABLE II.

Species		mean	s.d.	Comparison of Peak and Trough (i) Student's t (ii) F ratio	d.f.	P
Arenicola marina	P	59.48	19.95	(i) 6.81	23	$P<0.001^{***}$
	T	25.23	7.239	(ii) 7.595	12, 12	$P<0.001^{***}$
Bathyporeia guilliamsoniana	P	72.43	140.4	(i) -6.29	13	$P<0.001^{***}$
	T	1965	1638	(ii) 136.1	12, 12	$P<0.001^{***}$
Macoma balthica	P	0	0	(i) 4.331	12	$P<0.001^{***}$
	T	108.7	101.5	(ii) -	-	-
Nereis diversicolor	P	262.6	215.7	(i) -2.26	12	$0.05>P>0.02^{*}$
	T	633.8	195.4	(ii) 1.219	12, 12	$0.50>P>0.25$
Pygospio elegans	P	5831	3714	(i) 1.36	19	$0.2>P>0.1$
	T	4563	3673	(ii) 1.022	12, 12	$0.50>P>0.25$
Diversity Indices						
Shannon Wiener	P	0.2740	0.1250	(i) -7.74	19	$P<0.001^{***}$
	T	0.8202	0.2241	(ii) 3.214	12, 12	$0.05>P>0.025^{*}$
Simpson	P	0.1257	0.07065	(i) -7.18	17	$P<0.001^{***}$
	T	0.4475	0.1468	(ii) 4.317	12, 12	$0.01>P>0.005^{**}$
Sediment Parameters						
Shear strength ($kN.m^{-2}$)	P	8.307	1.260	(i) 12.01	14	$P<0.001^{***}$
	T	1.898	0.9343	(ii) 1.819	12, 12	$0.25>P>0.10$
Redox potential (mV)	P	+247.6	23.27	(i) 0.13	16	$P>0.9$
	T	+248.8	52.07	(ii) 5.007	12, 12	$0.005>P>0.001^{**}$

2.2. *Correlations between species abundances, sediment parameters, algal cover and water table*

The ln transformed data of species abundance, levels of sediment parameters and arcsine % algal cover were subjected to a series of correlation analyses. These analyses calculated correlation coefficients between pairs of species abundances and sediment parameters in turn and are presented below. The correlation coefficients represent relationships that are operating at a meso-scale, because they are calculated from pairs of data points taken from quadrats along the high or low tide transects. The interpretation of the significant coefficients are dealt with partly in the results but in more detail in the discussion.

Reference should be made to Figure 13 for a full understanding of sections 2.2.1. to 2.2.3.

2.2.1. *Comparisons of numbers of significant correlation coefficients at high and low tide*

Table 12 gives the numbers and percentages of correlation coefficients at high and low tide. The significant correlation coefficients have been grouped into negative and positive correlations and as animal/animal, animal/sediment, and sediment/sediment correlations. There are three major points about the data in this table.

Firstly, there are more significant correlation coefficients at low tide (20/45 = 44%) than at high tide (17/78 = 22%) ($2\times2\ \chi^2 = 6.960$, d.f.= 1, $0.01>P>0.001^{**}$).

Secondly, the proportion of positive to negative significant correlations at high tide (12:5) is not significantly different from that at low tide (8:12) ($2\times2\ \chi^2 = 3.462$, d.f. = 1, $0.1>P>0.05$).

Table 12 . Comparison of the total number of positive and negative correlation coefficients (on ln transformed data) for pairs of animal species and sediment parameters at high and low tide sites along the 50m transect (using χ^2 test).

Classification of Correlation Coefficients	HT No.	HT %	LT No.	LT %
Total significant	17	22%	20	44%
Total nonsignificant	61	78%	25	56%
Grand Total	78	100%	45	100%

HT/LT, sig./nonsig. : 2x2 χ^2

$\chi^2 = 6.960$, d.f. 1, $0.01>P>0.001^{**}$

Positively significant	12	15%	8	18%
Negatively significant	5	6%	12	27%
Grand Total	17		20	

HT/LT, +ve sig./-ve sig. : 2x2 χ^2

$\chi^2 = 3.462$, d.f. 1, $0.1>P>0.05$

Total significant				
Animal / animal	4	5%	5	11%
Animal / sediment	9	12%	12	27%
Sediment / sediment	4	5%	3	7%
Grand Total	17		20	
	$\chi^2 = 3.499$ d.f. 2 $0.2>P>0.1$		$\chi^2 = 6.428$ d.f. 2 $0.05>P>0.02^{*}$	

Animal/animal, animal/sediment, sediment/sediment sig. : 1x3 χ^2

Thirdly at low tide, there were more significant correlation coefficients between animal species and sediment parameters (animal/sediment) (12) than between pairs of animal species (animal/animal) (5) or between pairs of sediment parameters (sediment/sediment) (3) ($1x3\ \chi^2 = 6.428$, d.f. = 2, $0.05>P>0.02^*$). This means that at low tide there is more interaction between animal species and sediment parameters than there is between animal species or between sediment parameters. This effect is not significant at high tide site ($1x3\ \chi^2 = 3.499$, d.f.=2, $0.2>P>0.1$). In general therefore, at low tide site which is a high erosional environment, there is greater interaction between sediment properties and species abundance as compared to high tide site where conditions are not as extreme and the environment is more depositional.

Table 13 gives values of the correlation coefficients on the ln transformed data for (2.2.2.) high tide in the upper half (right hand side) and (2.2.3.) low tide in the lower half (left hand side). These will be now described.

2.2.2. High tide correlations

There were fewer significant correlations at high tide than at low tide. C. volutator was positively correlated with redox potential, and was therefore more abundant in the more aerobic sediments. N. diversicolor was positively correlated with water table and so was more abundant where the water table was well below the sediment surface. A. marina and C. volutator were both inversely correlated with arcsine % algal cover, and so were less abundant where the algal cover was high. P. elegans was inversely correlated with the standard deviation of the redox potential indicating a higher abundance of P. elegans associated with less variability in redox potential.

Figure 27 shows correlation coefficients between pairs of species. F. sabella was positively correlated with P. elegans, and C. volutator was positively correlated with both A. marina and N. diversicolor. This means that

Table 13.

Correlation coefficients beween species abundances and sediment parameters (ln transformed data). Upper right: High tide correlations. Lower left: Low tide correlations. Units: Shear strength : $kN.m^{-2}$; redox potential: mV; water table: cm; species abundance: $no.m^{-2}$. Probabilities: $0.05>P>0.02^{*}$; $0.02>P>0.01^{**}$; $P<0.01^{***}$.

	Shear Strength (mean)	*Shear Strength (s.d.)*	*Redox Potential (mean)*	*Redox Potential (s.d.)*	*Water Table*	*Arenicola marina*	*Bathyporeia guilliamsoniana*	*Corophium volutator*	*Fabricia sabella*	*Hydrobia neglecta*	*Macoma balthica*	*Nereis diversicolor*	*Pygospio elegans*	*Arcsine % algal cover*
Shear strength (mean)		0.899***	− 0.146	0.128	0.456***	− 0.168	—	0.121	0.004	0.135	− 0.161	0.320*	0.050	0.358***
Shear strength (s.d.)	0.822***		− 0.133	0.218	0.339**	− 0.060	—	0.074	− 0.103	0.109	− 0.044	0.235	− 0.021	0.315*
Redox Potential (mean)	0.277*	0.196		0.381***	0.201	− 0.032	—	0.371***	0.121	− 0.266	0.013	0.284	0.104	− 0.387***
Redox Potential (s.d.)	− 0.183	− 0.173	− 0.463***		0.146	− 0.067	—	0.019	− 0.172	− 0.110	− 0.050	0.054	− 0.312*	− 0.076
Water table	0.862***	0.716***	0.144	− 0.223		− 0.259	—	0.136	− 0.038	− 0.093	0.131	0.637***	0.011	0.164
Arenicola marina	0.456***	0.230	0.052	− 0.114	0.603***		—	0.309*	− 0.388***	0.090	− 0.022	− 0.136	− 0.209	− 0.504***
Bathyporeia guilliamsoniana	− 0.427***	− 0.350**	0.250	− 0.011	− 0.586***	− 0.404***		—	—	—	—	—	—	—
Corophium volutator	—	—	—	—	—	—	—		− 0.009	− 0.098	− 0.132	0.507***	− 0.087	− 0.397***
Fabricia sabella	—	—	—	—	—	—	—	—		− 0.128	− 0.025	− 0.071	0.523***	0.012
Hydrobia neglecta	—	—	—	—	—	—	—	—	—		− 0.101	− 0.085	0.032	0.089
Macoma balthica	− 0.479***	− 0.296*	− 0.062	0.210	− 0.535***	− 0.378***	0.485***	—	—	—		− 0.027	0.156	0.008
Nereis diversicolor	− 0.318*	− 0.379***	− 0.198	0.439***	− 0.360***	0.025	0.064	—	—	—	0.154		− 0.134	− 0.104
Pygospio elegans	0.160	0.075	− 0.197	0.173	0.125	− 0.023	− 0.138	—	—	—	− 0.049	0.012		− 0.109

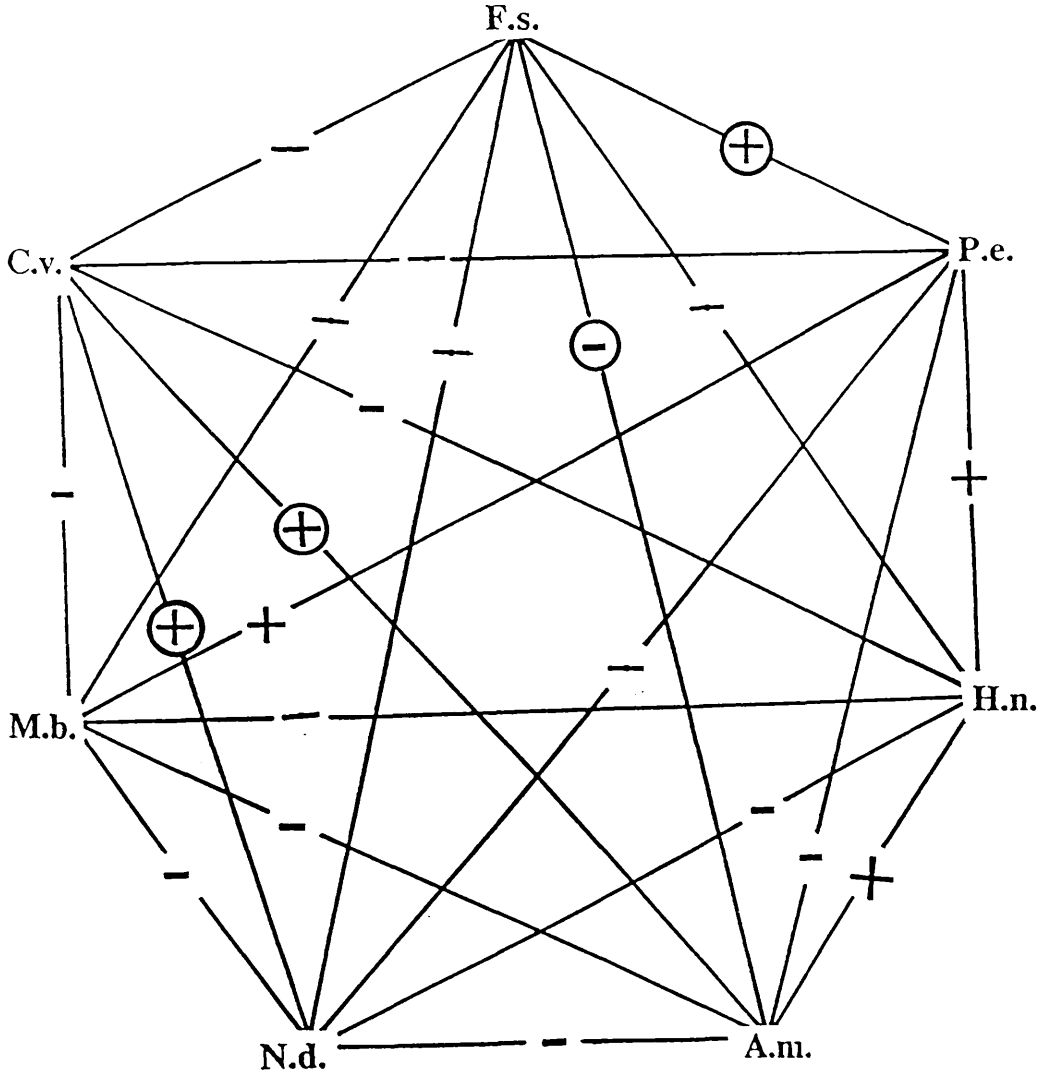


Figure 27. Correlation coefficients between species abundance at High tide site along the 50 m transect. The significant correlations are encircled.

A.m. Arenicola marina
C.v. Corophium volutator
F.s. Fabricia sabella
H.n. Hydrobia neglecta
M.b. Macoma balthica
N.d. Nereis diversicolor
P.e. Pygospio elegans

where one pair of species was abundant, so was the other. F. sabella was inversely correlated with A. marina. Hence where F. sabella was more abundant A. marina was less abundant, and vice versa.

Figure 28 shows correlation coefficients between pairs of sediment parameters. Shear strength and its standard deviation were positively correlated with both the arcsine % algal cover and water table. This reflects the high values of shear strength and its greater variability in the presence of algal cover and where the water depth was well below the sediment. Arcsine % algal cover was inversely correlated with redox potential and so areas having a high % algal cover had a lower redox potential. This was noticeable on the beach because the sediment in these areas was black just below the algal mat surface. The effect is probably caused by decaying algae and microbial degradation of the plant material.

2.2.3. Low tide correlations

There were more significant correlations at low tide than at high tide (Table 13). B guilliamsoniana and N. diversicolor were negatively correlated with mean shear strength and the water table. This means that B. guilliamsoniana and N. diversicolor were more abundant where the shear strength was low and the water table was close to or above the sediment surface. This tends to occur in the troughs of the sand waves. A. marina was positively correlated with mean shear strength and with level of the water table below the sediment surface. This means that A. marina was abundant where shear strength was high and the water table was below the sediment surface. This occurs at the peaks of the sand waves and reflects the greater abundance of A. marina there. M. balthica was negatively correlated with shear strength and also negatively correlated with the water table.

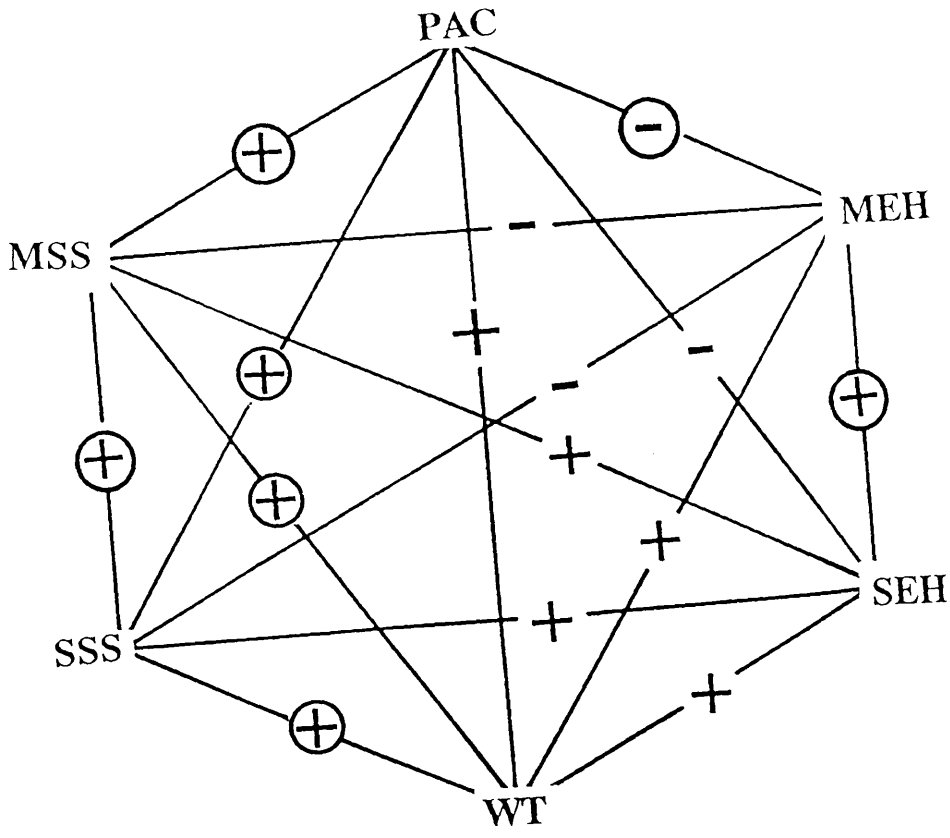


Figure 28. Correlation coefficients between sediment parameters at High tide site along the 50m transect. The significant correlations are encircled.

PAC Percent algal cover
MSS Mean shear strength
SSS Standard deviation in shear strength
MEH Mean Redox-potential (Eh)
SEH Standard deviation in Redox-potential (Eh)
WT Water table.

It is interesting to note that N. diversicolor is inversely correlated with the standard deviation of the shear strength but positively correlated with the standard deviation of the redox potential. N. diversicolor was therefore present in high numbers where variability in shear strength was low and where variability in redox potential was high. B. guilliamsoniana and M. balthica were negatively correlated with the standard deviation of shear strength and therefore occurred in low numbers where variation in shear strength was high.

Figure 29 shows the pairs of correlation coefficients between species. B. guilliamsoniana, and M. balthica were positively correlated with each other. A. marina was negatively correlated with M. balthica and B. guilliamsoniana.

Figure 30 shows correlation coefficients between the sediment parameters. The water table was positively correlated with the mean and standard deviation of the shear strength. This means that where the water depth was well below the sediment surface the shear strength was high and so was its variability (standard deviation). Shear strength was positively correlated with redox potential. This is to be expected, because shear strength will be high at the peaks of the sand waves where the sediment is exposed every tide and where it is therefore more aerobic.

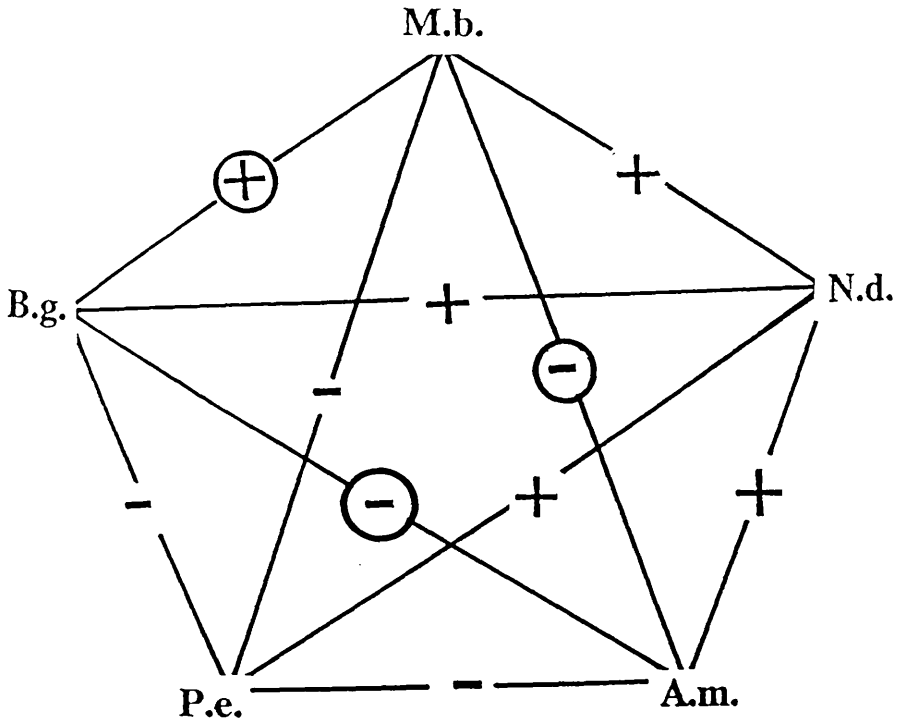


Figure 29. Correlation coefficients between species abundance at Low tide site along the 50 m transect. The significant correlations are encircled.

A.m. Arenicola marina
B.g. Bathyporeia guilliamsoniana
M.b. Macoma balthica
N.d. Nereis diversicolor
P.e. Pygospio elegans

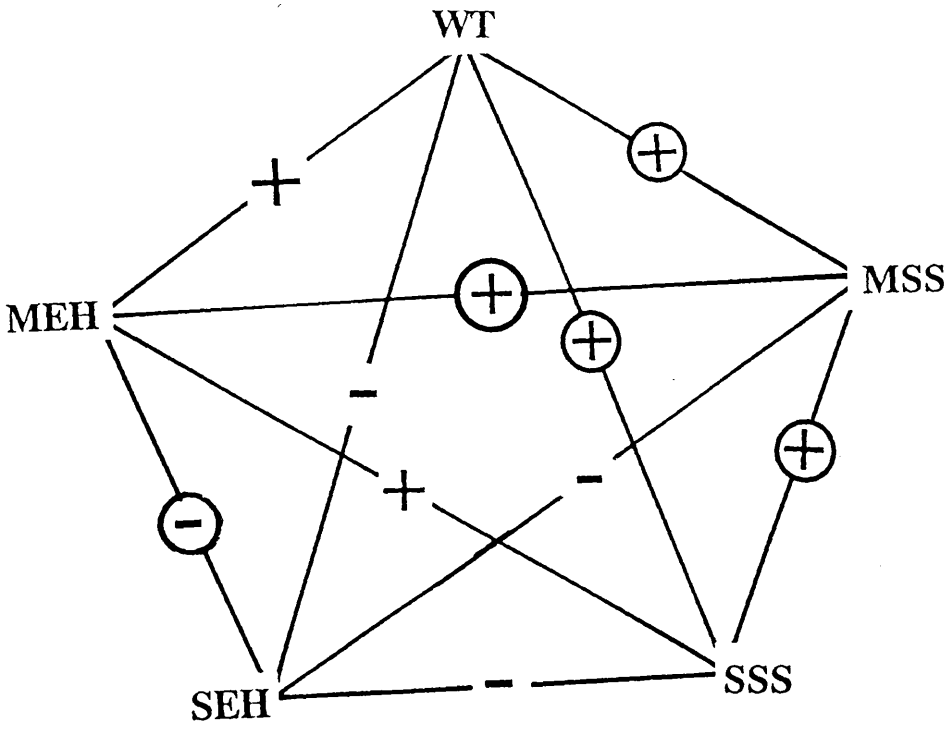


Figure 30. Correlation coefficients between sediment parameters at Low tide site along the 50 m transect. The significant correlations are encircled.

MSS Mean shear strength
SSS Standard deviation in shear strength
MEH Mean Redox-potential Eh
SEH Standard deviation in Redox-potential Eh
WT Water table.

2.3. Two additional methods of assessing heterogeneity

Two additonal methods were used to distinguish between macro-, meso- and micro-scale heterogeneity. Both methods compared scales of variability firstly along the high tide and low tide transects - micro-scale and meso-scale heterogeneity, and then between the high tide and low tide transects - macro-scale heterogeneity.

2.3.1. Method 1: Variance ratio method (sediment parameters only)

Reference should be made to Figure 14 for a full understanding of section 2.3.1. This method was applied to the shear strength and redox potential data, for which 4 readings were available in each quadrat. Four 1x50 one way analyses of variance were conducted on the ln transformed data (shear strength high tide, shear strength low tide, redox potential high tide, redox potential low tide). The results of these analyses are given in Tables 14 and 15 for shear strength at high and low tide, and in Tables 16 and 17 for redox potential at high and low tide. Each cell in each of the four analyses of variance contained 4 readings all of which had been taken within 1 m^2.

In the analyses of variance, the between quadrats variance (main effect) was taken as a measure of meso-scale variability between the quadrats along the transects (> 1m) (Figure 14). In a similar way, the within quadrats variance (residual effect) was taken as a measure of micro-scale variability within the $1m^2$ quadrats along the transects (< 1m) (Figure 14).

The comparison between meso-scale and micro-scale variability along each transect was assessed by the F ratios obtained from the one way analyses of variance (Figure 14). Tables 14 to 17 and Table 18 (upper half) give the F ratios of these analyses. All the four F ratios were statistically significant (shear strength HT, shear strength LT, redox potential HT, redox potential LT). This means that the meso-scale (between quadrat) variability

Table 14 . High tide site. 1x50 one-way analysis of variance comparing shear strength ($kN.m^{-2}$) between 1m quadrats along the 50m transect (1n transformed data).

Source of variation	SS	MS=SS/df	d.f.	F-ratio	P
Main Factor (Between quadrats)	67.83	1.384	49	4.856	$P<0.001^{***}$
Residual Error (Within quadrats)	42.72	0.285	150		
Total	110.5		199		

Table 15. Low tide site. 1x50 one-way analysis of variance comparing shear strength ($kN.m^{-2}$) between 1m quadrats along the 50m transect (1n transformed data).

Source of variation	SS	MS=SS/df	d.f.	F-Ratio	P
Main Factor (Between quadrats)	104.8	2.139	49	36.52	$P<0.001^{***}$
Residual Error (Within quadrats)	8.784	0.0586	150		
Total	113.6		199		

Table 16. High tide site. 1x50 one-way analysis of variance comparing Eh(mV) between and within 1m quadrats along the 50m transect (ln transformed data).

Source of variation	SS	MS=SS/df	d.f.	F-ratio	P
Main Factor (Between quadrats)	43.64	0.891	49	3.362	$P<0.001^{***}$
Residual Error (Within quadrats)	39.79	0.265	150		
Total	83.42		199		

Table 17. Low tide site. 1x50 one-way analysis of variance comparing Eh(mV) between and within 1m quadrats along the 50m transect (ln transformed data).

Source of variation	SS	MS=SS/df	d.f.	F-Ratio	P
Main Factor (Between quadrats)	2.716	0.0554	49	2.916	$P<0.001^{***}$
Residual Error (Within quadrats)	2.849	0.0190	150		
Total	5.565		199		

Table 18 . Comparison of meso-scale and micro-scale variability in the sediment parameters shear strength and redox potential at high and low tide sites (ln transformed data). The F ratios are calculated from the mean squares (MS) in the analyses of variance given in Tables 14-17

Comparison of Variability	$F = \frac{\text{greater MS}}{\text{lesser MS}}$	d.f.	P
Meso-scale/micro-scale variability			
Shear strength			
High Tide Site: Between/within $1m^2$ quadrats	$\frac{1.384}{0.285} = 4.856$	49,150	$P<0.001^{***}$
Low Tide Site: Between/within $1m^2$ quadrats	$\frac{2.139}{0.0586} = 36.50$	49,150	$P<0.001^{***}$
Redox Potential			
High Tide Site: Between/within $1m^2$ quadrats	$\frac{0.891}{0.265} = 3.362$	49,150	$P<0.001^{***}$
Low Tide Site: Between/within $1m^2$ quadrats	$\frac{0.0554}{0.0190} = 2.916$	49,150	$P<0.001^{***}$
High Tide Site/Low Tide Site variability			
Shear strength			
Meso-scale (between $1m^2$ quadrats) Low Tide/High Tide	$\frac{2.139}{1.384} = 1.546$	49,49	$0.1>P>0.05$
Micro-scale (within $1m^2$ quadrats) High Tide/Low Tide	$\frac{0.2850}{0.0586} = 4.863$	150,150	$P<0.001^{***}$
Redox Potential			
Meso-scale (between $1m^2$ quadrats) High Tide/Low Tide	$\frac{0.8910}{0.0554} = 16.08$	49,49	$P<0.001^{***}$
Micro-scale (within $1m^2$ quadrats) High Tide/Low Tide	$\frac{0.2650}{0.0190} = 13.95$	150,150	$P<0.001^{***}$

was greater than the micro-scale (within quadrat) variability for shear strength and for redox potential along both the high and low tide transects (see Figure 14).

The comparison of meso-scale variability at high tide site with meso-scale variability at low tide site which gave a macro-scale comparison was obtained by an F ratio which compared the anova between-quadrat variance at high tide with the anova between-quadrat variance at low tide site (Figure 14). In a similar way, the comparison of micro-scale variability at high tide with micro-scale variability at low tide site which gave a macro-scale comparison was obtained by an F ratio which compared the anova within-quadrat variance at high tide site with the anova within-quadrat variance at low tide site. Table 18 (lower half) gives the F ratios of these comparisons. Shear strength showed no difference in meso-scale variability between the high and low tide transects in spite of the very different sedimentary environments - the algal mats at high tide and the sand waves at low tide (Table 18, F = 1.546). Micro-scale variability in shear strength however was much higher at high tide site than at low tide site (Table 18, F = 4.863). Redox potential showed a highly significant difference in both meso-scale and micro-scale variability between the high and low tide transects. Hence for redox potential macro-scale variability between the high tide transect and the low tide transect occurred at both a meso- and micro-scale (Table 18, F = 16.08 and F = 13.95).

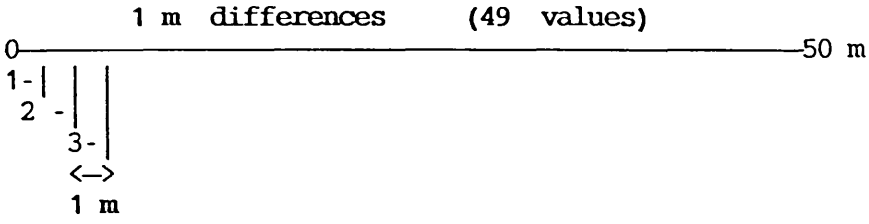
2.3.2. Method 2: Differences method

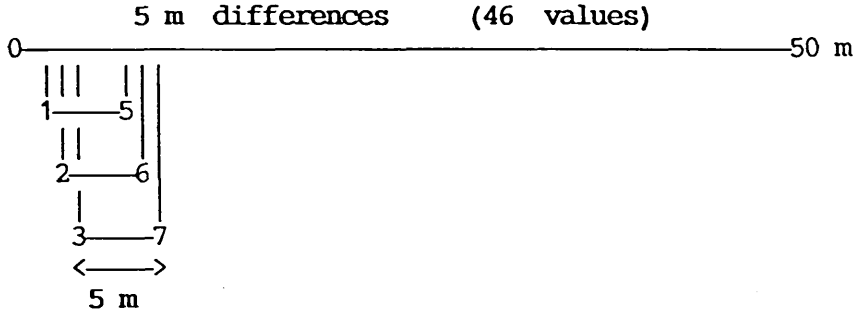
Reference should be made to Figures 15.1, 15.2 and 31 for a full understanding of section 2.3.2. In this method differences were obtained by subtraction of pairs of original data obtained from quadrats at successive 1m (micro-scale), 5m, 10m, 20m, 30m, and 40m (meso-scale) distances for species abundances, diversity indices and sediment parameters. For example for the 1m difference the abundance of a species in the first quadrat was subtracted from its abundance in the second quadrat, and the abundance in the second quadrat was subtracted from the abundance in the third quadrat, and so on. The 1m distances gave 49 differences, the 5m gave 46, the 10m gave 41, the 20m gave 31, the 30m gave 21, and the 40m distances gave 11 differences (Figure 31). In each case the absolute value of the difference was used. The differenced data for all the distances is given in Appendix 3 Tables 10 to 27. I wrote a computer program to calculate differences from the original data (I am grateful to Dr A.C. Reichelt for advice in computer programming). This program calculates the absolute values of the differences for pairs of distances. The flow chart, listing, and an example of a run of this computer program are given in Appendix 4.

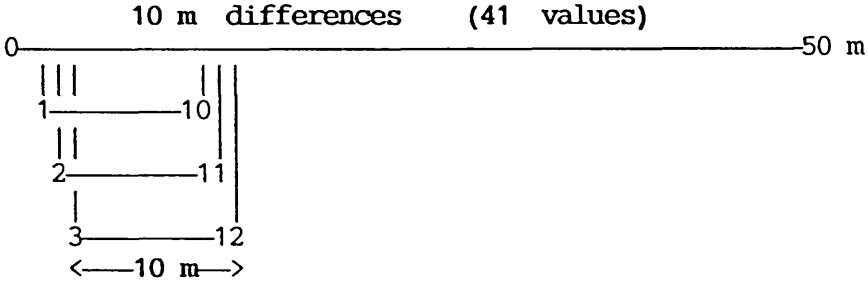
Table 19 gives the means and standard deviations of the 1m, 5m, 10m, 20m, 30m, and 40m differences data in species abundances and the Shannon Wiener diversity index for the high and low tide transects. The shear strength and redox potential data (means/quadrat) were also included, for comparison with method 1. The data in this table show that all 18 5m differences were greater than the 1m differences, that 15 out of the 18 10m differences were greater than the 5m differences, that 13 of the 18 10m differences were greater than the 20m, 30m, and 40m differences respectively. This means that in general the 1m differences were lowest and the 10m differences were highest.

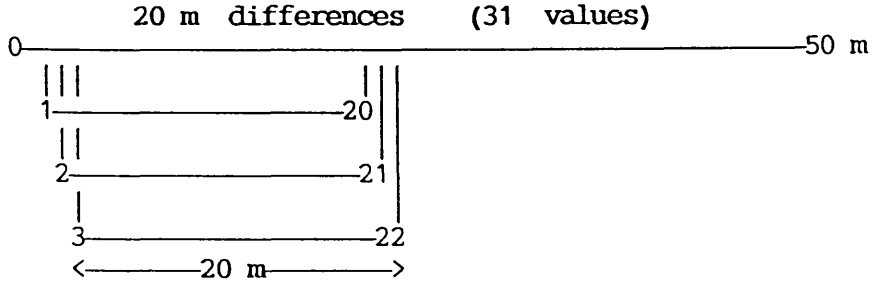
Figure 31. Meso- and micro-scale variability.

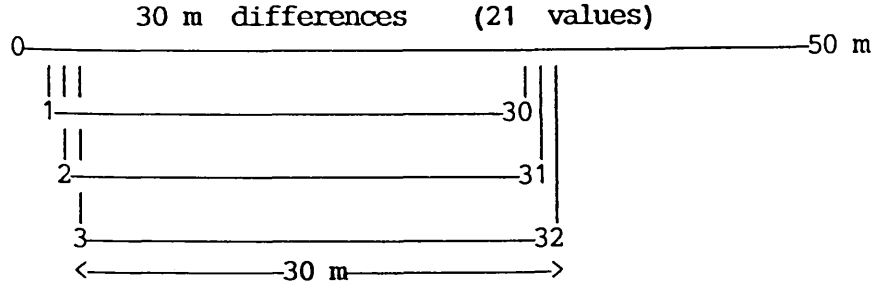
50 m transects showing how the 1m, 5m, 10m, 20m, 30m, and 40m differences were calculated. Values in brackets are the total number of differences obtained for the six distances, and figures directly below each transect line indicate the quadrat number (e.g. for the 5m differences: 1-5 means the difference between quadrat 1 and quadrat 5, 2-6 means the difference between quadrat 2 and 6, and so on).


1 m differences (49 values)
0
50 m
1-
2 -
3-
1 m


5 m differences (46 values)
0
50 m
1
5
2
6
3
7
5 m


10 m differences (41 values)
0
50 m
1
10
2
11
3
12
10 m


20 m differences (31 values)
0
50 m
1
20
2
21
3
22
20 m


30 m differences (21 values)
0
50 m
1
30
2
31
3
32
30 m

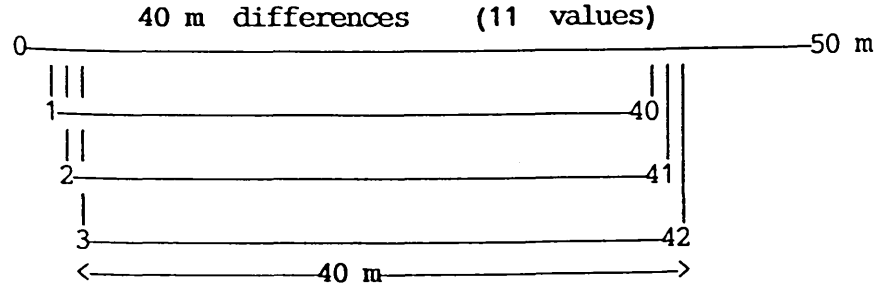

40 m differences (11 values)
0
50 m
1
40
2
41
3
42
40 m

Table 19.

Differences in species abundance (no.m^{-2}), in the Shannon Wiener diversity index, in values of shear strength (kN.m^{-2}) and redox potential (mV) at 1m, 5m, 10m, 20m, 30m amd 40m distances apart, along the high tide (HT) and low tide (LT) transects. Figures are means ± s.d.

Species		1m	5m	10m	20m	30m	40m
Arenicola marina	HT	29.8 ± 56.7	62.4 ± 92.4	67.1 ± 89.1	35.5 ± 78.5	72.1 ± 96.5	21.8 ± 28.3
	LT	12.4 ± 11.2	22.1 ± 17.7	24.4 ± 17.5	20.1 ± 18.1	22.7 ± 19.5	29.8 ± 23.7
Macoma balthica	HT	147 ± 212	174 ± 223	192 ± 231	178 ± 225	174 ± 231	278 ± 373
	LT	43.2 ± 62.2	81.9 ± 85.5	86.1 ± 91.3	64.5 ± 85.1	39.2 ± 56.9	96.3 ± 88.4
Nereis diversicolor	HT	826 ± 996	1223 ± 1315	1137 ± 1381	1435 ± 1402	1110 ± 996	1423 ± 1641
	LT	173 ± 140	271 ± 184	333 ± 217	273 ± 232	241 ± 172	300 ± 226
Pygospio elegans	HT	985 ± 976	1244 ± 1146	1476 ± 1244	1674 ± 1398	1300 ± 988	1337 ± 1390
	LT	3445 ± 3044	4030 ± 4058	4829 ± 4246	3987 ± 4168	5179 ± 4417	3167 ± 3547
Corophium volutator	HT	2613 ± 3338	3715 ± 3687	3301 ± 3222	4127 ± 3631	3380 ± 2856	2632 ± 2906
Fabricia sabella	HT	4218 ± 7307	6671 ± 10167	7059 ± 11130	10175 ± 13240	6642 ± 8432	6816 ± 10134
Hydrobia neglecta	HT	437 ± 425	473 ± 452	534 ± 389	520 ± 409	555 ± 536	439 ± 491
Bathyporeia guilliamsoniana	LT	1259 ± 1705	1568 ± 1728	2030 ± 1713	1033 ± 1599	1850 ± 1879	2044 ± 2305
Shannon Wiener diversity index	HT	0.304 ± 0.275	0.314 ± 0.266	0.360 ± 0.267	0.283 ± 0.243	0.309 ± 0.181	0.307 ± 0.211
	LT	0.205 ± 0.163	0.290 ± 0.235	0.493 ± 0.250	0.273 ± 0.247	0.393 ± 0.258	0.425 ± 0.286
Sediment parameters							
Shear Strength	HT	4.10 ± 5.95	5.33 ± 7.10	4.49 ± 4.05	4.48 ± 6.27	5.90 ± 8.00	3.80 ± 5.00
	LT	1.40 ± 1.08	3.20 ± 2.44	4.97 ± 2.74	3.29 ± 2.77	3.45 ± 2.45	2.81 ± 2.10
Redox Potential	HT	59.7 ± 47.4	85.6 ± 58.4	88.7 ± 62.0	99.0 ± 57.7	74.5 ± 60.0	65.9 ± 64.9
	LT	33.8 ± 30.5	38.3 ± 34.7	50.4 ± 35.4	38.4 ± 29.6	46.2 ± 43.4	36.6 ± 30.7

The differenced data was statistically analysed by a series of one way analyses of variance on the ln transformed data (Figures 15.1., 15.2). The results of these statistical analyses are presented below in 2.3.2.1. for micro-scale differences (1m) and meso-scale differences (5m, 10m, 20m, 30m and 40m), and in 2.3.2.2. for macro-scale differences (between the high and low tide differenced data).

2.3.2.1. Comparisons between meso- and micro-scale differences

A number of 1x6 one way analyses of variance were conducted to compare overall differences at 1m (micro-scale), and 5m, 10m, 20m, 30m, and 40m (meso-scale) distances along the high and low tide transects (Figure 15.1). This gave 18 anova in all. The 6 levels in the anova were the 1, 5, 10, 20, 30, and 40m differenced data for the species abundances, the Shannon Wiener diversity index, and the sediment parameters. The F ratios from these anovars are given in Table 20. Six out of the 18 comparisons were significant. Five of these were at low tide, and these included three of the four common species (A. marina, M. balthica, N. diversicolor), the Shannon Wiener diversity index and shear strength. The only significant anova at high tide was that for redox potential. In general, this indicates that there was more overall meso-scale and micro-scale variability along the low tide transect than along the high tide transect.

The 18 1x6 one way anova were followed by a series of 1x2 one way anova comparing pairs of differenced data (1/5, 1/10,....30/40m) for species abundances, the Shannon Wiener diversity index, and sediment parameters at high and low tide (Figure 15.1). These comparisons fell into two groups: 5 micro/meso-scale comparisons and 10 meso/meso-scale comparisons (Figure 15.1), giving 15 comparisons at high tide and 15 at low tide for each species, for the Shannon Wiener diversity index, for shear strength and for redox potential. The F ratios from these anovars are given in tables 21 to 31.

Table 20 . F ratios from the 18 1x6 one way analyses of variance comparing differences at 1m, 5m, 10m, 20m, 30m, and 40m distances apart along the 50m transect, for species abundances of (no.m^{-2}), values of diversity indices, and levels of sediment parameters at High and Low tide sites (ln transformed data).
Anovars not presented in thesis.

		F-ratio	d.f.'s	P
Species				
A. marina	HT	1.894	5, 193	0.1>P>0.05
	LT	2.729	5, 193	0.025>P>0.01*
M.balthica	HT	0.5143	5, 193	P>0.75
	LT	2.437	5, 193	0.05>P>0.025*
N.diversicolor	HT	1.991	5, 193	0.10>P>0.05
	LT	2.516	5, 193	0.05>P>0.025*
P.elegans	HT	0.9056	5, 193	0.50>P>0.25
	LT	1.075	5, 193	0.50>P>0.25
C.volutator	HT	0.4727	5, 193	P>0.75
F.sabella	HT	1.043	5, 193	0.50>P>0.25
H.neglecta	HT	0.4568	5, 193	P>0.75
B.guilliamsoniana	LT	1.802	5, 193	0.25>P>0.10
Diversity Index				
Shannon Wiener Diversity Index	HT	0.7330	5, 193	0.75>P>0.50
	LT	8.313	5, 193	P<0.001***
Sediment Parameters				
Shear strength	HT	0.4444	5, 193	P>0.75
	LT	7.368	5, 193	P<0.001***
Redox Potential	HT	2.783	5, 193	0.025>P>0.001*
	LT	1.355	5, 193	0.10>P>0.05

Table 21 . Shannon Wiener diversity index. Comparisons of differences between pairs of distances (m). F ratio from 30 one-way 1x2 anovars (ln transformed data). Anovars not presented in thesis.
Upper right: High tide site.
Lower left: Low tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		2.09	0.17	0.09	0.77	0.00
5	4.14*		0.92	2.49	0.09	0.73
10	43.48**	15.32***		0.43	0.25	0.05
20	2.08	0.10	14.09***		1.20	0.05
30	13.40***	2.59	2.21	2.89		0.40
40	11.73**	2.62	0.63	2.81	0.10	
	---------- Low tide site ----------					

Table 22 . Arenicola marina. Comparisons of differences in abundances between pairs of distances. F ratios from 30 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis. Upper right: High tide site.
Lower left: Low tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		3.12	5.00*	0.12	4.86*	0.18
5	2.56		0.28	1.54	0.66	0.54
10	12.98***	2.27		2.86	0.13	1.19
20	4.16*	0.10	2.47		3.31	0.03
30	2.68	0.05	1.72	0.00		2.11
40	3.75	0.65	0.00	0.82	0.56	
	---------- Low tide site ----------					

Table 23 . *Macoma balthica*. Comparisons of differences in abundances (no.m^{-2}) between pairs of distances (m). F ratios from 30 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis.
Upper right: High tide site.
Lower left: Low tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		0.48	1.32	0.48	0.24	1.88
5	6.16*		0.21	0.01	0.00	0.91
10	6.58*	0.04		0.11	0.16	0.46
20	1.49	0.82	1.06		0.01	0.67
30	0.05	4.18*	4.39*	1.28		0.64
40	5.29*	0.26	0.13	1.18	4.70*	
	---------- Low tide site ----------					

Table 24 . *Nereis diversicolor*. Comparisons of differences in abundances (no.m^{-2}) between pairs of distances (m). F ratios from 30 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis.
Upper right: High tide site.
Lower left: Low tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		8.40**	0.53	1.75	3.75	1.79
5	4.94*		4.15*	1.02	0.02	0.05
10	10.19**	1.14		0.44	1.81	0.82
20	1.54	0.46	2.60		0.40	0.15
30	3.02	0.00	0.83	0.33		0.01
40	2.40	0.10	0.14	0.48	0.09	
	---------- Low tide site ----------					

Table 25 . Pygospio elegans. Comparisons of differences in abundances ($no.m^{-2}$) between pairs of distances (m). F ratios from 30 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis.
Upper right: High tide site.
Lower left: Low tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		1.27	3.72	2.00	0.98	0.49
5	0.00		0.83	0.28	0.03	0.00
10	2.04	1.19		0.05	0.28	0.26
20	0.18	0.08	0.73		0.06	0.07
30	3.01	1.63	0.26	1.53		0.00
40	0.71	0.45	2.61	1.08	3.39	
	---------- Low tide site ----------					

Table 26 . Corophium volutator. Comparison of differences in abundances ($no.m^{-2}$) between pairs of distances (m). F ratios from 15 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis. High tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		2.27	0.11	0.63	0.33	0.00
5			1.06	0.21	0.31	0.90
10				0.20	0.08	0.04
20					0.01	0.24
30						0.14

Table 27. *Fabricia sabella*. Comparison of differences in abundances (no.m^{-2}) between pairs of distances (m). F ratios from 15 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis. High tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		0.33	0.48	4.85*	1.38	1.42
5			0.01	2.25	0.42	0.54
10				2.02	0.32	0.48
20					0.43	0.10
30						0.05

Table 28. *Hydrobia neglecta*. Comparison of differences in abundances (no.m^{-2}) between pairs of distances (m). F ratios from 15 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis. High tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		0.09	1.15	0.05	0.18	0.53
5			0.61	0.00	0.04	0.84
10				0.45	0.17	1.98
20					0.03	0.58
30						0.78

Table 29. Bathyporeia guilliamsoniana. Comparison of differences in abundances ($no.m^{-2}$) between pairs of differences (m). F ratios from 15 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis. Low tide site.

Metres	1	5	10	20	30
1					
5	0.25				
10	4.34*	2.18			
20	0.69	1.48	7.17**		
30	0.94	0.28	0.46	2.34	
40	1.74	0.87	0.00	3.15	0.27

---------- Low tide site ----------

Table 30 . Shear strength. Comparisons of differences in mean shear strength ($kN.m^{-2}$) between pairs of distances (m). F ratios from 30 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis.
Upper right: High tide site. Lower left: Low tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		0.97	1.66	0.79	0.73	0.01
5	6.80*		0.05	0.00	0.01	0.45
10	38.62***	6.56*		0.08	0.00	0.84
20	16.81***	0.71	3.80		0.02	0.47
30	13.05***	0.69	2.19	0.03		0.37
40	6.62*	0.15	2.34	0.05	0.11	
	---------- Low tide site ----------					

Table 31 . Redox potential (Eh). Comparisons of differences in mean redox potential (mV) between pairs of distances (m). F ratios from 30 1x2 one-way anovars (ln transformed data). Anovars not presented in thesis.
Upper right: High tide site. Lower left: Low tide site.

Metres	1	5	10	20	30	40
		---------- High tide site ----------				
1		5.61*	5.88*	11.36**	1.00	0.02
5	0.46		0.03	1.23	0.65	2.24
10	6.20*	3.03		0.78	0.81	2.32
20	0.57	0.01	2.28		2.83	4.98*
30	1.63	0.53	0.35	0.37		0.55
40	0.09	0.01	1.45	0.04	0.33	
	---------- Low tide site ----------					

Inspection of the F ratios in these tables and of the differenced data in Table 19 enabled me to draw up two tables which summarise the significant effects (Tables 32, 33). There were a number of cases where micro-scale differences (1m) were less than meso-scale differences (5, 10, 20, 30, and 40m). This was true for A. marina, M. balthica, N. diversicolor, F. sabella, B. guilliamsoniana, the Shannon Wiener diversity index and the two sediment parameters (Table 32). In contrast there were no cases where micro-scale differences were significantly greater than meso-scale differences. In some instances there were differences between different meso-scale distances. This was true for M. balthica, N. diversicolor, B. guilliamsoniana, the Shannon Wiener diversity index and the two sediment parameters (Table 32).

Table 33 shows that there were obvious differences between high and low tide in the numbers of significant micro/meso-scale comparisons, but no such difference in meso/meso-scale comparisons. Eighteen out of the 40 micro/meso-scale comparisons were significant at low tide but only 7 out of 50 at high tide. This difference was significant when tested by χ^2 (2×2 χ^2, 18/22 : 7/43, χ^2 = 10.60, d.f.=1, $0.01>P>0.001^{**}$). In contrast, there were few significant meso/meso-scale comparisons either at high tide or at low tide (2/100 and 7/80 respectively), although again there were significantly more at low tide (7/80) than at high tide (2/100) (2×2 χ^2, 2/98 : 7/73, χ^2 = 4.263, d.f.=1, $0.05>P>0.02^{*}$).

Overall, there were more significant micro/meso-scale comparisons (25 out of 90) than there were significant meso/meso-scale comparisons (9 out of 180) (2×2 χ^2, 25/65 : 9/171, χ^2 = 28.28, d.f.=1, $P<0.001^{***}$), and in all of these the micro-scale difference was less than the meso-scale difference (micro<meso in Table 33).

Table 32 . Number of significant F ratios for micro/meso-scale and meso/meso-scale differences at high and low tide sites from the 1x2 one way analyses of variance on species abundances, Shannon Wiener diversity index and sediment parameters.

		Number of significant F ratios		
		Micro/meso-scale		Meso/meso-scale
		Micro<meso	Micro>meso	
Species				
A. marina	HT	1m<10,30m	0	0
	LT	1m<10,20m	0	0
M.balthica	HT	0	0	0
	LT	1m<5,10,40m	0	30<5,10,40m
N.diversicolor	HT	1m<5m	0	10<5m
	LT	1m<5,10m	0	0
P.elegans	HT	0	0	0
	LT	0	0	0
C.volutator	HT	0	0	0
F.sabella	HT	1m<20m	0	0
H.neglecta	HT	0	0	0
B.guilliamsoniana	LT	1m<10m	0	20<10m
Diversity Index				
Shannon Wiener	HT	0	0	0
Diversity Index	LT	1m<5,10,30,40m	0	5<10m; 20<10m
Sediment Parameters				
Shear	HT	0	0	0
strength	LT	1m<5,10,20,30,40m	0	5<10m
Redox	HT	1m<5,10,20m	0	40<20m
Potential	LT	1m<10m	0	0

Table 33 . Numbers of significant (s) and nonsignificant (ns) micro- and meso-scale comparisons by 1x2 one way analyses of variance of differenced data.

	Micro/meso-scale comparisons				Total		
	Micro<meso		Micro>meso				
	s	ns	s	ns	s	ns	Total
HT	7	40	0	3	7	43	50
	47		3				
LT	18	19	0	3	18	22	40
	37		3				
Total	25	59	0	6	25	65	90

	Meso/meso-scale comparisons		
	s	ns	Total
HT	2	98	100
LT	7	73	80
Total	9	171	180

2.3.2.2. Macro-scale comparisons of differenced data between high and low tide

A series of 1x2 one way analyses of variance were conducted to compare macro-scale differences between high and low tide sites at 1m, 5m, 10m, 20m, 30m, and 40m for species abundances, Shannon Wiener diversity index and the sediment parameters (Figure 15.2). The F ratios of these analyses are given in Table 34. They show that most of the high tide differences were greater than the low tide differences for M. balthica, N. diversicolor and redox potential while the high tide differences were less than the low tide differences for P. elegans. Only one distance was different for the Shannon Wiener diversity index (10m, high tide < low tide) and only one for shear strength (1m, high tide > low tide).

Table 34. Comparison of differences in species abundances, Shannon Wiener diversity index, and sediment parameters at 1m, 5m, 10m, 20m, 30m, and 40m distances between high tide (HT) and low tide (LT).
F ratios from 42 1x2 one way analyses of variance (ln transformed data). Anovars not presented in thesis.

Distances(m)	1	5	10	20	30	40
Species						
A. marina	0.03	0.36	0.04	1.32	1.46	1.67
M. balthica	11.45*** HT>LT	6.35* HT>LT	7.79* HT>LT	6.80* HT>LT	7.13* HT>LT	1.95
N. diversicolor	5.68* HT>LT	19.35*** HT>LT	0.28	4.80* HT>LT	8.12** HT>LT	2.05
P. elegans	25.79*** HT<LT	15.51*** HT<LT	17.81*** HT<LT	7.78** HT<LT	11.48** HT<LT	1.87
Shannon Wiener Diversity Index	3.40	1.37	13.30*** HT<LT	0.02	0.80	1.76
Sediment Parameters						
Shear strength	11.10** HT>LT	1.49	1.25	0.14	0.07	0.08
Redox Potential	9.66** HT>LT	23.91*** HT>LT	10.59** HT>LT	30.25*** HT>LT	3.07	1.01

MICROBIAL COMMUNITIES

Colonisation and growth occurred on grains in all the sediment cores. The organisms included bacteria, blue-green algae, pennate diatoms, fungal mycelia and the fungus Thraustochytrium, some unidentified forms, and detrital material. The results are divided into two parts - a descriptive account of the microorganisms present in the different treatments and a quantitative analysis of their relative abundances. There is a small amount of overlap between the two parts, but this is necessary in order to provide a proper account of the data. In the descriptive part I have defined the scales as follows. For the comparison of species on an individual sand grain - micro-scale (≤1mm) (I have not studied), comparison of species on different sand grains in the same medium - meso-scale (>1mm - ≤10cm), and comparison of the same species in different media or environments - macro-scale (> 10cm).

1. Descriptive account of microorganisms present in different treatments

1.1. Sediment enriched with photosynthetic medium, incubated in the light (ML)

More growth occurred on subangular than on subrounded grains (Russell & Taylor, 1937; Weise & Rheinheimer, 1978; Nickels et al., 1981). The reasons for this interesting observation are discussed in the discussion. Clumps of 3 to 7 grains were sometimes bound together by dense growth of filamentous blue-green algae and pennate diatoms (Plate 6A).

The dominant pennate diatom, Amphora sp. B (Plate 6F), grew on flat surfaces either in monospecific colonies or in mixed colonies with filamentous blue-green algae. Dividing Amphora cells were often arranged in a pattern resembling the segments of an orange and were sometimes lodged in crevices. This diatom sometimes occurred on an unidentified biofilm (Plate

Plate 6. SEM photomicrographs. Microorganisms on sand grains in sediment enriched with photosynthetic medium, incubated in the light.

A. Clumping of sand grains caused by microbial growth. Scale bar, 200 μm.

B. Diatom: Amphora sp. A. Scale bar, 10 μm.

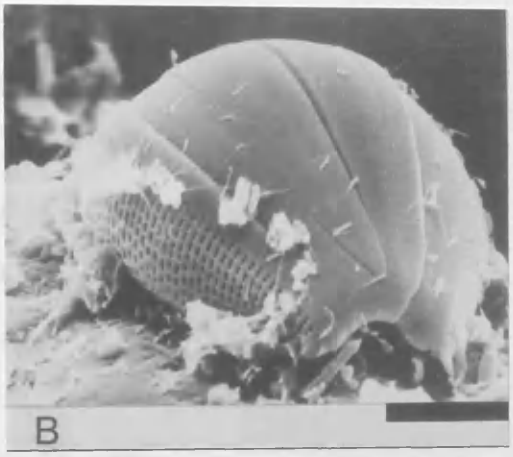
C. Aseptate blue-green alga forming loops (arrowed) among diatoms and detrital aggregates. Scale bar, 20 μm.

D. Biofilm (arrowed) with diatoms and blue-green algae. Scale bar, 20 μm.

E. Filamentous mat of blue-green alga Schizothrix and Amphora sp. B. Scale bar, 20 μm.

F. A colony of Amphora sp. B. Scale bar, 10 μm.


A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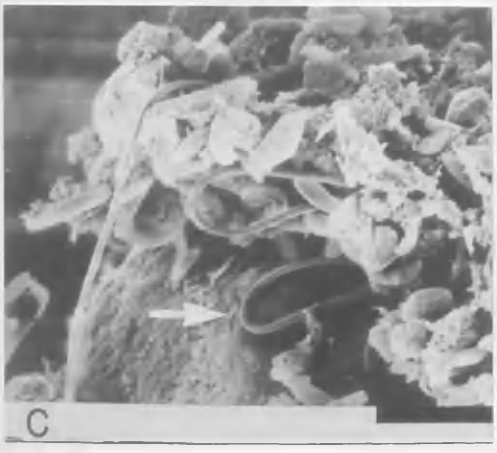
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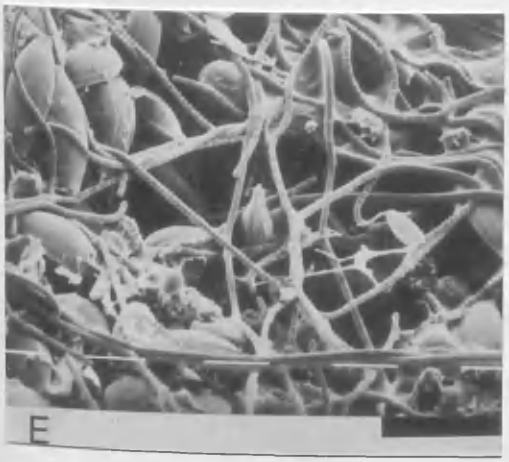

E


F

6D). An unusual pennate diatom (Amphora sp. A) was occasionally seen (Plate 6B). Its surface was covered by bacteria with pointed heads and cylindrical tails, whose average length was 3 μm. Other rods and cocci were also attached to the diatom's surface. A pennate diatom Rhaphoneis sp. formed chains (Plate 6G).

Two species of filamentous blue-green algae were observed. The more common species, Schizothrix sp. (Plate 6E), either grew in mixed colonies with Amphora sp. B cells and or in single species colonies in grooves. The other species appeared to be aseptate, and formed loops that emerged from dense growths of diatoms, bacteria, and detritus (Plate 6C).

A fine filamentous network of possible microbial origin was seen on one sand grain (Plate 7A). A less regular network has been recorded by Sieberth (1975) which he calls filamentous bacteria. Aggregates of 4 to 10 irregular cells (average diameter 6 μm) were sometimes found among the microbial growth (Plate 6I). Another unidentified species formed stellate colonies (Plate 6J). Each filament of this species had a nodulated structure with a tapering end and an average length of 8 μm. A hypotrichid ciliate was recorded (Plate 6H).

1.2. Sediment enriched with photosynthetic medium, incubated in the dark (MD).

Microbial growth occurred mainly in crevices and depressions. Blue-green algae and diatoms were very rare. Bacterial rods, cocci, a few filaments, and detrital aggregates were present. Clumping of sand grains was rare. Flakey material covered a large proportion of most grains particularly in hollows.

Long fungal-like hyphae were common (average diameter 0.3 μm). They either adhered to the grain surface or stretched from one point to another on the same grain or to an adjacent grain (Plate 7B). They originated in aggregates of bacteria and detritus. Very small clumps of material (diameter c. 3.3 μm) sometimes occurred along the length of the hyphae.

Plate 6 contd. SEM photomicrographs. Microorganisms on sand grains in sediment enriched with photosynthetic medium, incubated in the light.

G. A chain-colony of the diatom Rhaphoneis. Scale bar, 10 μm.

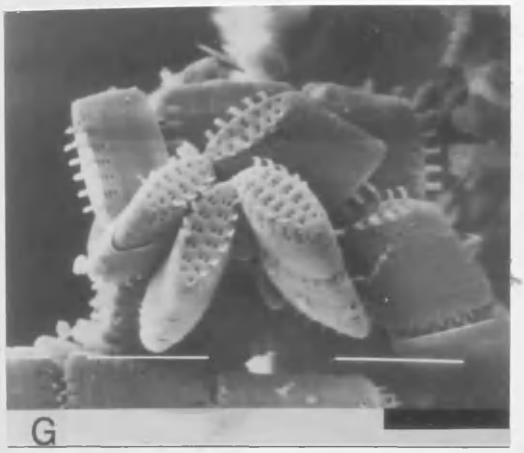
H. A Hypotrichid ciliate. Scale bar, 20 μm.

I. An aggregate of unidentified irregular-shaped cells (arrowed). Scale bar, 10 μm.

J. An assemblage of unidentified stellate colonies. Scale bar, 30 μm.

K. Two Thraustochytrium sporangia (left arrows) with a blue-green algal filament (right arrow). Scale bar, 20 μm.

L. A Thraustochytrium sporangium with pores (arrowed). Scale bar, 10 μm.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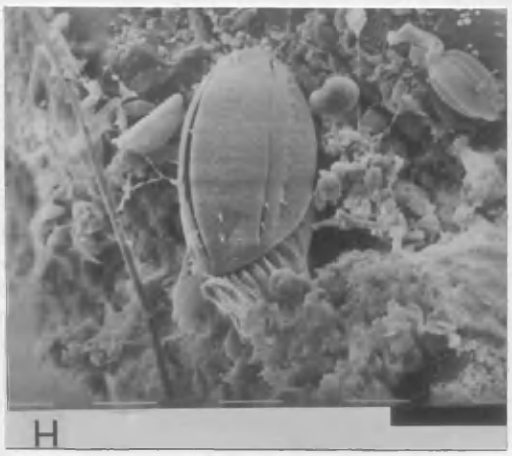
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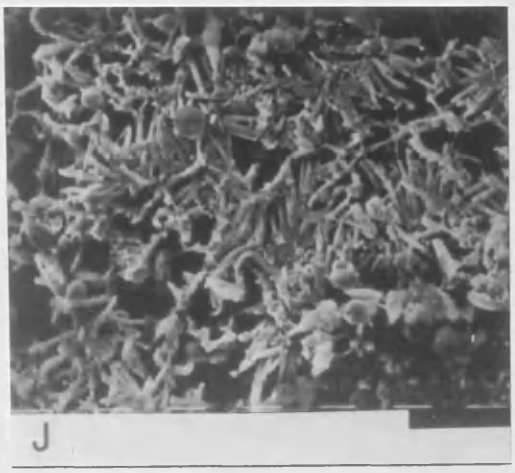
I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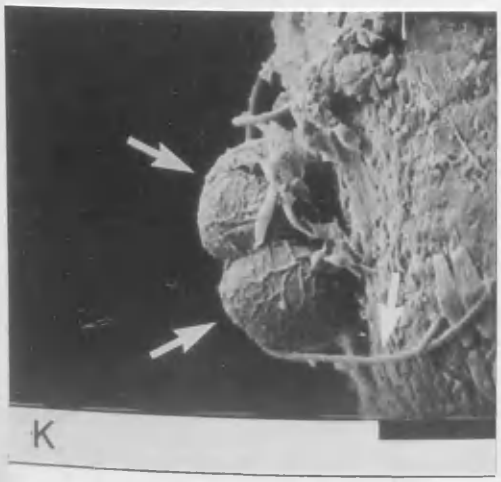

K

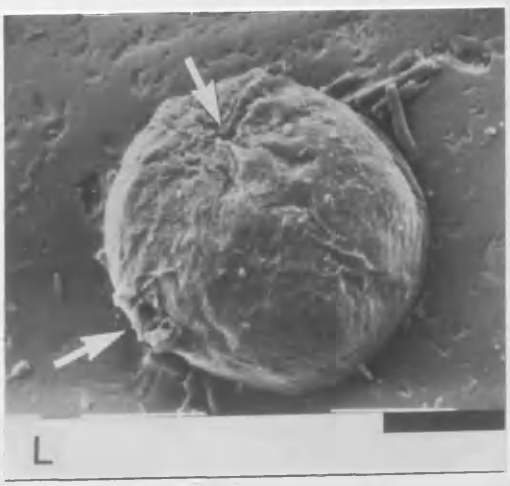

L

Plate 7. SEM photomicrographs. Microorganisms on sand grains in sediment enriched with: photosynthetic medium, incubated in the light (A), incubated in the dark (B), and bacterial medium, incubated in the light (C-F).

A. Fine filamentous network. Scale bar, 20 μm.

B. Fungal-like hyphae (arrowed). Scale bar, 30 μm.

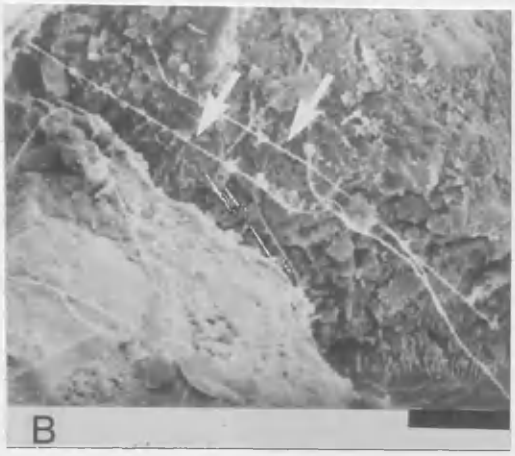
C. A sand grain with dense microbial growth. Scale bar, 200 μm.

D. Caulobacter. Scale bar, 10 μm.

E. A compact colony of coccoid bacteria with surrounding growth-free zone. Scale bar, 20 μm

F. A colony of coccoid bacteria. Scale bar, 10 μm.


A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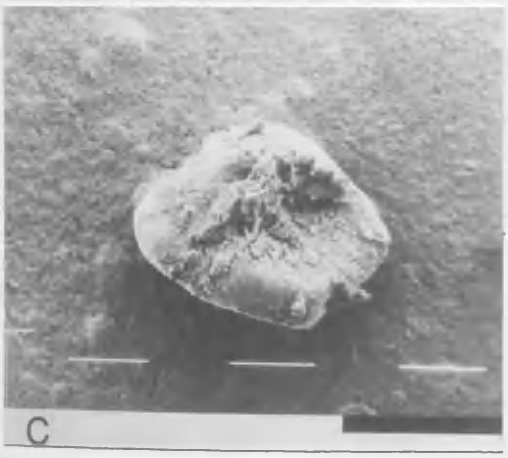
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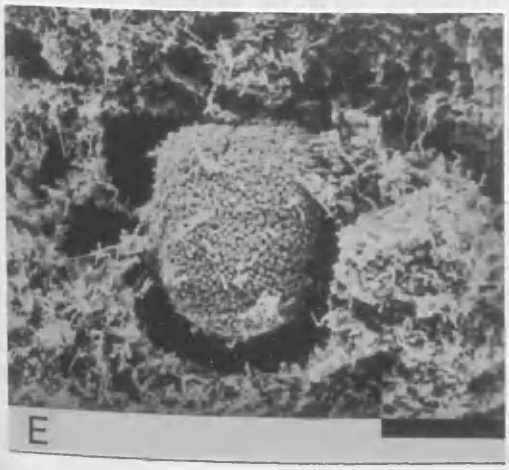
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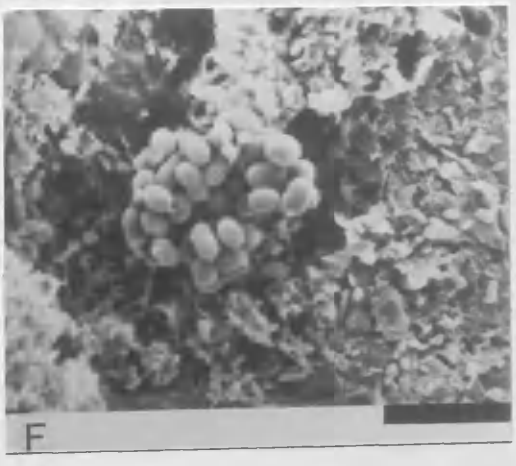

F

1.3 Sediment enriched with bacterial medium, incubated in the light (BL).

Microbial mats were common and contained rods, cocci, filaments and detrital aggregates. In some cases the microbial growth formed mounds (Plate 7C). Filamentous bacteria sometimes formed a characteristic network amongst and above other bacteria and detritus (Plate 7G). Scattered bacteria and detrital aggregates also occurred on flat bare surfaces, and Caulobacters were occasionally seen (Plate 7D).

Two types of coccoid bacteria were seen in this sediment and also in the sediment enriched with bacterial medium incubated in the dark. The first species had an average cell diameter of 2 μm and many of the cells were dividing. It either formed microcolonies of 15 to 50 cells (Plate 7F) or its cells were scattered; in both cases polymer strands connected the cells. The second species had an average diameter of 0.6 μm and formed compact spherical microcolonies of 50-150 cells with a distinct growth-free zone around them (Plate 7E).

1.4. Sediment enriched with bacterial medium, incubated in the dark (BD).

Dense growth occurred more often on subrounded than on subangular grains, and cocci and rods formed thick irregular mats. A few filamentous bacteria were also seen. Dense aggregates of a short bacillus (length c. 2 μm) were embedded in a characteristic film (Plate 7H). Similar films have been recorded by Sieberth (1975) on suspended particles. A number of other recognisable bacteria were seen including Caulobacter and Flexibacter (Plate 7I). Spirochaetes though few in number occurred in close association with other bacteria and detrital aggregates. Fine thread-like strands were observed on some surfaces. They appear to bridge between bacterial cells and detritus (Plate 7J).

Plate 7 contd. SEM photomicrographs. Microorganisms on sand grains in sediment enriched with: bacterial medium, incubated in the light (G), bacterial medium, incubated in the dark (H-J), and control unenriched sediment (K & L).

G. A characteristic network of filamentous bacteria (arrowed). Scale bar, 20 μm.

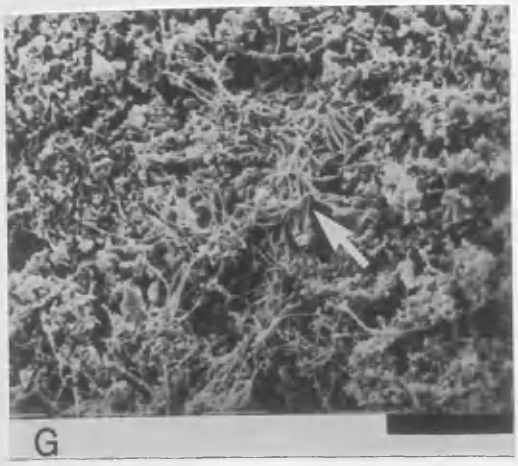
H. Bacilli embedded in a film. Scale bar, 10 μm.

I. A Flexibacter (arrowed) with other bacteria and detritus. Scale bar, 10 μm.

J. Very fine thread-like strands (arrowed) interconnecting rods, cocci and detrital aggregates. Scale bar, 5 μm.

K. Flakey material in a sand grain crevice. Scale bar, 20 μm.

L. Colony of blue-green alga Agmenellum. Scale bar, 10 μm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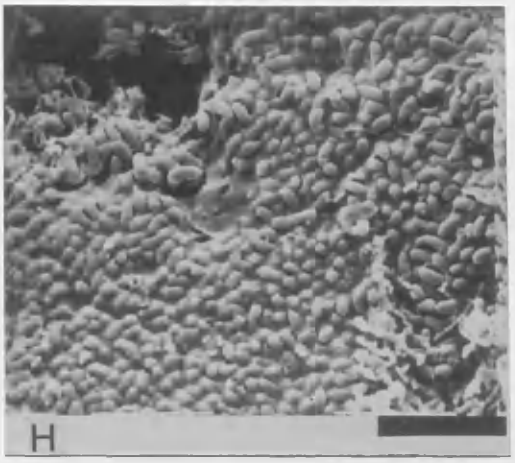
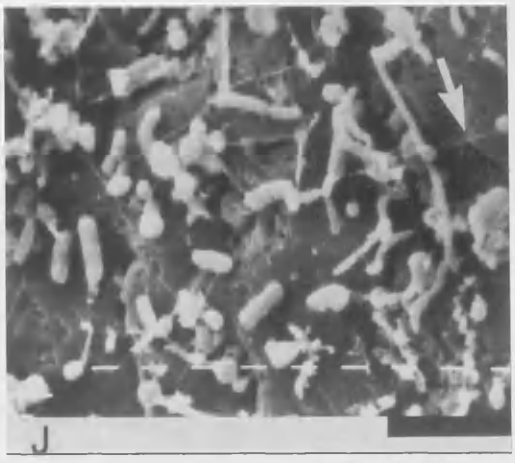

H


I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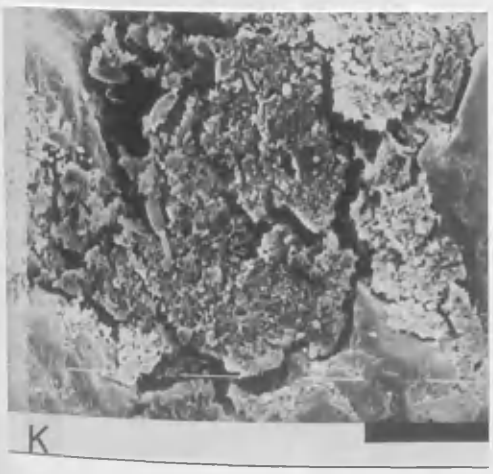
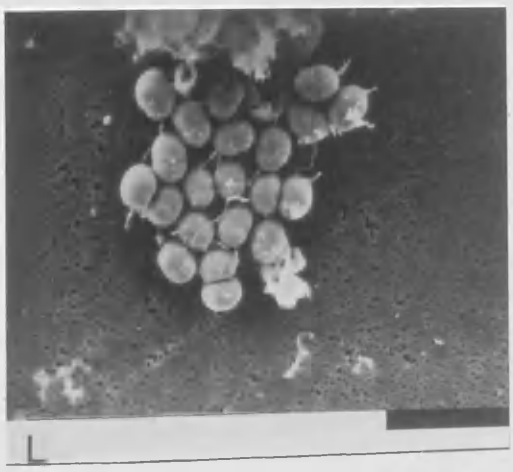

K


L

1.5. Control: unenriched sediment (C)

There were very few microbial cells and colonies on sand grains in the control sediment. A few bacterial microcolonies of 10 to 20 cells were found - mainly in depressions. Flakey material occurred in crevices (Plate 7K), and some flat colonies of the blue-green alga Agmenellum sp. were noted (Plate 7L).

1.6. Occurrence of Thraustochytrium sp.

Sporangia of an unusual marine fungal species, Thraustochytrium, occurred in the ML sediment.

The sporangium was a thick-walled semi-globular structure with a corrugated surface (Plate 6K). Nearly all the sporangia had a well-developed pore, and some had two (Plate 6L, arrows).

Their dimensions, abundance and distribution in relation to other microorganisms on sand grain surfaces are shown in Table 35. Thraustochytrids occurred among diatoms, bacteria and detritus, or near blue-green algal filaments. They were also found on flat bare surfaces. The mean number of Thraustochytrids per sand grain was 1.429 ± 0.6462. Some sporangia had bacteria on their surfaces; these bacteria were mainly cocci.

Table 35 . Dimensions, abundance and distribution of Thraustochytrium sporangia on grains enriched with photosynthetic medium, incubated in the light (No. sporangia = 20).

Sporangium dimensions	Mean	s.d.
Diameter (μm)	24.36	3.779
Surface area (μm^2)	1908.54	623.46
Abundance		
Number / sand grain	1.429	0.6462

Distribution in relation to other microorganisms	Percentage
Adjacent to diatoms	25
Amongst mats of blue-green algal filaments, diatoms, bacteria and detritus	10
Embedded in aggregates of bacteria, detritus and blue-green algal filaments	5
Amongst diatoms, bacteria and detritus	20
Near or below blue-green algal filaments	25
On flat bare surfaces of sand grains	10
On surface of biofilm	5

Number of bacteria/sporangium	Mean	s.d.
Cocci	6.833	9.488
Bacilli	1.944	3.421
Total	8.778	8.815

2. Quantitative analysis of data

Quantitative data on the abundances of the different groups of microorganisms on the sand grains in the different media (number of cells mm^{-2} sand grain surface) obtained from SEM photomicrographs, are given in Table 36 and show the following general points. The number of cells were always higher in the enriched sediments than in the control unenriched sediment. ML sediment contained a large number of diatoms and blue-green algae but relatively few bacteria. MD sediment contained no diatoms or blue-green algae, but more bacteria than the ML sediment. BL sediment contained no diatoms and only a few blue-green algae, but many morphological types of bacteria. BD sediment contained no diatoms or blue-green algae and fewer bacteria.

The data in Table 36 were then statistically analysed as follows.

(i) Analyses of variance were applied to the ln transformed data to compare overall differences between the means of the abundances. These were followed by Student's t-tests again applied to the ln transformed data comparing, differences between pairs of means.

(ii) F ratios were applied to the untransformed data to assess the relative variability between the two untransformed abundances being compared.

Note: It is important not to confuse these latter F ratios on untransformed abundance data (ii), with the F ratios that are an integral part of the one way analyses of variance that were conducted on the ln transformed abundance data in (i).

The statistical comparisons in (i) and (ii) were firstly conducted to test differences between media (differences between treatments) (macro-scale) for each species in turn (Table 36, comparisons between columns for each row in turn), and secondly to compare differences between species for each

Table 36 . Microbial mean abundance on enriched and control unenriched sand grains (No. cells mm^{-2} sand grain surface; S.D.= standard deviation; - = absent).

		Enriched Sediments				Control
		Photosynthetic medium		Bacterial medium		unenriched sediment
		Light ML	Dark MD	Light BL	Dark BD	C
DIATOMS						
Amphora	Mean	4.840	-	-	-	-
sp.A	S.D.	10.82	-	-	-	-
Amphora	Mean	1511	-	-	-	289
sp.B	S.D	1185	-	-	-	647
Rhaphoneis	Mean	2245	-	-	-	-
sp.	S.D.	2145	-	-	-	-
BLUE-GREEN ALGAE						
Schizothrix	Mean	97235	-	6942	-	-
sp.	S.D.	79657	-	15524	-	-
Agmenellum	Mean	-	-	-	-	92124
sp.	S.D.	-	-	-	-	56677
BACTERIA						
Cocci sp.	Mean	28927	51848	130831	9390	23031
(diam.0.6 μm)	S.D.	13568	40831	59209	2181	41872
Cocci sp.	Mean	-	-	108639	38799	-
(diam.2 μm)	S.D.	-	-	48716	31600	-
Bacilli	Mean	19670	39120	102690	86450	50057
	S.D.	3169	21869	40175	41890	95557
Caulobacter	Mean	-	-	12225	2445	-
	S.D.	-	-	17289	3348	-
Spirochetes	Mean	-	-	24450	9780	-
	S.D.	-	-	17289	13392	-
Filamentous	Mean	7204	733.5	21874	26764	4890
(isolated)	S.D.	10065	10934	18223	21596	10934
FUNGI						
Thraustochytrium	Mean	38.80	-	-	-	-
sp.	S.D.	53.13	-	-	-	-

medium (treatment) (meso-scale) in turn (Table 36 comparisons between rows for each column in turn). The results of these analyses are given in Tables 37 and 38.

It should be noted that when comparing the means, anovars were only used when there were more than two means. Secondly, some t-tests and F ratios were not conducted because some of the species were only observed in one treatment (medium). For example two of the three diatom species (Amphora sp. A, Rhaphoneis sp.) were only found in the ML treatment and one of the two blue-green algae (Agmenellum sp.) was only found in the control unenriched sediment.

2.1. Comparisons between treatments (media) macro-scale - between columns of Table 36

One way analyses of variance comparisons (Table 37) on the ln transformed abundances were only conducted on bacterial cocci (diameter 0.6 μm), bacterial bacilli, and filamentous bacteria. The anova for the cocci were both significant (ML/MD/BL/BD/C and ML/MD/BL/BD) showing that overall there were significant differences between the abundances in the treatments. These anovars were followed by Student's t-tests on the ln transformed data comparing differences between means, and then by F ratios on the untransformed data comparing differences between variances (relative variability of the two samples being compared).

The results of comparisons between treatments (media) by t-tests and by F ratios are given in Table 39. I have also drawn diagrams for each species showing (a) the significant and nonsignificant differences between the means of the abundances, and (b) the significant and nonsignificant differences between the variances of the abundances in the different media, so that the important effects that I wish to draw attention to can be more easily understood. These effects are as follows.

Table 37. One way analyses of variance (anovars) on abundances of microorganisms on sand grains. Anovars were conducted on ln transformed data. There were 5 readings per cell in each anovar (i.e. readings from 5 separate sand grains). Only the F ratios from the anovars are given. Comparison between media for Cocci (diam. 0.6 μm), Bacilli, and Filamentous bacterial species. Media: ML = photosynthetic light, MD = photosynthetic dark, BL = bacterial light, BD = bacterial dark, C = control.

Bacterial species	Media compared by anovars	F ratio	d.f.	P
Cocci (0.6 μm)	ML/MD/BL/BD/C	3.21	4, 20	0.05>P>0.025*
Cocci (0.6 μm)	ML/MD/BL/BD	25.31	3, 16	P<0.001***
Bacilli	ML/MD/BL/BD/C	2.04	4, 20	0.25>P>0.1
Bacilli	ML/MD/BL/BD	1.49	3, 16	0.25>P>0.1
Filamentous bacteria	ML/MD/BL/BD/C	2.54	4, 20	0.1>P>0.05
Filamentous bacteria	ML/MD/BL/BD	1.83	3, 16	0.25>P>0.1

Table 38. One way analyses of variance (anovars) on abundances of microorgaisms on sand grains. Anovars were conducted on ln transformed data. There were 5 readings per cell in each anovar (i.e. readings from 5 separate sand grains). Only the F ratios from the anovars are given. Comparison between species in each medium. Species: Amphora sp. A = AA, Amphora sp. B = AB, Rhaphoneis sp. = R, Agmenellum sp. = Am, Cocci (diam. 0.6 μm) = Cs, Cocci (diam. 2 μm) = Cb, Bacilli = B, Caulobacter sp. = C1, Spirochetes = Sp, Filamentous bacteria = F, Thraustochytrium sp. = T. Media: ML = photosynthetic light, MD = photosynthetic dark, BL = bacterial light, BD = bacterial dark, C = control; Schizothrix sp. = S.

Medium	Species compared by anovars	F ratio	d.f.	P
ML	AA/AB/R/S/Cs/B/F/T	6.03	7, 32	$P<0.001^{***}$
ML	AA/AB/R/S	4.87	3, 16	$0.025>P>0.01^{*}$
ML	Cs/B/F	4.06	2, 12	$0.05>P>0.025^{*}$
MD	Cs/B/F	3.44	2, 12	$0.1>P>0.05$
BL	S/Cs/Cb/B/C1/Sp/F	5.34	6, 28	$P<0.001^{***}$
BL	Cs/Cb/B/C1/Sp/F	3.62	5, 24	$0.025>P>0.01^{*}$
BD	Cs/Cb/B/C1/Sp/F	6.08	5, 24	$P<0.001^{***}$
C	AB/Am/Cs/B/F	4.84	4, 20	$0.01>P>0.005^{**}$
C	Cs/B/F	1.68	2, 12	$0.25>P>0.1$

Table 39. Abundance of species (no. mm^{-2} sand grain surface) in the five media.

ML photosynthetic medium incubated in the light
MD photosynthetic medium incubated in the dark
BL heterotrophic medium incubated in the light
BD heterotrophic medium incubated in the dark
C control

(i) Student's t comparing means of ln transformed data of the same species between pairs of media.

(ii) F ratio comparing variances of untransformed data of the same species between pairs of media.

TABLE 39.

Species	Medium	Mean	s.d.	(i) Student's t (ii) Fratio	d.f.	P
Amphora sp. B	M L	1511.2	1184.8	(i) 2.15	7	0.1 > P > 0.05
	C	289.2	646.7	(ii) 3.356	4,4	0.25 > P > 0.1
Schizothrix sp.	M L	97235	79657	(i) 2.30	7	0.1 > P > 0.05
	B L	6942	15524	(ii) 26.33	4,4	0.005 > P > 0.001**
Cocci sp. (diam. 0.6 µm)	M L	28927	13568	(i) -1.29	6	0.3 > P > 0.2
	M D	51848	40831	(ii) 9.056	4,4	0.05 > P > 0.025*
"	M L	28927	13568	(i) -5.40	7	0.01 > P > 0.001**
	B L	130831	59209	(ii) 19.04	4,4	0.01 > P > 0.005**
"	M L	28927	13568	(i) 5.00	6	0.01 > P > 0.001**
	B D	9390	2181	(ii) 38.7	4,4	0.005 > P > 0.001**
"	M L	28927	13568	(i) 1.38	4	0.3 > P > 0.2
	C	23031	41872	(ii) 9.524	4,4	0.05 > P > 0.025*
"	M D	51848	40831	(i) -2.85	7	0.05 > P > 0.02*
	B L	130831	59209	(ii) 2.103	4,4	0.25 > P > 0.1
"	M D	51848	40831	(i) 4.77	5	0.01 > P > 0.001**
	B D	9390	2181	(ii)350.5	4,4	P < 0.001***
"	M D	51848	40831	(i) 1.60	4	0.2 > P > 0.1
	C	23031	41872	(ii) 1.052	4,4	0.5 > P > 0.25
"	B L	130831	59209	(i) 10.94	6	P < 0.001***
	B D	9390	2181	(ii)737	4,4	P < 0.001***
"	B L	130381	59209	(i) 2.14	4	0.1 > P > 0.05
	C	23031	41872	(ii) 1.999	4,4	0.5 > P > 0.25
"	B D	9390	2181	(i) 0.83	4	0.5 > P > 0.4
	C	23031	41872	(ii)368.6	4,4	P < 0.001***
Cocci sp. (diam. 2 µm)	B L	108639	48716	(i) 2.85	6	0.05 > P > 0.02*
	B D	38799	31600	(ii) 2.377	4,4	0.25 > P > 0.1
Bacilli	M L	19670	3169	(i) 0.57	4	0.6 > P > 0.5
	M D	39120	21869	(ii) 47.62	4,4	0.005 > P > 0.001**
"	M L	19670	3169	(i) -9.48	5	P < 0.001***
	B L	102690	40175	(ii)160.7	4,4	P < 0.001***
"	M L	19670	3169	(i) -6.02	4	0.01 > P > P.001**
	B D	86450	41890	(ii)174.7	4,4	P < 0.001***
"	M L	19670	3169	(i) 1.41	4	0.3 > P > 0.2
	C	50057	95557	(ii)909.2	4,4	P < 0.001***
"	M D	39120	21869	(i) -1.32	4	0.3 > P > 0.2
	B L	102690	40175	(ii) 3.375	4,4	0.25 > P > 0.1

CONTD:

TABLE 39. contd:

Species	Medium	Mean	s.d.	(i) Student's t (ii) Fratio	d.f.	P
Bacilli	M D	39120	21869	(i) -1.21	4	0.3 > P > 0.2
	B D	86450	41890	(ii) 3.669	4,4	0.25 > P > 0.1
"	M D	39120	21869	(i) 0.72	7	0.5 > P > 0.4
	C	50057	95557	(ii) 19.09	4,4	0.01 > P > 0.005**
"	B L	102690	40175	(i) 0.80	7	0.5 > P > 0.4
	B D	86450	41890	(ii) 1.087	4,4	0.5 > P > 0.25*
"	B L	102690	40175	(i) 2.02	4	0.2 > P > 0.1
	C	50057	95557	(ii) 5.657	4,4	0.1 > P > 0.05
"	B D	86450	41890	(i) 1.94	4	0.2 > P > 0.1
	C	50057	95557	(ii) 5.204	4,4	0.1 > P > 0.05
Caulobacter	B L	12225	17289	(i) 0.19	7	0.9 > P > 0.8
	B D	2445	3348	(ii) 26.67	4,4	0.005 > P > 0.001**
Spirochetes	B L	24450	17289	(i) 1.30	7	0.3 > P > 0.2
	B D	9780	13392	(ii) 1.667	4,4	0.5 > P > 0.25
Filamentous (isolated)	M L	7204	10065	(i) 0.48	7	0.7 > P > 0.6
	M D	733.5	10934	(ii) 1.180	4,4	0.5 > P > 0.25
"	M L	7204	10065	(i) -0.85	7	0.5 > P > 0.4
	B L	21874	18223	(ii) 3.278	4,4	0.25 > P > 0.1
"	M L	7204	10065	(i) -1.87	4	0.2 > P > 0.1
	B D	26764	21596	(ii) 4.604	4,4	0.1 > P > 0.5
"	M L	7204	10065	(i) 1.14	7	0.3 > P > 0.2
	C	4890	10934	(ii) 1.180	4,4	0.5 > P > 0.25
"	M D	733.5	10934	(i) -1.33	7	0.3 > P > 0.2
	B L	21874	18223	(ii) 2.778	4,4	0.25 > P > 0.1
"	M D	733.5	10934	(i) -2.42	4	0.1 > P > 0.05
	B D	26764	21596	(ii) 3.901	4,4	0.25 > P > 0.1
"	M D	733.5	10934	(i) 0.60	7	0.6 > P > 0.5
	C	4890	10934	(ii) 1	4,4	0.75 > P > 0.5
"	B L	21874	18223	(i) -0.83	4	0.5 > P > 0.4
	B D	26764	21596	(ii) 1.404	4,4	0.5 > P > 0.25
"	B L	21874	18223	(i) 2.11	7	0.1 > P > 0.05
	C	4890	10934	(ii) 2.778	4,4	0.25 > P > 0.1
"	B D	26764	21596	(i) 3.75	4	0.02 > P > 0.01**
	C	4890	10934	(ii) 3.901	4,4	0.25 > P > 0.1

2.1.1. Student's t-tests

Cocci (diam. 0.6 μm) (Figure 32 upper): The abundances of coccoid bacteria were highest in the BL medium and lowest in the BD medium. Their abundance in the two photosynthetic media (ML, MD) and in the control were intermediate. Five out of the ten differences were statistically different.

Bacilli (Figure 33 upper): The abundance of bacilli was highest in the BL medium and lowest in the ML medium, while their abundances in the MD, BD medium and the control were intermediate. Only two out of the ten differences were statistically significant and so little importance can be attached to the observed differences.

Filamentous bacteria (Figure 34): The abundance of the filamentous bacteria was highest in the BD medium and lowest in the MD medium, while their abundances in the BL, ML medium and the control were intermediate. However, one of the t-tests comparing the abundances was significant.

2.1.2. F ratios

Cocci (diam. 0.6 μm) (Figure 32 lower): The variance of the abundance of the cocci was highest in the BL medium and lowest in the BD medium with the two photosynthetic media (ML, MD) and the control having intermediate variances. Seven out of the ten F ratios were significant and so the observed differences in the variances (differences in the variability of the two samples being compared) are significant.

Bacilli (Figure 33 lower): The variance of the abundance of the bacilli was highest in the control and lowest in the ML medium with the MD, BL and BD media being intermediate. Five out of the ten F ratios were significant and so the observed differences in the variances are vague.

Figure 32. Cocci.

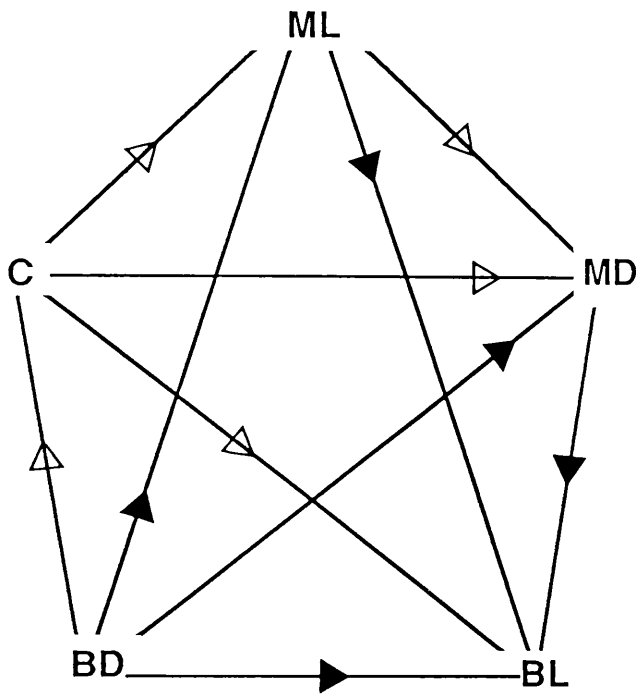
Upper : Student's t comparing means of ln transformed data between media.

Lower : F ratios comparing variances of untransformed data between media.

ML photosynthetic medium incubated in the light
MD photosynthetic medium incubated in the dark
BL heterotrophic medium incubated in the light
BD heterotrophic medium incubated in the dark
C control

▲ significant, △ nonsignificant.

Note: In each case the heads of the arrows point towards the higher value and the tails towards the lower value.


ML
C
MD
BD
BL

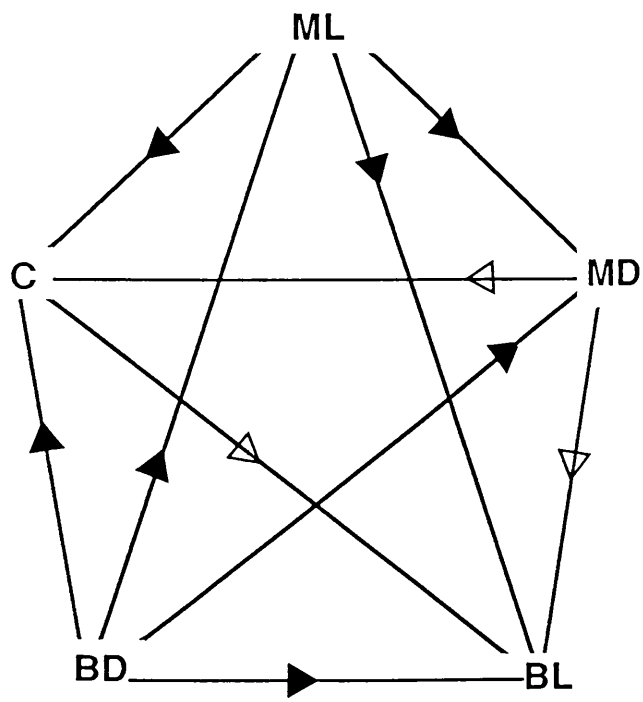

ML
C
MD
BD
BL

Figure 33 . Bacilli.

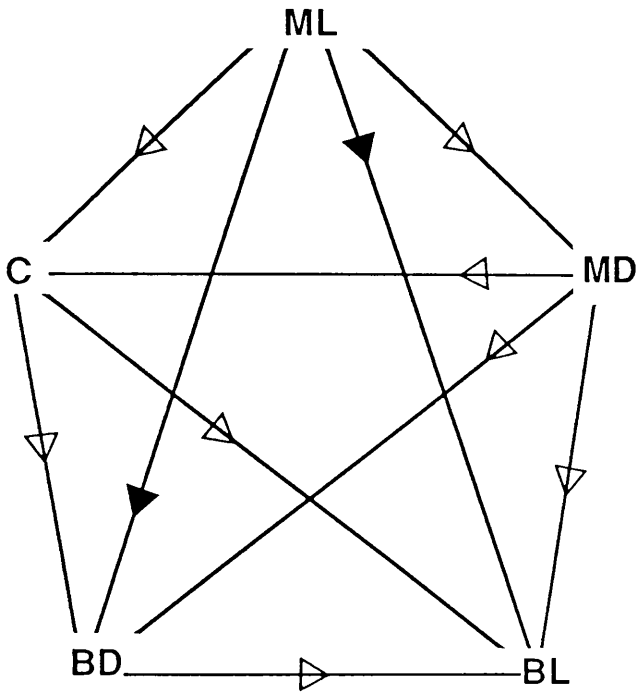
Upper : Student's t comparing means of ln transformed data between media.

Lower : F ratios comparing variances of untransformed data between media.

ML photosynthetic medium incubated in the light
MD photosynthetic medium incubated in the dark
BL heterotrophic medium incubated in the light
BD heterotrophic medium incubated in the dark
C control

▲ significant, △ nonsignificant.

Note: In each case the heads of the arrows point towards the higher value and the tails towards the lower value.


ML
C
MD
BD
BL

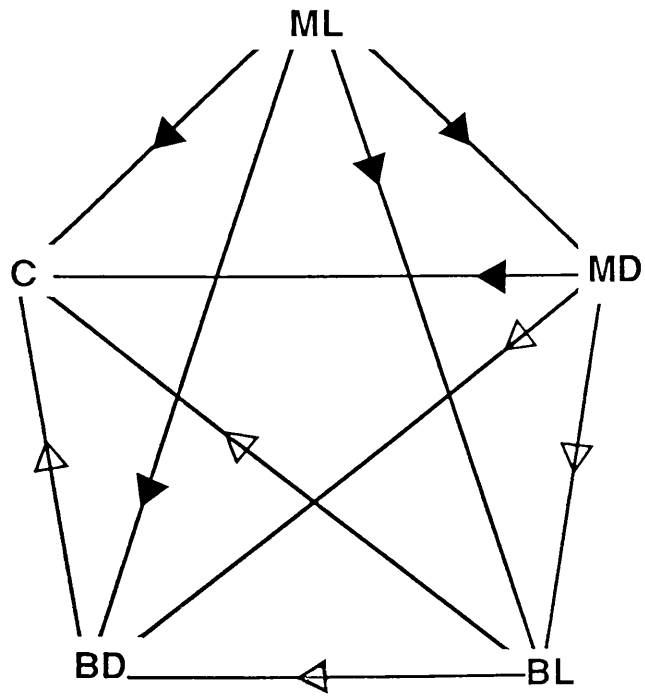

ML
C
MD
BD
BL

Figure 34. Filamentous bacteria.

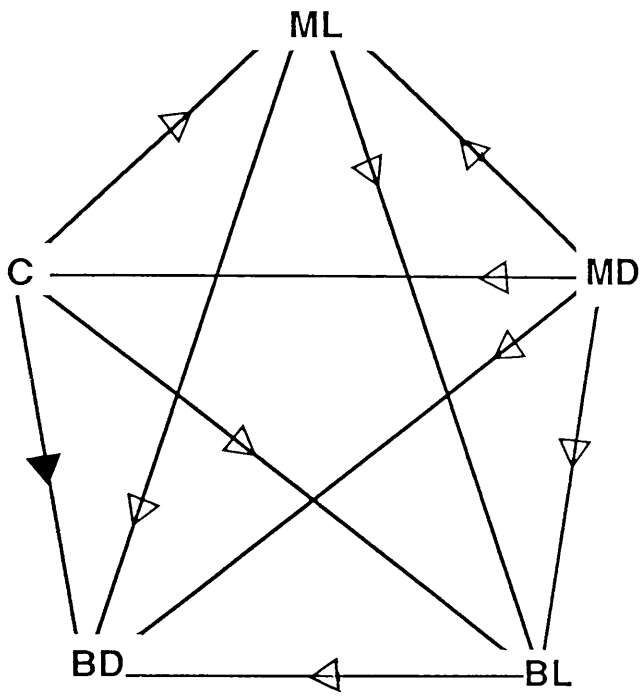
Upper : Student's t comparing means of ln transformed data between media.

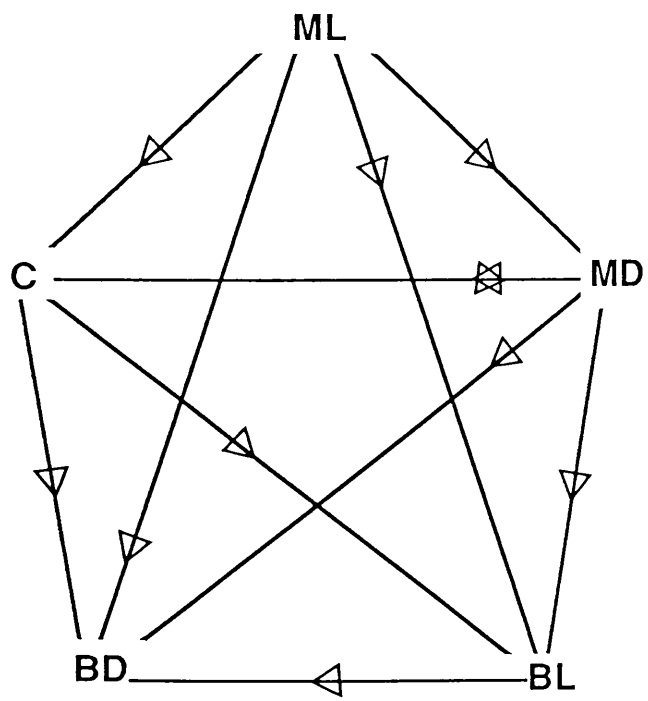
Lower : F ratios comparing variances of untransformed data between media.

ML photosynthetic medium incubated in the light
MD photosynthetic medium incubated in the dark
BL heterotrophic medium incubated in the light
BD heterotrophic medium incubated in the dark
C control

▲ significant, △ nonsignificant.

Note: In each case the heads of the arrows point towards the higher value and the tails towards the lower value.


ML
C
MD
BD
BL


ML
C
MD
BD
BL

Filamentous bacteria (Figure 34 lower): The variance of the abundance of the filamentous bacteria was highest in the BD medium and lowest in the ML medium, as well as in the control, with the BL and MD media being intermediate. However, none of the F ratios were significant.

2.2. Comparisons between species within each treatment (medium) meso-scale - between rows in each column of Table 36

These comparisons were conducted in a similar manner to those described in section 2.1. (comparison between treatments).

One way analyses of variance comparisons (Table 38) on the ln transformed abundances were conducted on the five different treatments (ML, MD, BL, BD and C media). All three anovars for the ML medium were statistically significant showing that there were overall significant differences between the abundances of the species in the ML medium.

The anovar for the MD medium (Cocci (diam. 0.6 μm)/Bacilli/Filamentous bacteria) was not significant. This indicates that overall there were no significant differences between the abundances of the bacterial species in the MD medium.

The two anovars for the BL medium and the single anovar for the BD medium were all significant, indicating overall differences between the abundances of the species in each medium.

In the control, one anovar (Amphora sp. B/Agmenellum sp./Cocci (diam. 0.6 μm)/Bacilli/Filamentous bacteria) was significant, indicating overall differences between the abundances of the photosynthetic and bacterial species, while the other anovar (Cocci (diam. 0.6 μm)/Bacilli/Filamentous bacteria) was not significant, indicating no significant differences between the abundances of the bacterial species. These anovars were followed by Student's

t-tests on the ln transformed abundances comparing differences between means, and then by F ratios on the untransformed abundances comparing differences between variances (relative variability of the two samples being compared).

The results of comparisons between species within each medium by t-tests and by F ratios are given in Table 40. As previously, I have also drawn diagrams showing (a) the significant and nonsignificant differences between the mean abundances and (b) the significant and nonsignificant differences between the variances of the abundances between the different species for each medium in turn. As previously this enables important effects to be more easily understood. These effects are as follows.

2.2.1. Student's t-tests

ML medium: In the ML medium (Figure 35 upper) the abundance of Schizothrix sp. was highest, and that of Amphora sp. A was lowest. The abundances of Amphora sp. B, Rhaphoneis sp., cocci (diam. 0.6 μm), bacilli, filamentous and Thraustochytrium sp. were intermediate. Nine out of the twenty eight differences were statistically different so little importance can be attached to the observed differences, except that five out of these nine concerned comparisons of the abundance of Amphora sp. A with other species.

MD medium: In this medium the abundance of the coccoid bacteria (diam. 0.6 μm) was highest, and that of filamentous bacteria was lowest. Bacilli had an intermediate abundance. Only one out of the three differences were statistically different, that between cocci (diam. 0.6 μm) and filamentous bacteria.

BL medium: In this medium (Figure 36 upper) the abundance of cocci (diam. 0.6 μm) was highest, and that of Schizothrix sp. was lowest. Cocci (diam. 2 μm), bacilli, Caulobacter sp., spirochetes, and filamentous bacteria had

Table 40. Abundance of species (no. mm^{-2} sand grain surface) in the five media.

ML photosynthetic medium incubated in the light
MD photosynthetic medium incubated in the dark
BL heterotrophic medium incubated in the light
BD heterotrophic medium incubated in the dark
C control

(i) Student's t comparing means of ln transformed data between pairs of species in the same medium.

(ii) F ratio comparing variances of untransformed data between pairs of species in the same medium.

TABLE 40.

Species	Medium	Mean	s.d.	(i) Student's t (ii) Fratio	d.f.	P
Amphora sp. A	M L	4.840	10.82	(i) -3.25	5	0.05 > P > 0.02*
Amphora sp. B		1511.2	1184.8	(ii)11990	4,4	P < 0.001***
Amphora sp. A	M L	4.840	10.82	(i) -3.28	5	0.05 > P > 0.02*
Rhaphoneis sp.		2245	2145	(ii)39300	4,4	P < 0.001***
Amphora sp. A	M L	4.840	10.82	(i) -3.57	4	0.05 > P > 0.02*
Schizothrix		97235	79657	(ii)54199261	4,4	P < 0.001***
Amphora sp. A.	M L	4.840	10.82	(i)-14.23	4	P < 0.001***
Cocci (0.6 µm)		28927	13568	(ii)1572451	4,4	P < 0.111***
Amphora sp. A	M L	4.840	10.82	(i)-14.22	4	P < 0.001***
Bacilli		19670	3169	(ii)85781	4,4	P < 0.001***
Amphora sp. A	M L	4.840	10.82	(i) -2.06	4	0.2 > P > 0.1
Filamentous		7204	10065	(ii)865313	4,4	P < 0.001***
Amphora sp. A	M L	4.840	10.82	(i) -0.92	6	0.4 > P > 0.3
Thraustochytrium sp.		38.80	53.13	(ii) 24.11	4,4	0.005 > P < 0.001***
Amphora sp. B	M L	1511.2	1184.8	(i) -0.12	7	P > 0.9
Rhaphoneis sp.		2245	2145	(ii) 3.278	4,4	0.25 > P > 0.1
Amphora sp. B	M L	1511.2	1184.8	(i) -1.20	6	0.3 > P > 0.2
Schizothrix sp.		97235	79657	(ii)4520	4,4	P < 0.001***
Rhaphoneis sp.	M L	2245	2145	(i) -1.90	7	0.1 > P > 0.05
Schizothrix sp.		97235	79657	(ii)1379	4,4	P < 0.001***
Cocci sp. (0.6 µm)	M L	28927	13568	(i) 1.63	5	0.2 > P > 0.1
Bacilli		19670	3169	(ii) 18.33	4,4	0.01 > P > 0.005***
Cocci sp. (0.6 µm)	M L	28927	13568	(i) 2.08	4	0.2 > P > 0.1
Filamentous		7204	10065	(ii) 1.817	4,4	0.5 > P > 0.25
Cocci sp. (0.6 µm)	M L	28927	13568	(i) 7.35	4	0.01 > P > 0.001**
Thraustochytrium sp.		38.80	53.13	(ii)65216	4,4	P < 0.001***
Bacilli	M L	19670	3169	(i) 1.95	4	0.2 > P > 0.1
Filamentous		7204	10065	(ii) 10.09	4,4	0.025 > P > 0.01**
Bacilli	M L	19670	3169	(i) 7.15	4	0.01 > P > 0.001**
Thraustochytrium sp.		38.80	53.13	(ii) 3558	4,4	P < 0.001***
Amphora sp. B	M L	1511.2	1184.8	(i) -2.80	4	0.05 > P > 0.02*
Cocci sp. (0.6 µm)		28927	13568	(ii)131.1	4,4	P < 0.001***
Amphora sp. B	M L	1511.2	1184.8	(i) -2.60	4	0.1 > P > 0.05
Bacilli		19670	3169	(ii) 7.154	4,4	0.05 > P > 0.025***

CONTD:

TABLE 40 CONTD:

Species	Medium	Mean	s.d.	(i) Student's t (ii) Fratio	d.f.	P
Amphora sp. B Filamentous	M L	1511.2 7204	1184.8 10065	(i) 0.17 (ii) 72.17	6 4,4	0.9 > P > 0.8 P < 0.001***
Amphora sp. B Thraustochytrium sp.	M L	1511.2 38.80	1184.8 53.13	(i) 2.20 (ii)497.3	7 4,4	0.1 > P > 0.05 P < 0.001***
Rhaphoneis sp. Cocci sp. (0.6 µm)	M L	2245 28927	2145 13568	(i) -2.51 (ii) 40.01	4 4,4	0.1 > P > 0.05 0.005 > P > 0.001**
Rhaphoneis sp. Bacilli	M L	2245 19670	2145 3169	(i) -2.32 (ii) 2.183	4 4,4	0.1 > P > 0.05 0.25 > P > 0.1
Rhaphoneis sp. Filamentous	M L	2245 7204	2145 10065	(i) 0.27 (ii) 22.02	7 4,4	0.8 > P > 0.7 0.01 > P > 0.005**
Rhaphoneis sp. Thraustochytrium sp.	M L	2245 38.80	2145 53.13	(i) 2.27 (ii)1630	7 4,4	0.1 > P > 0.05 P < 0.001***
Schizothrix sp. Cocci (0.6 µm)	M L	97235 28927	79657 13568	(i) -0.39 (ii) 34.47	4 4,4	0.8 > P > 0.7 0.005 > P > 0.001**
Schizothrix sp. Bacilli	M L	97235 19670	79657 3169	(i) -0.25 (ii)631.8	4 4,4	0.9 > P > 0.8 P < 0.001***
Schizothrix sp. Filamentous	M L	97235 7204	79659 10065	(i) 1.17 (ii) 62.64	7 4,4	0.4 > P > 0.3 P < 0.001***
Schizothrix sp. Thraustochytrium sp.	M L	97235 38.80	79659 53.13	(i) 2.88 (ii)2247968	5 4,4	0.05 > P > 0.02* P < 0.001***
Filamentous Thraustochytrium sp	M L	7204 38.80	10065 53.13	(i) 1.45 (ii) 35888	5 4,4	0.3 > P > 0.2 P < 0.001***
Cocci sp. (0.6 µm) Bacilli	M D	51848 39120	40831 21869	(i) 0.92 (ii) 3.486	4 4,4	0.5 > P > 0.4 0.25 > P > 0.1
Cocci sp. (0.6 µm) Filamentous	M D	51848 7335	40831 10934	(i) 2.8 (ii) 13.95	4 4,4	0.05 > P > 0.02* 0.025 > P > 0.01*
Bacilli Filamentous	M D	39120 7335	21869 10934	(i) 1.47 (ii) 4.0	7 4,4	0.2 > P > 0.1 0.25 > P > 0.1
Schizothrix sp. Cocci sp. (0.6 µm)	B L	97235 130831	79657 59209	(i) -4.57 (ii) 1.810	4 4,4	0.02 > P > 0.01* 0.5 > P > 0.25
Schizothrix sp. Cocci sp. (2 µm)	B L	97235 108639	79657 48716	(i) -4.48 (ii) 2.674	4 4,4	0.02 > P > 0.01* 0.25 > P > 0.1
Schizothrix sp. Bacilli	B L	97235 102690	79657 40175	(i) -4.48 (ii) 3.931	4 4,4	0.02 > P > 0.01* 0.25 > P > 0.1
Schizothrix sp. Caulobacter	B L	97235 12225	79657 17289	(i) -0.62 (ii) 21.23	7 4,4	0.6 > P > 0.5 0.01 > P > 0.005**

CONTD:

TABLE 40 CONTD:

Species	Medium	Mean	s.d.	(i) Student's t (ii) F ratio	d.f.	P
Schizothrix sp. Spirochetes	B L	97235 24450	79657 17289	(i) -2.09 (ii) 21.23	7 4,4	0.1 > P > 0.05 0.01 > P > 0.005**
Schizothrix sp. Filamentous	B L	97235 21874	79657 18223	(i) -2.05 (ii) 19.12	7 4,4	0.1 > P > 0.05 0.01 > P > 0.005**
Cocci sp. (0.6 µm) Cocci sp. (2 µm)	B L	130831 108639	59209 48716	(i) 0.63 (ii) 1.477	7 4,4	0.6 > P > 0.5 0.5 > P > 0.25
Cocci sp. (0.6 µm) Bacilli	B L	130831 102690	59209 40175	(i) 0.81 (ii) 1.477	7 4,4	0.5 > P > 0.4 0.5 > P > 0.25
Cocci sp. (0.6 µm) Caulobacter	B L	130831 12225	59209 17289	(i) 2.99 (ii) 11.73	4 4,4	0.05 > P > 0.02* 0.025 > P > 0.01*
Cocci sp. (0.6 µm) Spirochetes	B L	130831 24450	59209 17289	(i) 1.68 (ii) 11.73	4 4,4	0.2 > P > 0.1 0.025 > P > 0.01*
Cocci sp. (0.6 µm) Filamentous	B L	130831 21874	59209 18223	(i) 1.78 (ii) 10.56	4 4,4	0.2 > P > 0.1 0.025 > P > 0.01*
Cocci sp. (2 µm) Bacilli	B L	108639 102690	48716 40175	(i) 0.10 (ii) 1.470	7 4,4	P > 0.9 0.5 > P > 0.25
Cocci sp (2 µm) Caulobacter	B L	108639 12225	48716 17289	(i) 2.92 (ii) 7.940	4 4,4	0.05 > P > 0.02* 0.05 > P > 0.025*
Cocci sp. (2µm) Spirochetes	B L	108639 24450	48716 17289	(i) 1.59 (ii) 7.940	4 4,4	0.2 > P > 0.1 0.05 > P > 0.025*
Cocci sp. (2 µm) Filamentous	B L	108639 21874	48716 18223	(i) 1.69 (ii) 7.147	4 4,4	0.2 > P > 0.1 0.05 > P > 0.025*
Bacilli Caulobacter	B L	102690 12225	40175 17289	(i) 2.91 (ii) 5.400	4 4,4	0.05 > P > 0.02* 0.05 > P > 0.025*
Bacilli Spirochetes	B L	102690 24450	40175 17289	(i) 1.58 (ii) 5.400	4 4,4	0.2 > P > 0.1 0.05 > P > 0.025*
Bacilli Filamentous	B L	102690 21874	40175 18223	(i) 1.68 (ii) 15.93	4 4,4	0.2 > P > 0.1 0.025 > P > 0.01*
Caulobacter Spirochetes	B L	12225 24450	17289 17289	(i) -1.26 (ii) 1	7 4,4	0.3 > P > 0.2 0.5 > P > 0.25
Caulobacter Filamentous	B L	12225 21874	17289 18223	(i) -1.22 (ii) 1.111	7 4,4	0.3 > P > 0.2 0.5 > P > 0.25
Spirochetes Filamentous	B L	24450 21874	17289 18223	(i) -0.05 (ii) 1.111	7 4,4	P > 0.9 0.5 > P > 0.25
Cocci sp. (0.6 µm) Cocci sp. (2 µm)	B D	9390 38749	2181 31600	(i) -2.88 (ii) 209.9	4 4,4	0.05 > P > 0.02* P < 0.001***

CONTD:

TABLE 40 CONTD:

Species	Medium	Mean	s.d.	(i) Student's t (ii) Fratio	d.f.	P
Cocci sp. (0.6 μm) Bacilli	B D	9390 86450	2181 411889	(i) -8.70 (ii)368.9	5 4,4	$P < 0.001^{***}$ $P < 0.001^{***}$
Cocci sp. (0.6 μm) Caulobacter	B D	9390 2445	2181 3348	(i) 2.64 (ii) 2.356	4 4,4	0.1 > P > 0.05 0.25 > P > 0.1
Cocci sp. (0.6 μm) Spirochetes	B D	9390 9780	2181 13392	(i) 2.05 (ii) 37.70	4 4,4	0.2 > P > 0.1 $P < 0.001^{***}$
Cocci sp. (0.6 μm) Filamentous	B D	9390 26764	2181 21596	(i) -1.37 (ii) 98.05	4 4,4	0.3 > P > 0.2 $P < 0.001^{***}$
Cocci sp (2 μm) Bacilli	B D	38799 86450	31600 41889	(i) -2.25 (ii) 1.757	6 4,4	0.1 > P > 0.05 0.5 > P > 0.25
Cocci sp. (2 μm) Caulobacter	B D	38799 2445	31600 3348	(i) 3.13 (ii) 89.51	4 4,4	$0.05 > P > 0.02^{*}$ $P < 0.001^{***}$
Cocci sp. (2 μm) Spirochetes	B D	38799 9780	31600 13392	(i) 2.49 (ii) 13.23	4 4,4	0.1 > P > 0.05 $0.025 > P > 0.01^{*}$
Cocci sp. (2 μm) Filamentous	B D	38799 26764	31600 21596	(i) 0.76 (ii) 5.089	7 4,4	0.5 > P > 0.4 0.1 > P > 0.05
Bacilli Caulobacter	B D	86450 2445	41889 3348	(i) 3.63 (ii)156.5	4 4,4	$0.05 > P > 0.02^{*}$ $P < 0.001^{***}$
Bacilli Spirochetes	B D	86450 9780	41889 13392	(i) 2.91 (ii)156.5	4 4,4	$0.05 > P > 0.02^{*}$ $P < 0.001^{***}$
Bacilli Filamentous	B D	86450 26764	41889 21596	(i) 2.76 (ii) 3.762	5 4,4	$0.05 > P > 0.02^{*}$ 0.25 > P > 0.1
Caulobacter Spirochetes	B D	2445 9780	3348 13392	(i) -0.17 (ii) 15.99	7 4,4	0.9 > P > 0.8 $0.025 > P > 0.01^{*}$
Caulobacter Filamentous	B D	2445 26764	3348 21596	(i) -2.89 (ii) 41.61	4 4,4	$0.05 > P > 0.02^{*}$ $0.005 > P > 0.001^{**}$
Spirochetes Filamentous	B D	9780 21596	13392 21596	(i) -2.29 (ii) 2.60	4 4,4	0.1 > P > 0.05 0.25 > P > 0.1
Amphora sp. B Agmenellum sp	C	289.2 92124	646.7 56677	(i) -6.51 (ii)7681	4 4,4	$0.01 > P > 0.001^{**}$ $P < 0.001^{***}$
Amphora sp. B Cocci sp. (0.6 μm)	C	289.2 23021	646.7 41872	(i) -2.48 (ii)4192	7 4,4	$0.05 > P > 0.02^{*}$ $P < 0.001^{***}$
Amphora sp. B Bacilli	C	289.2 50057	646.7 95557	(i) -1.60 (ii)21833	6 4,4	0.2 > P > 0.1 $P < 0.001^{***}$
Amphora sp. B Filamentous	C	289.2 4890	646.7 10934	(i) -0.23 (ii)285.9	7 4,4	0.9 > P > 0.8 $P < 0.001^{***}$

CONTD:

TABLE 40 CONTD:

Species	Medium	Mean	s.d.	(i) Student's t (ii) F ratio	d.f.	P
Agmenellum sp.	C	92124	56677	(i) 1.87	4	0.2 > P > 0.1
Cocci sp. (0.6 um)		23031	41872	(ii) 1.83	4,4	0.5 > P < 0.25
Agmenellum sp.	C	92124	56677	(i) 1.90	4	0.2 > P > 0.1
Bacilli		50057	96557	(ii) 2.902	4,4	0.25 > P > 0.1
Agmenellum sp.	C	92124	56677	(i) 4.48	4	0.2 > P > 0.01*
Filamentous		4890	10934	(ii) 26.87	4,4	0.005 > P > 0.001**
Cocci sp. (0.6 um)	C	23031	41872	(i) 0.39	7	0.8 > P > 0.7
Bacilli		50057	95557	(ii) 5.208	4,4	0.1 > P > 0.05
Cocci sp. (0.6 um)	C	23031	41872	(i) 1.95	7	0.1 > P > 0.05
Filamentous		4890	10934	(ii) 14.66	4,4	0.01 > P > 0.005**
Bacilli	C	50057	95557	(i) 1.27	7	0.3 > P > 0.2
Filamentous		4890	10934	(ii) 76.38	4,4	P < 0.001***

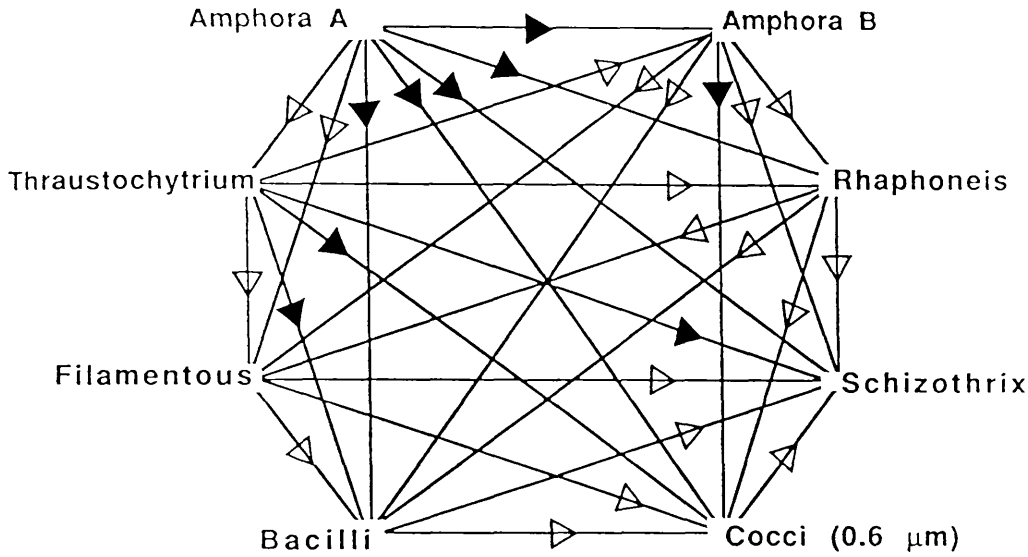
Figure 35 . Photosynthetic medium incubated in the light (ML).

Upper : Student's t comparing means of ln transformed data between media.

Lower : F ratios comparing variances of untransformed data between media.

▲ significant, △ nonsignificant.

Note: In each case the heads of the arrows point towards the higher value and the tails towards the lower value.


Amphora A
Amphora B
Thraustochytrium
Rhaphoneis
Filamentous
Schizothrix
Bacilli
Cocci (0.6 μm)

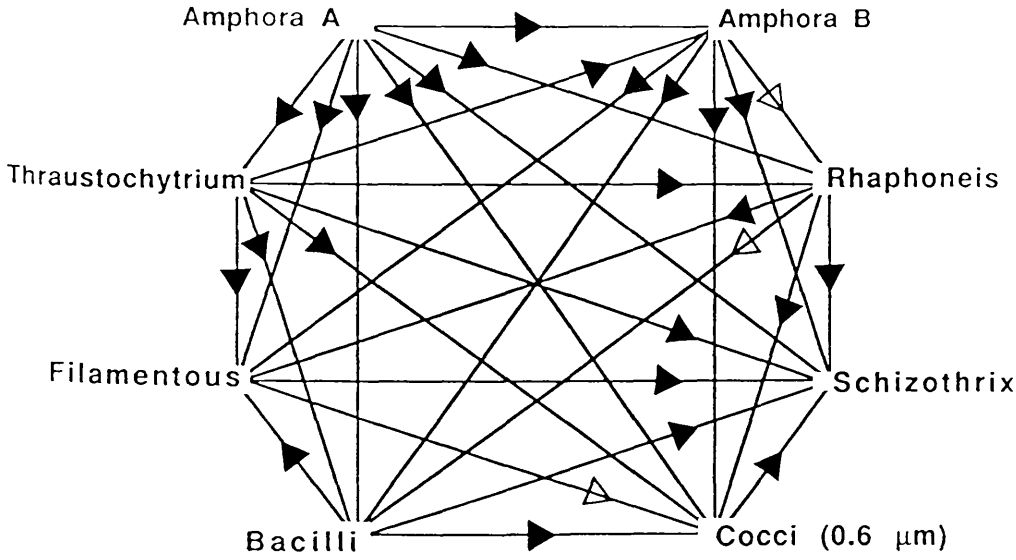

Amphora A
Amphora B
Thraustochytrium
Rhaphoneis
Filamentous
Schizothrix
Bacilli
Cocci (0.6 μm)

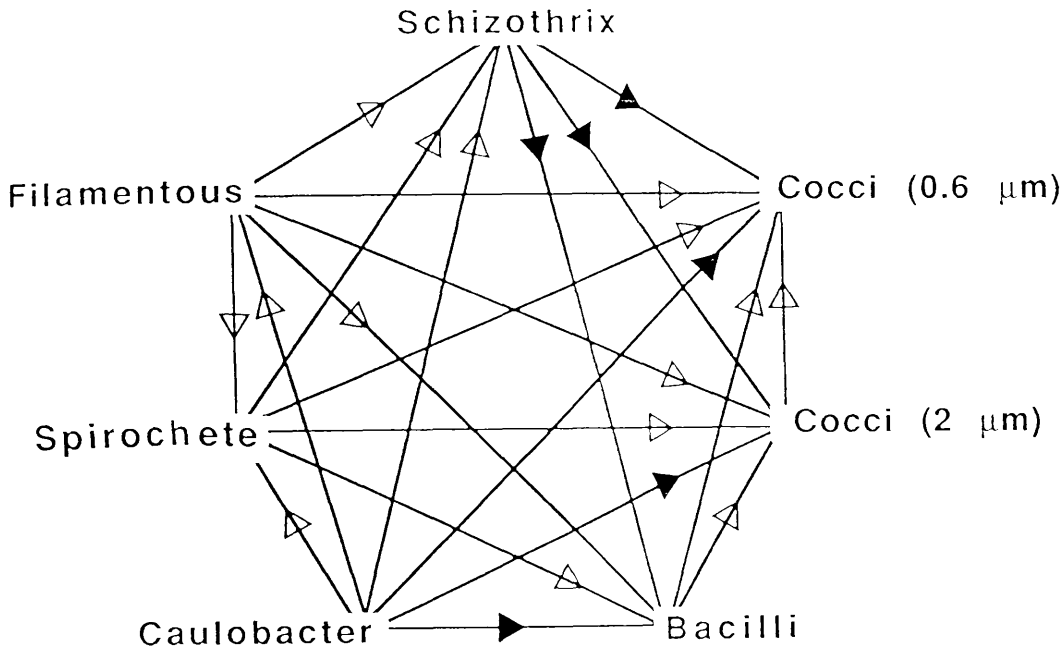
Figure 36. Heterotrophic medium incubated in the light (BL).

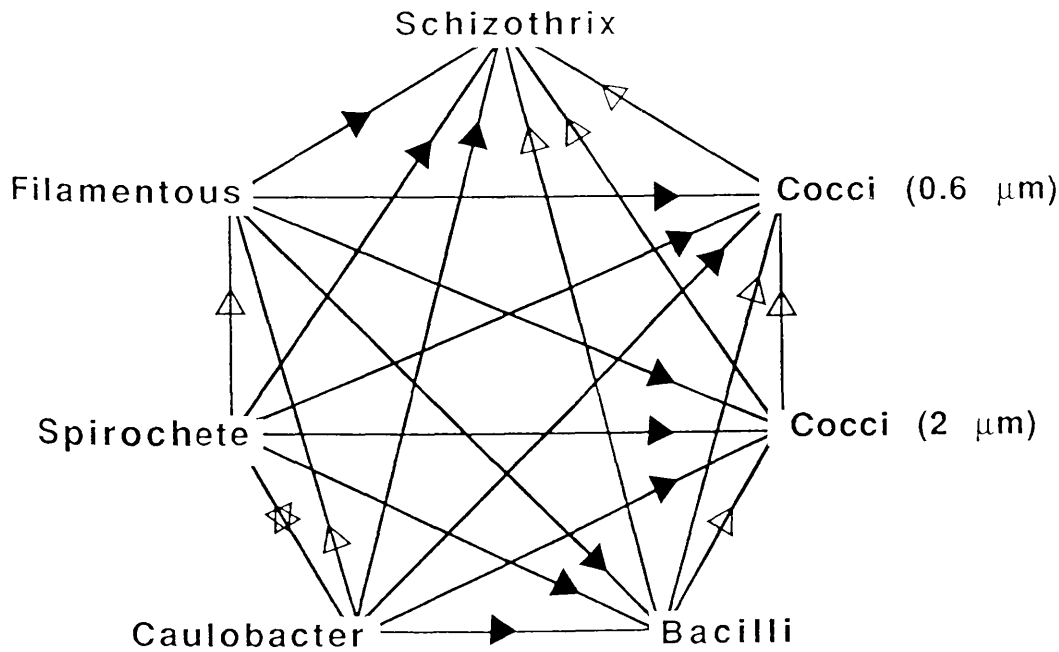
Upper : Student's t comparing means of ln transformed data between media.

Lower : F ratios comparing variances of untransformed data between media.

▲ significant, △ nonsignificant.

Note: In each case the heads of the arrows point towards the higher value and the tails towards the lower value.


Schizothrix
Filamentous
Cocci (0.6 µm)
Spirochete
Cocci (2 µm)
Caulobacter
Bacilli


Schizothrix
Filamentous
Cocci (0.6 µm)
Spirochete
Cocci (2 µm)
Caulobacter
Bacilli

intermediate abundances. Six out of the twenty one differences were statistically different, so little importance can be attached to the observed differences.

BD medium: In this medium (Figure 37 upper) the abundance of the bacilli was highest, and that of Caulobacter sp. was lowest. Cocci (diam. 0.6 μm), cocci (diam. 2 μm), spirochaetes and filamentous bacteria had intermediate abundances. Seven out of the fifteen differences were statistically different. Four out of these significant comparisons were between bacilli and other species.

Control: In the control (Figure 38 upper) the abundance of the Agmenellum sp. was highest, and that of Amphora sp. B was lowest. The abundances of cocci (diam. 0.6 μm), bacilli and filamentous bacteria were intermediate. Only three out of the ten differences were statistically different and so little importance can be attached to the observed differences, except that two out of the three comparisons of the abundances between Amphora sp. B and other species were significant.

2.2.2. F ratios

ML medium (Figure 35 lower): The variance of the abundance of the Schizothrix sp. was highest and that of Amphora sp. A was lowest. The variance of the abundance of Amphora sp. B, Rhaphoneis sp., cocci (diam. 0.6 μm), bacilli, filamentous bacteria, and Thraustochytrium sp. were intermediate. Twenty six out of the twenty eight F ratios were significant and so the observed differences in the variances (differences in the variability of the two samples being compared) are very important. It is interesting that all the F ratios were significant in which the highest variance (Schizothrix sp.) and the lowest variance (Amphora sp. A) were compared with other variances.

MD medium: The variance of the abundance of the cocci (diam. 0.6 μm) was

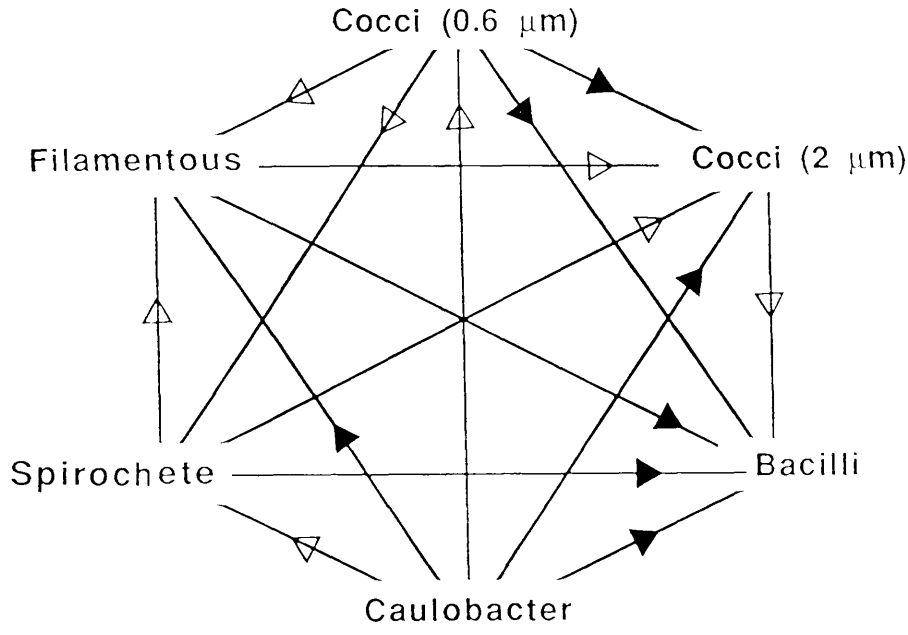
Figure 37 . Heterotrophic medium incubated in the dark (BD).

Upper : Student's t comparing means of ln transformed data between media.

Lower : F ratios comparing variances of untransformed data between media.

▲ significant, △ nonsignificant.

Note: In each case the heads of the arrows point towards the higher value and the tails towards the lower value.


Cocci (0.6 μm)
Filamentous
Cocci (2 μm)
Spirochete
Bacilli
Caulobacter

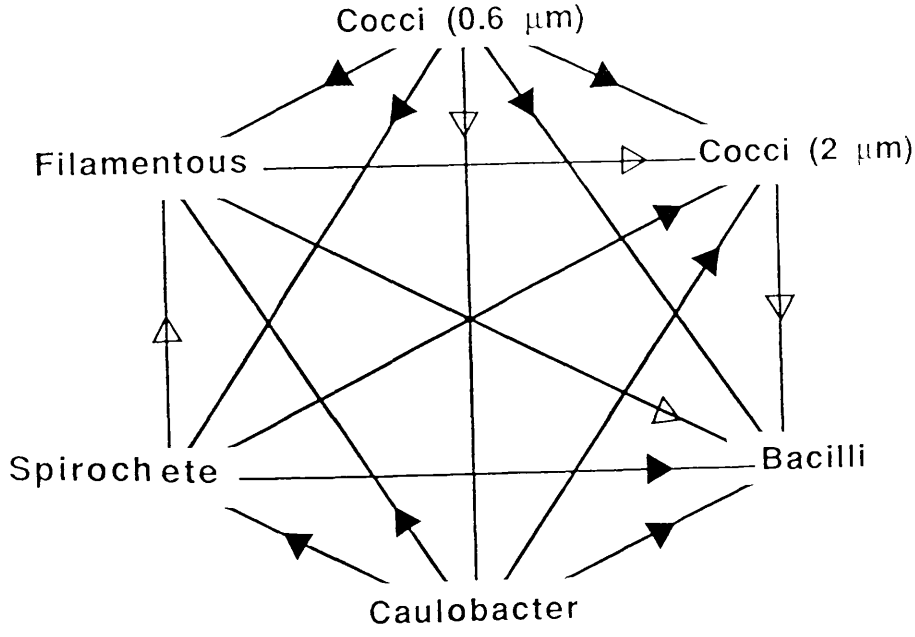

Cocci (0.6 μm)
Filamentous
Cocci (2 μm)
Spirochete
Bacilli
Caulobacter

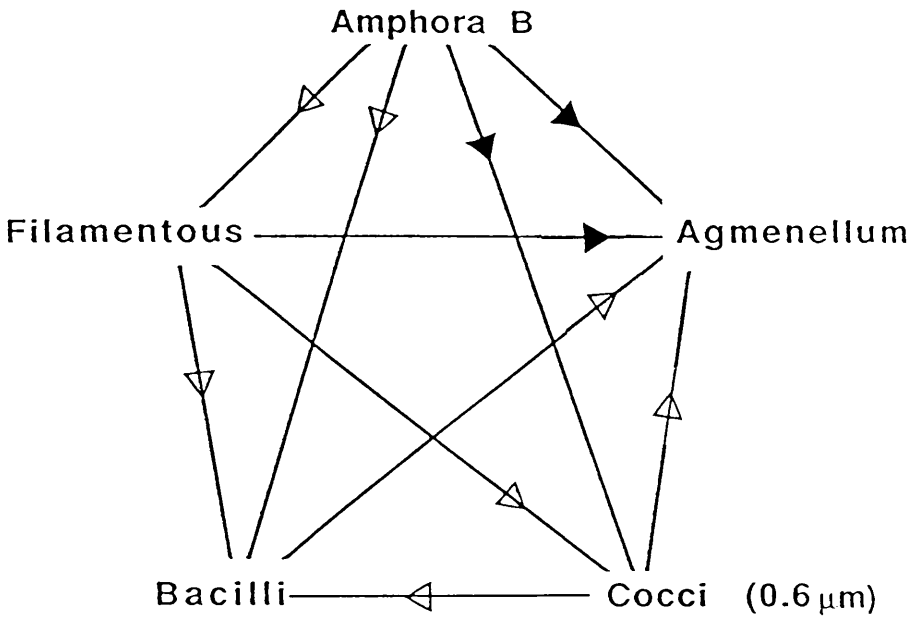
Figure 38. Control medium (C).

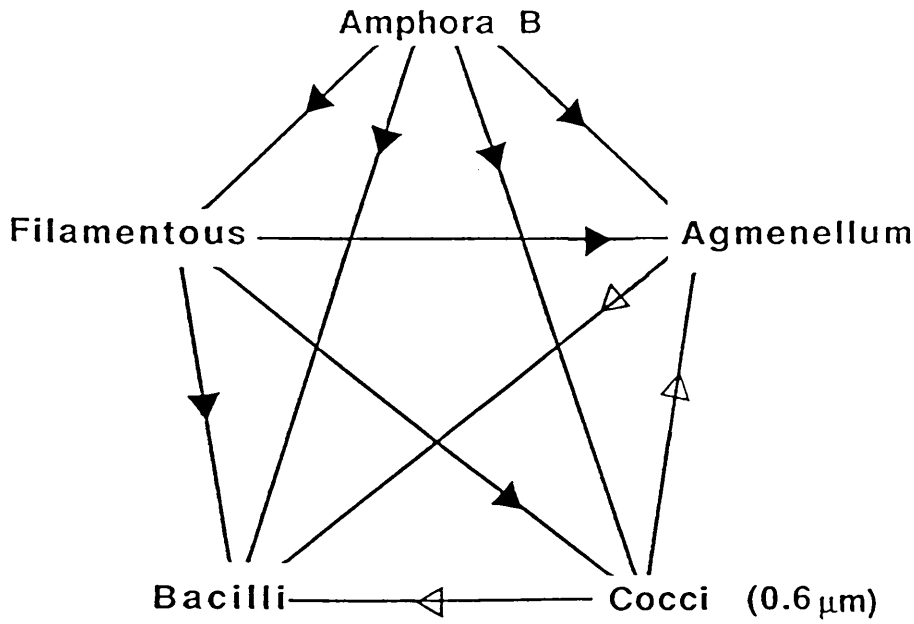
Upper : Student's t comparing means of ln transformed data between media.

Lower : F ratios comparing variances of untransformed data between media.

▲ significant, △ nonsignificant.

Note: In each case the heads of the arrows point towards the higher value and the tails towards the lower value.


Amphora B
Filamentous
Agmenellum
Bacilli
Cocci
(0.6 μm)


Amphora B
Filamentous
Agmenellum
Bacilli
Cocci
(0.6 μm)

highest, bacilli intermediate and filamentous bacteria lowest. One out of the three F ratios were significant - that between cocci (0.6 μm) and filamentous bacteria, so little importance can be attached to the observed differences.

BL medium (Figure 36 lower): The variance of the abundance of Schizothrix sp. was highest, and that of Spirochetes was lowest. The variance of the abundance of cocci (diam. 2 μm), bacilli, Caulobacter sp., cocci (0.6 μm) and filamentous bacteria were intermediate. Twelve out of the twenty one F ratios were significant and so the observed differences in the variances are fairly important.

BD medium (Figure 37 lower): The variance of the abundance of the bacilli was highest, and that of cocci (diam. 0.6 μm) was lowest. The variance of the abundance of cocci (diam. 2 μm), Caulobacter sp., spirochaetes, and filamentous bacteria were intermediate. Ten out of the fifteen F ratios were significant and so importance can be attached to the observed differences.

Control (Figure 38 lower): The variance of the abundance of bacilli was highest, and that of Amphora sp. B was lowest. The variance of the abundance of Agmenellum sp., cocci (diam. 0.6 μm), and filamentous bacteria were intermediate. Seven out of the ten F ratios were significant. It is interesting that all the F ratios were significant in which the lowest variance (Amphora sp. B) were compared with other variances.

DISCUSSION

"It is still too early to attempt scientific method in discussing this problem, nor is our present store of the necessary facts by any means complete enough to warrant me in promising any approach to fulness of statement respecting them."

(Marsh, 1874)

DISCUSSION

The work that I have presented in my thesis has been a study of benthic macrofaunal and microbial communities and their spatial variability. The macrofaunal communities and associated sediment parameters were studied by a field survey while the microbial communities were studied by enriching cores of sediment from Ardmore in the laboratory. I have therefore divided the discussion into two parts: the first deals with the field survey and the second with the laboratory enrichment experiments. I have decided to present the discussions separately because the macrofaunal and microbial communities are made up of organisms of very different sizes, and were investigated by contrasting methods.

The discussion on the field survey of macrofauna is approximately three times the length of that on the microbial communities in the enrichment cores. One of the main reasons for this is the enormous literature on the former when compared with that on the latter - I refer to about 150 references when discussing the macrofaunal field survey but only about 50 when discussing the microbial work. A secondary reason is that the macrofaunal field survey included a considerable amount of work on sediment properties and their relationship to species abundance. No work on sediment properties was done on the microbial enrichment cores.

MACROFAUNAL COMMUNITIES

The main objectives of my study of the intertidal communities of infaunal macrofauna at Ardmore was to investigate them in relation to the contrasting sedimentary environments on the beach. This involved comparing means and spatial variability of species abundances with those of sedimentary parameters in the algal and nonalgal areas towards high tide and the peaks and troughs of the sand waves towards low tide. It also involved investigating correlations between species abundances and sediment parameters, and comparing differences in diversity, between the different areas.

I therefore first discuss the effects of sediments on the abundance of infaunal species, and follow this with a consideration of scales of spatial heterogeneity in benthic communities, and the relations between algal mats, sand waves and benthic communities. I then discuss correlations between species abundances and sedimentary parameters at the high tide and low tide sites. I complete my discussion by considering the spatial differences in species diversity at Ardmore in the light of Margalef's (1968), Sanders (1968) and Abele and Walter's (1979) theories on the environmental factors influencing diversity.

There is a vast literature in most of these subject areas, only a small proportion of which I have referred to in detail because I have preferred to be selective. There is also a certain amount of overlap between the different parts of the discussion. This is inevitable when covering such closely related aspects of infaunal communities and sedimentary environments.

1. Sediment Properties

It is well known that the structure of benthic infaunal communities and the abundance of their constituent species is often closely related to the properties of the sediments in which they live. For example it would be unusual to find Corophium volutator and Macoma balthica in a gravelly sand or Bathyporeia guilliamsoniana and Cerastoderma (Cardium) edule in a fine clay. There is a large literature on these relationahips dating back to the early parts of the twentieth century (Petersen, 1913, 1915, 1918; Petersen & Jensen, 1911; Spark, 1935; Jones, 1950; Thorson, 1957; Holme, 1966; Sanders, 1968).

I want to consider some of the more recent literature which concentrates on the relationship between sediment properties and benthic communities per se, rather than the literature which is concerned with community structure itself. Some of this literature and its relation to my results is covered below in item (3.2.) sand waves and item (4) correlations, and to avoid repetition is not dealt with here.

A large number of authors have conducted field surveys in which sediment characteristics have been correlated with intertidal and subtidal benthic communities or with the abundance of a single species (Barnard, 1963; Evans, 1965; Cassie & Michael, 1968; Longbottom, 1970; Field, 1971; Hughes & Thomas, 1971; Rhoads & Young, 1971; Ward, 1975; Beukema, 1976; Erwin, 1977; Giere, 1977; Tyler, 1977; Tyler & Banner, 1977; Warwick & Davies, 1977; Buchannan et al., 1978; Pearson & Eleftheriou, 1981; Rhoads & Boyer, 1982; Creutzberg et al., 1984; Eleftheriou et al., 1986; Meadows & Tufail, 1986; Pearson et al., 1986; Ishikawa, 1989; Sorbe, 1989; Basford et al., 1990; Miron & Desrosiers, 1990).

A selection of these references is given in table 41 identifying the major sediment parameters measured. Many of these studies include measurements of particle size parameters such as mean and sorting (s.d.) while

Table 41 . Sediment properties affecting benthic communities.

Author(s)	Site	Sediment property(ies) & organism(s)
Beukema (1976)	Wadden Sea Denmark (mud flat)	High sand or silt contents correlated with low macrobenthic biomass.
Buchanan et al., (1978)	Northumberland coast, UK (subtidal)	Significant negative correlation between diversity and percentage silt. No correlation between biomass and sediment type.
Cassie & Michael (1968)	Karore Bank New Zealand (intertidal mud flat)	Chione stutchburyi and Macomona liliana community positively correlated with coarse sediment and negatively with fine sediment.
Creutzberg et al., (1984)	North Sea (subtidal)	Particle size positively correlated with current velocity which in turn determines distribution of food resources for benthos.
Erwin (1977)	Irish Sea (subtidal)	Ten communities identified at 10m and 50m depth, their distribution is related to low wave action.
Evans (1965)	The Wash UK (intertidal)	Distribution of organisms varies in salt marsh, mudflat and sand flat areas. Pygospio tubes in troughs of ripple marks.
Field (1971)	False Bay South Africa (subtidal)	Number of benthos high in stable sand, but low in shallow sediment with high wave surge.
Giere (1977)	Subtropical beach, Bermuda (intertidal flat & slope)	Eh, pH, salinity, and temperature restrict oligochaete species to uppermost layers - intertidally. More animals found in subsurface layers of slope.
Harrison & Wass (1965)	Chesapeake Bay USA, (subtidal)	Water content determines frequencies of infaunal invertebrates.
Hogue & Miller (1981)	Yaquina Bay Oregon, USA (intertidal sand flat)	Most nematodes found in the vicinity of crests of sand ripples rather than troughs.

contd:

Table 41 contd:

Author(s)	Site	Sediment property(ies) & organism(s)
Howes et al., (1981)	Sippewissett USA (intertidal saltmarsh)	Water logging in sediments inhibits aboveground growth of the seagrass Spartina alterniflora by decreasing oxygen release and thus lowering Eh.
Hughes & Thomas (1971)	Bideford River Canada (subtidal)	Yoldia - Tellina community associated with finer sediments while remaining benthos not associated with sediment type.
Longbottom (1970)	Swale Estuary UK (intertidal)	Arenicola marina found in deposits of median particle diameter of < 80 μm.
McCall (1978)	Long Island Sound USA (tidal embayment)	Benthos distribution affected by substrate disturbance, a result of bottom storms.
Miron & Desrosiers (1990)	St Lawrence Estuary Canada (intertidal)	Nereis virens had highest densities towards the shore and lowest at the lower tidal level. Nephtys caeca showed the opposite trend. N. virens increased with high organic content.
Moore (1931)	Clyde Sea Area Scotland (subtidal)	Harpacticoids restricted to top 1cm of mud.
Palmer & Gust (1985)	North Inlet Estuary USA (intertidal mud flat creek)	Meiofaunal dispersal is affected by strong water currents.
Pearson & Eleftheriou (1981)	Sullom Voe Scotland (subtidal)	Faunal distributions vary in relation to type of sediment. Current speed & organic content in certain areas affect macrofauna.
Pearson & Stanley (1979)	Loch Linnhe & Loch Eil Scotland (subtidal)	Sediment with low organic matter and high Eh have a diverse fauna. Annelid size is directly related to Eh.
Rhoads & Young (1971)	Cape Cod Bay USA (subtidal)	Molpadia oolitica (holothurian) is found in sediment with a silt/clay content greater than 20%.

contd:

Table 41 contd:

Author(s)	Site	Sediment property(ies) & organism(s)
Sameoto (1969b)	Sippewissett Creek, USA (intertidal)	Sand bars affect distribution of Amphipods (Haustoriidae).
Tyler & Banner (1977)	Oxwich Bay UK (subtidal)	Benthic echinoderm distribution is positively correlated with the distribution of fine sediment and hydrodynamic conditions.
Ward (1975)	Liverpool Bay UK (subtidal)	Nematode distribution affected by sediment granulometry; a wider range of nematode lengths found in more heterogeneous sediments.
Warwick & Davies (1977)	Bristol Channel UK (subtidal)	Substrate type characterises different benthic communities.
Wieser (1959)	Puget Sound USA (intertidal)	Interstitial fauna not found in sediments finer than 200 μm particle size.

others cover organic carbon, redox potential, oxygen, sediment water content and water movement above the sediment water interface.

The bay at Ardmore has a number of different sedimentary environments ranging from higher energy erosional conditions towards the mouth which produce the stable sand wave configuration there, to lower energy depositional environments in the high tide area where well established algal mats exist (Plate 1). Both the algal mats towards high tide (Plate 2) and the sand waves in the lower part of the beach (Plate 3) have been stable features of the beach for many years and have retained their relative position, although the algal mats are more obvious in summer.

The properties of the sediment at the high tide and low tide sites are different. In general particle size is finer at the high tide site than at the low tide site, shear strength is lower (except in the troughs at low tide), redox potential is lower, and pH is lower (Tables 4, 5). All of these differences emphasise that the high tide site is a lower energy environment than the low tide one, probably caused by the combined effect of the shape of the bay, the direction of the prevailing winds and the dissipation of wave energy towards high tide (Figure 2). In this context it is interesting to note that work by Tyler (1977), Tyler and Banner (1977), Warwick and Uncles (1980), and Kunitzer (1990) stress the importance of hydrodynamic conditions in determining benthic community structure in the subtidal zone. It is certainly true that similar effects will be operating in Ardmore Bay either by directly affecting the infaunal benthic community or by controlling the sedimentary environment there, and a similar hypothesis was put forward for the intertidal zone many years ago by Bruce (1928a, p 551) after studying the intertidal zone at Port Erin Bay.

The infaunal animal communities at the two sites contain relatively few species, 5 at the low tide site and 7 at the high tide site (Tables 2, 3, 6), which indicates that the whole area can be regarded as a marginal habitat in which relatively few species can survive but in which those that do are very

successful (see Discussion section 5 (species diversity)).

The species composition of the two communities is surprisingly similar in view of the different sedimentary environments (sand waves and algal mats). Only one of the species at low tide B. guilliamsoniana is not found at high tide while 3 out of the 7 species at high tide (C. volutator, F. sabella, and H. neglecta) are not found at low tide. There are however very significant differences between the structure of two communities which must be caused by the different sedimentary environments - at least in part. These differences which are considered in more detail below consist of a higher diversity at the high tide site, greater variability in the abundance of species at high tide and large populations at high tide of C. volutator, H. neglecta, M. balthica, and N. diversicolor (Table 6). These four species are characteristic of more muddy sediments which agrees with the more sheltered conditions existing towards high tide at Ardmore. The only species which is found at low tide but not at high tide is B. guilliamsoniana which is very characteristic of coarser sediments and higher energy conditions.

2. Scales of Spatial Heterogeneity in Benthic Communities

I have made a distinction in my macrobenthos study between micro-scale variability - defined as operating up to a distance of 1m apart horizontally, meso-scale variability - defined as operating between 1m and 50m (Figure 31, Table 18, 19), and macro-scale variability - defined as operating above 50m. This is an arbitrary distinction but was appropriate to the area that I was studying, in that spatial heterogeneity in the high tide algal mats and in the low tide sand waves was of this order of magnitude (Plates 2, 3, Figure 2 lower, Table 19). However, there is considerable need for standardisation of terminology (Connell & Sousa, 1983, p. 292-294), and agreed definitions for micro, meso, macro, and mega-scale effects are required. For example in the same issue of the journal Limnology and

Oceanography (1985 vol. 30 (6),pp 1246-1252), Paerl refers to microzones and micro-scale effects in cyanobacterial-bacterial aggregates of the order of 50 μm to 250 μm (loc. cit. p 1250, Fig. 2), and Seitzinger and Nixon (1985) use what they term microcosms (loc. cit. p. 1333) containing 13 m^3 water and a 40cm deep sediment layer to study denitrification in coastal marine sediments.

A number of authors have considered the scales at which spatial heterogeneity occurs in benthic infaunal communities in sediments (Eckman, 1979; Maurer et al., 1979; Findlay, 1981; Schaffner, 1990).

Schaffner (1990) studied faunal abundance and horizontal and vertical distribution patterns in 70 box core samples taken from sub-tidal sediments in lower Chesapeake Bay, USA, covering an area of about 20x10 km. The box cores were separated by about 5km from each other, which in my classification would be regarded as macro-scale. These distances are at least 2 orders of magnitude greater than the distances over which I was sampling at Ardmore (< 1m to 50m). In spite of this, some of Schaffner's results are of direct relevance to my own work. She identified 5 functional groups of infaunal benthos:

(i) large tube and burrow builders with modal depth distributions below 2cm and depth ranges extending below 10cm.

(ii) small tube builders with modal depth distributions above 2cm and depth ranges generally not exceeding 5cm.

(iii) shallow burrowers with modal depth distribution above 2cm and depth ranges not exceeding 10cm.

(iv) deep burrowers with modal depth distribution below 2cm and depth ranges extending below 10cm.

(v) epifauna and tube or burrow co-inhabitants.

Three of the species in my study (Tables 2, 3, 6) fall into Schaffner's group (i) (A. marina (Plate 5, 8), N. diversicolor and P. elegans (Plate 9)), two of my species fall into Schaffner's group (ii) (F. sabella and C. volutator), two of my species fall into Schaffner's group (iii) (H. neglecta and

Plate 8. Ardmore bay. Low tide. Peak sediment split to show Arenicola marina burrow c.12cm long. Note the top aerobic sediment with anaerobic sediment below and the aerobic lining of the burrow throughout its length.

Plate 9. Ardmore bay. Low tide sediment on the peak of the sand waves showing small-scale sand ripples. Note Pygospio elegans tubes (golden brown) protruding from ripple troughs.

Plate 10. Ardmore bay. High tide. Algal mat sediment split to show the sub-surface black ferrous sulphide layer.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B. guilliamsoniana) and one of my species falls into Schaffner's group (iv) (M. balthica).

Maurer et al. (1979) investigated spatial heterogeneity in coastal benthic invertebrates using cluster analysis. They identified 3 spatially separate groups (clusters) at the HCS (Hen and Chickens Shoal) site, but none at the SBB (South Bethany Beach) site (USA). The stations at the HCS site separated into a near shore group which were similar to all the SBB site stations, and a mid-shore, and off-shore group which were different. The distance between the near-shore group and the mid-shore group, and between the mid-shore group and the off-shore group was about 1km and so differences between the groups would be regarded as macro-scale effects in my classification. The near-shore group of stations had relatively few species at low densities. The off-shore group of stations had more species at higher densities. This means that the near-shore group has a lower species diversity than the off-shore group. Maurer et al. (1979, Table 1) also show that the off-shore group of stations contained finer sediment (higher mud and clay %) than the near-shore group. Although operating on a larger spatial scale than mine, these differences in species diversity and sediment characteristics are interesting. The high tide site at Ardmore had a higher species diversity (Table 6) and a finer sediment than the low tide site (Tables 4, 5). The high tide and low tide sites at Ardmore, although less than a kilometre apart (Figure 2 lower), can therefore be regarded as an intertidal analogue of the off-shore and near-shore groups of stations in Maurer et al's. study. It would be interesting to find out whether this was generally true by studying a range of intertidal sites and comparing these with a range of subtidal sites both of which had fine and coarse sediments.

As an example of micro-scale spatial variability, Eckman (1979) has shown that clustering at scales of one to several centimetres occurs commonly in small macrofaunal species inhabiting environments where protruding structures such as animal tubes, shell fragments and stones affect the pattern

of water flow at the benthic boundary layer. Like my work, Eckman has investigated spatial distribution of macrofaunal species, but the scales used by Eckman are smaller than the ones I used. His results are interesting because several of the species he studied exhibited gregariousness at scales of between 1-3cm (Manayunkia aestuarina and a Tanais sp.) while larger scale periodicities and interdependence in species abundance at a 10cm level were seen in M. aestuarina, P. elegans and Pseudopolydora kempi japonica. It is probable that similar micro-scale effects may be detectable at Ardmore with a suitably designed sampling protocol, and this would be a fruitful area for future research. For example it would be possible to lay out a 50cm transect and sample along it at 1cm intervals using mini-cores. The same statitical procedures could then be applied to this data as I have used in my study (Tables 18, 19, 20, 34).

Findlay (1981) has studied spatial distribution in meiofaunal communities. He selected two different sediment sites, a sand and a mudflat, and used four different sized cores, ranging in area from $0.3cm^2$ (radius c. 3.0mm) to $32.0cm^2$ (radius c. 3.2cm). Findlay showed that at a scale of 3 to $5cm^2$ a micro-scale patchiness existed in the meiofauna at both the mud and sand sites. This approach is an interesting one which could well be relevant to a site such as that at Ardmore when studying macrofauna. Taking into account the size of the macrofauna in sediments at Ardmore appropriate core sizes would probably be $3cm^2$ (radius c. 1.0cm) to $0.32\ m^2$ (radius c. 32.0cm). These could be used at either regular or random positions in a given area on the beach or along a transect. It would also be interesting to conduct this study at different times of the year to determine any seasonal effects, because Findlay demonstrated higher spatial aggregation for copepods in February than in September.

3. Algal mats and sand waves

One of the most interesting features at Ardmore is the meso-scale spatial heterogeneity on a scale of 1 to 50m (Figures 16 to 26, 31 & Tables 18, 19) imposed by the presence of algal mats at the high tide site and sand waves at the low tide site (Plates 2, 3), and it was this visible spatial heterogeneity produced by two different phenomena, the algal mats at high tide site and the sand waves at low tide site, which determined my transect sampling strategy at the two sites.

There is a significant literature on the effects of algal mats and also of seagrass beds (a related phenomenon) on benthic communities but less is known of the effects of sand waves.

3.1. Algal mats

Algal mats and also seagrass beds can have a major impact on intertidal and shallow subtidal sediments and their faunal communities (Gingsburg & Lowenstam, 1958; O'Gower & Wacasey, 1967; Wood et al., 1969; Coull, 1970; Hartog, 1970; Neumann et al., 1970; Scoffin, 1970; Taylor & Lewis, 1970; Perkins & Abbott, 1972; Zieman, 1972; Orth, 1973; 1977; Rasmussen, 1973; Santos & Simon, 1974; Woodin, 1974; McRoy & Helfferich, 1977; Reise, 1977, 1983; Lubchenco, 1978; Frostick & McCave, 1979; Suchanek, 1983; Norton, 1986; Gambi et al., 1990). They can stabilize sediments (Gingsburgh & Lowenstam, 1958; Neumann et al., 1970; Scoffin, 1970; Orth, 1977; Frostick & McCave, 1979), increase larval settlement, decrease predation, prevent adults from being washed away, and increase species richness and diversity (O'Gower & Wacasey, 1967; Wood et al. 1969; Coull, 1970; Hartog, 1970; Taylor & Lewis, 1970; Warme, 1971; Zieman, 1972; Orth, 1973, 1977; Santos & Simon, 1974; Woodin, 1974; Thayer et al., 1975; Reise, 1977, 1983; Nicholls et al., 1981; Gambi et al., 1990).

Nicholls et al., (1981) looked at the effect of the growth of the green algae Enteromorpha and Ulva on intertidal macrobenthic communities and their predators. They studied two sites in Langstone Harbor, the Solent, Hampshire, one an open mudflat and the other with a rich cover of algae. The species composition of the two sites was very similar but the relative abundances of the species differed significantly. The algal mat area had fewer species with higher numbers, while the mud-flat area had more species with fewer individuals per species. This means that the mud site had a higher diversity than the algal mat site, although the authors did not actually calculate diversity indices for their data. There are interesting similarities and differences between this study and my results at Ardmore, although Nicholls et al. did not submit their data to statistical analysis. At Ardmore the species composition was broadly similar between the high and low tide sites (Table 6) and between the algal and nonalgal areas at high tide site (Table 10). However in contrast to Nicholls et al.'s study, the diversity index of the low tide site at Ardmore where there were no algae was significantly lower than the diversity index of the high tide site where algal mats were present (Table 6).

The algal mats that I studied at the high tide site at Ardmore (Plate 2, 10) are permanent features of the beach there and have a very marked effect on the structure and variability of the benthic infaunal communities and on sediment parameters (Figures 8, 9, 10, 11 & Tables 2, 10). However even when algal mats are ephemeral they can have significant effects on the infauna. Reise (1983) studied Enteromorpha mats which became established by the algae becoming anchored in the feeding funnels of Arenicola marina. These mats were destroyed one month later by wave action. He counted the abundance of infaunal polychaetes and of a large number of turbellarian species and showed that although the polychaetes were not markedly affected the turbellarians decreased in abundance and species numbers. The turbellarians which fed on diatoms were affected the most and those that fed

on bacteria were affected the least. Reise cleared a $100m^2$ area of algal mats by daily hand removal, and found that in this area the abundance of the turbellaria had doubled relative to their numbers at the beginning of the formation of the algal mat and were 5 times higher than below the algal mats. Although Reise's paper is difficult to interpret because of the way in which it is written, his results are of great significance because they show the importance of short term algal cover in introducing spatial heterogeneity in the abundance of some members of the benthic community - the turbellaria. I did not measure turbellaria in my study and so no detail comparisons can be made between my work and Reise's (1983) study. However the first effect of algal cover may be to cause spatial heterogeneity in smaller infauna such as turbellaria which then in turn affect the larger organisms perhaps by predator-prey relationships.

There are a number of further points about my own results which require comment in relation to the presence or absence of algal mats. The first is that although there are considerable differences between the high and low tide sites (Plates 2, 3, Figures 8, 9, 10, 11 & Tables 2, 3, 4, 5, 6, 18) I found fewer differences in mean abundance between the algal and nonalgal areas at the high tide than I had expected (Table 10). There are no differences in abundances of F. sabella, H. neglecta, M. balthica, N. diversicolor, or P. elegans and there were also no differences in the diversity indices as assessed by the Shannon-Wiener and Simpson's indices (Table 10). On the other hand there were significantly more A. marina and C. volutator in the nonalgal than the algal areas along the transect (Table 10) and this may well be related to the significantly lower shear strengths and higher redox potentials (more aerobic sediment) in the nonalgal sediment (Table 10). At a scale of upto 50m then, the abundance of five out of the seven species and the diversity indices are not affected by the patchiness of the algal mats along the transect.

However one has to use very careful reasoning in this context, because to determine whether algal mats increased or decreased abundance and

diversity at high tide it would be necessary to conduct an equivalent 50m transect at the same tidal level on the same intertidal beach which contained no algae at all. This was not possible at Ardmore because there was no such area at that tidal level. However it might be possible to tackle the problem by removing algae from the beach and then comparing the abundance of species in the area from which algae had been removed with an adjacent area from which the algae had not been removed (c.f. Reise, 1983).

There were considerably greater differences in the variability of the species abundances between the algal and nonalgal areas than there was between the means of the abundances themselves (Table 10). The only species not to show such an effect was P. elegans. The variability in abundances of A. marina and C. volutator were greater in the nonalgal than in the algal areas. However this might have been expected because the mean abundances were also higher in the nonalgal areas.

The significant differences in the variability of the abundances of the other four species (F. sabella, H. neglecta, M. balthica, and N. diversicolor) are extremely interesting, because their abundances were the same in the algal and nonalgal areas. Two of the species, F. sabella and N. diversicolor, were more variable in the nonalgal areas in other words their patchiness was greater there, and two of the species, H. neglecta and M. balthica, had a greater variation in the algal areas and hence were more patchily distributed there. The difference between the two pairs of species might be related to their mode of life or feeding (Newell, 1965; Fenchel, 1972). F. sabella and N. diversicolor both construct permanent tubes as adults while H. neglecta and M. balthica are mobile deposit feeders, feeding on microorganisms and sometimes Enteromorpha (Green, 1968; Hughes, 1986).

3.2. Sand waves

Sand waves, also called sand banks or sand dunes similar to those at Ardmore (Plate 3) are well recognised meso- and macro-scale intertidal and subtidal sedimentological phenomena (Marsh, 1874; Carey & Oliver, 1918; Coleman, 1969; Klein, 1970; Stride, 1970; Caston, 1972; Langhorne, 1973, 1982; Swift et al., 1978; Reineck & Singh, 1980; Bridge, 1981; Caston, 1981; Kidd & Roberts, 1982; Wilson, 1982; Gardner & Kidd, 1983; Allen, 1985; Boothroyd, 1985; Reise, 1985; Odum et al., 1987; Siever, 1988) and there is some ecological evidence reviewed by Wilson (1982) that they can have a significant effect on the subtidal infauna inhabiting them.

Actively moving subtidal sand banks (Jones et al., 1965; Salsman et al., 1966; Langhorne, 1982) have a low species diversity (Wilson, 1982, p. 154). For example Tyler and Shackley (1980) record an impoverished fauna from inshore subtidal sandbanks in the Bristol Channel which includes the mysid Gastrosaccus spinifer, the amphipod Pontocrates arenarius and the polychaete Nephthys cirrosa. The tops and sides of subtidal sand banks can however contain high populations of some species - for example the irregular echinoid Echinocardium cordatum and the sand eels (Ammodytes marinus) and Hyperoplus (Ammodytes) lanceolatus (Reineck, 1963; Macer, 1966; Houbolt, 1968; Wilson, 1982). The troughs of subtidal sand waves appear to support a more varied fauna. According to Wilson (1982), a well-established infauna occurs if the sand waves only move occasionally or are separated by a wide area of gravel. This author reports a personal communication from J. Ulrich that the polychaete Lanice conchilega is found in large numbers in sand wave troughs in the German Bight, and Werner et al. (1974) report large colonies of Mya arenaria at densities of up to $400m^{-2}$ in the troughs of sand waves in the Kiel Bight, Baltic Sea.

My own data on the intertidal non-migrating stable sand waves at Ardmore show marked meso-scale differences in sediment properties,

abundances of the 5 indicator species and diversity indices between the peaks and troughs of the sand waves (Figures 6, 8 to 11, 16 to 18, 20 to 25, & Tables 3, 5, 11). The peaks of the sand wave are made up of well-drained sand and the troughs usually contain water (Figure 6, Plate 3), and this difference undoubtedly partly explains the significantly higher shear strength of the sediment making up the peaks (Table 5).

There is also a meso-scale difference in the redox potential data obtained from the peaks and troughs. However these data are more difficult to interpret as there is an apparent inconsistency in the statistical significance of the differences between the redox potentials in the peaks and troughs, given in Tables 5 and 11. In Table 5 the redox potential is significantly lower in the troughs than in the peaks while in Table 11 there is no significant difference. This may be because the 2 quadrats in which measurements were taken were sited exactly at the top of the peak and exactly at the bottom of the trough respectively, while some of the 13 peak and 13 trough quadrats along the 50m transect from which the data in Table 11 were obtained inevitably did not sit exactly at the top of the peaks and at the bottom of the troughs because they were part of the 50m transect. If the lower redox potential in the troughs recorded in Table 5 is a genuine difference it may well be caused by a higher content of detrital material there. This detrital material would stimulate heterotrophic microbial activity (Gerlach, 1978) which in turn would use up oxygen hence lowering the redox potential.

One species was more abundant at the peaks than in the troughs - A. marina (Table 3, 11). The reasons for this are not clear but similar effects occur subtidally with a few species (see above). The peak sediments have a higher shear strength and therefore may be more difficult to burrow in. However once a burrow is constructed it might retain its integrity for longer than in a lower shear strength sediment. But one should be cautious about reading too much into the differences of shear strength because the shear

strength of the sediment may become significantly less - and the differences in shear strength between the peaks and troughs might hence be reduced - when the tide covers the site.

Three species were significantly more abundant in the troughs than in the peaks of the sand waves, B. guilliamsoniana, M. balthica and N. diversicolor (Table 3, 11) and this effect has also been noted for other species in subtidal troughs (see above). Again the reasons are not obvious although they might be related to detrital material in the troughs, to being almost always covered by water, or to avoidance of the higher shear strength in drained sediment on the peaks. The diversity indices were higher in the troughs than at the peaks (Table 11) and the same effect is recorded subtidally (see above).

All of these differences must be produced by some local property of the sediment that differs between the peaks and the troughs. Shear strength, sediment permeability and drainage or lack of it, redox potential and pH (Table 5), and detrital material are possible causes as outlined above. Others might be differences in particle size distribution. For example the trough sediment had a significantly larger particle size and was less well sorted than the peak sediment (Tables 5).

There is evidence in the literature for the importance of differences in microtopography of the sediment surface, which although on a different scale from the sand waves at the Ardmore low tide site, are of interest to my work. Several authors have shown that alterations in microtopography produced by macrobenthic bioturbation can change community structure, albeit on a smaller scale than the sand waves. Rhoads and Young (1971) showed that the cone-shaped faecal mounds produced by the burrowing sea cucumber Molpadia oolitica increased species richness. The mounds were colonised by 3 tube-building polychaetes Euchone incolor, Ninoe nigripes and Spio limicola, which in turn made the faecal mounds suitable habitats for the caprellid amphipod Aeginina longicornis and the bivalve Thyasira gouldi.

Similar effects have been demonstrated by Reise (1981) for the funnels and faecal mounds of Arenicola marina which are colonised by small zoobenthos, and by Billheimer and Coull (1988) for the effects of feeding pits produced by juvenile spot (Leiostomus xanthurus) (Pisces) on meiobenthic community structure. It is however unwise to draw too close a parallel between these effects and my sand wave data. Faecal mounds and similar structures are on a smaller scale than the sand waves, but more significantly they may have quantitatively or qualitatively different chemical and microbiological properties than the surrounding sediment.

Three papers are particularly relevant to my results on the abundance of infauna in the peaks and troughs because they are both concerned with intertidal communities (Sameoto, 1969a, b; Hogue & Miller, 1981).

Hogue and Miller (1981) investigated the effects of sediment microtopography on the micro-scale spatial distribution of meiobenthic nematodes by studying nematode abundance in the peaks and troughs of sediment ripples. Although the scales that Hogue and Miller studied were much smaller than mine, their techniques were similar and their results are very interesting. Hogue and Miller chose an intertidal sand flat characterised by regularly spaced assymetrical sediment ripples whose wavelength was about 8cm. They laid out two transects each 1m long at right angles to the ripples. They then sampled along the transects by contiguous 6mm diameter cores (drinking straws) and were able to demonstrate a clear association between high densities of nematodes and the ripple crests.

Their results show that micro-scale environmental heterogeneity imposed by ripples produces detectable differences in meiobenthic organisms similar to, but at a different scale from, the effects that I noted at the Ardmore low tide site (Tables 3, 11). Hogue and Miller (1981) suggested that the reasons for the nematodes being higher in the peaks than in the troughs -

an observation that they had not expected - was related to the migration of ripple crests along the sediment surface once every tide. This caused the organic material which was at the surface of the sediment in the ripple troughs on the previous low tide to aggregate in a subsurface layer below the peaks of the ripple on the subsequent tide. A similar effect has been recorded by Jenness and Duineveld (1985).

Hogue and Miller (1981) suggest that the nematodes find the subsurface layer of organic material attractive and aggregate in it, thus producing the higher nematode numbers below the ripple peaks. However an effect such as this is unlikely to occur at Ardmore because the sand waves at the low tide site are stable and do not migrate. In the light of these investigations it would be interesting to study meiofaunal abundance and sediment properties in the ripples (Plate 9) that occur on the peaks of the large sand waves at the Ardmore low tide site.

Sameoto (1969a) studied the distribution of three species of Haustoriidae (amphipods) (Haustorius canadensis, Neohaustorius biarticulatus and Acanthohaustorius millsi) at Sippewissett Creek and Black Beach, Cape Cod, Massachusetts. The area at Sippewissett Creek consisted of a sand bar and a bank, the tops of which were drained and the sides of which were not, and a channel between the bank and the sand bar which was always covered by water. The parallel to my own low tide site at Ardmore is fairly close. One of the species N. biarticulatus was most abundant in drained sediment at the top of the sand bar and bank , the second H. canadensis appears from his table 2 (loc.cit. p. 367) to have been more abundant in the sides of the sand bar below the water table and also in the Creek channel, and the third A. millsi was most abundant in the channel. Sameoto (1969a) also measured mean sediment particle size and sorting, interstitial water content, and organic content of the sand bar, the bank, and the channel. The only one of these parameters that Sameoto was able to correlate with the different species distribution (loc. cit. Table 2 p. 366) was interstitial water content which was

low at the top of the sand bars and creek where N. biarticulatus was abundant. However Sameoto also comments in his discussion (p. 387) that the distribution of H. canadensis and A. millsi was positively correlated with anaerobic sands in the channels and low sand bars, while N. biarticulatus preferred the drained tops of the sand bars which were more aerobic. Sameoto (1969a) did not make any quantitative measurements of redox potential so these observations can only be regarded as qualitative. The only amphipod I found at the low tide site at Ardmore was B. guilliamsoniana which since it occurred in the troughs of the sand waves (Tables 3, 11) is broadly similar to A. millsi in its habitat requirements. It is interesting that B. guilliamsoniana is negatively correlated with shear strength and with the level of the sediment surface above the water table (Table 13).

In a second paper Sameoto (1969b) reports that three species of essentially subtidal haustoriids are "almost entirely found in the troughs of sand ripples that remained water-saturated" - presumably at low tide - (loc. cit. p. 1336) but Sameoto gives no further details, so a detailed comparison with my results is not possible.

These papers and my own research show that the effects of large sand waves on benthic community diversity and structure at a meso-scale and macro-scale is a fruitful area for future research which should firstly involve field surveys and then field and laboratory experiments.

4. Correlations between species abundances, between species abundances and sediment parameters and between sediment parameters

Correlations between species abundance, between species abundance and sediment parameters, and between sediment parameters, can have a major effect on the structure and variability of infaunal benthic communities in sediments. For example if the abundance of two species are positively

correlated, high numbers of one species would be associated with high numbers of the other, and low numbers of one would be associated with low numbers of the other. This occurs at the high tide site at Ardmore between C. volutator and N. diversicolor, between C. volutator and A. marina, and between F. sabella and P. elegans (Table 13, Figure 27) and at the low tide site between B. guilliamsoniana and M. balthica (Table 13, Figure 29). As another example, if a species is negatively correlated with an environmental parameter such as shear strength, when the shear strength of the sediment is high there will be few individuals and when the shear strength of the sediment is low there would be many. This sort of effect occurs at the low tide site at Ardmore, where B. guilliamsoniana, M. balthica and N. diversicolor are all negatively correlated with shear strength (Table 13) (see below p 213).

Relationships such as these are obviously of major significance in determining structure and variability in the benthic ecosystem, but in themselves give no information about cause and effect. In the latter example, for instance, B. guilliamsoniana, M. balthica and N. diversicolor might be negatively correlated with shear strength for several reasons. Low shear strength might actually be preferred by the species, and this would be a cause and effect relationship. On the other hand a third factor might reduce shear strength and might at the same time be favorable to the species: microbial growth (Meadows & Anderson, 1966, 1968; Frankel, 1977) might decrease shear strength by making the particles more slippery hence reducing shear strength while at the same time being a good source of food for the species (Zobell & Felthan, 1938; Newell, 1965; Hargrave, 1970; Fenchel, 1972) and hence increasing species abundance. Alternative hypotheses of this sort can only be proved or disproved by carefully controlled experiments in the field and in the laboratory.

Having made these points, it is certainly true that a number of authors including myself in this thesis have calculated correlations between

species and sediment parameters, and between different species (Buchanan, 1963; Lie, 1968; Wade, 1972; Parker, 1975; Schaffner, 1990; Brekhovskikh et al., 1991), and then speculated on the meaning of the correlations in relation to species abundance and its variation. In my work, since the correlation analyses were conducted on pairs of data points from successive quadrats along the transects (e.g. abundance of C. volutator, shear strength) the resultant correlations can also be viewed as meso-scale effects.

Chapman and Newell (1949) demonstrated in a classic paper that Arenicola marina on mud flats at Whitstable, Kent were most abundant on the muddy sand flats and fell off in abundance in shingle banks towards high tide and in clay towards low tide. There was a strong positive correlation between population density and the depth of the muddy sand overlying the clay substrate. This is interesting because although I did not analyse it in detail a similar effect may be occurring at Ardmore. At high tide the muddy sand at the surface overlies a more clayey sediment and the interface between the two occurs at c. 5-10cm. At the low tide site the sediment is a muddy sand to a depth of at least 40 to 60cm which is the depth to which A. marina normally bioturbates the sediment. There is strong evidence from my results (Table 7) that A. marina adults are less abundant at the high tide site than at the low tide site. One explanation for Chapman and Newell's (1949) and my observations are that adult A. marina prefer a reasonably deep muddy sand sediment of the order of 40 to 60cm in which to construct their vertical burrows.

Witte and Wilde (1979) conducted a series of experiments to demonstrate the effects of Nereis diversicolor on juvenile Arenicola marina. Nereis was found to intrude into Arenicola burrows and settle in their upper parts, thus competing for space. Nereis also predates on the tails of Arenicola and sometimes even kills them. Witte and Wilde found in the field that Nereis can cause considerable damage to Arenicola and that there was an inverse relationship between the densities of the two species. However, I found no

significant negative correlation between N. diversicolor and A. marina either at the high or low tide sites (Table 13). This suggests that the mechanisms reported by Witte and Wilde (1979) may not be occurring on the beach at Ardmore.

Olafsson and Persson (1986) studied interactions between Corophium volutator and Nereis diversicolor in a field study of an estuarine shallow-water soft-bottom sediment on the south coast of Sweden and also conducted behavioural experiments on the interactions between the two species. Over a two-year period they studied a Corophium patch containing high densities of Corophium and low densities of Nereis and a Nereis patch containing high densities of Nereis and low densities of Corophium. Their laboratory experiments suggested that high densities of Nereis reduced the density of Corophium mainly by sediment disturbance - not by predation. However their experiments did not show any impact of Corophium on the abundance of Nereis. My field results do not agree with those of Olafsson and Persson since C. volutator was positively correlated with N. diversicolor at the high tide site where both species occurred together (Figure 27, Table 13). The explanation for this very obvious difference between Olafsson and Persson's (1986) data and my results is obscure, although it might be related in some way to the different environmental characteristics of the two sites (Tables 4, 5, 6, 18). My high tide station is covered by water for only a small proportion of time during the tidal cycle while Olafsson and Persson's site although in very shallow water (30-40cm) was essentially a subtidal habitat.

I now want to consider the results of my own correlation analyses at Ardmore in a little more detail (Table 13, Figures 27 to 30). At low tide there was a group of 3 species which were positively correlated with each other (Figure 29). These were Bathyporeia guilliamsoniana, Macoma balthica, and Nereis diversicolor, although only B. guilliamsoniana and M. balthica are significantly correlated. These 3 species are also negatively correlated with

shear strength and with the height of sediment above the water table (Table 13, Figures 29, 30). Inspection of the abundance data along the transect shows (Figures 17, 20, 21) that all three species occur in the troughs in higher abundances than in the peaks of the sand waves. The troughs of the sand waves have a lower shear strength and are covered with water. This explains the positive correlations between the species and the negative correlations between the species and the two sediment parameters shear strength and water table. The correlations associated with A. marina substantiate this view. A. marina tends to be more abundant in the peaks of the sand waves than in the troughs (Plate 5). One would expect this to lead to negative correlations between A. marina and the three species in the troughs. In fact two of the correlations are statistically negatively significant (with M. balthica and B. guilliamsoniana), while A. marina and N. diversicolor are not significantly correlated. It should also lead to positive correlations between A. marina and shear strength and with the height of sediment above the water table (Figure 6) both of these correlations are positive and highly significant (Table 13).

All of these correlation coefficients between species and sediment parameters emphasise the important role played by sand waves in determining the meso-scale structure and variability of the benthic infaunal community at the low tide site.

The high tide site correlation coefficients are more difficult to interpret (Figure 27, Table 13). However, there are three pairs of species which are positively correlated (F. sabella/P. elegans; C. volutator/N. diversicolor; A. marina/C. volutator). The reasons for these positive correlations are not obvious, although some of them might be related to the presence of algal cover. For example both A. marina and C. volutator are negatively correlated with algal cover being more abundant in the nonalgal areas and hence a positive correlation between the two species is to be expected.

There are two further points about the significant correlation coefficients at high tide which require comment. The first of these concerns

N. diversicolor. N. diversicolor is strongly positively correlated with the height of the sediment above the water table (Figure 6, Table 13) - which is exactly the opposite effect to that observed at the low tide site where the correlation is negative. This means that N. diversicolor occurs in large numbers in exposed sediment at high tide site and in large numbers in sediment underwater in the troughs at low tide site. As might be expected from this, the species is positively correlated with shear strength at high tide and negatively correlated with shear strength at low tide. However, this does not explain the contrasting habitat of the species at the high and low tide sites.

The second point concerns C. volutator. C. volutator is strongly positively correlated with positive redox potential. This means that it favours aerobic sediment. Deans et al., (1977) showed that C. volutator avoided irradiated sediment which had very low Eh values but preferred control unirradiated sediment. These findings substantiate my results that C. volutator favours sediment with positive Eh values.

A final point needs to be made about the correlation coefficients in Table 13. There were a larger number of significant correlations at the low tide site than there were at the high tide site, 20 (44%) out of 45 as compared with 17 (22%) out of 78 (Table 12). The reasons for this may be the major role played by the large sand waves at the low tide site (Plate 3). Perhaps a regular spatial variation of this sort produces more significant correlations between species and sediment parameters than does the less regular spatial variation between algal mat and nonalgal mat areas at the high tide site (Plate 2). In this context it may be significant that the sand waves at low tide are permanent features at all seasons on the beach while the algal mats at high tide although being permanent show much greater growth in the summer than in the winter.

5. Species Diversity

Differences in the relative abundance of different species can be measured by a number of diversity indices (Simpson, 1949; Lloyd & Ghelardi, 1964; Margalef, 1968, 1978; Sanders, 1968; Odum, 1971; Fager, 1972; Pielou, 1977; May, 1981; Valiela, 1984; Baker & Wolff, 1987; Magurran, 1988) which distinguish between a continuum of communities ranging from those having a low diversity with a few species and many individuals per species, to those having a high diversity with a large number of species and relatively few individuals per species.

I applied two commonly used indices, the Shannon-Wiener index and Simpson's diversity index, to my data for the high and low tide transects because these two are recommended by a number of authors (Odum, 1971; Krebs, 1972; Pielou, 1977; Margalef, 1978; May, 1981; Levinton, 1982; Holme & McIntyre, 1984; Valiela, 1984; Baker et al., 1987; Magurran, 1988; Meadows & Campbell, 1988). The results (Table 6) show clearly that on a macro-scale the community at the high tide site has a significantly higher diversity than the community at the low tide site and that diversity fluctuates less along the transect at high tide - in other words shows less meso-scale variability - than it does at low tide (Table 6). These results are of great interest in relation to studies on the diversity of intertidal and subtidal sedimentary infauna and to hypotheses about factors causing diversity.

Some authors report that there is a decrease in the number of infaunal species from subtidal sedimentary environments through low tide to high tide areas (Johnson, 1970; McIntyre & Eleftheriou, 1968), but there is considerable variation between different beaches. For example Beukema (1976) in a study of species richness of macrofauna communities living in intertidal flats of the Dutch Wadden Sea, found the highest density of species at about mid tide level associated with a low silt content at that point. The number of species decreased towards high tide where the sediments became more muddy,

and towards low tide where sediments became more sandy. In contrast I found a higher species diversity at the high tide transect than at the low tide transect (Table 6). This macro-scale difference may be due to the contrast between the sandy sediment and sand waves at the low tide site and the rather more muddy sand with more food (detrital and algal material) (Gerlach, 1978) for infauna at the high tide site (Tables 4 & 5).

Rather than discussing the large literature on diversity indices in benthic communities (e.g. Paine, 1966; 1974; Hessler & Sanders, 1967; Fager, 1972; Reise, 1978; Watling et al., 1978; Baker et al., 1987; Outridge, 1987; Saenger et al., 1988) I now propose to consider my results in the light of Margalef's (1968), Sanders's (1968) and Abele and Walter's (1979) theories on diversity.

In his book on "Perspectives in Ecological Theory" Margalef (1968) identifies a spectrum of marine communities ranging from pioneering or immature ones with a relatively low diversity in which the relative abundances of species vary considerably in space and time, to mature communities having a high species diversity and a relative constancy of number of individuals. According to Margalef's classification, my low tide site is a relatively immature community and my high tide site a more mature community. Margalef states that instability in the environment may hold a community indefinitely at a given level on his scale (c.f. Johnson, 1970). If the low tide site at Ardmore Bay can be regarded as an immature community in Margalef's sense, the higher exposure to wave action at that site could be the instability holding the communities at a relatively immature stage with a low diversity.

The relationship between the communities at my high and low tide sites to Margalef's (1968) views on the differences between immature and mature communities, regarded by him as a process of succession, can be examined in more detail. Margalef identifies these differences as follows.

(i) A mature community has a higher diversity. This is certainly true of my high tide site, when compared with the low tide one (Table 6).

(ii) A mature community has a higher biomass. I did not measure biomass, but there were greater numbers of individuals at the high tide transect ($5.3605 \times 10^5 m^{-2}$) than at the low tide transect ($3.7875 \times 10^5 m^{-2}$). These data were calculated from those in Table 6 by summing the mean abundances of all the high tide species and multiplying by 50, and then doing the same for the low tide species.

(iii) A mature community has a higher primary production. The high tide site almost certainly has a higher primary production than the low tide site because of the abundance of algal material there (Plate 2), although microbial primary production will occur at both sites.

(iv) A mature community contains a greater proportion of inert organic matter and biogenic structures. The high tide site has more inert organic material in the form of decaying algal mat below the sediment surface (Plate 10) (c.f. Fenchel, 1970) (c.f. the resultant low redox potentials below the mat surface), and probably has more biogenic structures - burrows are more obvious at the high tide site than at the low tide site (Plate 2).

(v) A mature community has a more constant number of individuals in space and time. The high tide community has a less variable diversity than the low tide community along their respective transects (Table 6). However the abundances of 3 of the 4 species common to the high and low tide sites (A. marina, M. balthica, N. diversicolor) are more variable at high tide than at low tide so the picture is not a simple one (Table 6).

These detailed comparisons broadly confirm my view that the high tide site is a more mature community than the low tide site, using the phrase mature community as defined by Margalef (1968).

Sanders (1968) in a comparative study of marine benthic diversity envisaged a continuum (loc. cit. p. 253, Fig. 6) ranging from communities which are physically controlled to those in which the physical environment is not a critical controlling factor. He termed the former physically controlled communities, and the latter biologically accommodated communities. He based his reasoning on data collected from a wide range of soft-bottom marine and estuarine environments (Arabian Sea, Bay of Bengal, Vellar River Estuary, India, continental shelf, the slope, and abyssal rise off New England, USA and South America, and the Pocasset River and Buzzards Bay, Massachusetts). Sanders (1968, p. 252) defined physically controlled communities as those in which the physical conditions fluctuate widely, the animals are exposed to severe physiological stress and the community has a low diversity. Examples are communities in boreal estuaries and hypersaline bays. He defined biologically accommodated communities as those in which the physical conditions are rather constant and uniform and are not critical in controlling the success or failure of the species. These communities have a high species diversity (tropical shallow water, continental slope, abyssal rise).

It is more difficult to relate my high and low tide communities to Sanders's (1968) concepts than to Margalef's (1968). The high tide site has a higher diversity, more species (Table 6) and may therefore be regarded as a more biologically accommodated community, while the low tide community could be viewed as a more physically controlled community because of its lower diversity (Table 6). However at both sites physical conditions fluctuate widely over one tidal cycle and also between summer and winter. Perhaps one should regard them both as different levels of a physically controlled community and this broadly agrees with Sanders' (1968) view that boreal shallow water and estuarine communities are physically controlled ones. This would include areas such as the Clyde Estuary and the Clyde sea area.

However my difficulty in relating the high and low tide

communities to Sanders' model may be caused by the model itself being false. An alternative interpretation of Sanders (1968) results has been given by Abele and Walters (1979). They erected a hypothesis (loc. cit. p. 121) that "the differences in species richness among the boreal estuary, shallow water, shelf and deep sea regions are due to differences in the areal extent of the regions". According to Abele and Walters (1979) this was first suggested by Grassle (1967) in his unpublished Ph.D. dissertation (not consulted by me), and also by Bambach (1977). When Abele and Walters tested their hypothesis on Sanders's (1968) data (Abele & Walters, 1979, table 4, p. 122), there proved to be highly significant positive correlations between the number of species and the area of the sea bed. In their discussion they regard the species/area relationship as an empirical one, not a mechanism explaining species richness. However they go on to suggest that the relationship might be caused by an increase in the number of habitats with increasing area. Abele and Walters' (1979) species/area phenomenon is unlikely to explain the differences I recorded between the low and high tide sites because I sampled exactly the same size of area at both sites ($50m^2$). On the other hand the algal mats at high tide might provide more microhabitats within the $50m^2$ sampled than were provided by the sand waves at the low tide site. This would be a fruitful area for further research.

MICROBIAL COMMUNITIES

The microbial enrichment experiments reported in the second part of my thesis are relevant to a range of environmental conditions encountered in temperate continental shelf waters, and show how enrichment cores simulating different environments can produce very different microbial communities. There are a number of reports of sediment cores being used to investigate these interactions (see Introduction p 25) and I now propose to review the most relevant of these (Wormald & Stirling, 1979; Cox & Bazin, 1980; Nickels et al., 1981; Hennig et al., 1983) and then to discuss in more detail a number of aspects of the microbial communities and their variability that developed in my cores.

Hennig et al. (1983) studied mineralisation and fixation of organic material by bacteria and meiofauna in columns of beach sand. They interpreted their data to show that more organic material was fixed by meiofauna and bacteria than by meiofauna alone, and that net mineralisation only occurred when meiofauna were present alone. I did not assess meiofauna in my cores which may with hind sight have been an error. However all cores received identical sediment from the same area of the beach, and I did not notice any of the larger forms such as nematodes and harpacticoid copepods when the sediment was allowed to settle through water in the columns at the beginning of the experiment, or when samples were taken for SEM work at the end of the experiment. Furthermore on the area of the beach from which I obtained the sediment for my microbial experiments, harpacticoids and nematodes constitute over 90% of the meiofauna in abundance (Hariri, 1990; Saleh, 1990). I consider, therefore, that any meiofauna would have been present in very small numbers and would have had only a marginal effect on the progress of the experiments. Having said this, since extraction methods for meiofauna are fairly routine, future experiments should be directed towards

studying their effects on microbial communities on the shore under conditions such as those used in my own work.

Wormald and Stirling (1979) studied the effects of phosphate, nitrate and domestic sewage on bacteria and meiofauna in sand columns. The columns were incubated for 83 days during which time media were continuously circulated through them. Bacterial and meiofaunal abundances were measured at the end of the experiment. Nematodes were significantly more abundant in the nitrate and phosphate enriched columns. In contrast bacteria and harpacticoids showed no significant increase with any of the treatments. The lack of any increase in bacteria is surprising particularly in the sewage treated cores because they would have contained large quantities of organic material, and also because in my BL and BD cores which contained heterotrophic organic rich media there was a large increase in bacterial numbers. However Wormald & Stirling's paper is not clearly written and is therefore difficult to interpret.

Nickels et al., (1981) conducted an elegant field incubation experiment to demonstrate the effects of sand grain microtopography and substrate location on the structure and distribution of microbial communities. These authors ran two parallel sets of samples, each set consisted of three different silicate substrates: glass beads (45 to 500 μm in diameter), Santa Rosa beach sand and sand dredged from the bottom (near the platform where the first set of samples was to be incubated). The first set was exposed to running seawater pumped from a depth of 26m. The second set was incubated on the sea bed at a depth of 32m. Both sets were incubated for 8 weeks after which cores were taken. Their results from SEM show that the glass beads which have a smooth surface had very little microflora. The sand grains from Santa Rosa beach had surface irregularities which contained a diverse microflora. The sand grains from the sea floor were irregular and had a morphologically diverse microbial community. My results show similar effects where irregular sand grains had more microbial growth than the smooth

sand grains. The most important conclusion drawn from Nickels et al.'s (1981) work is the presence of spatial heterogeneity in microbial communities on three different types of substrate when incubated under the same, as well as different environmental conditions.

Nickels et al's (1981) findings broadly relate to my work even though they do not define any scales of heterogeneity. In my study the photosynthetic and heterotrophic media would equal Nickel et al's two different sites of incubation. Both studies indicate that when the same type of substrate is incubated under different environmental conditions it results in different microbial communities showing different scales of spatial heterogeneity, although in Nickels et al's work there is also an input of new microorganisms from the surrounding water medium. However, Nickels et al.'s (1981) different types of substrate incubated under the same environmental conditions can be considered as showing a meso-scale effect, as my within media effect, and the two sets incubated under different environmental conditions an example of macro-scale effects, as my between media effects.

Cox & Bazin (1980) conducted a laboratory experiment using glass beads packed in a column. These authors inoculated two species of nitrifying bacteria Nitrosomonas europaea and Nitrobacter agilis into a 35cm long column supplied with nutrient solution containing $(NH_4)_2SO_4$ maintained at a constant flow rate. The column was incubated for seven months. At the end of the experiment the column was divided into 11 contiguous sections each approximately 3cm long and samples from each section were examined under the electron microscope. The first section (0-3cm) showed monolayers of bacteria and in some regions a layer 20 cells thick was observed. The second section (3-6cm) showed relatively fewer bacteria and frequent slime layers. In the third section (6-9cm) there were very few bacteria and most of the beads had slime layers. No bacterial growth was seen in sections 4 to 8. In sections 9, 10 and 11 only a few contaminant bacteria were present. Their results

therefore show vertical spatial heterogeneity in microbial abundance on glass beads under laboratory conditions. Cox & Bazin (1980) hypothesise that the absence of bacteria in the lower sections of the column is due to factors like changes in nutrient concentration, pH, CO_2 concentration or growth inhibition by either metabolic products, or the slime layer. Although I did not study spatial heterogeneity at a scale of centimetres vertically in my sand cores, future investigations should study vertical and horizontal spatial heterogeneity at this scale in benthic microbial communities grown under laboratory conditions in sediment cores.

There are a number of aspects of the microbial communities that developed in my cores that are interesting. The ML cores show a community containing large growths of photosynthetic microorganisms such as diatoms and blue-green algae which would develop in highly illuminated sheltered sediments occurring intertidally or in the immediate subtidal range.

The BL and BD cores with their communities containing a wide range of morphological types and high numbers of heterotrophic bacteria demonstrate the effect of high levels of nutrients such as would occur near sewage outlets, one of the effects of which would be the establishment of very diverse microbial communities. This is interesting, because the number of species in macrofaunal communities are usually impoverished in similar situations (Pearson et al., 1986, loc. cit. p. 343, Fig. 8b) and often one species predominates - Capitella capitata around the Firth of Clyde dumping site off Garroch Head at the south end of Bute (Clark, 1986).

Heterotrophic bacteria were present in the communities that developed in all four ML, MD, BL, and BD sediments but were much more abundant in the BL and BD than in the ML and MD sediments. Their abundance in the ML and MD sediments was not affected by light since the numbers were the same. If this result can be extrapolated to field conditions, it means that subtidal illumination or lack of it, will not have a major impact on the numbers of heterotrophic bacteria. A purple-pink top layer of growth was

seen in both the BL and BD cores. The SEM photomicrographs show many short rods and cocci which are consistent with this.

The occurrence of Thraustochytrids in the ML cores is of great interest. The type species was described by Sparrow (1936), and Thraustochytrids have been isolated from seawater (Johnson, 1976) and sediments (Kumar, 1980; Rieman & Scharge, 1983). My work shows that it is possible to grow Thraustochytrid sporangia from marine sediments under controlled conditions that mimic their natural environment.

A number of points in the descriptive account of the microbial communities in the different treatments require comment.

There tended to be more growth on subangular (sharp) sand grains than on subrounded (smooth) sand grains (Russell & Taylor, 1937; Weise & Rheinheimer, 1978; Nickels et al., 1981) and hence microbial communities may be better developed in sediments made up of particles that are less weathered or are exposed to less wave action. This is likely to occur in more sheltered sedimentary environments, on low energy beaches. It is interesting in this context that Meadows and Anderson (1968) in describing microbial communities on sand grains sampled from an intertidal high energy sandy beach in Etterick Bay, Clyde Estuary, state that diatoms were sparse on grains taken from higher reaches of the beach but more abundant towards low tide and subtidally (loc. cit. p. 167, Table 1). These authors also conducted a simple abrasion experiment with sand grains maintained in culture media. Flasks were either shaken or not shaken and more growth occurred in the sediments in the nonshaken flasks. They concluded that abrasion was an important factor limiting growth to depressions on the sand grain surface, and of course subangular sand grains would have more depressions than subrounded sand grains. However abrasion does not account for the observations that I have recorded in my experiments because the sediments were maintained in columns under static conditionns. Another cause might be grazing by microfauna and

meiofauna (Alongi, 1985) because these organisms if they eat microorganisms on sand grain surfaces would find it easier to eat them from flat surfaces than from concavities. However this is unlikely to be a causative agent in my experiments because larger invertebrates were excluded by the initial sieving process although there might have been a few meiofauna in the columns (see above).

There are other explanations of the greater growth in the microbial communities on subangular grains. Fluid flow through a sediment might be more likely to dislodge microorganisms from exposed surfaces than from concavities, and since the medium was allowed to flow through the sediment every two days this may have had an effect. Another explanation might be natural abrasion effects before collection. The subangular grains with more concavities on their surfaces would then have more microorganisms on them than the subrounded sand grains from the start of the experiment.

Both monospecific colonies and mixed species colonies occurred in the communities on the sand grains. The Agmenellum sp., the Bacillus sp. and the two coccoid bacterial species all occurred in monospecific colonies while Amphora sp. B and Schizothrix sp. occurred both in monospecific and mixed species colonies. The reasons for these differences are probably complex. A monospecific colony might be monospecific because it produces some inhibitory extracellular material which stops other microorganisms invading the colony. In this context it is interesting to note that there appeared to be a growth-free zone around one of the microcolonies of coccoid bacteria (Plate 10E). Conversely species in mixed species colonies might obtain some mutual benefit from the other species present. This would be a fruitful area for future research.

A number of different examples of binding were noted on and between sand grains in the different media. There is now considerable evidence from field observations and laboratory experiments that microbial binding may be an important factor in determining the stability and ersoion

properties of naturally occurring subtidal and intertidal coastal sediments (Bathurst, 1967; Neumann et al., 1970; Frankel & Mead, 1973; Holland et al., 1974; Frostick & McCave, 1979; Stal et al., 1985; Paterson, 1989; Brekhovskikh et al., 1991). Biofilms were noted in the ML medium (Plate 6D)., microbial mats (Plate 7C), filamentous network (Plate 7G) and strands connecting coccoid cells (Plate 7F) were noted in the BL medium, and thread-like strands were observed between bacterial cells and detritus (Plate 7J) in the BD medium. All of these illustrate the importance of binding materials in my columns and have important implications for field studies.

One of the purposes of the microbial work described in this section was to assess differences in variability of the abundance of microorganisms in the communities in the same (between sand grains - meso-scale) and different (between media - macro-scale) environments (i.e. different enrichment culture conditions). This was done by counts from randomly chosen sand grains. There can be a number of possible reasons for variability in the abundances of microorganisms between individual sand grains (meso-scale), and it should be remembered here that my abundance data are all based on counts of five randomly selected sand grains for each species in each medium. This is a small sample, but SEM preparation and photographic assessment of the results is very time consuming.

There may be differences in the physical nature of the sand grains themselves such as differences in concavities and the micro-smoothness or roughness of the surface (Meadows & Anderson, 1966, 1968; Krumbein, 1971; Rades-Rohkohl et al. 1978; Weise & Rheinheimer, 1978; Nickels et al., 1981; DeFlaun & Mayer, 1983) and individual sand grains may have different mineralogical compositions (Paerl, 1975; Rades-Rohkohl et al., 1978). There may also be chemical effects such as nutrient concentrations (Ellwood et al., 1982; Paerl, 1985) or biological effects, such as competition for space on sand grain surface (Patrick, 1977; Gooday, 1988), parasitism of one species on

another (Patrick, 1977; Gooday, 1988), and specific inhibitory or enhancement effects between species by the production of ECPM (extra-cellular polymeric material) and antibiotics (Bell & Lang, 1974; Patrick, 1977; Cox & Bazin, 1980; Nicholson et al., 1987; Gooday, 1988). For example a number of species are known to produce ECPM (Lewin, 1955, 1958; Duguid & Wilkinson, 1953; Huntsman & Sloneker, 1971; Allan et al., 1972; Bell & Lang, 1974; Huang & Boney, 1984; Hsieh et al., 1985, 1990; Bartlett et al., 1988).

Finally, the well-known existence of micro-scale spatial heterogeneity in naturally occurring and laboratory maintained sediments as micro-environments, micro-layers, and micro-zones is likely to be very important (Meadows & Anderson, 1968; Norkrans, 1980; Revsbeck & Jorgensen, 1981; Anderson & Ineson, 1982; Wimpenny, 1982; Revsbeck et al., 1983; Revsbeck & Ward, 1984; Wilson & Noonan, 1984; Wimpenny et al., 1984; Jorgensen & Revesbech, 1985; Paerl, 1985; Seitzinger & Nixon, 1985; Bebout et al., 1987; Nicholson et al., 1987). Each of these possibilities could be tested by suitably designed experiments under laboratory conditions although I was unable to do so through lack of time. All of them might have caused the differences in variability that I observed although it is difficult to be more specific than this.

There were a number of interesting meso-scale and macro-scale differences in variability in my data that were demonstrated by the application of appropriate F ratio tests. These are discussed in the following paragraphs.

There were 21 out of 25 (84%) significant meso-scale F ratio tests between pairs of species in the photosynthetic medium maintained in the light, only 11 out of 21 (52%) and 10 out of 15 (67%) respectively between species in the bacterial medium maintained in the light and dark. The higher number of significant meso-scale F ratios between species in the communities in the photosynthetic medium maintained in the light means that the species growing in highly illuminated conditions show greater meso-scale variability between sand grains. It is not easy to account for this, although it might be caused by

gradients of light in the sediment.

The number of significant macro-scale F ratios for cocci (diam. 0.6 μm) and bacilli growing in the different media, are almost identical - 7 out of 10 and 6 out of 10 respectively. This probably means that the factors producing macro-scale differences in variability in both groups of organisms when compared between the different media may be the same. This is not surprising because both cocci and bacilli are likely to be similar in their requirements for growth and space, being of the same size and almost certainly both being heterotrophic and utilizing similar nutrients.

There is an interesting contrast between the meso-scale variability of the blue-green alga Schizothrix sp. and the diatom Amphora sp. A in the community that developed in the photosynthetic medium maintained in the light. Schizothrix sp. showed a significantly greater variability between different sand grains than all the other species, while Amphora sp. A showed a significantly lower variability than all the other species. The reasons for this very obvious difference is not clear. Schizothrix sp. is a chain-forming organism while Amphora sp. A exists as individual cells that form colonies. But this does not explain the effect. Amphora sp. A is a motile diatom and therefore in principle could move readily between sand grains, while Schizothrix sp. being filamentous might be less likely to do so. This possible difference in motility might be one of the causes of their different variability, the more motile species being able to colonise other sand grains more easily thus leading to a more uniform meso-scale distribution between the sand grains.

A similar effect might account for the observed differences in variability between other species. In this context it would be interesting to test sand grain colonisation by two closely related species (same genus with similar nutritional requirements) one of which was known to be more motile than the other, and then to record the abundance and variability of the two species between different sand grains at successive intervals of time.

FULL SUMMARY

"Systematic observation in relation to this subject has hardly yet begun, and the scattered data which have chanced to be recorded have never been collected."

(Marsh, 1874)

FULL SUMMARY

The overall objectives of my thesis have been to study levels of abundances and their spatial heterogeneity in macrofaunal and microbial communities living in sediments on an intertidal muddy sand beach at Ardmore bay, Clyde Estuary, Scotland. The macrofaunal communities were studied by a field survey, and the microbial communities by nutrient enriched cores in the laboratory. The rationale for these two contrasting approaches is given in the introduction of the thesis.

MACROFAUNAL COMMUNITIES

1. Spatial heterogeneity and abundance in infaunal benthic communities have been studied in relation to their sedimentary environments at two intertidal sites on Ardmore bay in summer.

2. The high tide site (HT) was a low energy depositional environment dominated by patches of algal mats (Enteromorpha spp.). The low tide site (LT) was a higher energy erosional environment dominated by large sand waves. Each site had two visibly distinct areas. At high tide these were algal mats of Enteromorpha (diameter c 0.75m to 2m) and bare sediment with no algal mats - termed algal and nonalgal areas respectively. At low tide these were the peaks and troughs of large sand waves (wavelength c. 25m).

3. The work consisted of an initial survey followed by a detailed transect survey. Both surveys were done on all four areas (High tide: algal, nonalgal; Low tide: peak, trough).

4. The objectives of the initial survey were to identify and assess the abundances of the infaunal species, to test out sedimentary techniques and to obtain an assessment of the sedimentary environments, at the two high tide and two low tide areas.

5. The objectives of the more detailed transect survey were to assess mean values of and spatial heterogeneity (variability) in the species abundances and sediment parameters, to test statistical correlations between species abundances and between sediment parameters, and to measure diversity by two diversity indices and its spatial variability.

6. Overall, the results showed that the high tide and low tide sites were significantly different sedimentary environments and that there were also clear differences between the algal and nonalgal areas at the high tide site and between the peaks and troughs of the sand waves at the low tide site. The abundance and spatial variability in abundance of the infaunal macrofauna also showed highly significant differences both between the two sites and between the two areas at each site. These differences are very probably related to the different sedimentary environments but causal effects can only be established by future experimentation. A number of significant correlations were established between species abundances, between species abundances and sedimentary parameters, and between sedimentary parameters themselves. These results are summarised in detail below.

7. Both surveys showed that the following infaunal species were present in order of decreasing abundance. High tide site: Fabricia sabella, Corophium volutator, *Pygospio elegans, *Nereis diversicolor, Hydrobia neglecta, *Macoma balthica, *Arenicola marina; Low tide site: *Pygospio elegans, Bathyporeia guilliamsoniana, *Nereis diversicolor, *Macoma balthica and *Arenicola marina. (* = species common to high tide and low tide sites).

8. In the **initial survey** I measured species abundances of infaunal macrofauna and sediment parameters of surface sediment (shear strength, water content, permeability, particle size, redox potential, and pH). I also measured vertical profiles of shear strength, water content, redox potential and pH.

8.1. In general the sediment from the two high tide areas was finer than the two low tide areas and the sediment parameters were very different between the four areas emphasing the different sedimentary environments. At high tide, the algal areas contained more finer sediment than the nonalgal areas. At low tide the trough sediment was more widely distributed between the particle sizes (less well sorted) than the peak sediment. The permeability and shear strength of the algal area were higher than the nonalgal area, and the permeability and shear strength of the peak area were higher than the trough area. Redox potential was lower in the algal than the nonalgal area and in the trough area than in the peak area. Vertical profiles of sedimentary parameters showed that shear strength increased and water content decreased with depth. Redox potential profiles decreased or remained the same with depth.

8.2. In the **initial survey** there were fewer statistically significant differences in species abundances between the four areas than in the **transect survey**. This is attributed to the small number of replicates in the initial survey. Apart from this there were no inconsistencies between the two surveys. At the high tide site juvenile A. marina were more abundant in the nonalgal than algal area. At the low tide site total A. marina and B. guilliamsoniana were more abundant in the peak than in the trough areas.

9. In the **transect survey** I established two 50m transects. One was in the high tide area which crossed algal mats and areas of bare sediment (termed nonalgal areas), and one was in the low tide area which crossed the peaks and troughs of the sand waves at right angles. Measurements were taken at 1m intervals

along each transect using a $1m^2$ metal quadrat. I measured species abundances of infaunal macrofauna, surface shear strength, surface redox potential, height of the sediment surface above the water table, and percent algal cover at high tide. The following scales of spatial heterogeneity were defined:

micro-scale $\leq$ 1m — within and between contiguous $1m^2$ quadrats - distances of up to and including 1m.

meso-scale > 1m - $\leq$ 50m — between quadrats along each transect - distances greater than 1m and up to and including 50m, the length of the transect.

macro-scale > 50m — between transects - distances greater than 50m.

10. The results of the transect survey are divided into three parts: 10.1, 10.2, and 10.3.

10.1. Mean species abundance, diversity indices, and sediment parameters and their spatial heterogeneity. Comparisons of means were done by Student's t tests. Comparisons of variability were done by F ratio test on the variances of the two samples being compared.

10.1.1. Macro-scale comparisons between high and low tide showed the following. A. marina and P. elegans were more abundant at low tide, diversity indices were higher at high tide, redox potential was lower at high tide. Spatial variability in abundance of A. marina, M. balthica, and N. diversicolor was higher at high tide, and of P. elegans was higher at low tide. Spatial variability of Simpson's diversity index was higher at low tide. Shear strength and redox potential showed more spatial variability at high tide.

10.1.2. Meso-scale differences along the high tide and along the low tide transects showed the following. At high tide F. sabella was most abundant and showed the greatest variability along the transect and the opposite was true of A. marina. At low tide P.elegans was most abundant and showed the greatest variability along the transect and the opposite was true of A. marina.

10.1.3. Meso-scale differences between algal and nonalgal areas along the high tide transect showed the following. A. marina and C. volutator were less abundant in the algal areas. Shear strength was higher and redox potential lower in the algal than in the nonalgal areas. A. marina, C. volutator, F. sabella and N. diversicolor showed more variability in the nonalgal than in the algal areas while the reverse was true for H. neglecta and M. balthica. Shear strength was more variable in the algal than in the nonalgal areas.

10.1.4. Meso-scale differences between the peaks and troughs along the low tide transect showed the following. B. guilliamsoniana and N. diversicolor were less abundant in the peaks and M. balthica was totally absent from the peaks. A. marina was more abundant in the peaks. Both diversity indices were higher in the troughs than in the peaks. Shear strength was higher in the peaks. A. marina was more variable in the peaks and B. guilliamsoniana in the troughs. The two diversity indices and redox potential showed a higher variability in the troughs than in the peaks.

10.2. Correlations between species abundance, sediment parameters, algal cover and water table. Correlation coefficients represent relationships that are operating at a meso-scale because they are calculated from pairs of data points taken from successive quadrats along the two transects. There were more significant correlations at low tide site than at high tide site and significantly more of these were between animal species and sediment parameters than between pairs of animal species or between pairs of sediment parameters. This suggests that

at low tide site which is a high erosional environment there is greater interaction between sediment properties and species abundances as compared to high tide site where conditions are not as extreme and the environment is more depositional.

10.2.1. High tide site correlations. C. volutator was positively correlated with redox potential, N. diversicolor with the water table, A. marina and C. volutator were both negatively correlated with percent algal cover. F. sabella was positively correlated with P. elegans, and C. volutator with both A. marina and N. diversicolor. F. sabella was negatively correlated with A. marina.

10.2.2. Low tide site correlations. B. guilliamsoniana and N. diversicolor were negatively correlated with shear strength and water table. A. marina was positively correlated with shear strength and water table, M. balthica was negatively correlated with shear strength and also with the water table.

10.3. Two additional methods were used to distinguish between macro-, meso-, and micro-scale heterogeneity.

10.3.1. The first method used the between and within quadrats variance from analyses of variance on the shear strength and redox potential data. The between quadrats variance represents meso-scale spatial variability. The within quadrats variance represents micro-scale spatial variability. Meso-scale (between quadrat) variability was greater than micro-scale (within quadrat) variability for shear strength and for redox potential along both the high tide and low tide transects. Shear strength showed no difference in meso-scale variability between high tide site and low tide site but showed a much greater micro-scale variability at high tide site than at low tide site. Redox potential showed a much greater meso-scale and micro-scale variability at high tide site than at low tide site. Both of these effects are at a macro-scale level because they compare between the transects.

10.3.2. The second method used differences between pairs of data at successive 1m, 5m, 10m, 20m, 30m, and 40m distances along the transects. The method was applied to species abundances, diversity indices and also to shear strength and redox potential. The 1m differences are classified as micro-scale and the 5m, 10m, 20m, 30m, and 40m differences as meso-scale spatial variability. There was a tendecy for the 1m micro-scale differences to be lower than the 5, 10, 20, and 30m meso-scale differences, with the peak sometimes occurring at 10m. For example, A. marina, M. balthica, N. diversicolor, F. sabella, Shannon Wiener diversity index, and the two sediment parameters (shear strength and redox potential) all showed higher meso-scale differences (5, 10, 20, 30 and 40m) than micro-scale differences (1m).

In general, there was more overall meso-scale and micro-scale variability along the low tide transect than along the high tide transect. Macro-scale comparisons of the differences were made between the high tide transect and low tide transect for each distance in turn. For most of the distances, the differenced data for M. balthica, N. diversicolor and redox potential tended to be greater at high tide site than at low tide site, and the differenced data for P.elegans greater at low tide site than at high tide site.

11. In the discussion I review some of the huge literature on sediment properties affecting macrobenthic infaunal communities and consider the ecological implications of my results in relation to this literature under the following topics: sediment properties, scales of spatial heterogeneity, algal mats and sand waves, correlations and species diversity.

MICROBIAL COMMUNITIES

1. The abundance and spatial heterogeneity of microbial communities on sand grains from the low tide area at Ardmore bay have been studied in nutrient enriched sediment columns in the laboratory. The sediment was collected on a flat area of the beach near the sand waves at the low tide site. The columns consisted of sediment cores through which media were percolated every two days over a 25 day period. Columns were maintained under 17h light/7h dark (L) and total dark (D) regimes. Photosynthetic (M) and heterotrophic (B) media were used in both regimes. The sediments incubated in the light (ML, BL) were designed to simulate intertidal and inshore surface sediments, while sediments incubated in the dark (MD, BD) simulated subsurface sediments in the same environments and also surface sediments which are below the euphotic zone. The sediments enriched with photosyntheic medium (ML, MD) were intended to mimic sediments where inorganic nutrients in soil run-off occurs from the land. The sediments enriched with heterotrophic medium (BL, BD) were intended to mimic sediments with a higher organic content such as those near sewage outlets. Control columns (C) contained formalin.

2. At the end of the experiment surface samples from each column were examined by scanning electron microscopy (SEM) and the numbers and types of microorganisms on sand grains were recorded as numbers mm^{-2} sand grain surface.

3. A detailed description of the microbial communities on the sand grains in the different media is presented with the aid of scanning electron microscope photographs. The main results of the qualitative description and quantitative analyses of the microbial communities that developed in the different media are as follows.

3.1. Both monospecific and mixed species colonies of a wide range of microorganisms were noted and more growth occurred on subangular (sharp) sand grains than on subrounded (smooth) sand grains. This may be because there are more depressions and crevices on the former.

3.2. There were considerable differences in the microbial communities that developed on the sand grains in the different media. These differences reflected the different media used, and hence the different sedimentary environments that were being simulated.

3.3. Large populations of photosynthetic micro-organisms (diatoms, blue-green algae) developed in the illuminated columns containing photosynthetic medium (ML). The most abundant species was the blue green alga Schizothrix sp.

3.4. Many coccoid and rod shaped bacteria developed in the columns containing photosynthetic medium incubated in the dark (MD), but very few photosynthetic organisms grew.

3.5. A wide range and high abundance of heterotrophic bacteria developed in the columns containing heterotrophic medium, whether incubated in the light or dark (BL, BD). There were many rods, cocci and filamentous bacteria, but no photosynthetic microorganisms. More filamentous bacteria were found in the light incubated columns than in the dark columns. Two distinct types of cocci were observed.

3.6. Thraustochytrids developed in the ML columns. This is an exciting discovery because it means that these interesting fungi can be grown in mixed cultures in the laboratory.

3.7. Binding materials such as biofilms, microbial mats, and filamentous networks were observed on sand grains in the BL and BD columns.

4. There were a number of differences between species in the variability of their abundances on sand grains in the same medium. This is termed meso-scale variability. The differences were as follows. In the ML medium Schizothrix sp. had the highest variability in abundance and Amphora sp. A the lowest. In the MD medium cocci (diam. 0.6 μm) had the highest variability and filamentous bacteria the lowest. In the BL medium, cocci (0.6 diam. μm) had the highest variability and Schizothrix sp. the lowest. In both the BD and control media bacilli had the highest variability and in the former cocci had the lowest variability while in the latter Amphora sp. B.

5. There were a number of macro-scale differences in the variability of the microbial species between different media. Cocci had the highest variability in the BL medium and lowest in the BD medium. Bacilli had the highest variability in the control medium and the lowest in the ML medium. Filamentous bacteria had the highest variability in the BD medium and lowest in the ML medium.

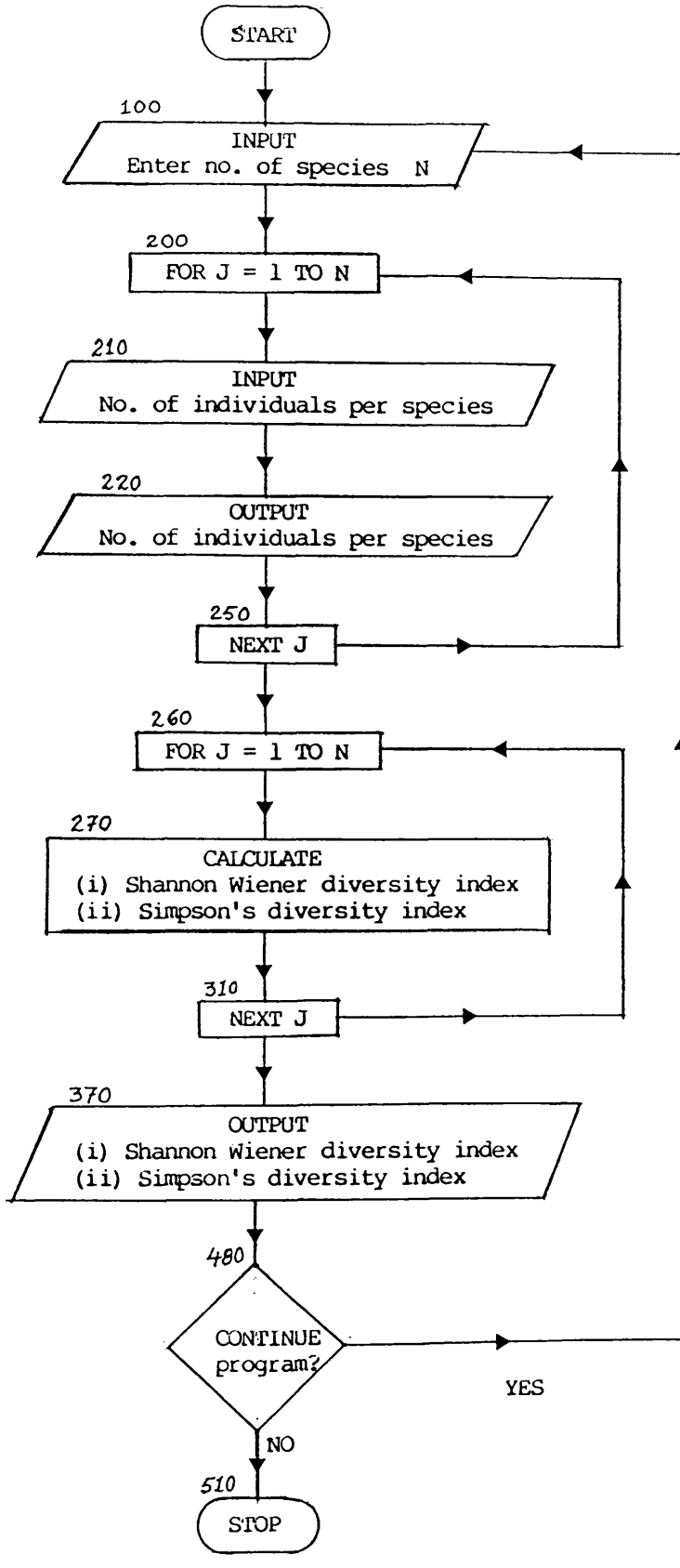
6. In an ecological field context spatial variability in microbial communities can be defined as micro-scale ($\leq$ 1mm), meso-scale ($>$ 1mm to $\leq$ 10cm), and macro-scale ($\geq$ 10cm), although it was difficult to draw an exact parallel with the laboratory experiments.

7. In the discussion I relate my results to the rather sparse literature on enrichment cores simulating different sedimentary environments. This includes consideration of the possible role of meiofauna in affecting microbial communities in my cores, the significance of spatial heterogeneity in the microbial communities in my and other's work at a micro-, meso-, and macro-scale, and the presence of monospecific and mixed species colonies. I also discuss the occurrence of sedimentary binding materials produced by microorganisms that I observed, and of grain shape and surface topography in determining microbial colonisation.

APPENDICES

Appendix 1

Computer program used to calculate the (i) Shannon Wiener diversity index, (ii) Simpson's diversity index in each of the 50 quadrats along the HT and LT transects.


START
100
INPUT
Enter no. of species N
200
FOR J = 1 TO N
210
INPUT
No. of individuals per species
220
OUTPUT
No. of individuals per species
250
NEXT J
260
FOR J = 1 TO N
270
CALCULATE
(i) Shannon Wiener diversity index
(ii) Simpson's diversity index
310
NEXT J
370
OUTPUT
(i) Shannon Wiener diversity index
(ii) Simpson's diversity index
480
CONTINUE
program?
YES
NO
510
STOP

LISTING:

```
10 T=0: A(J)=0: N=0: Q(J)=0: R(J)=0: P=0: S=0: U=0
20 PRINT "THIS PROGRAM CALCULATES THE SHANNON WIENER AND SIMPSON INDICES OF DIVE
RSITY"
30 LPRINT "THIS PROGRAM CALCULATES THE SHANNON WIENER AND SIMPSON INDICES OF DIV
ERSITY"
40 PRINT:PRINT
50 LPRINT:LPRINT
60 INPUT "DETAILS OF SAMPLE ";A$
70 LPRINT "DETAILS OF SAMPLE :      ";A$
80 PRINT:PRINT
90 LPRINT:LPRINT
100 INPUT "ENTER NUMBER OF SPECIES";N
110 LPRINT "NUMBER OF SPECIES:       ";N
120 LPRINT:LPRINT:LPRINT
130 PRINT:PRINT
140 LPRINT:LPRINT
150 PRINT "ENTER NO. INDIVIDUALS PER SQUARE METRE FOR EACH SPECIES IN TURN"
160 PRINT "NOTE: use same units throughout , i.e. no./m2"
170 PRINT:PRINT
180 LPRINT "NO. INDIVIDUALS PER SQUARE METRE FOR EACH SPECIES ENTERED:"
190 LPRINT:LPRINT
200 FOR J=1 TO N
210 INPUT A(J)
220 LPRINT "                                                    ";A(J)
230 LPRINT:LPRINT
240 T=T+A(J)
250 NEXT J
260 FOR J=1 TO N
270 Q(J)=(A(J)/T)*(LOG(A(J)/T))
280 R(J)=(A(J)/T)^2
290 P=P+Q(J)
300 S=S+R(J)
310 NEXT J
320 P=-P
330 U=1-S
340 PRINT:PRINT
350 LPRINT:LPRINT:LPRINT
360 LPRINT "-------------------------------------------------------------------"
370 LPRINT:LPRINT:LPRINT
380 PRINT "SHANNON WIENER (natural log) DIVERSITY INDEX    ";P
390 LPRINT "SHANNON WIENER (NAT.LOG) DIVERSITY INDEX         ";P
400 PRINT:PRINT
410 LPRINT:LPRINT
420 PRINT "SIMPSON'S DIVERSITY INDEX      ";U
430 LPRINT "SIMPSON'S DIVERSITY INDEX       ";U
440 PRINT:PRINT:PRINT
450 LPRINT:LPRINT:LPRINT
460 PRINT "-----------------------------------------------------------"
470 LPRINT "-------------------------------------------------------------------"
480 PRINT:PRINT:PRINT:PRINT:PRINT
490 LPRINT:LPRINT:LPRINT:LPRINT:LPRINT
500 INPUT "PRINT Y TO CONTINUE OR NO TO TERMINATE PROGRAM";B$
510 PRINT:PRINT:PRINT:PRINT:PRINT
520 IF B$="Y" THEN 10
530 END
```

RUN:

THIS PROGRAM CALCULATES THE SHANNON WIENER AND SIMPSON INDICES OF DIVERSITY

DETAILS OF SAMPLE : ARDMORE H.T. VARIABILITY. QUAD. 1 (10/8/87)

NUMBER OF SPECIES: 6

NO. INDIVIDUALS PER SQUARE METRE FOR EACH SPECIES ENTERED:

5.985

5649

2824

823.9

6355

823.9

SHANNON WIENER (NAT.LOG) DIVERSITY INDEX 1.33913

SIMPSON'S DIVERSITY INDEX .699503

Appendix 2.

Original data - macrofaunal communities

1.	0.17300	0.070900	1.33900	0.700000	3.
2.	0.25700	0.111000	1.50000	0.749000	2.
3.	0.20100	0.075900	0.72500	0.391000	3.
4.	0.12200	0.045200	1.22000	0.647000	3.
5.	0.15200	0.058000	1.03100	0.527000	2.
6.	0.35300	0.150000	1.29800	0.668000	3.
7.	0.19800	0.086800	1.41700	0.718000	1.
8.	0.82700	0.510000	1.35000	0.731000	1.
9.	0.55900	0.273000	0.52200	0.305000	1.
10.	0.96200	0.571000	0.45100	0.278000	1.
11.	0.80900	0.409000	1.22200	0.681000	1.
12.	1.12400	0.634000	1.04600	0.632000	1.
13.	1.01600	0.539000	0.64700	0.351000	2.
14.	0.72300	0.358000	0.80000	0.346000	2.
15.	0.84400	0.490000	1.03500	0.485000	2.
16.	0.63800	0.335000	1.07100	0.540000	3.
17.	0.78000	0.431000	1.35800	0.703000	2.
18.	0.64700	0.373000	0.97500	0.585000	1.
19.	0.10900	0.042900	1.36000	0.681000	1.
20.	0.18800	0.083300	1.21500	0.617000	1.
21.	0.27900	0.119000	0.61100	0.420000	3.
22.	0.15400	0.060700	1.17500	0.621000	2.
23.	0.22900	0.019700	0.79800	0.436000	1.
24.	0.23400	0.096900	1.11900	0.627000	1.
25.	0.36100	0.157000	1.24900	0.685000	3.
26.	0.27300	0.121000	1.23500	0.616000	2.
27.	0.49500	0.248000	1.20500	0.620000	3.
28.	0.37500	0.193000	0.46700	0.218000	3.
29.	0.25800	0.113000	0.90800	0.461000	3.
30.	0.95100	0.537000	0.84200	0.447000	3.
31.	0.29200	0.138000	1.15200	0.638000	3.
32.	0.62100	0.396000	0.99300	0.577000	3.
33.	0.92300	0.495000	0.86900	0.406000	1.
34.	0.92700	0.549000	1.42000	0.705000	2.
35.	0.94600	0.568000	1.44000	0.700000	2.
36.	0.86000	0.531000	1.02400	0.592000	3.
37.	1.08600	0.640000	0.95700	0.577000	3.
38.	0.71200	0.371000	1.11900	0.615000	1.
39.	0.74600	0.370000	1.21200	0.653000	3.
40.	1.04200	0.597000	0.94500	0.552000	3.
41.	0.28300	0.111000	0.98000	0.547000	2.
42.	0.61900	0.294000	0.82800	0.428000	3.
43.	0.72400	0.381000	0.94100	0.504000	3.
44.	0.51900	0.252000	1.34900	0.676000	1.
45.	0.22700	0.088900	1.48000	0.700000	1.
46.	0.41500	0.185000	1.40500	0.714000	1.
47.	0.29600	0.134000	1.34800	0.724000	1.
48.	0.47400	0.255000	0.67700	0.484000	1.
49.	0.26500	0.120000	0.97400	0.589000	1.
50.	0.07400	0.027900	0.62000	0.301000	1.

Table 1. Shannon Wiener and Simpson's diversity indices.

Columnl 1m quadrats 1 to 50 along transect.
Column 2 Shannon Wiener diversity index. Low tide site.
Column 3 Simpson's diversity index. Low tide site.
Column 4 Shannon Wiener diversity index. High tide site.
Column 5 Simpson's diversity index. High tide site.
Column 6 1 , > 70% algal cover.
2 , < 30% algal cover.
3 , 30-70% algal cover.

1.	83.7900	5.985	3.
2.	82.5930	9.576	2.
3.	49.0770	39.501	3.
4.	34.7130	65.835	3.
5.	51.4710	17.955	2.
6.	49.0770	5.985	3.
7.	43.0920	0.000	1.
8.	43.0920	0.000	1.
9.	21.5460	3.591	1.
10.	51.4710	0.000	1.
11.	32.3190	0.000	1.
12.	14.3640	0.000	1.
13.	28.7280	354.312	2.
14.	22.7430	323.190	2.
15.	21.5460	160.398	2.
16.	26.3340	92.169	3.
17.	28.7280	39.501	2.
18.	27.5310	7.182	1.
19.	16.7580	0.000	1.
20.	26.3340	32.319	1.
21.	17.9550	0.000	3.
22.	26.3340	35.910	2.
23.	40.6980	35.910	1.
24.	94.5630	0.000	1.
25.	57.4560	2.394	3.
26.	70.6230	3.591	2.
27.	61.0470	0.000	3.
28.	40.6980	10.773	3.
29.	38.3040	9.576	3.
30.	39.5010	0.000	3.
31.	35.9100	16.758	3.
32.	31.1220	15.561	3.
33.	33.5160	15.561	1.
34.	53.8650	102.942	2.
35.	58.6530	137.655	2.
36.	41.8950	47.880	3.
37.	23.9400	16.758	3.
38.	28.7280	19.152	1.
39.	22.7430	25.137	3.
40.	15.5610	44.289	3.
41.	20.3490	89.775	2.
42.	27.5310	9.576	3.
43.	27.5310	0.000	3.
44.	39.5010	13.167	1.
45.	74.2140	8.379	1.
46.	88.5780	7.182	1.
47.	71.8200	2.394	1.
48.	73.0170	0.000	1.
49.	50.2740	1.197	1.
50.	37.1070	3.591	1.

Table 2. Arenicola marina abundance (original data).

Column 1 1m quadrats 1 to 50 along transect.
Column 2 no.m^{-2}. Low tide site.
Column 3 no.m^{-2}. High tide site.
Column 4 1 , > 70% algal cover.
2 , < 30% algal cover.
3 , 30-70% algal cover.

1.	0.000	0.00	2.
2.	0.000	117.70	2.
3.	0.000	0.00	1.
4.	0.000	0.00	2.
5.	0.000	0.00	2.
6.	0.000	0.00	1.
7.	0.000	0.00	1.
8.	117.700	0.00	1.
9.	0.000	0.00	1.
10.	117.700	0.00	1.
11.	117.700	117.70	1.
12.	235.400	0.00	1.
13.	235.400	0.00	1.
14.	117.700	117.70	2.
15.	0.000	235.40	2.
16.	117.700	117.70	2.
17.	0.000	0.00	1.
18.	0.000	117.70	2.
19.	0.000	0.00	2.
20.	0.000	0.00	1.
21.	0.000	470.80	2.
22.	0.000	0.00	2.
23.	117.700	0.00	1.
24.	0.000	0.00	1.
25.	0.000	470.80	2.
26.	0.000	117.70	1.
27.	0.000	235.40	1.
28.	0.000	0.00	2.
29.	0.000	0.00	2.
30.	0.000	235.40	1.
31.	0.000	235.40	2.
32.	0.000	235.40	2.
33.	117.700	235.40	2.
34.	117.700	235.40	2.
35.	0.000	0.00	1.
36.	0.000	0.00	1.
37.	0.000	0.00	1.
38.	0.000	0.00	1.
39.	235.400	235.40	1.
40.	235.400	0.00	2.
41.	117.700	0.00	2.
42.	235.400	0.00	2.
43.	117.700	0.00	2.
44.	0.000	235.40	1.
45.	0.000	941.60	1.
46.	0.000	588.50	1.
47.	0.000	235.40	1.
48.	0.000	0.00	1.
49.	0.000	0.00	1.
50.	0.000	1059.30	1.

Table 3. Macoma balthica abundance (original data).

Column 1 1m quadrats 1 to 50 along transect.
Column 2 no.m^{-2}. Low tide site.
Column 3 no.m^{-2}. High tide site.
Column 4 1 , alga present.
2 , alga absent.

1.	470.800	5649.60	2.
2.	117.700	2824.80	2.
3.	117.700	1177.00	1.
4.	0.000	1530.10	1.
5.	117.700	235.40	2.
6.	235.400	1412.40	2.
7.	470.800	2942.50	1.
8.	235.400	941.60	1.
9.	235.400	588.50	1.
10.	706.200	588.50	1.
11.	706.200	941.60	1.
12.	941.600	1059.30	1.
13.	588.500	0.00	2.
14.	706.200	235.40	2.
15.	706.200	117.70	2.
16.	706.200	1530.10	2.
17.	941.600	2118.60	1.
18.	588.500	470.80	1.
19.	470.800	470.80	1.
20.	470.800	706.20	2.
21.	353.100	0.00	2.
22.	117.700	117.70	2.
23.	0.000	235.40	2.
24.	117.700	235.40	1.
25.	470.800	353.10	1.
26.	235.400	4001.80	2.
27.	706.200	4119.50	2.
28.	353.100	588.50	1.
29.	117.700	4119.50	2.
30.	235.400	2118.60	1.
31.	0.000	0.00	1.
32.	0.000	470.80	2.
33.	353.100	706.20	2.
34.	353.100	117.70	2.
35.	353.100	353.10	2.
36.	353.100	0.00	1.
37.	706.200	0.00	1.
38.	353.100	0.00	2.
39.	588.500	0.00	1.
40.	588.500	0.00	1.
41.	353.100	470.80	2.
42.	588.500	2236.30	1.
43.	588.500	1294.70	2.
44.	353.100	235.40	1.
45.	353.100	823.90	1.
46.	353.100	117.70	1.
47.	235.400	117.70	1.
48.	470.800	0.00	1.
49.	235.400	0.00	1.
50.	0.000	0.00	1.

Table 4. Nereis diversicolor abundance (original data).

Column 1 1m quadrats 1 to 50 along transect.
Column 2 no.m^{-2}. Low tide site.
Column 3 no.m^{-2}. High tide site.
Column 4 1 , alga present.
2 , alga absent.

1.	14594.8	2824.80	2.
2.	4237.2	2942.50	2.
3.	9886.8	117.70	1.
4.	6473.5	353.10	2.
5.	5531.9	1059.30	2.
6.	6002.7	1412.40	1.
7.	10828.4	1059.30	1.
8.	4237.2	588.50	1.
9.	2707.1	0.00	1.
10.	5296.5	0.00	1.
11.	353.1	0.00	1.
12.	3177.9	0.00	1.
13.	3531.0	0.00	1.
14.	4943.4	353.10	2.
15.	2000.9	353.10	2.
16.	13770.9	117.70	2.
17.	6708.9	706.20	1.
18.	14241.7	0.00	2.
19.	21774.5	235.40	2.
20.	10946.1	1294.70	1.
21.	7297.4	706.20	2.
22.	4472.6	117.70	2.
23.	10239.9	0.00	1.
24.	4001.8	1177.00	1.
25.	10946.1	117.70	2.
26.	4472.6	1883.20	1.
27.	5414.2	1412.40	1.
28.	3295.6	3766.40	2.
29.	2471.7	3766.40	2.
30.	1412.4	5531.90	1.
31.	3413.3	1530.10	2.
32.	2354.0	1883.20	2.
33.	3177.9	353.10	2.
34.	3295.6	2824.80	2.
35.	2589.4	235.40	1.
36.	4354.9	1883.20	1.
37.	1530.1	3060.20	1.
38.	2589.4	235.40	1.
39.	3413.3	1883.20	1.
40.	3060.2	2000.90	2.
41.	9886.8	706.20	2.
42.	9533.7	1059.30	2.
43.	8239.0	117.70	2.
44.	6002.7	2118.60	1.
45.	11299.2	1059.30	1.
46.	5061.1	235.40	1.
47.	4001.8	0.00	1.
48.	3177.9	0.00	1.
49.	4237.2	3177.90	1.
50.	2589.4	4472.60	1.

Table 5. Pygospio elegans abundance (original data).

Column 1 1m quadrats 1 to 50 along transect.
Column 2 no.m^{-2}. Low tide site.
Column 3 no.m^{-2}. High tide site.
Column 4 1 , alga present.
2 , alga absent.

1.	0.00	18.8000	2.00000	49.	44.4300
2.	0.00	17.7000	2.00000	26.	30.6600
3.	235.40	17.1000	1.50000	49.	44.4300
4.	117.70	15.0000	0.00000	36.	36.8700
5.	0.00	12.3000	0.50000	15.	22.7900
6.	235.40	12.0000	1.00000	24.	29.3300
7.	0.00	9.8000	2.00000	81.	64.1600
8.	6708.90	7.0000	2.50000	98.	81.8700
9.	235.40	4.0000	2.00000	80.	63.4300
10.	4943.40	2.0000	3.50000	100.	90.0000
11.	3648.70	0.0000	3.00000	100.	90.0000
12.	2589.40	-1.0000	3.50000	99.	84.2600
13.	1177.00	-1.4000	0.00000	26.	30.6600
14.	470.80	-1.3000	-1.50000	0.	0.0000
15.	5414.20	-1.3000	2.50000	0.	0.0000
16.	2589.40	0.0000	0.00000	45.	42.1300
17.	1530.10	0.0000	-1.00000	10.	18.4300
18.	3766.40	2.1000	2.50000	94.	75.8200
19.	0.00	3.4000	3.50000	100.	90.0000
20.	0.00	5.2000	-2.00000	100.	90.0000
21.	117.70	7.2000	-1.75000	36.	36.8700
22.	0.00	10.0000	-1.50000	0.	0.0000
23.	353.10	12.3000	-1.50000	87.	68.8700
24.	0.00	13.5000	3.00000	73.	58.6900
25.	470.80	14.9000	3.50000	58.	49.6000
26.	0.00	15.5000	4.00000	28.	31.9500
27.	117.70	15.5000	5.00000	40.	39.2300
28.	0.00	14.7000	4.50000	49.	44.4300
29.	0.00	12.5000	4.00000	34.	35.6700
30.	588.50	11.0000	3.00000	45.	42.1300
31.	235.40	9.0000	0.50000	64.	53.1300
32.	823.90	7.5000	1.50000	33.	35.0600
33.	1059.30	5.5000	0.00000	80.	63.4300
34.	4472.60	4.0000	0.00000	6.	14.1800
35.	2118.60	1.2000	0.50000	6.	14.1800
36.	2942.50	0.0000	-1.50000	42.	40.4000
37.	1059.30	-0.5000	-2.50000	65.	53.7300
38.	353.10	-2.0000	-2.75000	90.	71.5700
39.	117.70	-1.5000	-2.50000	62.	51.9400
40.	3531.00	-1.0000	-2.25000	49.	44.4300
41.	117.70	0.0000	1.50000	16.	23.5800
42.	1059.30	1.3000	4.50000	63.	52.5400
43.	1765.50	2.1000	4.50000	33.	35.0600
44.	588.50	3.7000	3.50000	100.	90.0000
45.	117.70	5.5000	2.50000	100.	90.0000
46.	117.70	7.2000	3.00000	100.	90.0000
47.	0.00	8.5000	2.50000	82.	64.9000
48.	0.00	10.0000	0.50000	100.	90.0000
49.	0.00	10.5000	0.00000	100.	90.0000
50.	0.00	10.5000	0.00000	78.	62.0300

Table 6. Bathyporeia guilliamsoniana abundance, water table level, and % algal cover (original data).

Column 1 1m quadrats 1 to 50 along transect.
Column 2 no.m^{-2}. Bathyporeia guilliamsoniana. Low tide site.
Column 3 water table height (cm). Low tide site.
Column 4 water table height (cm). High tide site.
Column 5 % algal cover. High tide site.
Column 6 arcsine of % algal cover. High tide site.
Note : If water table is above sediment surface then value of water table is negative and vice versa.

1.	6355.8	823.90	2.	823.9	2.
2.	6708.9	1177.00	2.	5414.2	2.
3.	4472.6	117.70	1.	0.0	1.
4.	5178.8	235.40	1.	3413.3	2.
5.	7062.0	353.10	2.	2118.6	2.
6.	7297.4	706.20	2.	4354.9	1.
7.	1059.3	353.10	1.	1294.7	1.
8.	0.0	470.80	1.	470.8	1.
9.	117.7	823.90	1.	0.0	1.
10.	0.0	117.70	1.	0.0	1.
11.	0.0	588.50	1.	588.5	1.
12.	0.0	470.80	1.	706.2	1.
13.	4001.8	706.20	2.	0.0	1.
14.	5178.8	235.40	2.	0.0	2.
15.	3648.7	706.20	2.	0.0	2.
16.	6238.1	117.70	2.	1530.1	2.
17.	3884.1	2118.60	1.	235.4	1.
18.	0.0	588.50	1.	0.0	2.
19.	588.5	353.10	1.	1647.8	2.
20.	4237.2	117.70	2.	1059.3	1.
21.	0.0	0.00	2.	1647.8	2.
22.	0.0	470.80	2.	823.9	2.
23.	2236.3	588.50	2.	0.0	1.
24.	0.0	235.40	1.	1412.4	1.
25.	0.0	706.20	1.	0.0	2.
26.	10828.4	706.20	2.	1530.1	1.
27.	9416.0	117.70	2.	1765.5	1.
28.	588.5	117.70	1.	36957.8	2.
29.	8121.3	117.70	2.	40018.0	2.
30.	0.0	353.10	1.	20597.5	1.
31.	0.0	1412.40	1.	3295.6	2.
32.	12947.0	0.00	2.	20597.5	2.
33.	2471.7	823.90	2.	14359.4	2.
34.	1059.3	1059.30	2.	3884.1	2.
35.	941.6	588.50	2.	2000.9	1.
36.	0.0	470.80	1.	1059.3	1.
37.	0.0	941.60	1.	4590.3	1.
38.	1530.1	1177.00	2.	3531.0	1.
39.	0.0	706.20	1.	941.6	1.
40.	0.0	823.90	1.	4237.2	2.
41.	7768.2	470.80	2.	12829.3	2.
42.	470.8	0.00	1.	10475.3	2.
43.	2824.8	235.40	2.	8827.5	2.
44.	117.7	470.80	1.	1765.5	1.
45.	353.1	470.80	1.	3531.0	1.
46.	0.0	470.80	1.	1059.3	1.
47.	117.7	235.40	1.	0.0	1.
48.	0.0	1530.10	1.	1059.3	1.
49.	0.0	1294.70	1.	5061.1	1.
50.	0.0	2000.90	1.	36369.3	1.

Table 7. Corophium volutator, Hydrobia neglecta and Fabricia sabella abundance (original data). High tide site.

Column 1 1m quadrats 1 to 50 along transect.
Column 2 no.m^{-2}. Corophium volutator.
Column 3 no.m^{-2}. Hydrobia neglecta.
Column 5 no.m^{-2}. Fabricia sabella.
Columns 4 and 6 1 , alga present.
2 , alga absent.

1.	7.2150	1.60800	5.6270	1.9400	3.
2.	7.7590	0.88940	4.8610	1.5310	2.
3.	8.3340	1.94100	7.0690	5.2720	3.
4.	9.0960	3.04300	5.1600	1.1740	3.
5.	8.8390	1.41600	3.8930	0.3480	2.
6.	9.1390	1.14300	14.1600	13.3600	3.
7.	8.4500	0.87870	38.9500	62.6400	1.
8.	9.6800	1.45800	8.3990	4.2440	1.
9.	6.9180	1.87300	9.3830	4.4570	1.
10.	5.7590	1.18900	6.0700	1.1930	1.
11.	2.3800	0.89670	4.8180	1.6470	1.
12.	1.7920	0.17540	10.7700	4.4430	1.
13.	0.9565	0.16340	7.6260	4.9580	2.
14.	1.3660	0.12300	4.3840	3.0690	2.
15.	1.2080	0.24320	2.7470	0.5696	2.
16.	1.3610	0.43290	2.2530	0.7978	3.
17.	2.9820	0.38430	7.7050	2.9050	2.
18.	5.1540	0.19220	1.2020	0.1418	1.
19.	6.9160	1.28800	8.8150	4.8690	1.
20.	9.5320	2.97600	8.5460	3.9580	1.
21.	10.3100	2.04900	1.2200	0.1916	3.
22.	9.7980	3.48700	1.5290	0.3216	2.
23.	7.3330	1.73900	6.5180	4.2980	1.
24.	9.6340	1.12400	6.1720	1.7340	1.
25.	6.7720	1.59500	8.3160	4.6850	3.
26.	6.9720	1.53200	4.8690	0.9262	2.
27.	11.1700	1.85400	6.7170	5.4270	3.
28.	8.7340	3.58400	5.4150	0.1264	3.
29.	7.0290	1.10700	8.0700	3.6300	3.
30.	9.2930	2.04100	13.3200	13.5500	3.
31.	9.8660	2.77700	6.3620	3.2190	3.
32.	8.5280	1.43700	5.5650	2.1120	3.
33.	9.8100	3.30800	5.1300	0.5076	1.
34.	5.9550	1.57800	3.9390	0.6522	2.
35.	4.7310	0.64250	3.5160	1.9970	2.
36.	4.0330	1.57300	2.1310	0.1532	3.
37.	1.8400	0.46290	3.7250	1.4150	3.
38.	1.0870	0.14580	2.2760	0.3943	1.
39.	1.1910	0.34190	2.0260	0.2480	3.
40.	1.4720	0.52620	2.4980	0.5221	3.
41.	3.0030	1.00200	4.4710	0.6184	2.
42.	6.3190	1.96600	6.5470	2.4400	3.
43.	7.8860	1.12100	5.7270	2.0990	3.
44.	7.8160	1.23600	5.0480	2.7280	1.
45.	7.4070	1.61700	6.3960	3.0920	1.
46.	9.2240	0.79510	22.0300	22.3000	1.
47.	6.2770	1.35800	10.6600	9.6600	1.
48.	7.9110	0.52640	10.9200	7.2820	1.
49.	8.1480	2.22000	12.5500	10.0400	1.
50.	9.2210	3.05800	3.7600	1.7880	1.

Table 8. Shear strength ($KN.m^{-2}$) mean and s.d.

Column 1 1m quadrats 1 to 50 along transect.
Columns 2 and 3 mean and s.d. Low tide site.
Columns 4 and 5 mean and s.d. High tide site.
Column 6 1 , > 70% algal cover.
2 , < 30% algal cover.
3 , 30-70% algal cover.

1.	213.500	23.500	216.300	90.530	3.
2.	252.000	34.190	85.500	29.870	2.
3.	205.300	45.940	222.300	148.700	3.
4.	282.500	9.036	112.500	100.500	3.
5.	275.800	30.570	191.500	44.090	2.
6.	322.300	8.992	187.800	83.140	3.
7.	297.800	17.760	73.250	79.670	1.
8.	299.800	26.550	29.500	65.140	1.
9.	291.000	22.110	31.000	70.810	1.
10.	308.500	12.180	13.500	65.920	1.
11.	262.500	50.950	-63.750	35.980	1.
12.	277.000	76.800	-16.500	49.510	1.
13.	282.500	10.120	24.500	61.920	2.
14.	172.300	99.410	-3.500	37.750	2.
15.	290.300	5.849	149.800	72.010	2.
16.	260.500	57.100	160.500	66.280	3.
17.	289.500	45.210	88.000	97.040	2.
18.	273.000	39.560	228.500	42.850	1.
19.	229.500	27.960	124.800	138.400	1.
20.	239.500	58.400	-31.250	9.979	1.
21.	255.800	22.590	111.800	130.900	3.
22.	214.800	64.320	128.800	81.170	2.
23.	269.800	17.050	1.000	66.110	1.
24.	250.300	41.380	12.000	60.910	1.
25.	248.000	36.210	-1.500	58.810	3.
26.	266.800	43.960	9.000	87.470	2.
27.	244.500	51.800	36.250	86.400	3.
28.	214.800	54.020	76.500	26.740	3.
29.	258.000	41.240	113.800	30.210	3.
30.	310.800	10.560	87.000	75.570	3.
31.	314.000	11.830	85.000	68.680	3.
32.	306.000	10.890	168.000	67.460	3.
33.	305.300	11.270	55.500	51.490	1.
34.	298.800	29.540	85.500	41.460	2.
35.	321.000	7.703	61.250	50.550	2.
36.	290.500	56.670	5.000	62.120	3.
37.	265.500	89.030	5.000	47.170	3.
38.	154.800	26.540	40.500	82.530	1.
39.	152.800	66.110	4.000	18.220	3.
40.	279.500	39.310	-1.500	48.610	3.
41.	255.000	104.300	59.000	42.600	2.
42.	225.300	65.330	147.000	47.520	3.
43.	235.800	64.050	85.250	37.740	3.
44.	270.500	103.100	123.000	55.840	1.
45.	225.000	28.310	28.500	44.900	1.
46.	282.500	54.300	99.750	100.800	1.
47.	229.000	10.100	-17.500	59.640	1.
48.	257.500	36.810	-8.500	83.460	1.
49.	272.300	20.890	-12.000	40.280	1.
50.	253.300	8.692	53.500	33.360	1.

Table 9. Eh(mV) mean and s.d.

Column 1 1m quadrats 1 to 50 along transect.
Columns 2 and 3 mean and s.d. Low tide site.
Columns 4 and 5 mean and s.d. High tide site.
Column 6 1 , > 70% algal cover.
2 , < 30% algal cover.
3 , 30-70% algal cover.

Appendix 3.

Differenced data - macrofaunal communities

COLUMN	C8	C9	C10	C11	C12	C13
COUNT	49	46	41	31	21	11
ROW						
1	0.161 00	0.30800	0.88800	0.124000	0.497000	0.392000
2	0.775 00	0.20200	0.27800	0.889000	0.348000	0.520000
3	0.495 00	0.69200	0.32100	0.450000	0.268000	0.103000
4	0.189 00	0.13000	0.57300	0.422000	0.351000	0.279000
5	0.267 00	0.50900	0.23100	0.088000	0.389000	0.318000
6	0.119 00	0.84700	0.26300	0.049000	0.142000	0.182000
7	0.067 00	0.19500	0.34600	0.182000	0.393000	0.012000
8	0.828 00	0.30400	0.00800	0.145000	0.393000	0.002000
9	0.072 00	0.12400	0.45200	0.055000	0.597000	0.446000
10	0.771 00	0.34900	0.90900	0.458000	0.761000	0.524000
11	0.176 00	0.18700	0.00700	0.380000	0.275000	0.602000
12	0.399 00	0.02500	0.43500	0.106000	0.066000	
13	0.153 00	0.71100	0.52800	0.346000	0.181000	
14	0.235 00	0.17500	0.00200	0.070000	0.141000	
15	0.036 00	0.32500	0.08400	0.385000	0.314000	
16	0.287 00	0.14400	0.17800	0.369000	0.409000	
17	0.383 00	0.74700	0.12300	0.334000	0.047000	
18	0.385 00	0.20000	0.23000	0.017000	0.373000	
19	0.145 00	0.56200	0.89300	0.241000	0.284000	
20	0.604 00	0.09600	0.30700	0.003000	0.241000	
21	0.564 00	0.63800	0.23100	0.336000	0.009000	
22	0.377 00	0.06000	0.02300	0.195000		
23	0.321 00	0.40700	0.19500	0.029000		
24	0.130 00	0.65200	0.25000	0.178000		
25	0.014 00	0.34100	0.17100	0.100000		
26	0.030 00	0.39300	0.20500	0.245000		
27	0.738 00	0.05300	0.18100	0.200000		
28	0.441 00	0.52300	0.49000	0.881000		
29	0.066 00	0.03900	0.21100	0.832000		
30	0.310 00	0.57800	0.37000	0.132000		
31	0.159 00	0.28800	0.20500	0.532000		
32	0.124 00	0.03100	0.01300			
33	0.551 00	0.08800	0.04200			
34	0.020 00	0.30100	0.47900			
35	0.416 00	0.22800	0.09100			
36	0.067 00	0.07700	0.45600			
37	0.162 00	0.02300	0.44800			
38	0.093 00	0.29100	0.22900			
39	0.265 00	0.27100	1.13600			
40	0.033 00	0.40200	0.02800			
41	0.152 00	0.50000	0.36000			
42	0.113 00	0.57700				
43	0.408 00	0.40700				
44	0.131 00	1.27300				
45	0.075 00	0.50600				
46	0.057 00	0.78500				
47	1.271 00					
48	0.898 00					
49	0.354 00					

Table 10. Shannon Wiener diversity index. Differences in abundance along the 50m transect. High tide site.

C8 1m differences in abundance.
C9 5m differences in abundance.
C10 10m differences in abundance.
C11 20m differences in abundance.
C12 30m differences in abundance.
C13 40m differences in abundance.

COLUMN	C68	C69	C70	C71	C72	C73
COUNT	49	46	41	31	21	11
ROW						
1	3.591	11.97	5.985	26.334	5.985	38.3040
2	29.925	3.591	9.576	9.576	7.182	80.1990
3	26.334	39.501	39.501	3.591	23.940	29.9250
4	47.880	65.835	288.477	29.925	50.274	65.8350
5	11.970	14.364	305.235	17.955	84.987	4.7880
6	5.985	5.985	154.413	3.591	131.670	2.3940
7	0.000	0.000	92.169	3.591	47.880	7.1820
8	3.591	0.000	39.501	0.000	16.758	2.3940
9	3.591	350.721	3.591	7.182	15.561	3.5910
10	0.000	323.190	0.000	9.576	25.137	1.1970
11	0.000	160.398	32.319	0.000	44.289	3.5910
12	354.312	92.169	0.000	16.758	89.775	
13	31.122	314.811	318.402	338.751	344.736	
14	162.792	316.008	287.28	307.629	323.190	
15	68.229	160.398	160.398	57.456	147.231	
16	52.668	59.850	89.775	45.486	83.790	
17	32.319	39.501	35.910	8.379	32.319	
18	7.182	28.728	7.182	9.576	4.788	
19	32.319	35.910	10.773	19.152	0.000	
20	32.319	32.319	22.743	7.182	31.122	
21	35.910	2.394	0.000	44.289	3.591	
22	0.000	32.319	19.152	53.865		
23	35.910	35.910	20.349	26.334		
24	2.394	10.773	15.561	0.000		
25	1.197	7.182	100.548	10.773		
26	3.591	3.591	134.064	4.788		
27	10.773	16.758	47.880	7.182		
28	1.197	4.788	5.985	8.379		
29	9.576	5.985	9.576	9.576		
30	16.758	102.942	25.137	1.197		
31	1.197	120.897	27.531	13.167		
32	0.000	32.319	74.214			
33	87.381	1.197	5.985			
34	34.713	83.790	102.942			
35	89.775	112.518	124.488			
36	31.122	3.591	39.501			
37	2.394	73.017	9.576			
38	5.985	9.576	16.758			
39	19.152	25.137	25.137			
40	45.486	31.122	43.092			
41	80.199	81.396	86.184			
42	9.576	2.394				
43	13.167	2.394				
44	4.788	13.167				
45	1.197	7.182				
46	4.788	3.591				
47	2.394					
48	1.197					
49	2.394					

Table 11. Arenicola marina. Differences in abundance along the 50m transect. High tide site.

C68 1m differences in abundance.
C69 5m differences in abundance.
C70 10m differences in abundance.
C71 20m differences in abundance.
C72 30m differences in abundance.
C73 40m differences in abundance.

COLUMN	C2	C3	C4	C5	C6	C7
COUNT	49	46	41	31	21	11
ROW						
1	353.1	706.2	6355.8	2118.6	6355.80	6355.80
2	2236.3	588.5	6708.9	6708.9	6708.90	1059.30
3	706.2	3413.3	4472.6	4472.6	8474.40	4001.80
4	1883.2	5178.8	1177.0	2942.5	2707.10	2354.00
5	235.4	6944.3	1883.2	7062.0	6002.70	6944.30
6	6238.1	7297.4	3648.7	7297.4	6355.80	6944.30
7	1059.3	1059.3	5178.8	9769.1	1059.30	1059.30
8	117.7	0.0	3884.1	9416.0	0.00	117.70
9	117.7	3884.1	117.7	470.8	1412.40	117.70
10	0.0	5178.8	588.5	8121.3	0.00	0.00
11	0.0	3648.7	4237.2	0.0	0.00	0.00
12	4001.8	6238.1	0.0	0.0	7768.20	
13	1177.0	117.7	4001.8	8945.2	3531.00	
14	1530.1	5178.8	2942.5	2707.1	2354.00	
15	2589.4	3060.2	3648.7	2589.4	3531.00	
16	2354.0	2000.9	6238.1	5296.5	5885.00	
17	3884.1	3884.1	6944.3	3884.1	3884.10	
18	588.5	0.0	9416.0	0.0	117.70	
19	3648.7	1647.8	0.0	941.6	588.50	
20	4237.2	4237.2	3884.1	4237.2	4237.20	
21	0.0	0.0	0.0	0.0	0.00	
22	2236.3	10828.4	0.0	7768.2		
23	2236.3	7179.7	10710.7	1765.5		
24	0.0	588.5	2471.7	2824.8		
25	10828.4	8121.3	1059.3	117.7		
26	1412.4	10828.4	9886.8	10475.3		
27	8827.5	9416.0	9416.0	9416.0		
28	7532.8	12358.5	588.5	470.8		
29	8121.3	5649.6	6591.2	8121.3		
30	0.0	1059.3	0.0	0.0		
31	12947.0	941.6	0.0	0.0		
32	10475.3	12947.0	5178.8			
33	1412.4	2471.7	2000.9			
34	117.7	470.8	1765.5			
35	941.6	941.6	823.9			
36	0.0	0.0	353.1			
37	1530.1	7768.2	0.0			
38	1530.1	1059.3	1412.4			
39	0.0	2824.8	0.0			
40	7768.2	117.7	0.0			
41	7297.4	7415.1	7768.2			
42	2354.0	470.8				
43	2707.1	2707.1				
44	235.4	117.7				
45	353.1	353.1				
46	117.7	0.0				
47	117.7					
48	0.0					
49	0.0					

Table 12. Corophium volutator. Differences in abundance along the 50m transect. High tide site.

C2 1m differences in abundance.
C3 5m differences in abundance.
C4 10m differences in abundance.
C5 20m differences in abundance.
C6 30m differences in abundance.
C7 40m differences in abundance.

COLUMN	C8	C9	C10	C11	C12	C13
COUNT	49	46	41	31	21	11
ROW						
1	4590.3	1294.7	823.9	235.4	19773.6	3413.3
2	5414.2	1059.3	4825.7	3766.4	2118.6	7415.1
3	3413.3	1294.7	706.2	823.9	14712.5	10475.3
4	1294.7	2942.5	3413.3	3413.3	10946.1	5414.2
5	2236.3	2118.6	2118.6	1059.3	1765.5	353.1
6	3060.2	4354.9	4354.9	4354.9	2354.0	823.9
7	823.9	706.2	235.4	235.4	235.4	235.4
8	470.8	235.4	235.4	1294.7	4119.5	4943.4
9	0.0	0.0	0.0	36957.8	3531.0	1059.3
10	588.5	0.0	1647.8	40018.0	941.6	5061.1
11	117.7	588.5	470.8	20009.0	3648.7	35780.8
12	706.2	823.9	941.6	2589.4	12123.1	
13	0.0	235.4	823.9	14712.5	10475.3	
14	0.0	0.0	0.0	14359.4	8827.5	
15	1530.1	1647.8	1412.4	3884.1	1765.5	
16	1294.7	470.8	1530.1	470.8	2000.9	
17	235.4	1412.4	1294.7	823.9	823.9	
18	1647.8	823.9	1765.5	4590.3	0.0	
19	588.5	1647.8	35310.0	1883.2	588.5	
20	588.5	353.1	38958.7	117.7	4001.8	
21	823.9	1647.8	18949.7	235.4	34721.5	
22	823.9	706.2	2471.7	12005.4		
23	1412.4	1765.5	14712.5	10475.3		
24	1412.4	35545.4	12947.0	7415.1		
25	1530.1	40018.0	3884.1	1765.5		
26	235.4	19067.4	470.8	2000.9		
27	35192.3	1530.1	706.2	706.2		
28	3060.2	22245.3	32367.5	36957.8		
29	19420.5	25658.6	36487.0	38958.7		
30	17301.9	16713.4	19655.9	15536.4		
31	11416.9	1294.7	941.6	33779.9		
32	353.1	13653.2	1883.2			
33	10475.3	9769.1	3884.1			
34	1883.2	353.1	4943.4			
35	941.6	1059.3	235.4			
36	3531.0	3177.9	2471.7			
37	1059.3	8239.0	3531.0			
38	2589.4	6944.3	3531.0			
39	3295.6	7885.9	117.7			
40	8592.1	2471.7	823.9			
41	2354.0	9298.3	23540.0			
42	1647.8	9416.0				
43	7062.0	8827.5				
44	1765.5	706.2				
45	2471.7	1530.1				
46	1059.3	35310.0				
47	1059.3					
48	4001.8					
49	31308.2					

Table 13. Fabricia sabella. Differences in abundance along the 50m transect. High tide site.

C8 1m differences in abundance.
C9 5m differences in abundance.
C10 10m differences in abundance.
C11 20m differences in abundance.
C12 30m differences in abundance.
C13 40m differences in abundance.

COLUMN	C14	C15	C16	C17	C18	C19
COUNT	49	46	41	31	21	11
ROW						
1	353.10	470.80	706.20	706.20	470.80	0.00
2	1059.30	470.80	588.50	1177.00	235.40	706.20
3	117.70	235.40	353.10	353.10	117.70	117.70
4	117.70	235.40	470.80	353.10	588.50	0.00
5	353.10	470.80	117.70	117.70	706.20	117.70
6	353.10	588.50	0.00	0.00	117.70	235.40
7	117.70	235.40	235.40	353.10	117.70	117.70
8	353.10	0.00	1647.80	353.10	470.80	235.40
9	706.20	117.70	235.40	706.20	353.10	706.20
10	470.80	117.70	235.40	0.00	588.50	1177.00
11	117.70	117.70	470.80	235.40	235.40	1412.40
12	235.40	353.10	470.80	941.60	0.00	
13	470.80	1412.40	235.40	706.20	706.20	
14	470.80	353.10	353.10	588.50	0.00	
15	588.50	353.10	470.80	353.10	235.40	
16	2000.90	0.00	588.50	470.80	353.10	
17	1530.10	2118.60	1412.40	1647.80	1647.80	
18	235.40	117.70	470.80	353.10	353.10	
19	235.40	235.40	235.40	823.90	1177.00	
20	117.70	117.70	0.00	588.50	1177.00	
21	470.80	706.20	353.10	823.90	2000.90	
22	117.70	235.40	941.60	0.00		
23	353.10	470.80	588.50	588.50		
24	470.80	117.70	588.50	0.00		
25	0.00	588.50	353.10	235.40		
26	588.50	353.10	117.70	235.40		
27	0.00	1294.70	353.10	353.10		
28	0.00	117.70	823.90	117.70		
29	235.40	706.20	1059.30	1412.40		
30	1059.30	706.20	353.10	941.60		
31	1412.40	823.90	588.50	588.50		
32	823.90	470.80	470.80			
33	235.40	117.70	823.90			
34	470.80	117.70	823.90			
35	117.70	117.70	117.70			
36	470.80	353.10	0.00			
37	235.40	470.80	470.80			
38	470.80	1177.00	941.60			
39	117.70	470.80	823.90			
40	353.10	353.10	470.80			
41	470.80	0.00	1530.10			
42	235.40	470.80				
43	235.40	0.00				
44	0.00	1059.30				
45	0.00	823.90				
46	235.40	1530.10				
47	1294.70					
48	235.40					
49	706.20					

Table 14. Hydrobia neglecta. Differences in abundance along the 50m transect. High tide site.

C14 1m differences in abundance.
C15 5m differences in abundance.
C16 10m differences in abundance.
C17 20m differences in abundance.
C18 30m differences in abundance.
C19 40m differences in abundance.

COLUMN	C44	C45	C46	C47	C48	C49
COUNT	49	46	41	31	21	11
ROW						
1	117.70	0.000	0.00	0.000	235.400	0.000
2	117.70	117.700	0.00	353.100	117.700	117.700
3	0.00	0.000	0.00	0.000	235.400	0.000
4	0.00	0.000	0.00	0.000	235.400	0.000
5	0.00	0.000	117.70	0.000	235.400	235.400
6	0.00	0.000	235.40	470.800	0.000	941.600
7	0.00	117.700	117.70	117.700	0.000	588.500
8	0.00	0.000	0.00	235.400	0.000	235.400
9	0.00	0.000	117.70	0.000	0.000	0.000
10	117.70	117.700	0.00	0.000	235.400	0.000
11	117.70	117.700	117.70	117.700	117.700	941.600
12	0.00	117.700	470.80	235.400	0.000	
13	117.70	0.000	0.00	235.400	0.000	
14	117.70	0.000	117.70	117.700	117.700	
15	117.70	235.400	235.40	0.000	0.000	
16	117.70	117.700	353.10	117.700	823.900	
17	117.70	470.800	117.70	0.000	588.500	
18	117.70	117.700	117.70	117.700	117.700	
19	0.00	0.000	0.00	0.000	0.000	
20	470.80	0.000	0.00	235.400	0.000	
21	470.80	0.000	235.40	470.800	588.500	
22	0.00	117.700	235.40	0.000		
23	0.00	235.400	235.40	0.000		
24	470.80	0.000	235.40	0.000		
25	353.10	470.800	235.40	235.400		
26	117.70	117.700	117.70	823.900		
27	235.40	0.000	235.40	353.100		
28	0.00	235.400	0.00	235.400		
29	235.40	235.400	0.00	0.000		
30	0.00	0.000	0.00	235.400		
31	0.00	235.400	235.40	823.900		
32	0.00	235.400	235.40			
33	0.00	235.400	235.40			
34	235.40	235.400	235.40			
35	0.00	235.400	235.40			
36	0.00	0.000	941.60			
37	0.00	0.000	588.50			
38	235.40	0.000	235.40			
39	235.40	235.400	235.40			
40	0.00	235.400	0.00			
41	0.00	941.600	1059.30			
42	0.00	588.500				
43	235.40	235.400				
44	706.20	235.400				
45	353.10	941.600				
46	353.10	470.800				
47	235.40					
48	0.00					
49	1059.30					

Table 15. Macoma balthica. Differences in abundance along the 50m transect. High tide site.

C44 1m differences in abundance.
C45 5m differences in abundance.
C46 10m differences in abundance.
C47 20m differences in abundance.
C48 30m differences in abundance.
C49 40m differences in abundance.

COLUMN	C80	C81	C82	C83	C84	C85
COUNT	49	46	41	31	21	11
ROW						
1	2824.80	5414.20	5061.10	4943.40	3531.00	5649.60
2	1647.80	1412.40	1883.20	2824.80	2824.80	2354.00
3	353.10	1765.50	117.70	1059.30	706.20	1059.30
4	1294.70	588.50	1530.10	1294.70	823.90	235.40
5	1177.00	353.10	0.00	0.00	117.70	0.00
6	1530.10	823.90	1294.70	1059.30	1059.30	588.50
7	2000.90	2000.90	1412.40	1059.30	2942.50	2824.80
8	353.10	117.70	1177.00	3177.90	941.60	823.90
9	0.00	588.50	117.70	0.00	588.50	588.50
10	353.10	353.10	117.70	3531.00	588.50	588.50
11	117.70	823.90	235.40	1177.00	941.60	941.60
12	1059.30	470.80	1059.30	1059.30	588.50	
13	235.40	2118.60	117.70	470.80	2236.30	
14	117.70	235.40	0.00	470.80	1059.30	
15	1412.40	353.10	117.70	0.00	117.70	
16	588.50	823.90	1177.00	1177.00	706.20	
17	1647.80	2118.60	1883.20	2118.60	2000.90	
18	0.00	353.10	3648.70	470.80	353.10	
19	235.40	235.40	117.70	470.80	470.80	
20	706.20	470.80	3413.30	706.20	706.20	
21	117.70	353.10	2118.60	0.00	0.00	
22	117.70	3884.10	117.70	353.10		
23	0.00	3884.10	235.40	2000.90		
24	117.70	353.10	470.80	1059.30		
25	3648.70	3766.40	235.40	117.70		
26	117.70	1883.20	3648.70	3177.90		
27	3531.00	4119.50	4119.50	4001.80		
28	3531.00	117.70	588.50	470.80		
29	2000.90	3413.30	4119.50	4119.50		
30	2118.60	2000.90	2118.60	2118.60		
31	470.80	353.10	0.00	0.00		
32	235.40	470.80	0.00			
33	588.50	706.20	1530.10			
34	235.40	117.70	1177.00			
35	353.10	353.10	117.70			
36	0.00	0.00	823.90			
37	0.00	470.80	117.70			
38	0.00	2236.30	117.70			
39	0.00	1294.70	0.00			
40	470.80	235.40	0.00			
41	1765.50	353.10	470.80			
42	941.60	2118.60				
43	1059.30	1177.00				
44	588.50	235.40				
45	706.20	823.90				
46	0.00	117.70				
47	117.70					
48	0.00					
49	0.00					

Table 16. Nereis diversicolor. Differences in abundance along the 50m transect. High tide site.

C80 1m differences in abundance.
C81 5m differences in abundance.
C82 10m differences in abundance.
C83 20m differences in abundance.
C84 30m differences in abundance.
C85 40m differences in abundance.

COLUMN	C92	C93	C94	C95	C96	C97
COUNT	49	46	41	31	21	11
ROW						
1	117.70	1765.50	2824.80	1530.10	2707.10	823.90
2	2824.80	1530.10	2942.50	2236.30	1412.40	2236.30
3	235.40	941.60	117.70	0.00	1765.50	941.60
4	706.20	235.40	353.10	353.10	0.00	235.40
5	353.10	1059.30	706.20	117.70	1765.50	1059.30
6	353.10	1412.40	1059.30	1294.70	1177.00	353.10
7	470.80	1059.30	941.60	823.90	823.90	823.90
8	588.50	588.50	117.70	823.90	2471.70	588.50
9	0.00	0.00	0.00	3766.40	235.40	0.00
10	0.00	353.10	235.40	3766.40	1883.20	3177.90
11	0.00	353.10	1294.70	5531.90	2000.90	4472.60
12	0.00	117.70	706.20	1530.10	706.20	
13	353.10	706.20	117.70	1883.20	1059.30	
14	0.00	353.10	353.10	0.00	235.40	
15	235.40	117.70	823.90	2471.70	1765.50	
16	588.50	1177.00	0.00	117.70	941.60	
17	706.20	0.00	1177.00	1177.00	470.80	
18	235.40	117.70	1412.40	3060.20	0.00	
19	1059.30	235.40	3531.00	0.00	235.40	
20	588.50	117.70	2471.70	588.50	1883.20	
21	588.50	588.50	4825.70	1294.70	3766.40	
22	117.70	1765.50	1412.40	588.50		
23	1177.00	1412.40	1883.20	1059.30		
24	1059.30	2589.40	823.90	1059.30		
25	1765.50	3648.70	2707.10	2000.90		
26	470.80	3648.70	1647.80	823.90		
27	2354.00	117.70	470.80	1177.00		
28	0.00	1883.20	706.20	3766.40		
29	1765.50	3413.30	3531.00	3766.40		
30	4001.80	2707.10	3648.70	2354.00		
31	353.10	1294.70	470.80	2942.50		
32	1530.10	0.00	1177.00			
33	2471.70	2707.10	706.20			
34	2589.40	2589.40	2707.10			
35	1647.80	1647.80	1883.20			
36	1177.00	117.70	823.90			
37	2824.80	2354.00	2824.80			
38	1647.80	823.90	235.40			
39	117.70	1765.50	1883.20			
40	1294.70	117.70	1177.00			
41	353.10	353.10	3766.40			
42	941.60	823.90				
43	2000.90	117.70				
44	1059.30	2118.60				
45	823.90	2118.60				
46	235.40	4237.20				
47	0.00					
48	3177.90					
49	1294.70					

Table 17. Pygospio elegans. Differences in abundance along the 50m transect. High tide site.

C92 1m differences in abundance.
C93 5m differences in abundance.
C94 10m differences in abundance.
C95 20m differences in abundance.
C96 30m differences in abundance.
C97 40m differences in abundance.

COLUMN	C32	C33	C34	C35	C36	C37
COUNT	49	46	41	31	21	11
ROW						
1	0.7660	1.7340	0.4430	2.9190	7.6930	3.1290
2	2.2080	9.2990	0.0430	3.6410	1.5010	0.3900
3	1.9090	31.8810	3.7010	5.5400	1.5040	0.5220
4	1.2670	3.2390	2.4660	1.4210	0.0300	0.5670
5	10.2670	5.4900	0.4910	2.2790	0.0460	1.1550
6	24.7900	8.0900	11.4130	5.8440	10.6440	7.7640
7	30.5510	34.1320	2.2530	34.0810	36.8190	16.9200
8	1.0440	2.3710	0.6940	1.6820	4.6740	2.2610
9	3.3130	1.7570	8.1810	3.9680	7.1070	1.5370
10	1.2520	1.6860	2.7450	2.0000	4.0440	6.4800
11	5.9520	2.0710	3.7280	8.5020	2.3200	1.0580
12	3.1440	8.5170	9.5500	4.4080	6.2990	
13	3.2420	0.0790	6.0970	2.0610	1.0790	
14	1.6370	3.1820	2.1970	0.7460	1.3430	
15	0.4940	6.0680	3.4250	1.1920	2.3010	
16	5.4520	6.2930	6.0630	1.2630	4.1430	
17	6.5030	6.4850	2.8360	5.5740	14.3250	
18	7.6130	0.3270	5.5150	2.5230	9.4580	
19	0.2690	2.2340	3.4000	6.5390	2.1050	
20	7.3260	2.3740	0.4760	6.5200	4.0040	
21	0.3090	7.0960	12.1000	1.2780	2.5400	
22	5.0520	3.3400	4.8330	2.9420		
23	0.4090	0.1360	1.0160	0.0340		
24	2.1440	0.7570	1.0420	0.4450		
25	3.4470	0.2460	4.3770	3.2680		
26	1.8480	8.4510	1.3530	1.5270		
27	1.3020	0.3550	4.5860	15.3130		
28	2.6550	0.1500	1.6900	5.2450		
29	5.2500	2.9400	5.7940	2.8500		
30	6.9580	9.3810	11.2940	0.7700		
31	0.7970	2.8460	3.8640	2.6020		
32	0.4350	3.4340	1.0940			
33	1.1910	1.4050	1.4170			
34	0.4230	1.6630	1.7880			
35	1.3850	1.4900	1.5320			
36	1.5940	0.3670	4.2650			
37	1.4490	0.7460	18.3050			
38	0.2500	4.2710	8.3840			
39	0.4720	3.7010	8.8940			
40	1.9730	2.5500	10.0520			
41	2.0760	1.9250	0.7110			
42	0.8200	15.4830				
43	0.6790	4.9330				
44	1.3480	5.8720				
45	15.6340	6.1540				
46	11.3700	18.2700				
47	0.2600					
48	1.6300					
49	8.7900					

Table 18. Shear strength ($KN.m^{-2}$). Differences in mean values along the 50m transect. High tide site.

C32 1m differences in mean values.
C33 5m differences in mean values.
C34 10m differences in mean values.
C35 20m differences in mean values.
C36 30m differences in mean values.
C37 40m differences in mean values.

COLUMN	C20	C21	C22	C23	C24	C25
COUNT	49	46	41	31	21	11
ROW						
1	131.	25.	203.	248.	129.	218.
2	137.	102.	149.	26.	1.	27.
3	110.	149.	239.	94.	54.	15.
4	79.	83.	88.	112.	57.	27.
5	4.	161.	195.	180.	106.	69.
6	115.	174.	38.	189.	127.	159.
7	44.	137.	87.	64.	68.	27.
8	2.	46.	59.	7.	25.	47.
9	18.	7.	198.	46.	10.	40.
10	77.	17.	111.	100.	10.	26.
11	47.	214.	33.	151.	62.	10.
12	41.	177.	128.	102.	76.	
13	28.	64.	104.	144.	123.	
14	153.	232.	5.	59.	89.	
15	11.	25.	138.	64.	27.	
16	73.	192.	162.	99.	132.	
17	141.	24.	79.	83.	12.	
18	104.	100.	192.	224.	246.	
19	156.	124.	48.	84.	133.	
20	143.	43.	145.	35.	19.	
21	17.	113.	25.	113.	58.	
22	128.	120.	44.	70.		
23	11.	35.	167.	146.		
24	14.	65.	44.	73.		
25	11.	115.	87.	125.		
26	27.	78.	52.	20.		
27	40.	49.	31.	64.		
28	37.	92.	72.	94.		
29	27.	58.	73.	122.		
30	2.	2.	83.	99.		
31	83.	24.	87.	32.		
32	113.	163.	109.			
33	30.	51.	92.			
34	24.	45.	0.			
35	56.	57.	62.			
36	0.	7.	24.			
37	36.	54.	95.			
38	37.	107.	58.			
39	6.	81.	13.			
40	61.	125.	11.			
41	88.	31.	6.			
42	62.	47.				
43	38.	103.				
44	95.	132.				
45	71.	41.				
46	117.	46.				
47	9.					
48	4.					
49	66.					

Table 19. Eh(mV). Differences in mean values along the 50m transect. High tide site.

C20 1m differences in mean values.
C21 5m differences in mean values.
C22 10m differences in mean values.
C23 20m differences in mean values.
C24 30m differences in mean values.
C25 40m differences in mean values.

COLUMN	C2	C3	C4	C5	C6	C7
COUNT	49	46	41	31	21	11
ROW						
1	0.085000	0.021000	0.789000	0.015000	0.778000	0.869000
2	0.056000	0.096000	0.552000	0.021000	0.035000	0.026000
3	0.079000	0.004000	0.923000	0.048000	0.420000	0.418000
4	0.030000	0.705000	0.894000	0.107000	0.801000	0.602000
5	0.201000	0.407000	0.571000	0.082000	0.775000	0.367000
6	0.155000	0.609000	0.491000	0.008000	0.593000	0.126000
7	0.630000	0.612000	0.441000	0.075000	0.662000	0.217000
8	0.268000	0.297000	0.047000	0.333000	0.259000	0.532000
9	0.403000	0.457000	0.088000	0.184000	0.153000	0.086000
10	0.152000	0.239000	0.853000	0.703000	0.206000	0.697000
11	0.315000	0.035000	0.622000	0.142000	0.233000	0.735000
12	0.108000	0.486000	0.845000	0.832000	0.841000	
13	0.294000	0.236000	0.862000	0.395000	0.397000	
14	0.122000	0.075000	0.493000	0.201000	0.002000	
15	0.206000	0.735000	0.610000	0.083000	0.325000	
16	0.142000	0.451000	0.278000	0.307000	0.411000	
17	0.133000	0.502000	0.508000	0.079000	0.366000	
18	0.539000	0.494000	0.152000	0.439000	0.351000	
19	0.079000	0.121000	0.267000	0.604000	0.365000	
20	0.091000	0.047000	0.071000	0.558000	0.077000	
21	0.125000	0.082000	0.672000	0.763000	0.204000	
22	0.075000	0.119000	0.138000	0.130000		
23	0.005000	0.266000	0.392000	0.390000		
24	0.126000	0.141000	0.689000	0.490000		
25	0.088000	0.102000	0.567000	0.158000		
26	0.222000	0.678000	0.673000	0.045000		
27	0.120000	0.203000	0.365000	0.080000		
28	0.117000	0.246000	0.711000	0.079000		
29	0.693000	0.665000	0.454000	0.215000		
30	0.659000	0.024000	0.205000	0.686000		
31	0.330000	0.654000	0.750000	0.218000		
32	0.302000	0.238000	0.338000			
33	0.004000	0.163000	0.304000			
34	0.018000	0.215000	0.203000			
35	0.086000	0.200000	0.427000			
36	0.227000	0.183000	0.632000			
37	0.374000	0.803000	0.671000			
38	0.033000	0.093000	0.416000			
39	0.297000	0.021000	0.272000			
40	0.259000	0.523000	0.777000			
41	0.336000	0.056000	0.209000			
42	0.105000	0.205000				
43	0.205000	0.428000				
44	0.291000	0.045000				
45	0.187000	0.038000				
46	0.119000	0.340000				
47	0.178000					
48	0.209000					
49	0.191000					

Table 20. Shannon Wiener diversity index. Differences in abundance along the 50m transect. Low tide site.

C2 1m differences in abundance.
C3 5m differences in abundance.
C4 10m differences in abundance.
C5 20m differences in abundance.
C6 30m differences in abundance.
C7 40m differences in abundance.

COLUMN	C62	C63	C64	C65	C66	C67
COUNT	49	46	41	31	21	11
ROW						
1	1.1970	32.3190	32.3190	57.4560	44.2890	68.2290
2	33.5160	33.5160	50.2740	64.6380	46.6830	62.2440
3	14.3640	5.9850	34.7130	22.7430	17.9550	21.5460
4	16.7580	8.3790	5.9850	5.9850	1.1970	7.1820
5	2.3940	29.9250	28.7280	43.0920	2.3940	11.9700
6	5.9850	2.3940	27.5310	8.3790	9.5760	25.1370
7	0.0000	10.7730	16.7580	27.5310	1.1970	45.4860
8	21.5460	28.7280	14.3640	17.9550	19.1520	28.7280
9	29.9250	7.1820	5.9850	19.1520	7.1820	51.4710
10	19.1520	28.7280	34.7130	13.1670	28.7280	1.1970
11	17.9550	10.7730	5.9850	7.1820	16.7580	4.7880
12	14.3640	11.9700	3.5910	9.5760	5.9850	
13	5.9850	0.0000	2.3940	2.3940	1.1970	
14	1.1970	4.7880	17.9550	10.7730	4.7880	
15	4.7880	4.7880	73.0170	32.3190	17.9550	
16	2.3940	0.0000	31.1220	32.3190	47.8800	
17	1.1970	10.7730	41.8950	13.1670	59.8500	
18	10.7730	1.1970	33.5160	3.5910	44.2890	
19	9.5760	23.9400	23.9400	11.9700	56.2590	
20	8.3790	68.2290	11.9700	3.5910	23.9400	
21	8.3790	39.5010	21.5460	2.3940	19.1520	
22	14.3640	44.2890	9.5760	5.9850		
23	53.8650	20.3490	9.5760	13.1670		
24	37.1070	53.8650	61.0470	67.0320		
25	13.1670	19.1520	3.5910	17.9550		
26	9.5760	31.1220	11.9700	3.5910		
27	20.3490	25.1370	19.1520	27.5310		
28	2.3940	9.5760	16.7580	31.1220		
29	1.1970	4.7880	9.5760	34.7130		
30	3.5910	14.3640	16.7580	10.7730		
31	4.7880	22.7430	20.3490	1.1970		
32	2.3940	10.7730	10.7730			
33	20.3490	9.5760	5.9850			
34	4.7880	25.1370	26.3340			
35	16.7580	35.9100	19.1520			
36	17.9550	26.3340	32.3190			
37	4.7880	3.5910	64.6380			
38	5.9850	1.1970	43.0920			
39	7.1820	4.7880	50.2740			
40	16.7580	23.9400	34.7130			
41	7.1820	53.8650	16.7580			
42	0.0000	61.0470				
43	11.9700	44.2890				
44	34.7130	33.5160				
45	14.3640	23.9400				
46	16.7580	51.4710				
47	1.1970					
48	22.7430					
49	13.1670					

Table 21. Arenicola marina. Differences in abundance along the 50m transect. Low tide site.

C62 1m differences in abundance.
C63 5m differences in abundance.
C64 10m differences in abundance.
C65 20m differences in abundance.
C66 30m differences in abundance.
C67 40m differences in abundance.

COLUMN	C20	C21	C22	C23	C24	C25
COUNT	49	46	41	31	21	11
ROW						
1	0.00	0.00	4943.40	0.00	588.50	3531.00
2	235.40	235.40	3648.70	117.70	235.40	117.70
3	117.70	235.40	2354.00	235.40	588.50	823.90
4	117.70	6591.20	1059.30	235.40	941.60	1647.80
5	235.40	235.40	470.80	0.00	4472.60	588.50
6	235.40	4708.00	5178.80	235.40	1883.20	117.70
7	6708.90	3648.70	2589.40	0.00	2942.50	117.70
8	6473.50	4119.50	5178.80	6591.20	5649.60	6708.90
9	4708.00	941.60	3531.00	235.40	117.70	235.40
10	1294.70	4472.60	4943.40	4943.40	4825.70	4943.40
11	1059.30	1765.50	3648.70	3060.20	117.70	3648.70
12	1412.40	0.00	2471.70	2354.00	2471.70	
13	706.20	353.10	1177.00	353.10	117.70	
14	4943.40	3295.60	117.70	588.50	1294.70	
15	2824.80	5414.20	5414.20	941.60	4825.70	
16	1059.30	2589.40	2118.60	470.80	2471.70	
17	2236.30	1412.40	1530.10	1412.40	1412.40	
18	3766.40	3766.40	3648.70	2707.10	3766.40	
19	0.00	353.10	0.00	353.10	0.00	
20	117.70	0.00	0.00	117.70	0.00	
21	117.70	353.10	470.80	3413.30	117.70	
22	353.10	0.00	235.40	117.70		
23	353.10	235.40	470.80	706.20		
24	470.80	0.00	1059.30	1765.50		
25	470.80	470.80	4001.80	117.70		
26	117.70	588.50	2118.60	117.70		
27	117.70	117.70	2824.80	0.00		
28	0.00	823.90	1059.30	0.00		
29	588.50	1059.30	353.10	0.00		
30	353.10	3884.10	470.80	588.50		
31	588.50	1883.20	3295.60	235.40		
32	235.40	2118.60	706.20			
33	3413.30	0.00	0.00			
34	2354.00	4119.50	2707.10			
35	823.90	2000.90	1530.10			
36	1883.20	588.50	2824.80			
37	706.20	941.60	941.60			
38	235.40	706.20	353.10			
39	3413.30	1647.80	117.70			
40	3413.30	2942.50	3531.00			
41	941.60	0.00	117.70			
42	706.20	941.60				
43	1177.00	1765.50				
44	470.80	588.50				
45	0.00	117.70				
46	117.70	117.70				
47	0.00					
48	0.00					
49	0.00					

Table 22. Bathyporeia guilliamsoniana. Differences in abundance along the 50m transect. Low tide site.

C20 1m differences in abundance.
C21 5m differences in abundance.
C22 10m differences in abundance.
C23 20m differences in abundance.
C24 30m differences in abundance.
C25 40m differences in abundance.

COLUMN	C38	C39	C40	C41	C42	C43
COUNT	49	46	41	31	21	11
ROW						
1	0.000	0.000	117.700	0.000	0.000	235.400
2	0.000	0.000	117.700	0.000	0.000	117.700
3	0.000	0.000	235.400	0.000	0.000	235.400
4	0.000	117.700	235.400	117.700	117.700	117.700
5	0.000	0.000	117.700	0.000	117.700	0.000
6	0.000	117.700	0.000	0.000	0.000	0.000
7	117.700	117.700	117.700	0.000	0.000	0.000
8	117.700	117.700	117.700	117.700	117.700	117.700
9	117.700	235.400	0.000	0.000	0.000	0.000
10	0.000	0.000	117.700	117.700	117.700	117.700
11	117.700	117.700	117.700	117.700	117.700	117.700
12	0.000	117.700	235.400	235.400	117.700	
13	117.700	235.400	235.400	235.400	0.000	
14	117.700	117.700	0.000	0.000	0.000	
15	117.700	0.000	0.000	117.700	0.000	
16	117.700	117.700	117.700	117.700	117.700	
17	0.000	0.000	0.000	0.000	0.000	
18	0.000	0.000	0.000	0.000	0.000	
19	0.000	117.700	0.000	0.000	0.000	
20	0.000	0.000	0.000	235.400	0.000	
21	0.000	0.000	0.000	235.400	0.000	
22	117.700	0.000	0.000	117.700		
23	117.700	117.700	117.700	117.700		
24	0.000	0.000	117.700	117.700		
25	0.000	0.000	117.700	0.000		
26	0.000	0.000	0.000	0.000		
27	0.000	0.000	0.000	0.000		
28	0.000	0.000	0.000	0.000		
29	0.000	117.700	0.000	0.000		
30	0.000	117.700	235.400	0.000		
31	0.000	0.000	235.400	0.000		
32	117.700	0.000	117.700			
33	0.000	117.700	117.700			
34	117.700	117.700	0.000			
35	0.000	235.400	0.000			
36	0.000	235.400	0.000			
37	0.000	117.700	0.000			
38	235.400	235.400	0.000			
39	0.000	117.700	235.400			
40	117.700	235.400	235.400			
41	117.700	117.700	117.700			
42	117.700	235.400				
43	117.700	117.700				
44	0.000	0.000				
45	0.000	0.000				
46	0.000	0.000				
47	0.000					
48	0.000					
49	0.000					

Table 23. Macoma balthica. Differences in abundance along the 50m transect. Low tide site.

C38 1m differences in abundance.
C39 5m differences in abundance.
C40 10m differences in abundance.
C41 20m differences in abundance.
C42 30m differences in abundance.
C43 40m differences in abundance.

COLUMN	C74	C75	C76	C77	C78	C79
COUNT	49	46	41	31	21	11
ROW						
1	353.100	353.100	235.400	0.000	235.400	117.700
2	0.000	117.700	588.500	235.400	117.700	235.400
3	117.700	353.100	823.900	0.000	117.700	470.800
4	117.700	235.400	588.500	0.000	353.100	588.500
5	117.700	117.700	588.500	0.000	235.400	235.400
6	235.400	470.800	470.800	235.400	117.700	117.700
7	235.400	235.400	235.400	235.400	117.700	117.700
8	0.000	706.200	706.200	470.800	470.800	0.000
9	470.800	353.100	353.100	117.700	117.700	235.400
10	0.000	0.000	235.400	588.500	117.700	470.800
11	235.400	0.000	235.400	470.800	117.700	706.200
12	353.100	235.400	588.500	941.600	588.500	
13	117.700	353.100	470.800	588.500	0.000	
14	0.000	117.700	706.200	353.100	117.700	
15	0.000	235.400	588.500	353.100	353.100	
16	235.400	235.400	235.400	353.100	353.100	
17	353.100	588.500	706.200	588.500	588.500	
18	117.700	470.800	117.700	117.700	353.100	
19	0.000	470.800	117.700	117.700	0.000	
20	117.700	353.100	353.100	117.700	235.400	
21	235.400	117.700	117.700	235.400	353.100	
22	117.700	117.700	117.700	235.400		
23	117.700	706.200	0.000	588.500		
24	353.100	235.400	235.400	470.800		
25	235.400	353.100	117.700	117.700		
26	470.800	0.000	117.700	117.700		
27	353.100	706.200	353.100	353.100		
28	235.400	353.100	353.100	117.700		
29	117.700	235.400	235.400	353.100		
30	235.400	117.700	353.100	0.000		
31	0.000	353.100	588.500	0.000		
32	353.100	353.100	353.100			
33	0.000	353.100	235.400			
34	0.000	0.000	235.400			
35	0.000	235.400	0.000			
36	353.100	235.400	0.000			
37	353.100	353.100	353.100			
38	235.400	235.400	117.700			
39	0.000	0.000	117.700			
40	235.400	235.400	353.100			
41	235.400	0.000	353.100			
42	0.000	235.400				
43	235.400	353.100				
44	0.000	117.700				
45	0.000	117.700				
46	117.700	353.100				
47	235.400					
48	235.400					
49	235.400					

Table 24. Nereis diversicolor. Differences in abundance along the 50m transect. Low tide site.

C74 1m differences in abundance.
C75 5m differences in abundance.
C76 10m differences in abundance.
C77 20m differences in abundance.
C78 30m differences in abundance.
C79 40m differences in abundance.

COLUMN	C86	C87	C88	C89	C90	C91
COUNT	49	46	41	31	21	11
ROW						
1	10357.6	9062.9	9298.3	3648.7	13182.4	11534.6
2	5649.6	1765.5	3884.1	3060.2	823.9	5649.6
3	3413.3	941.6	6708.9	5414.2	7532.8	353.1
4	941.6	2236.3	2942.5	3766.4	3295.6	1765.5
5	470.8	2824.8	588.5	1530.1	2236.3	470.8
6	4825.7	706.2	4001.8	4943.4	3413.3	5296.5
7	6591.2	10475.3	2942.5	6355.8	6473.5	5767.3
8	1530.1	1059.3	2471.7	1177.0	2707.1	235.4
9	2589.4	823.9	11534.6	588.5	117.7	470.8
10	4943.4	353.1	16478.0	2824.8	1883.2	1059.3
11	2824.8	1647.8	10593.0	1059.3	2707.1	2236.3
12	353.1	10593.0	4119.5	235.4	6708.9	
13	1412.4	3177.9	941.6	1177.0	6002.7	
14	2942.5	9298.3	5296.5	1765.5	3295.6	
15	11770.0	19773.6	2000.9	1294.7	4001.8	
16	7062.0	2824.8	2824.8	11181.5	2471.7	
17	7532.8	588.5	2236.3	2354.0	1647.8	
18	7532.8	9769.1	8827.5	12711.6	10239.9	
19	10828.4	11534.6	18478.9	19185.1	18596.6	
20	3648.7	6944.3	8474.4	7532.8	6708.9	
21	2824.8	3648.7	5885.0	4237.2	4708.0	
22	5767.3	0.0	1059.3	5414.2		
23	6238.1	4825.7	7885.9	706.2		
24	6944.3	706.2	823.9	4237.2		
25	6473.5	8356.7	7650.5	4943.4		
26	941.6	3060.2	1883.2	6826.6		
27	2118.6	2000.9	1059.3	353.1		
28	823.9	941.6	1765.5	706.2		
29	1059.3	706.2	117.7	706.2		
30	2000.9	1883.2	2000.9	2824.8		
31	1059.3	823.9	353.1	823.9		
32	823.9	2000.9	7532.8			
33	117.7	1647.8	6355.8			
34	706.2	706.2	4943.4			
35	1765.5	823.9	3413.3			
36	2824.8	1294.7	6944.3			
37	1059.3	8356.7	3531.0			
38	823.9	6944.3	1412.4			
39	353.1	4825.7	235.4			
40	6826.6	2942.5	1177.0			
41	353.1	1412.4	7297.4			
42	1294.7	4472.6				
43	2236.3	4237.2				
44	5296.5	2824.8				
45	6238.1	7062.0				
46	1059.3	2471.7				
47	823.9					
48	1059.3					
49	1647.8					

Table 25. Pygospio elegans. Differences in abundance along the 50m transect. Low tide site.

C86 1m differences in abundance.
C87 5m differences in abundance.
C88 10m differences in abundance.
C89 20m differences in abundance.
C90 30m differences in abundance.
C91 40m differences in abundance.

COLUMN	C26	C27	C28	C29	C30	C31
COUNT	49	46	41	31	21	11
ROW						
1	0.54400	1.62400	1.45600	2.31700	2.07800	5.74300
2	0.57500	1.38000	5.37900	2.55100	2.10700	4.75600
3	0.76200	0.11600	6.54200	1.46400	0.19400	2.01500
4	0.25700	0.58400	8.13950	1.76300	0.71400	1.21000
5	0.30000	1.92100	7.47300	3.79500	2.88400	1.02300
6	0.68900	3.38000	7.93100	2.36700	4.40800	1.73200
7	1.23000	6.07000	7.08900	1.47800	4.41700	0.77400
8	2.76200	7.88800	6.69800	1.49000	7.84000	3.40300
9	1.15900	5.96150	1.76400	1.81600	5.83100	0.99300
10	3.37000	4.39300	1.15700	1.27000	4.56800	2.38900
11	0.58800	1.17200	7.15200	6.91300	0.90800	6.84100
12	0.83550	0.43100	8.51800	8.07400	1.21100	
13	0.40950	2.02550	8.84150	7.57150	5.36250	
14	0.15800	3.78800	5.96700	8.44400	6.52000	
15	0.15300	5.70800	8.42600	4.74700	6.60800	
16	1.62100	8.17100	5.41100	3.37000	6.04600	
17	2.17200	7.32800	3.99000	1.05100	6.24200	
18	1.76200	4.64400	6.01600	3.31400	1.12300	
19	2.61600	0.41700	1.81800	5.82900	0.99400	
20	0.77800	0.10200	2.50300	8.34100	1.38400	
21	0.51200	3.53800	1.01700	8.83800	1.08900	
22	2.46500	2.82600	0.06800	6.79500		
23	2.30100	3.83700	1.19500	1.01400		
24	2.86200	0.90000	0.17600	1.74800		
25	0.20000	0.25700	0.81700	1.04400		
26	4.19800	2.32100	2.24100	0.43500		
27	2.43600	1.30400	7.13700	1.94600		
28	1.70500	0.20600	6.89400	2.45700		
29	2.26400	2.78100	5.94200	0.88200		
30	0.57300	3.33800	8.10200	1.14500		
31	1.33800	5.13500	8.39400	0.64500		
32	1.28200	4.49500	5.52500			
33	3.85500	7.97000	3.49100			
34	1.22400	4.86800	1.93100			
35	0.69800	7.17900	3.08500			
36	2.19300	2.56100	3.37400			
37	0.75300	1.16300	7.38400			
38	0.10400	5.23200	5.19000			
39	0.28100	4.02400	6.72000			
40	1.53100	6.34400	6.67600			
41	3.31600	4.40400	6.21800			
42	1.56700	2.90500				
43	0.07000	1.60900				
44	0.40900	0.09500				
45	1.81700	0.74100				
46	2.94700	0.00300				
47	1.63400					
48	0.23700					
49	1.07300					

Table 26. Shear strength ($KN.m^{-2}$). Differences in mean values along the 50m transect. Low tide site.

C26 1m differences in mean values.
C27 5m differences in mean values.
C28 10m differences in mean values.
C29 20m differences in mean values.
C30 30m differences in mean values.
C31 40m differences in mean values.

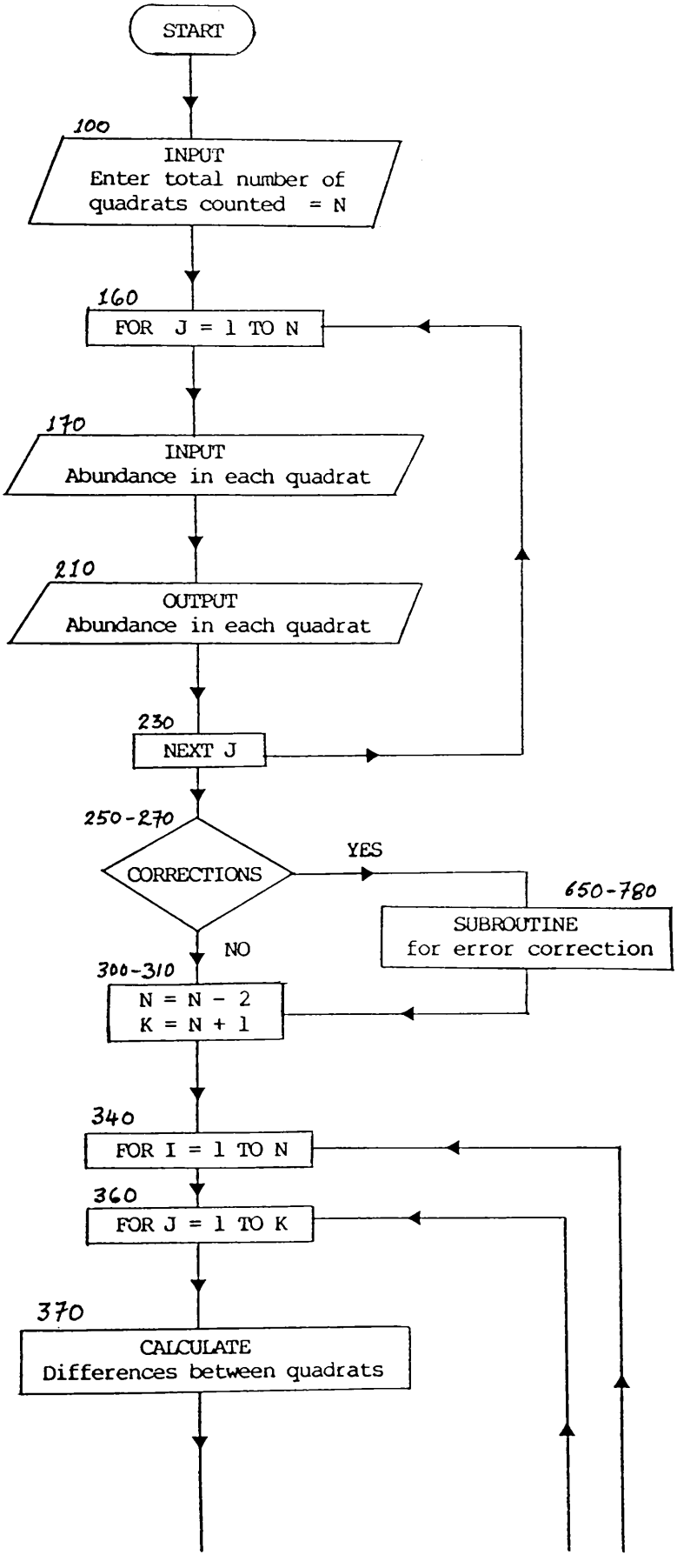
COLUMN	C14	C15	C16	C17	C18	C19
COUNT	49	46	41	31	21	11
ROW						
1	39.	62.	95.	26.	97.	66.
2	47.	70.	11.	4.	62.	3.
3	77.	93.	72.	10.	101.	19.
4	7.	17.	0.	13.	22.	47.
5	47.	15.	104.	26.	23.	5.
6	25.	14.	32.	74.	1.	97.
7	2.	35.	37.	31.	7.	15.
8	9.	23.	10.	55.	34.	71.
9	18.	9.	18.	76.	136.	33.
10	46.	136.	79.	51.	157.	37.
11	15.	28.	23.	48.	17.	10.
12	6.	17.	21.	37.	22.	
13	110.	7.	68.	24.	58.	
14	118.	101.	98.	133.	64.	
15	30.	61.	40.	9.	19.	
16	29.	21.	13.	61.	36.	
17	17.	34.	22.	1.	7.	
18	44.	58.	29.	8.	44.	
19	10.	40.	15.	75.	28.	
20	16.	11.	19.	87.	32.	
21	41.	8.	55.	24.	3.	
22	55.	52.	101.	40.		
23	20.	25.	36.	45.		
24	2.	36.	55.	15.		
25	19.	10.	51.	23.		
26	22.	56.	54.	42.		
27	30.	31.	46.	38.		
28	43.	11.	51.	14.		
29	53.	47.	103.	1.		
30	3.	12.	158.	39.		
31	8.	7.	35.	61.		
32	1.	16.	51.			
33	7.	40.	80.			
34	22.	14.	63.			
35	31.	168.	51.			
36	25.	11.	66.			
37	111.	11.	17.			
38	2.	71.	74.			
39	127.	83.	105.			
40	25.	9.	7.			
41	30.	30.	2.			
42	11.	57.				
43	35.	7.				
44	46.	23.				
45	58.	47.				
46	54.	29.				
47	29.					
48	15.					
49	19.					

Table 27. Eh(mV). Differences in mean values along the 50m transect. Low tide site.

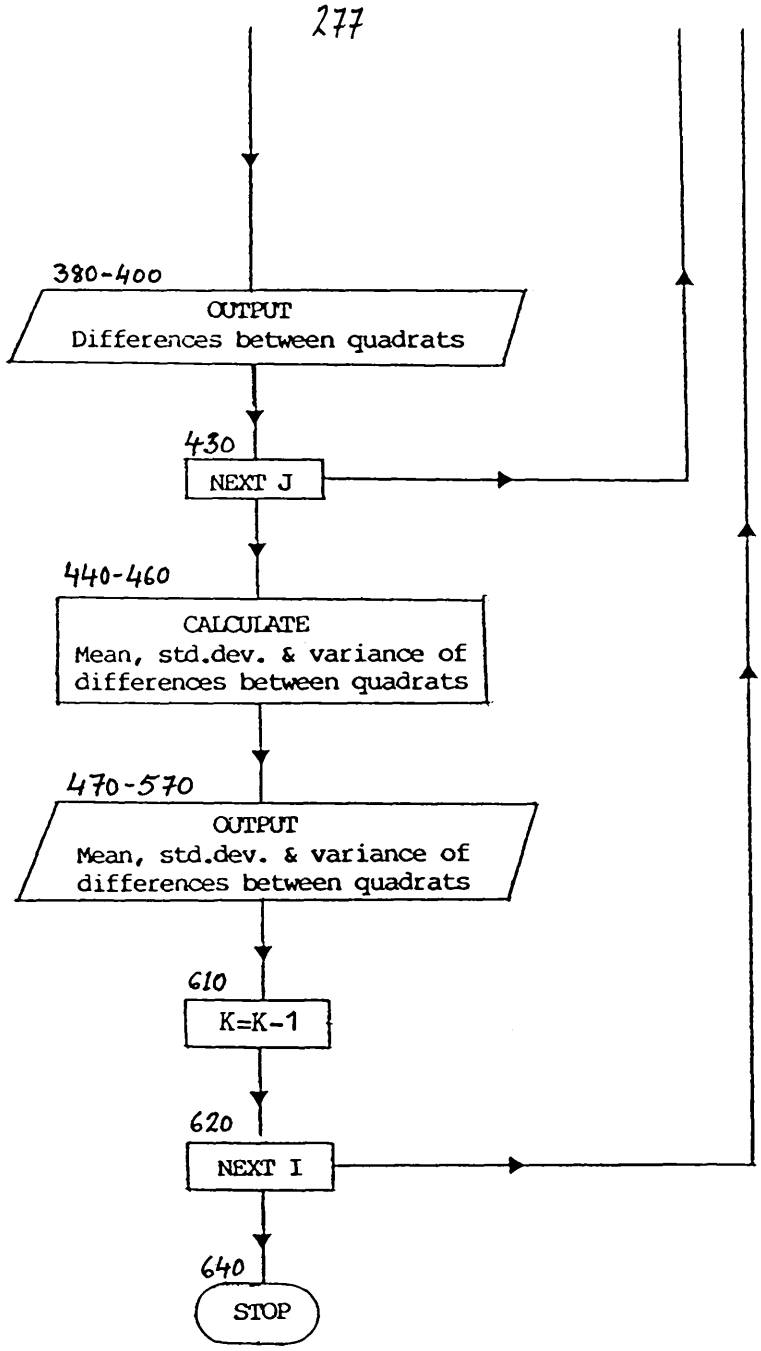
C14 1m differences in mean values.
C15 5m differences in mean values.
C16 10m differences in mean values.
C17 20m differences in mean values.
C18 30m differences in mean values.
C19 40m differences in mean values.

Appendix 4.

Computer program used to calculate differences in animal abundances and sediment parameters between quadrats along the HT and LT transects.


START
100
INPUT
Enter total number of
quadrats counted = N
160
FOR J = 1 TO N
170
INPUT
Abundance in each quadrat
210
OUTPUT
Abundance in each quadrat
230
NEXT J
250-270
CORRECTIONS
YES
650-780
SUBROUTINE
for error correction
NO
300-310
N = N - 2
K = N + 1
340
FOR I = 1 TO N
360
FOR J = 1 TO K
370
CALCULATE
Differences between quadrats

CONTD:


380-400
OUTPUT
Differences between quadrats
430
NEXT J
440-460
CALCULATE
Mean, std.dev. & variance of
differences between quadrats
470-570
OUTPUT
Mean, std.dev. & variance of
differences between quadrats
610
K=K-1
620
NEXT I
640
STOP

LISTING:

```
10 DIM X(500)
20 REM***THIS PROGRAM CALCULATES DIFFERENCES IN ANIMAL ABUNDANCES (9-9-87)***
30 INPUT "ENTER TOTAL NUMBER OF QUADRATS COUNTED = ";N
40 A$="THIS PROGRAM CALCULATES THE DIFFERENCES IN ANIMAL ABUNDANCES OR ANY OTHER
"
50 B$="       PARAMETER BETWEEN QUADRATS, ALONG A TRANSECT"
60 LPRINT A$;B$
70 LPRINT "=========================================================================
=========="
80 LPRINT
90 LPRINT:LPRINT
100 LPRINT "TOTAL NUMBER OF QUADRATS COUNTED= ";N
110 LPRINT:LPRINT
120 INPUT "ENTER SPECIES OR PARAMETER NAME=  ";Z$
130 LPRINT "SPECIES OR PARAMETER NAME:    ";Z$
140 LPRINT:LPRINT:LPRINT
150 REM***LOOP FOR ENTERING DATA VALUES : LINES 120-160***
160 FOR J=1 TO N
170 INPUT "ENTER ABUNDANCE (NO./M2 OR NO./CORE) OF ANIMALS= ";X(J)
180 PRINT J
190 LPRINT J
200 PRINT X(J)
210 LPRINT "ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = ";X(J)
220 LPRINT:LPRINT
230 NEXT J
240 PRINT:PRINT
250 PRINT "CHECK ENTERED DATA ON PRINTOUT"
260 PRINT:PRINT
270 INPUT "ARE CORRECTIONS NEEDED?  YES/NO";D$
280 IF D$="NO" GOTO 300
290 GOSUB 660
300 N=N-2
310 K=N+1
320 REM***OUTER LOOP SUCCESIVELY GREATER DISTANCES***
330 REM***INNER LOOP ALL DIFFERENCES FOR ONE DISTANCE***
340 FOR I=1 TO N
350 Q=0: R=0
360 FOR J=1 TO K
370 A=ABS(X(J)-X(J+I))
380 PRINT "ABSOLUTE VALUE IN DIFFERENCE IN ABUNDANCE = ";A
390 PRINT:PRINT
400 LPRINT "ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE ";J;" TO ";J+I;" QUAD
RATS =";A
410 Q=Q+A
420 R=R+A^2
430 NEXT J
440 M=Q/K
450 S=SQR((R-Q^2/K)/(K-1))
460 V=(R-Q^2/K)/(K-1)
470 E$="TOTAL NO. DIFF."
480 F$="MEAN"
490 G$="STD.DEV."
500 H$="VARIANCE"
510 PRINT TAB(4);E$;TAB(28);F$;TAB(42);G$;TAB(58);H$
520 LPRINT:LPRINT
530 LPRINT TAB(4);E$;TAB(28);F$;TAB(42);G$;TAB(58);H$
540 LPRINT
550 PRINT TAB(8);K;TAB(26);M;TAB(41);S;TAB(58);V
560 PRINT:PRINT
570 LPRINT TAB(8);K;TAB(25);M;TAB(41);S;TAB(57);V
580 LPRINT:LPRINT
590 LPRINT "------------------------------------------------------------------
----------"
600 LPRINT
610 K=K-1
620 NEXT I
630 LPRINT:LPRINT
640 END
650 REM ***SUBROUTINE TO CHANGE A MISTAKE IN ENTERING DATA VALUES***
660 PRINT:PRINT
670 INPUT "C FOR CHANGE, T TO RETURN";C$
680 IF C$="T" THEN 300
690 PRINT:PRINT
700 INPUT "WHICH QUADRAT NUMBER?";J
710 PRINT:PRINT
720 INPUT "CORRECT DATA VALUE";C
730 PRINT:PRINT
740 LPRINT "QUADRAT NO. IN WHICH WRONG DATA VALUE ENTERED = ";J
750 LPRINT "CORRECT DATA VALUE =";C
760 LPRINT:LPRINT
770 LET X(J)=C
780 GOTO 660
```

RUN:

THIS PROGRAM CALCULATES THE DIFFERENCES IN ANIMAL ABUNDANCES OR ANY OTHER PARAMETER BETWEEN QUADRATS, ALONG A TRANSECT.

TOTAL NUMBER OF QUADRATS COUNTED= 50

SPECIES OR PARAMETER NAME: A. MARINA (HIGH TIDE)

1
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 5.985

2
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 9.576

3
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 39.501

4
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 65.835

5
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 17.955

6
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 5.985

7
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

8
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

9
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 3.591

10
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

11
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

12
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

13
ABUNDANCE (NO/M^2 OR NO./CORE OF ANIMALS = 354.312

14
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 323.19

15
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 160.398

16
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 92.169

17
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 39.501

18
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 7.182

19
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

20
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 32.319

21
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

22
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 35.91

23
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 35.91

24
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

25
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 2.394

26
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 3.591

27
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

28
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 10.773

29
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 9.576

30
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

31
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 16.758

32
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 15.561

33
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 15.561

34
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 102.942

35
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 137.655

36
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 47.88

37
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 16.758

38
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 19.152

39
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 25.137

40
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 44.289

41
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 89.775

42
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 9.576

43
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

44
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 13.167

45
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 8.379

46
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 7.182

47
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 2.394

48
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 0

49
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 1.197

50
ABUNDANCE (NO/M^2 OR NO./CORE) OF ANIMALS = 3.591

ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 1 TO 2 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 2 TO 3 QUADRATS = 29.925
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 3 TO 4 QUADRATS = 26.334
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 4 TO 5 QUADRATS = 47.88
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 5 TO 6 QUADRATS = 11.97
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 6 TO 7 QUADRATS = 5.985
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 7 TO 8 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 8 TO 9 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 9 TO 10 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 10 TO 11 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 11 TO 12 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 12 TO 13 QUADRATS = 354.312
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 13 TO 14 QUADRATS = 31.122
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 14 TO 15 QUADRATS = 162.792
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 15 TO 16 QUADRATS = 68.229
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 16 TO 17 QUADRATS = 52.668
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 17 TO 18 QUADRATS = 32.319
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 18 TO 19 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 19 TO 20 QUADRATS = 32.319
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 20 TO 21 QUADRATS = 32.319
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 21 TO 22 QUADRATS = 35.91
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 22 TO 23 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 23 TO 24 QUADRATS = 35.91
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 24 TO 25 QUADRATS = 2.394
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 25 TO 26 QUADRATS = 1.197
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 26 TO 27 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 27 TO 28 QUADRATS = 10.773
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 28 TO 29 QUADRATS = 1.197
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 29 TO 30 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 30 TO 31 QUADRATS = 16.758
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 31 TO 32 QUADRATS = 1.197
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 32 TO 33 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 33 TO 34 QUADRATS = 87.381
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 34 TO 35 QUADRATS = 34.713
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 35 TO 36 QUADRATS = 89.775
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 36 TO 37 QUADRATS = 31.122
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 37 TO 38 QUADRATS = 2.394
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 38 TO 39 QUADRATS = 5.985
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 39 TO 40 QUADRATS = 19.152
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 40 TO 41 QUADRATS = 45.486
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 41 TO 42 QUADRATS = 80.199
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 42 TO 43 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 43 TO 44 QUADRATS = 13.167
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 44 TO 45 QUADRATS = 4.788
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 45 TO 46 QUADRATS = 1.197
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 46 TO 47 QUADRATS = 4.788
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 47 TO 48 QUADRATS = 2.394
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 48 TO 49 QUADRATS = 1.197
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 49 TO 50 QUADRATS = 2.394

TOTAL NO. DIFF.	MEAN	STD. DEV.	VARIANCE
49	29.8029	56.7141	3216.49

ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 1 TO 5 QUADRATS = 11.97
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 2 TO 6 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 3 TO 7 QUADRATS = 39.501
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 4 TO 8 QUADRATS = 65.835
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 5 TO 9 QUADRATS = 14.364
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 6 TO 10 QUADRATS = 5.985
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 7 TO 11 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 8 TO 12 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 9 TO 13 QUADRATS = 350.721
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 10 TO 14 QUADRATS = 323.19
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 11 TO 15 QUADRATS = 160.398
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 12 TO 16 QUADRATS = 92.169
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 13 TO 17 QUADRATS = 314.811
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 14 TO 18 QUADRATS = 316.008
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 15 TO 19 QUADRATS = 160.398
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 16 TO 20 QUADRATS = 59.85
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 17 TO 21 QUADRATS = 39.501
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 18 TO 22 QUADRATS = 28.728
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 19 TO 23 QUADRATS = 35.91
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 20 TO 24 QUADRATS = 32.319
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 21 TO 25 QUADRATS = 2.394
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 22 TO 26 QUADRATS = 32.319
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 23 TO 27 QUADRATS = 35.91
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 24 TO 28 QUADRATS = 10.773
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 25 TO 29 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 26 TO 30 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 27 TO 31 QUADRATS = 16.758
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 28 TO 32 QUADRATS = 4.788
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 29 TO 33 QUADRATS = 5.985
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 30 TO 34 QUADRATS = 102.942
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 31 TO 35 QUADRATS = 120.897
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 32 TO 36 QUADRATS = 32.319
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 33 TO 37 QUADRATS = 1.197
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 34 TO 38 QUADRATS = 83.79
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 35 TO 39 QUADRATS = 112.518
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 36 TO 40 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 37 TO 41 QUADRATS = 73.017
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 38 TO 42 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 39 TO 43 QUADRATS = 25.137
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 40 TO 44 QUADRATS = 31.122
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 41 TO 45 QUADRATS = 81.396
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 42 TO 46 QUADRATS = 2.394
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 43 TO 47 QUADRATS = 2.394
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 44 TO 48 QUADRATS = 13.167
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 45 TO 49 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 46 TO 50 QUADRATS = 3.591

TOTAL NO. DIFF.	MEAN	STD.DEV.	VARIANCE
46	62.6343	92.2821	8515.98

ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 1 TO 10 QUADRATS = 5.985
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 2 TO 11 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 3 TO 12 QUADRATS = 39.501
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 4 TO 13 QUADRATS = 288.477
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 5 TO 14 QUADRATS = 305.235
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 6 TO 15 QUADRATS = 154.413
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 7 TO 16 QUADRATS = 92.169
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 8 TO 17 QUADRATS = 39.501
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 9 TO 18 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 10 TO 19 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 11 TO 20 QUADRATS = 32.319
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 12 TO 21 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 13 TO 22 QUADRATS = 318.402
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 14 TO 23 QUADRATS = 287.28
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 15 TO 24 QUADRATS = 160.398
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 16 TO 25 QUADRATS = 89.775
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 17 TO 26 QUADRATS = 35.91
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 18 TO 27 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 19 TO 28 QUADRATS = 10.773
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 20 TO 29 QUADRATS = 22.743
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 21 TO 30 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 22 TO 31 QUADRATS = 19.152
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 23 TO 32 QUADRATS = 20.349
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 24 TO 33 QUADRATS = 15.561
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 25 TO 34 QUADRATS = 100.548
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 26 TO 35 QUADRATS = 134.064
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 27 TO 36 QUADRATS = 47.88
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 28 TO 37 QUADRATS = 5.985
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 29 TO 38 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 30 TO 39 QUADRATS = 25.137
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 31 TO 40 QUADRATS = 27.531
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 32 TO 41 QUADRATS = 74.214
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 33 TO 42 QUADRATS = 5.985
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 34 TO 43 QUADRATS = 102.942
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 35 TO 44 QUADRATS = 124.488
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 36 TO 45 QUADRATS = 39.501
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 37 TO 46 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 38 TO 47 QUADRATS = 16.758
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 39 TO 48 QUADRATS = 25.137
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 40 TO 49 QUADRATS = 43.092
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 41 TO 50 QUADRATS = 86.184

TOTAL NO. DIFF.	MEAN	STD.DEV.	VARIANCE
41	69.1924	88.4328	7820.36

ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 1 TO 20 QUADRATS = 26.334
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 2 TO 21 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 3 TO 22 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 4 TO 23 QUADRATS = 29.925
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 5 TO 24 QUADRATS = 17.955
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 6 TO 25 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 7 TO 26 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 8 TO 27 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 9 TO 28 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 10 TO 29 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 11 TO 30 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 12 TO 31 QUADRATS = 16.758
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 13 TO 32 QUADRATS = 338.751
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 14 TO 33 QUADRATS = 307.629
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 15 TO 34 QUADRATS = 57.456
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 16 TO 35 QUADRATS = 45.486
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 17 TO 36 QUADRATS = 8.379
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 18 TO 37 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 19 TO 38 QUADRATS = 19.152
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 20 TO 39 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 21 TO 40 QUADRATS = 44.289
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 22 TO 41 QUADRATS = 53.865
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 23 TO 42 QUADRATS = 26.334
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 24 TO 43 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 25 TO 44 QUADRATS = 10.773
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 26 TO 45 QUADRATS = 4.788
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 27 TO 46 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 28 TO 47 QUADRATS = 8.379
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 29 TO 48 QUADRATS = 9.576
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 30 TO 49 QUADRATS = 1.197
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 31 TO 50 QUADRATS = 13.167

TOTAL NO. DIFF.	MEAN	STD.DEV.	VARIANCE
31	35.5239	78.4788	6158.92

ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 1 TO 34 QUADRATS = 5.985
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 2 TO 35 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 3 TO 36 QUADRATS = 23.94
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 4 TO 37 QUADRATS = 50.274
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 5 TO 38 QUADRATS = 84.987
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 6 TO 39 QUADRATS = 131.67
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 7 TO 36 QUADRATS = 47.88
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 8 TO 37 QUADRATS = 16.756
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 9 TO 38 QUADRATS = 15.561
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 10 TO 39 QUADRATS = 25.137
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 11 TO 40 QUADRATS = 44.289
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 12 TO 41 QUADRATS = 89.775
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 13 TO 42 QUADRATS = 344.736
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 14 TO 43 QUADRATS = 323.19
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 15 TO 44 QUADRATS = 147.231
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 16 TO 45 QUADRATS = 83.79
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 17 TO 46 QUADRATS = 32.319
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 18 TO 47 QUADRATS = 4.786
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 19 TO 48 QUADRATS = 0
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 20 TO 49 QUADRATS = 31.122
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 21 TO 50 QUADRATS = 3.591

TOTAL NO. DIFF.	MEAN	STD.DEV.	VARIANCE
21	72.105	96.4562	9303.79

ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 1 TO 40 QUADRATS = 38.304
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 2 TO 41 QUADRATS = 80.199
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 3 TO 42 QUADRATS = 29.925
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 4 TO 43 QUADRATS = 65.835
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 5 TO 44 QUADRATS = 4.788
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 6 TO 45 QUADRATS = 2.394
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 7 TO 46 QUADRATS = 7.182
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 8 TO 47 QUADRATS = 2.394
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 9 TO 48 QUADRATS = 3.591
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 10 TO 49 QUADRATS = 1.197
ABSOLUTE VALUE IN ABUNDANCE DIFFERENCE FOR THE 11 TO 50 QUADRATS = 3.591

TOTAL NO. DIFF.	MEAN	STD.DEV.	VARIANCE
11	21.7636	28.3404	803.181

REFERENCES

REFERENCES

Abele, L.G. & Walters, K. 1979. Marine benthic diversity: a critique and alternative explanation. Journal of Biogeography, 6: 115-126.

Allan, G.G., Lewin, J. & Johnson, P.G. 1972. Marine polymers. IV. Diatom polysaccharides. Botanica Marina, 15: 102-108.

Allen, E.J. 1899. On the fauna and bottom-deposits near the thirty- fathom line from the Eddystone Grounds to Start Point. Journal of the Marine Biological Association of the United Kingdom, 5: 365- 542.

Allen, E.J. & Todd, R.A. 1900. The fauna of the Salcombe Estuary. Journal of the Marine Biological Association of the United Kingdom, 6: 151-217.

Allen, E.J. & Todd, R.A. 1902. The fauna of the Exe Estuary. Journal of the Marine Biological Association of the United Kingdom, 6: 295-335.

Allen, J.R.L. 1968. Current Ripples. Their relation to Patterns of Water and Sediment Motion. North-Holland Publishing Company, Amsterdam.

Allen, J.R.L. 1970. Physical Processes of Sedimentation. An Introduction. Allen and Unwin, London.

Allen, J.R.L. 1973. A classification of climbing - ripple cross-lamination. Journal of the Geological Society of London, 129: 537-541.

Allen, J.R.L. 1978. Polymodal dune assemblages: an interpretation in terms of dune creation - destruction in periodic flows. Sedimentary Geology, 20: 17-28.

Allen, J.R.L. 1985. Principles of Physical Sedimentology. George Allen & Unwin, London.

Allen, T.F.H. & Starr, T.B. 1982. Hierarchy. Perspectives for Ecological Complexity. The University of Chicago Press, Ltd. London.

Alongi, D.M. 1985. Microbes, meiofauna, and bacterial productivity on tubes constructed by the polychaete Capitella capitata. Marine Ecology Progress Series, 23: 207-208.

Anderson, J.G. & Meadows, P.S. 1969. Bacteria on intertidal sand grains. Hydrobiologia, 33: 33-46.

Anderson, J.G. & Meadows, P.S. 1978. Microenvironments in marine sediments. Proceedings of the Royal Society of Edinburgh, 76B: 1- 16.

Anderson, J.G., Boonruang, P. & Meadows, P.S. 1981. Interrelationships between chlorophylls, carbon, nitrogen and heterotrophic bacteria in an intertidal sediment transect. Marine Ecology Progress Series, 6: 277-283.

Anderson, J.M. & Ineson, P. 1982. A soil microcosm system and its application to measurements of respiration and nutrient leaching. Soil Biology Biochemistry, 14: 415-416.

Angel, M.V. 1991. Variations in time and space: is biogeography relevant to studies of long-time scale change? Journal of the Marine Biological Association of the United Kingdom., 71: 191- 206.

Ardakani, M.S., Rehbock, J.T. & McLaren, A.D. 1973. Oxidation of nitrite to nitrate in a soil column. Proceedings. Soil Science Society of America, 37: 53-56.

Atkinson, R.J.A. 1986. Mud-burrowing megafauna of the Clyde Sea Area. Proceedings of the Royal Society of Edinburgh, 90 B: 351-361.

Asher, A. & Spalding, D.F. (Eds.) 1982. List of Strains 1982. Culture Centre of Algae and Protozoa. Institute of Terrestrial Ecology, Cambridge.

BS 1377. 1975. Methods of Test for Soils for Civil Engineering Purposes. BSI, London.

Bailey, N.T.J. 1981. Statistical Methods in Biology. 2nd edn.. Hodder and Stoughton, London.

Baillie, P.W. 1987. Diatom size distributions and community stratification in estuarine intertidal sediments. Estuarine and Coastal Shelf Science, 25: 193-209.

Bainbridge, R. 1952. Underwater observations on swimming of marine zooplankton. Journal of the Marine Biological Association of the United Kingdom 31: 107-112.

Bainbridge, R. 1953. Studies on the interrelationships of zooplankton and phytoplankton. Journal of the Marine Biological Association of the United Kingdom, 32: 385-447

Baker, J.M. & Wolff, W.J. (Eds.). 1987. Biological Surveys of Estuaries and Coasts. EBSA Handbook. Cambridge University Press, Cambridge.

Baker, J.M., Hartley, J.P. & Dicks, B. 1987. Planning biological surveys. In: Biological Surveys of Estuaries and Coasts, (Eds.) Baker, J.M. & Wolff, W.J., pp. 1-26. Cambridge University Press, Cambridge.

Balch, W.M., Reid, P.C. & Surrey-Gent, S.C. 1983. Spatial and temporal variability of dinoflagellate cyst abundance in a tidal estuary. Canadian Journal of Fisheries & Aquatic Sciences, 40: 244-261.

Bambach, R.K. 1977. Species richness in marine benthic habitats through the Phanerozoic. Paleobiology, 3: 152-167.

Barnard, J.L. 1963. Relationship of benthic Amphipoda to invertebrate communities of inshore sublittoral sand of southern California. Pacific Naturalist, 3: 439-468.

Barrett, J.H. & Yonge, C.M. 1980. Collins Pocket Guide to the Sea Shore. Collins, London.

Barnett, P.R.O. 1968. Distribution and ecology of harpacticoid copepods of an intertidal mud-flat. Internationale Revue der gesamten Hydrobiologie, 53: 177-209.

Barnett, P.R.O. & Watson, J. 1986. Long-term changes in some benthic species in the Firth of Clyde, with particular reference to Tellina tenuis da Costa. Proceedings of the Royal Society of Edinburgh, 90B: 287-302.

Bartlett, D.H., Wright, M.E. & Silverman, M. 1988. Variable expression of extracellular polysaccharide in the marine bacterium Pseudomonas atlantica is controlled by genome rearrangement. Proceedings of the National Academy of Sciences, 85: 3923-3927.

Basford, D.J., Eleftheriou, A. & Raffaelli, D. 1990. The infauna and epifauna of the northern North Sea. Netherlands Journal of Sea Research, 25: 165-173.

Bathurst, R.G.C. 1967. Subtidal gelatinous mat, sand stabilizer and food, Great Bahama Bank. Journal of Geology, 75: 736-738.

Bebout, B.M., Paerl, H.W., Crocker, K.M. & Prufert, L.E. 1987. Diel interactions of oxygenic photosynthesis and N_2 fixation (acetylene reduction) in a marine microbial mat community. Applied & Environmental Microbiology, 53: 2353-2362.

Beckett, P.H.T. & Webster, R. 1971. Soil variability: A Review. Soils & Fertilizers, 34: 1-15.

Belderson, R.H., Kerryon, N.H., Stride, A.H. & Stubbs, A.R. 1972. Sonographs of the Sea Floor. A Picture Atlas. Elsiver, Amsterdam.

Bell, W.H. & Lang, J.M. 1974. Selective stimulation of marine bacteria by algal extracellular products. Limnology & Oceanography, 19: 833-839.

Beukema, J.J. 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. Netherlands Journal of Sea Research, 10: 236-261.

Beukema, J.J., Cadee, G.C. & Jansen, J.J.M. 1977. Variability of growth rate of Macoma balthica (L.) in the Wadden Sea in relation to availability of food. In: Biology of Benthic Organisms, (Eds.) Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 69-77. Pergamon Press, Oxford.

Billheimer, L.E. & Coull, B.C. 1988. Bioturbation and recolonization of meiobenthos in juvenile spot (Pisces) feeding pits. Estuarine Coastal and Shelf Science, 27: 335-340.

Bird, E.C.F. 1984. Coasts, 3rd edn. Blackwell, Oxford.

Blanchard, G.F. 1990. Overlapping microscale dispersion patterns of meiofauna and microphytobenthos. Marine Ecology Progress Series, 68: 101-111.

Blegvad, H. 1925. Continued studies on the quantity of fish food in the sea bottom. Report of the Danish Biological Station, 31: 27- 56.

Boney, A.D. 1989. Phytoplankton, 2nd edn. Edward Arnold, London.

Boothroyd, J.C. 1985. Tidal inlets and tidal deltas. In: Coastal Sedimentary Environments. 2nd edn. (Ed.) Davis, R.A. Jr., pp. 445-532. Springer-Verlag, New York.

Boynton, W.R. & Kemp, W.M. 1985. Nutrient regeneration and oxygen consumption by sediments along an estuarine salinity gradient. Marine Ecology Progress Series, 23: 45-55.

Brekhovskikh, V.F., Debolsky, V.K., Vishnevskaya, G.N. & Zolotareva, N.S. 1991. Erosion of cohesive bottom sediments: The influence of benthos. Journal of Hydraulic Research, 29: 149-160.

Bridge, J.S. 1981. Bed shear stress over subaqueous dunes, and the to upper-stage plane beds. Sedimentology, 28: 33-36.

Briggs, D. 1977. Sediments. Sources and Methods in Geography. Butterworths, London.

Bruce, J.R. 1928a. Physical factors on the sandy beach. Part I. Tidal, climatic, and edaphic. Journal of the Marine Biological Association of the United Kingdom, 15: 535-552.

Bruce, J.R. 1928b. Physical factors on the sandy beach. Part II. Chemical changes - carbon dioxide concentration and sulphides.Journal of the Marine Biological Association of the United Kingdom, 15: 553-565.

Buchanan, J.B. 1963. The bottom fauna communities and their sediment relationships off the coast of Northunmberland. Oikos, 14: 154- 175.

Buchanan, J.B. 1984. Sediment analysis. In: Methods for the study of Marine Benthos 2nd edn. IBP Handbook 16. (Eds.) Holme, N.A. & McIntyre, A.D. pp. 41-65. Blackwell Scientific Publications, Oxford.

Buchanan, J.B., Sheader, M. & Kingston, P.F. 1978. Sources of variability in the benthic macrofauna off the south Northumberland coast, 1971-6. Journal of the Marine Biological Association of the United Kingdom, 58: 191-209.

Buller, A.T. & McManus, J. 1975. Sediments of the Tay Estuary. I. Bottom sediments of the upper and upper middle reaches. Proceedings of the Royal Society of Edinburgh B, 75: 41-64.

Cadee, G. 1976. Sediment reworking by Arenicola marina in tidal flats in the Dutch Wadden Sea. Netherlands Journal of Sea Research, 10 : 440-460.

Cammen, L. 1982. Effect of particle size on organic content and microbial abundance within four marine sediments. Marine Ecology Progress Series, 9: 273-280.

Campbell, A.C. 1982. The Country Life Guide to the Seashore and Shallow Seas of Britain and Europe. The Hamyln Publishing Group Ltd. London. 321 pp.

Capper, P.L. & Cassie, W.F. 1976. The Mechanics of Engineering Soils, 6th S.I. edtn. E. & F.N. Spon Ltd., London.

Carey, A.E. & Oliver, F.W. 1918. Tidal Lands. A Study of Shore Problems. Blackie and Son, Glasgow.

Cassie, R.M. & Michael, A.D. 1968. Fauna and sediments of an intertidal mud flat: a Multivariate analysis. Journal of Experimental Marine Biology and Ecology, 2: 1-23.

Castenholz, R.W. 1963. An experimental study of the vertical distribution of littoral marine diatoms. Limnology & Oceanography, 8: 450-462.

Caston, G.F. 1981. Potential gain and loss of sand by some sand banks in the Southern Bight of the North Sea. Marine Geology, 41: 239- 250.

Caston, V.N.D. 1972. Linear sand banks in the Southern North Sea. Sedimentology, 18: 63-78.

Chapman, G. & Newell, G.E. 1949. The distribution of lugworms (Arenicola marina L.) over the flats at Whitstable. Journal of the Marine Biological Association of the United Kingdom, 28: 627-634.

Chester, R. 1990. Marine Geochemistry. Unwin Hyman, London.

Christensen, P.B. & Sorensen, J. 1986. Temporal variation of denitrification activity in plant-covered, littoral sediment from Lake Hampen, Denmark. Applied & Environmental Microbiology, 51: 1174-1179.

Chumley, J. 1918. The Fauna of the Clyde Sea Area. University Press, Glasgow.

Clark, R.B. 1986. Marine Pollution. Claredon Press, Oxford.

Clutter, R.I. 1969. The microdistribution and social behaviour of some pelagic mysid shrimps. Journal of Experimental Marine Biology and Ecology, 3: 125-155.

Coleman, J.M. 1969. Brahmaputra River: Channel processes and sedimentation. Sedimentary Geology, 3: 129-239.

Colijn, F. & Dijkema, K.S. 1981. Species composition of benthic diatoms and distribution of chlorophyll a on an intertidal flat in the Dutch Wadden Sea. Marine Ecology Progress Series, 4: 9-21.

Collinson, J.D. & Thompson, D.B. 1989. Sedimentary Structures. 2nd edn.. Unwin Hyman, London.

Connell, J.H. & Sousa, W.P. 1983. On the evidence needed to judge ecological stability or persistence. The American Naturalist, 121: 789-824.

Coull, B.C. 1970. Shallow water meiobenthos of the Bermuda platform. Oecologia (Berl.), 4: 325-357.

Coull, B.C. & Bell, S.S. 1979. Perspectives of marine meiofaunal ecology. In: Ecological Processes in Coastal and Marine Systems. (Ed.) Livingston, R.J., pp. 189-216. Plenum Press, New York.

Cox, D.J. & Bazin, M.L. 1980. Distribution of bacteria in a continuous-flow nitrification column. Soil Biology Biochemistry, 12: 241-246.

Creutzberg, F., Wapenaar, P., Duineveld, G. & Lopez, N. 1984. Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditons. Rapport et proces-verbaux des reunions Conseil permanent international pour l'exploration de la mer, 183: 101- 110.

Crozier, W.J. 1918. The amount of bottom material ingested by holothurians (Stichopus). Journal of Experimental Biology, 26: 379-389.

Cruickshank, R., Duguid, J.P., Marmion, B.P. & Swain, R.A.H. 1975. Medical Microbiology Vol. II, 12th (edn.). Churchill Livingston, London.

Cushing, D.H. & Tungate, D.S. 1963. Studies of a Calanus patch. I. The identification of a Calanus patch. Journal of the Marine Biological Association of the United Kingdom, 43: 327-337.

D'Olier, B. 1979. Side-scan sonar and reflection seismic profiling. In: Estuarine Hydrography and Sedimentation, (Ed.) Dyer, K.R., pp. 57-86. Cambridge University Press, Cambridge.

Dapples, E.C. 1942. The effect of macro-organisms upon near-shore marine sediments. Journal of Sedimentary Petrology, 12:118-126.

Davis, N. & van Blaricom, G.R. 1978. Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow water. Limnology and Oceanography, 23: 417-427.

Deans, E.A., Anderson, J.G. & Meadows, P.S. 1977. Responses of a benthic marine invertebrate to -irradiated sediment. Nature, 70: 595-596.

Decho, A.W. & Castenholz, R.W. 1986. Spatial patterns and feeding of meiobenthic harpacticoid copepods in relation to resident microbial flora. Hydrobiologia, 131: 87-96.

Deegan, C.E., Kirby, R., Rae, I. & Floyd, R. 1973. The superficial deposits of the Firth of Clyde and its sea lochs. Report of the Institute of Geological Sciences, 73(9) 42 pp.

DeFlaun, M.F. & Mayer, L.W. 1983. Relationships between bacteria and grain surfaces in intertidal sediments. Limnology & Oceanography, 28: 873-881.

Dillon, W.P. & Zimmerman, H.B. 1970. Erosion by biological activity in two England submarine canyons. Journal of Sedimentary Petrology, 40: 542-547.

Dobbs, F.C. & Guckert, J.B. 1988. Callinassa trilobata (Crustacea: Thalassinidae) influences abundance of meiofauna and biomass, composition and physiologic state of microbial communities within its burrow. Marine Ecology Progress Series, 45: 69-79.

Doemel, W.N. & Brock, T.D. 1977. Structure, growth, and decomposition of laminated algal-bacterial mats in alkaline hot springs. Applied & Environmental Microbiology, 34: 433-452.

Dorjes, J., Gadow, S., Reineck, H.-E., & Singh, I.B. 1969. Die rinnen der Jade (Sudliche Nordsee). Sedimente und makrobenthos. Senckenbergiana maritima, 50: 5-62.

Downing, J.A. & Rath, L.C. 1988. Spatial patchiness in the lacustrine sedimentary environment. Limnology and Oceanography, 33: 447-458.

Ducklow, H.W. 1984. Geographical ecology of marine bacteria: physical and biological variability at the mesoscale. In: Current Perspectives in Microbial Ecology (Eds.) Klug, M.J. & Reddy, C.A. pp. 22-31. American Society for Microbiology, Washington.

Duguid, J.P. & Wilkinson, J.F. 1953. The influence of cultural conditions on polysaccharide production by Aerobacter aerogenes. Journal of General Microbiology, 9: 174-189.

Dyer, K.R. (Ed.). 1979. Estuarine Hydrography and Sedimentation. Cambridge University Press, Cambridge.

Eagle, R.A. & Hardiman, P.A. 1977. Some observations on the relative abundance of species in a benthic community. In: Biology of Benthic Organisms, (Eds.) Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 197-208. Pergamon Press, Oxford.

Eckman, J.E. 1979. Small-scale patterns and processes in a soft- substratum, intertidal community. Journal of Marine Research, 37: 437-457.

Ehrlich, R. 1983. Editorial - size analysis wears no clothes, or have moments come and gone? Journal of Sedimentary Petrology, 53: 1.

Eleftheriou, A., Robertson, M.R., Murison, D.J. 1986. The benthic fauna of sandy bays, with particular reference to Irvine Bay. Proceedings of the Royal Society of Edinburgh, 90B: 317-327.

Ellwood, D.C., Keevil, C.W., Marsh, P.D., Brown, C.M. & Wardell, J.N. 1982. Surface-associated growth. Philosophical Transactions of the Royal Society of London, B, 297: 517-532.

Erwin, D.G. 1977. A diving survey of Strangford Lough: The benthic communities and their relation to substrate - A preliminary account. In: Biology of Benthic Organisms. Proceedings of the 11th Marine Biology Symposium, (Eds.) Keegan, B.F. & Ceidigh, P.O., pp. 215-224. Pergamon Press, Oxford.

Esselink, P. & Zwarts, L. 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of Nereis diversicolor. Marine Ecology Progress Series, 56: 243-254.

Evans, G. 1965. Intertidal flat sediments and their environments of deposition in the Wash. Quarterly Journal of the Geological Society of London, 121: 209-245.

Evans, R.A. 1977. The shallow-water soft bottom benthos in Lindaspollene, western Norway : II - estimates of biomass for some macrofauna species. Sarsia, 63 : 97-111.

Fager, E.W. 1968. A sand-botom epifaunal community of invertebrates in shallow water. Limnology and Oceanography, 13: 448-464.

Fager, E.W. 1972. Diversity: a sampling study. The American Naturalist, 106: 293-310.

Farke, H., Wilde, P.A.W. de., & Berghuis, E.M. 1979. Distribution of juvenile and adult Arenicola marina on a tidal mud flat and the importance of nearshore areas for recruitment. Netherlands Journal of Sea Research, 13: 354-361.

Fauvel, P. 1923. Fauna de France. 5 Polychetes Erranntes. Paul Lechevalier, Paris.

Fauvel, P. 1927. Faune de France. 16 Polychaetes Sedentaries. Paul Lechevalier, Paris.

Fenchel, T. 1970. Studies on the decomposition of organic detritus derived from the turtle grass Thalassia testudinum. Limnology and Oceanography, 15: 14-20.

Fenchel, T. 1972. Aspects of decomposer food chains in marine benthos. Verhandlungen der Deutschen zoologischen Gesellschaft Jahresversammlung, 65: 14-22.

Field, J.G. 1971. A numerical analysis of changes in the soft-bottom fauna along a transect across False Bay, South Africa. Journal of Experimental Marine Biology and Ecology, 7: 215-253.

Findlay, S.E.G. 1981. Small-scale spatial distribution of meiofauna on a mud- and sandflat. Estuarine, Coastal and Shelf Science, 12: 471-484.

Fisher, R.A. & Yates, F. 1963. Statistical Tables for Biological, Agricultural and Medical Research. 6th edn. Oliver and Boyd, London.

Folk, R.L. 1974. Petrology of Sedimentary Rock. Hemphill, Texas.

Ford, E. 1923. Animal communities of the level sea-bottom in the waters adjacent to Plymouth. Journal of the Marine Biological Association of the United Kingdom, 13: 164-224.

Frankel, L. 1977. Microorganism induced weathering of biotite and hornblende grains in estuarine sands. Journal of Sedimentary Petrology, 47: 849-854.

Frankel, L. & Mead, D.J. 1973. Mucilaginous matrix of some estuarine sands in Connecticut. Journal of Sedimentary Petrology, 43: 1090- 1095.

Frostick, L.E. & McCave, I.N. 1979. Seasonal shifts of sediment within an estuary mediated by algal growth. Estuarine and Coastal Marine Science, 9: 569-576.

Gage, J.D., Lightfoot, R.H., Pearson, M. & Tyler, P.A. 1980. An introduction to a sample time-series of abyssal benthos: methods and principal sources of variability. Oceanologica Acta, 3: 169- 176.

Gambi, M.C., Nowell, A.R.M. & Jumars, P.A. 1990. Flume observations on flow dynamics in Zostera marina (eelgrass) beds. Marine Ecology Progress Series, 61: 159-169.

Gardner, J.V., Kidd, R.B. 1983. Sedimentary processes on the Iberian continental margin viewed by long-range side-scan sonar. Part 1: Gulf of Cadiz. Oceanologica Acta, 6: 245-254.

Gerlach, S.A. 1978. Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. Oecologia, 33: 55-69.

Gibb, A. 1983. Glasgow: the making of a City. Croom Helm, London.

Giere, O. 1977. An ecophysiological approach to the micro-distribution of meiobenthic oligochaeta. I. Phallodrilus monospermathecus (Knollner) (Tubificidae) from a subtropical beach at Bermuda. In: Biology of Benthic Organisms, (Eds.) Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 285-296. Pergamon Press, Oxford.

Giere, O. & Pfannkuche, O. 1982. Biology and ecology of marine oligochaeta. A review. Oceanography and Marine Biology. An Annual Review, 23: 399-489.

Gingsburg, R.N. & Lowenstam, H.A. 1958. The influence of marine bottom communities on the depositional environment of sediments. Journal of Geology, 66: 310-318.

Girling, A.E. 1984. Interactions between marine benthic macroinvertebrates and their sedimentary environment. Ph.D. Thesis, Glasgow University.

Goldring, R. & Seilacher, A. 1971. Limulid undertracks and their sedimentological implications. Neues Jahrbuch fur Palaeontologie Abhanlung, 137: 422-442.

Gooday, G.W. 1988. The potential of the microbial cell and its interaction with other cells. In: Micr-organisms in Action: Concepts and Applications in Microbial Ecology. 2nd edn. (Eds.) Lynch, J.M. & Hobbie, J.E. pp. 7-32. Blackwell Scientific Publications, Oxford.

Gooday, A.J. & Turley, C.M. 1990. Responses by benthic organisms to inputs of organic material to the ocean floor: a review. Philosophical Transactions of the Royal Society of London, A331: 119-138.

Gordon, D.C. 1966. The effects of the deposit feeding polychaete, Pectinaria gouldii on the intertidal sediments of Barnstable Harbor. Limnology and Oceanography, 11: 327-332.

Grassle, F. 1967. Influence of environmental variation on species diversity in benthic communities of the continental shelf and slope. Unpublished Ph.D. dissertation, Duke University, Durham, N.C.

Gray, J.S. 1974. Animal-sediment relationships. Oceanography and Marine Biology, Annual Reviews, 12: 223-261.

Gray, J.S., Valderhaug, V. & Ugland, K.I. 1985. The stability of a benthic community of soft sediment. In: Proceedings of the 19th European Marine Biology Symposium, (Ed.) Gibbs, P.E., pp. 245- 253. Cambridge University Press, Cambridge.

Green, J. 1968. The Biology of Estuarine Animals. Sidgwick & Jackson, London. 401 pp.

Green, R.H. & Hobson, K.D. 1970. Spatial and temporal structure in a temperate intertidal community, with special emphasis on Gemma gemma (Pelecypoda: Mollusca). Ecology, 51: 999-1011.

Gregory, S. 1968. Statistical Methods and the Geographer. 2nd edn. Longmans, Green & Co. London.

Grieve, J. 1863. Notes on some marine invertebrata of the Firth of Clyde. Proceedings of the Natural History Society of Glasgow, 1: 57-68.

Grieve, J. & Robertson, D. 1869. On the marine Zoology and Botany of Loch Ryan, Bay of Luce, and Portpatrick, from observations made during a recent excursion. Proceedings of the Natural History Society of Glasgow, 1: 21-36.

Groffman, P.M. & Tiedje, J.M. 1989. Denitrification in North temperate forest soils: spatial and temporal patterns at the landscape and seasonal scales. Soil Biology Biochemistry, 21: 613-620.

Hansbo, S. 1957. A new approach to the determination of the shear strength of clay by the fall-cone test. Royal Swedish Geotechnical Institute Proceedings, 14: 1-49.

Hansen, D.V. & Rattray, M. 1966. New dimensions in estuary classification. Limnology & Oceanography, 11: 319-326.

Hargrave, B.T. 1970. The utilization of benthic microflora by Hyallela azteca (Amphipoda). Journal of Animal Ecology, 39: 427-437.

Hargrave, B.T. & Nielsen, L.K. 1977. Accumulation of sedimentary organic matter at the base of steep bottom gradients. In: Interactions between sediments and freshwater. (Ed.) Golterman, H.L., pp. 168-173. Junk, The Hague.

Hariri, M.S.B. 1990. Ecological and experimental studies on sedimentary infauna with particular reference to sediment stability, the physical and chemical properties of sediments and bioturbation. Ph.D. Thesis, Glasgow University.

Harris, R.P. 1972. Seasonal changes in population density and vertical distribution of harpacticoid copepods on an intertidal sand beach. Journal of the Marine Biological Association of the United Kingdom, 52: 493-505.

Harrison, P.G. & Harrison, B. 1980. Interactions of bacteria, microalgae, and copepods in a detritus microcosm: through a flask darkly. In: Marine Benthic Dynamics, (Eds.) Tenore, K.R. & Coull, B.C. pp. 373-385. Univeristy of South Carolina Press, South Carolina.

Harrison, W. & Wass, M.L. 1965. Frequencies of infaunal invertebrates related to water content of Chesapeake Bay sediments. Southeastern Geographer,6: 177-187.

Hartog, C. den. 1970. The seagrasses of the world. Verh K... Ned... Akad Wet Afd Natuurkd Recks, 159: 1-275.

Haury, L.R., McGowan, J.A. & Wiebe, P.H. 1978. Patterns and processes in the time-space scales of plankton distributions. In: Spatial Pattern in Plankton Communities, (Ed.) Steele, J.H., pp. 277-327, Plenum Press, New York.

Heip, C., Vincx, M. & Vranken, G. 1985. The ecology of marine nematodes. Oceanography and Marine Biology. An Annual Review, 23: 399-489.

Henderson, J.R. 1886. Th Echinodermata of the Firth of Clyde. Proceedings of the Royal Physical Society of Edinburgh, 9: 328- 337.

Hennig, H.F-K.O., Fricke, A.H. & Martin, C.T. 1983. The effect of meiofauna and bacteria on nutrient cycles in sandy beaches. In: Sandy Beaches as Ecosystems, (Ed.) McLachlan, A. & Erasmus, T. pp. 235-247. Junk, The Hague.

Herdman, W.A. 1880. On the invertebrate fauna of Lamlash Bay. Proceedings of the Royal Physical Society of Edinburgh, 5: 193- 219.

Hessler, R.R. & Sanders, H.L. 1967. Faunal diversity in the deep-sea. Deep-sea Research, 14: 65-78.

Heydemann, B. 1979. Responses of animals to spatial and temporal environmental heterogeneity within salt marshes. In: Ecological Processes in Coastal Environments, (Eds.) Jefferies, R.L. & Davy, A.J., pp. 145-163. Blackwell Scientific Publications, Oxford.

Hjulstrom, F. 1939. Transportation of detritus by moving water. In: Recent Marine Sediments, (Ed.) Trask, P.D., pp. 5-31. T. Murphy & Co., London.

Hogue, E.W. & Miller, C.B. 1981. Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. Journal of Experimental Marine Biology and Ecology, 53: 181-191.

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.

Holligan, P.M. 1978. Patchiness in subsurface phytoplankton populations on the northwest European continental shelf. In: Spatial Pattern in Plankton Communities, (Ed.) Steele, J.H. pp. 221-238. Plenum Press, New York.

Holm, R.F. 1978. The community structure of a tropical marine Lagoon. Estuarine and Coastal Marine Science, 7: 329-345.

Holme, N.A. 1949. The fauna of sand and mud banks near the mouth of the Exe Estuary. Journal of the Marine Biological Association of United Kingdom, 28 : 189-238.

Holme, N.A. 1953. The biomass of the bottom fauna in the English channel off Plymouth. Journal of the Marine Biological Association of the United Kingdom, 32: 1-49.

Holme, N.A. 1961. The bottom fauna of the English Channel. Journal of the Marine Biological Association of the United Kingdom, 41: 397- 461.

Holme, N.A. 1966. The bottom fauna of the English Channel, Part II. Journal of the Marine Biological Association of the United Kingdom, 46: 401-493.

Holme, N.A. & McIntyre, A.D. (Eds.). 1984. Methods for the Study of Marine Benthos. IBP Handbook 16. Blackwell Scientific, Oxford.

Houbolt, J.J.H.C. 1968. Recent sediments in the Southern Bight of the North Sea. Geologie en Mijnbouw, 47: 245-273.

Hovland, M. & Gudmestad, O.T. 1984. Potential influence of gas-induced erosion on seabed installations. In: Seabed Mechanics, (Ed.) Denness, B., pp. 255-263. Graham & Trotman, London.

Howard, J.D. & Frey, R.W. 1975. Estuaries of the Georgia Coast, U.S.A.: Sedimentology and Biology. II. Regional animal-sediment characteristics of Georgia estuaries. Senckenbergiana marit, 7: 33-103.

Howes, B.L., Howarth, R.W., Teal, J.M. & Valiela, I. 1981. Oxidation- reduction potentials in a salt marsh: spatial patterns and interactions with primary production. Limnology & Oceanography, 26: 350-360.

Hsieh, K.M., Lion, L.W. & Shuler, M.L. 1985. Bioreactor for the study of defined interactions of toxic metals and biofilms. Applied and Environmental Microbiology, 50: 1155-1161.

Hsieh, K.M., Lion, L.W. & Shuler, M.L. 1990. Production of extracellular and cell-associated biopolymers by Pseudomonas atlantica. Biotechnology Letters, 12: 449-454.

Huang, R. & Boney, A.D. 1984. Growth interactions between littoral diatoms and juvenile marine algae. Journal of Experimental Marine Biology and Ecology, 81: 21-45

Hughes, R.N. 1986. A Functional Biology of Marine Gastropods. Croom Helm, London.

Hughes, R.N. & Thomas, M.L.H. 1971. The classification and ordination of shallow-water benthic samples from Prince Edward Island, Canada. Journal of Experimental Marine Biology and Ecology, 7: 1- 39.

Hull, S.C. 1987. Macroalgal mats and species abundance: a field experiment. Estuarine, Coastal and Shelf Science, 25: 519-532.

Hummon, W.D. & Hummon, M.R. 1977. Meiobenthic subcommunity structure: Spatial vs. temporal variability. In: Biology of Benthic Organisms, (Eds.)Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 339-347. Pergamon Press, Oxford.

Huntsman, S.A. & Sloneker, J.H. 1971. An exocellular polysaccharide from the diatom Gomphonema olivaceum. Journal of Phycology, 7: 261-264.

Huxley, A. 1943. The Art of Seeing. Chatto & Windus, London.

Ishikawa, K. 1989. Relationship between bottom characteristics and benthic organisms in the shallow water of Oppa Bay, Miyagi. Marine Biology, 102: 265-273.

Jardine, W.G. 1986. The geological and geomorphological setting of the Estuary and Firth of Clyde. In: The Environment of the Estuary and the Firth of Clyde. (Eds.) Allen, J.A., Barnett, P.R.O., Boyd, J.M., Kirkwood, R.C., MacKay, D.W. & Smyth, J.C. Proceedings of the Royal Society of Edinburgh B, 90: 25-41.

Jenness, M.I. & Duineveld, G.C.A. 1985. Effects of tidal currents on chlorophyll a content of sandy sediments in the southern North Sea. Marine Ecology Progress Series, 21: 283-287.

Jensen, K.T. 1985. The presence of the bivalve Cerastoderma edule affects migration, survival and reproduction of the amphipod, Corophium volutator. Marine Ecology Progress Series, 25: 269-277.

Jensen, K.T. & Kristensen, L.D. 1990. A field experiment on competition between Corophium volutator (Pallas) and Corophium arenarium (Crawford) (Crustacea: Amphipoda): effects on survival, reproduction and recruitment. Journal of Experimental Marine Biology and Ecology, 137: 1-24.

Johnson, R.G. 1970. Variations in diversity within benthic marine communities. American Naturalist, 104: 285-300.

Johnson, T.W. 1976. The phycomycetes: morphology and taxonomy. In: Recent Advances in Aquatic Mycology, (Ed.) Jones, E.B.G., pp. 193-211. Elek Science, London.

Jones, N.S. 1950. Marine bottom communities. Biological Reviews, 25: 283-313.

Jones, N.W., Kain, J.M. & Stride, A.H. 1965. The movement of sand waves on Warts Bank, Isle of Man. Marine Geology, 3: 329-336.

Jorgensen, B.B. 1977. Bacterial sulfate reduction within reduced microniches of oxidized marine sediments. Marine Biology, 47: 7- 17.

Jorgensen, B.B. & Revsbech, N.P. 1985. Diffusive boundary layers and the oxygen uptake of sediments and detritus. Limnology & Oceanography, 30: 111-112.

Jorgensen, B.B., Revsbech, N.P., Blackburn, T.H. & Cohen, Y. 1979. Diurnal cycle of oxygen and sulphide microgradients and microbial photosynthesis in a cyanobacterial mat sediment. Applied Environmental Microbiology, 38: 46-58.

Jorgensen, B.B. , Revsbech, N.P. & Cohen, Y. 1983. Photosynthesis and structure of benthic microbial mats: Microelectrode and SEM studies of four cyanobacterial communities. Limnology & Oceanography, 28: 1075-1093.

Josefson, A.B. 1981. Persistence and structure of two deep macrobenthic communities in the Skagerrak (western coast of Sweden). Journal of Experimental Marine Biology and Ecology, 50: 63-97.

Jumars, P.A. & Eckman, J.E. 1983. Spatial structure within deep-sea benthic communities. In: Deep-Sea Biology, The Sea, Vol. 8 (Ed.) Rowe, G.T., pp 399-451. John Wiley & Sons, New York.

Kamamura, A. 1974. Food and feeding ecology in the Southern Sei whale. Science Reports of the Whales Research Institute, Tokyo, 26: 25- 144.

Kidd, R.B. & Roberts, D.G. 1982. Long-range sidescan sonar studies of large-scale sedimentary features in the North Atlantic. Actes Colloque International CNR, Bordeoux, Sept. 1981. Bulletin Institut Geologie Bassin Aquitaine Bordeaux, 31: 11-29.

King, G.M. 1990. Effects of added manganic and ferric oxides on sulfate reduction and sulfide oxidation in intertidal sediments. FEMS Microbiology Ecology, 73: 131-138.

Klein, G. deVries. 1970. Depositional and dispersal dynamics of intertidal sand bars. Journal of Sedimentary Petrology, 40: 1095- 1127.

Klein, G. deVries. 1985. Intertidal flats and intertidal sand bodies. In: Coastal Sedimentary Environments 2nd edn. (Ed.) Davies, R.A., pp. 187-224. Springer-Verlag, New York.

Krebs, C.J. 1972. Ecology. The Experimental Analysis of Distribution and Abundance. Harper & Row, New York.

Krumbein, W.C. & Pettijohn, F.J. 1938. Manual of Sedimentary Petrography. Appleton.-Century Crofts, New York.

Krumbein, W.E. 1971. Sediment microbiology and grain-size distribution, as related to tidal movement during the first mission of the West German underwater laboratory "Helgoland". Marine Biology, 10: 101-112.

Kumar, S.R. 1980. Thraustochytrium benthicola sp. nov. A new marine fungus from the North Sea. Transactions of the British Mycological Society, 74: 607-614.

Kunitzer, A. 1990. A comparison of the Amphiura filiformis - associations North-east of the Dogger Bank and of the German Bight. Netherlands Journal of Sea Research, 25: 199-208.

Kushner, D.J. (Ed.). 1978. Microbial Life in Extreme Environments. Academic Press, London.

Lambe, T.W. & Whitman, R.V. (Eds.). 1979. Soil Mechanics, S.I. Version. John Wiley & Sons, New York.

Landry, E.F., Vaughn, J.M., Penello, W.F. 1980. Polio-virus retention in 75-cm soil cores after sewage and rainwater application. Applied & Environmental Microbiology, 40: 1032-1038.

Langhorne, D.N. 1973. A sandwave field in the outer Thames Estuary, Great Britain. Marine Geology, 14: 129-143.

Langhorne, D.N. 1982. A study of the dynamics of a marine sand wave. Sedimentology, 29: 571-594.

Lee, I. K., White, W. & Ingles, O.G. 1983. Geotechnical Engineering. Pitman, Boston.

Levinton, J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. American Naturalist, 106: 472-486.

Levinton, J.S. 1982. Marine Ecology. Prentice-Hall Inc., New Jersey.

Lewin, J.C. 1955. The capsule of the diatom Navicula pelliculosa. Journal of General Microbiology, 13: 162-169.

Lewin, R.A. 1958. The mucilage tubes of Amphipleura rutilans. Limnology & Oceanography, 3: 111-113.

Lewin, J.C. & Lewin, R.A. & Phillpot, D.E. 1958. Observations on Phaeodactylum tricornutum. Journal of General Microbiology, 18: 418-426.

Lewis, D.B. 1968. Some aspects of the ecology of Fabricia sabella (Ehr.) (Annelida, Polychaeta). Journal of the Linnean Society (Zool), 47 : 515-526.

Lie, U. 1968. A quantitative study of benthic infauna in Puget Sound, Washington, U.S.A. in 1963-64. Fiskeridirektoratets Skrifter. Serie Havundersokelser, 14: 229-556.

Lin, C.K. 1977. Continuous flow culture of benthic diatoms and its application to bioassay. Journal of Phycology, 13: 267-271.

Lincoln, R.J. 1979. British Marine Amphipoda: Gammaridea. British Museum (Natural History). London. 68 pp.

Lindholm, R. 1987. A Practical Approach to Sedimentology. Allen & Unwin, London.

Longbottom, M.R. 1970. The distribution of Arenicola marina (L) with particular reference to the effects of particle size and organic matter of the sediments. Journal of Experimental Marine Biology and Ecology, 5 : 138-158.

Lloyd, M. & Ghelardi, R.J. 1964. A table for calculating the 'equitability'component of species diversity. Journal of Animal Ecology, 33: 217-225.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive ability. American Naturalist, 112: 23-39.

Lyle, M. 1983. The brown-green color transition in marine sediments: a marker of the Fe (II) - Fe(III) redox boundary. Limnology & Oceanography, 28: 1026-1033.

McCall, P.L. 1978. Spatial-temporal distributions of Long Island Sound infauna: The role of bottom disturbance in a nearshore marine habitat. In: Estuarine Interactions, (Ed.) Wiley, M., pp. 191- 219. Academic Press, New York.

McCormack, D.E. & Wilding, L.P. 1969. Variation of soil properties within mapping units of soils with contrasting substrata in Northwestern Ohio. Soil Science Society of America Proceedings, 33: 587-593.

McIntyre, A.D. 1969. Ecology of marine meiobenthos. Biological Reviews of the Cambridge Philosophical Society, 44: 245-290.

McIntyre, A.D. & Eleftheriou, A. 1968. The bottom fauna of a flatfish nursery ground. Journal of the Marine Biological Association of the United Kingdom, 48: 113-142.

McIntyre, A.D. & Murison, D.J. 1973. The meiofauna of a flatfish nursery ground. Journal of the Marine Biological Association of the United Kingdom, 53: 93-118.

McLusky, D.S. 1971. Ecology of Estuaries. Heinemann Educational Books, London.

McMillan, N.F. 1968. British Shells. Frederick Warne & Co. Ltd. London. 196 pp.

McRoy, C.P. & Helfferich, C. (eds.) 1977. Seagrass Ecosystems: a Scientific Perspective. M. Dekker, New York.

Macer, C.T. 1966. Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. Ministry of Agriculture, Fisheries and Food, Fishery Investigations, Series 2, 24: 1-55, HMSO, London.

Mader, D.L. 1963. Soil variability - A serious problem in soil-site stiudies in the Northeast. Soil Science of America Proceedings, 27: 707-709.

Magurran, A.E. 1988. Ecological Diversity and its Measurement. Croom Helm, London.

Margalef, R. 1968. Perspectives in Ecological Theory. The University of Chicago Press, Chicago.

Margalef, R. 1978. Diversity. In: Phytoplankton Manual, (Ed.) Sournia, A., pp. 251-327. Unesco, Paris.

Marsh, G.P. 1874. The Earth as Modified by Human Action, 2nd edn. Sampson Low, Marston Low, and Searle, London.

Matthews, J.B.L. 1964. On the biology of some bottom-living copepods (Aetideidae and Phaennidae) from Western Norway. Sarsia, 16: 1- 46.

Maul, G.A., Norris, D.R & Johnson, W.F. 1974. Satellite photography of eddies in the Gulf Loop current. Geophysical Research Letters, 1: 256-258

Maurer, D., Leathem, W., Kinner, P. & Tinsman, J. 1979. Seasonal fluctuations in coastal benthic invertebrate assemblages. Estuarine and Coastal Marine Science, 8: 181-193.

May, R.M. (Ed.). 1981. Theoretical Ecology. Blackwell, Oxford.

Meadows, P.S. & Anderson, J.G. 1966. Micro-organisms attached to marine and fresh-water sand grains: Nature, 212: 1059-1060.

Meadows, P.S. & Anderson, J.G. 1968. Micro-organisms attached to marine sand grains. Journal of the Marine Biological Association of the Untied Kingdom, 48: 161-175.

Meadows, P.S. & Campbell, J.I. 1988. Marine Science. 2nd edn. Blackie, Glasgow.

Meadows, P.S. & Tait, J. 1985. Bioturbation, geotechnics and microbiology at the sediment-water interface in deep-sea sediments. In: Proceedings of the 19th European Marine Biology Symposium, (Ed.) Gibbs, P.E. pp. 191-199. Cambridge University Press, Cambridge.

Meadows, P.S. & Tufail, A. 1986. Bioturbation, microbial activity and sediment properties in estuarine ecosystem. Proceedings of the Royal Society of Edinburgh, 90B: 129-142.

Miron, G.Y. & Desrosiers, G.L. 1990. Distributions and population structures of two intertidal estuarine polychaetes in the lower St Lawrence Estuary, with special reference to environmental factors. Marine Biology, 105: 297-306.

Mooney, N.T. 1974. An analysis of the vane shear test at varying rates of shear. In: Deep-Sea Sediments, Inderbitzen, A.L. (Ed.). pp. 151-167. Plenum Press, New York.

Moore, H.B. 1931. The muds of the Clyde Sea area: III. Chemical and physical conditions; rate and nature of sedimentation; and fauna. Journal of the Marine Biological Association of the United Kingdom, 17: 325-358.

Moore, D.R. 1963. Turtle grass in the deep sea. Science, 139: 1234- 1235.

Murphy, P.W. (Ed.). 1962. Progress in Soil Zoology Papers from a colloquia on research methods organised by the soil Zoological Committee of the International Societies of Soil Science. Butterworths, London.

Muus, B.J. 1963. Some Danish Hydrobiidae with the description of a new species, Hydrobia neglecta. Proceedings of the Malacological Society of London, 35 : 131-138.

Muus, B.J. 1967. The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. Meddelelser fra Danmarks Fiskeri- og Havundersogelser. Kobenhaven, 5: 1-316.

Myers, A.C. 1977. Sediment processing in a marine subtidal sandy bottom community. I. Physical aspects. Journal of Marine Research, 35: 609-632.

Naylor, E. 1962. Seasonal changes in population of Carcinus maenas (L) in the littoral zone. Journal of Animal Ecology, 31: 601-609.

Neumann, A.C., Gebelein, C.D. & Scoffin, T.P. 1970. The composition, structure and erodability of subtidal mats, Abaco, Bahamas. Journal of Sedimentary Petrology, 40: 274-297.

Newell, R. 1965. The role of detritus in the nutrition of two deposit feeders, the prosobranch Hydrobia ulvae and the bivalve Macoma balthica. Proceedings of the Zoological Society of London, 144: 25-45.

Newell, R.C. 1970. Biology of Intertidal Animals. Logos Press Ltd. London. 555 pp.

Newton, R.S., Cunningham, R.C. & Schubert, C.E. 1980. Mud volcanoes and pockmarks: seafloor engineering hazards or geological curiosities. 12th Annual O.T.C. Houston, Texas, pp. 425-435.

Nicholls, D.J., Tubbs, C.R. & Haynes, F.N. 1981. The effect of green algal mats on intertidal macro-benthic communities and their predators. Kieler Meeresforsch, (Sonderh), 5: 511-520.

Nicholson, J.M., Stolz, J.F., & Pierson, B.K. 1987. Structure of a microbial mat at Great Sippewissett Marsh, Cape Cod, Massachusetts. FEMS Microbiology Ecology, 45: 343-364.

Nickels, J.S., Bobbie, R.J., Martz, R.F., Smith, G.A., White, D.C. & Richards, N.L. 1981. Effect of silicate grain shape, structure, and location on the biomass and community structure of colonizing marine microbiota. Applied Environmental Microbiology, 41: 1262- 1268.

Nicol, J.A.C. 1967. The Biology of Marine Animals. 2nd edn. Pitman, London.

Norkrans, B. 1980. Surface microlayers in aquatic environments. Advances in Microbial Ecology, 4: 51-85.

Norton, T.A. 1986. The ecology of macroalgae in the Firth of Clyde. Proceedings of the Royal Society of Edinburgh, 90B: 255-269.

Nygaard, K., Borsheim, K.Y., Thingstad, T.F. 1988. Grazing rates on bacteria by marine heterotrophic microflagellates compared to uptake rates of bacterial-sized monodisperse fluorescent latex beads. Marine Ecology Progress Series, 44: 159-165.

O'Gower, A.K. & Wacasey, J.W. 1967. Animal communities associated with Thalassia, Diplanthera and sand beds in Biscayne Bay. I. Analysis of communities in relation to water movements. Bulletin of Marine Science, 17: 175-210.

Odum, E.P. 1971. Fundamentals of Ecology, 3rd edn. Saunders, London.

Odum, W.E., Smith, T.J. & Dolan, R. 1987. Suppression of natural disturbance: Long-term ecological change on the outer banks of North Carolina. In: Landscape Heterogeneity and Disturbance, (Ed.) Turner, M.G., pp. 123-135. Springer-Verlag, New York.

Olafsson, E.B. & Persson, L-E. 1986. The interaction between Nereis diversicolor O.F. Muller and Corophium volutator Pallas as a structuring force in a shallow brackish sediment. Journal of Experimental Marine Biology and Ecology, 103: 103-117.

Outridge, P.M. 1987. Possible causes of high species diversity in tropical Australian freshwater macrobenthic communities. Hydrobiologia, 150: 95-107.

Orth, R.J. 1973. Benthic infauna of eelgrass, Zostera marina, beds. Chesapeake Science 14: 258-269.

Orth, R.J. 1977. The importance of sediment stability in seagrass communities. In: Ecology of Marine Benthos, (Ed.) Coull, B.C. pp. 281-306. University of South Carolina Press, Columbia.

Paerl, H.W. 1975. Microbial attachment to particles in marine and fresh water ecosystems. Microbial Ecology, 2: 73-83.

Paerl, H.W. 1985. Microzone formation: Its role in the enhancement of aquatic N_2 fixation. Limnology & Oceanography, 30: 1246-1252.

Paine, R.T. 1966. Food web complexity and species diversity. The American Naturalist, 100: 65-75.

Paine, R.T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia, 15: 93-120.

Palmer, M.A. & Gust, G. 1985. Dispersal of meiofauna in a turbulent tidal creek. Journal of Marine Research, 43: 179-210.

Parker, R.H. 1975. The Study of Benthic Communities. A Model and a Review. Elsevier, Amsterdam.

Paterson, D.M. 1989. Short-term cahnges in the erodibility of intertidal cohesive sediments related to migratory behaviour of epipelic diatoms. Limnology & Oceanography, 34: 223-234.

Patrick, R. 1977. Ecology of freshwater diatoms - diatom communities. In: The Biology of Diatoms. (Ed.) Werner, D. pp. 284-332. Blackwell Scientific Publications, Oxford.

Pearse, A.S., Humm, H.J. & Wharton, G.W. 1942. Ecology of sand beaches at Beaufort, N.C. Ecological Monographs, 12: 136-190.

Pearson, T.H., Ansell, A.D. & Robb, L. 1986. The benthos of the deeper sediments of the Firth of Clyde, with particular reference to organic enrichment. Proceedings of the Royal Society of Edinburgh, 90B: 329-350.

Pearson, T.H. & Eleftheriou, A. 1981. The benthic ecology of Sullom Voe. Proceedings of the Royal Society of Edinburgh, 80B: 241-269.

Pearson, T.H. & Stanley, S.O. 1979. Comparative measurement of the redox potential of marine sediments as a rapid means of assessing the effect of organic pollution. Marine Biology, 53: 371-379.

Pennings, S.C. 1991. Spatial and temporal variation in recruitment of Aplysia californica Cooper: patterns mechanisms and consequences. Journal of Experimental Marine Biology & Ecology, 146: 253-274..

Perkins, E.J. 1974. The Biology of Estuaries and Coastal Waters. Academic Press, London.

Perkins, E.J. & Abbott, O.J. 1972. Nutrient enrichment and sand-flat fauna. Marine Pollution Bulletin, 3: 70-72.

Petersen, C.G.J. 1913. Valuation of the sea. II. Animal communities of the sea bottom and their importance for marine zoogeography. Report of the Danish Biological Station to the Board of Agriculture. No. 21.

Petersen, C.G.J. 1915. On the animal communities of the sea bottom in Skagerak, the Christiania Fjord, and the Danish Waters. Report of the Danish Biological Station to the Board of Agriculture, No. 23.

Petersen, C.G.J. 1918. The sea-bottom and its production of fish food. Report of the Danish Biological Station to the Board of Agriculture, No. 25.

Petersen, C.G.J. & Jensen, P.B. 1911. Valuation of the sea. I. Report of the Danish Biological Station to the Board of Agriculture, No. 20.

Peterson, B.H. 1979. Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Ecological Processes in Coastal and Marine Systems, (Ed.) Livingston, R.J., pp. 233-264. Plenum Press, New York.

Pfarl, C., Ditzelmuller, G., Loidl, M. & Streichsbier, F. 1990. Microbial degradation of xenobiotic compounds in soil columns. FEMS Microbioloy Ecology, 73: 255-262.

Pielou, E.C. 1977. Mathematical Ecology. Wiley-Interscience, New York.

Pierce, J.W. & Graus, R.R. 1981. Use and misuses of the phi-scale: discussion. Journal of Sedimentary Petrology, 51: 1348-1350

Pierson, B., Oesterle, A., & Murphy, G.L. 1987. Pigments, light penetration, and photosynthetic activity in the multilayered microbial mats of Great Sippewissett Salt Marsh, Massachusetts. FEMS Microbiology Ecology, 45: 365-376.

Pirrie, M.E. & Moore, H.B. 1932. A quantitative study of the fauna of the sandy beach at Port Erin. Journal of the Marine Biological Association of the United Kingdom, 18: 279-296.

Plante, R., Plante-Cunny, M-R. & Reys, J. 1986. Photosynthetic pigments of sandy sediments on the north Mediterrnean coast: their spatial distribution and its effect on sampling strategies. Marine Ecology Progress Series, 34: 133-141.

Pringle, C.M. & Bowers, J.A. 1984. An in situ substratum fertilization technique: diatom colonization on nutrient- enriched, sand substrata. Canadian Journal of Fisheries Aquatic Science, 41: 1247-1251.

Radach, G. & Mann, K.H. 1981. Statistical design of field programmes. In: Mathematical Models in Biological Oceanography. Monographs on Oceanographic Methodology. (Eds.) Platt, T., Mann, K.H. & Ulanowicz, R.E., pp. 124-126. The Unesco Press, Paris.

Rades-Rohkohl, E., Franzle, O. & Hirsch, P. 1978. Behaviour, activities, and effects of bacteria on synthetic quartz monocrystal surfaces. Microbial Ecology, 4: 189-205.

Ramm, A.E. & Bella, D.A. 1974. Sulphide production in anaerobic microcosms. Limnology & Oceanography, 19: 110-118.

Rasmussen, E. 1973. Systematics and Ecology of the Isefjord Marine fauna (Denmark) with a survey of the eelgrass (Zostera) vegetation and its communities. Ophelia, 11: 1-507.

Raymont, J.E.G. 1949. Further observations on changes in the bottom fauna of a fertilized sea loch. Journal of the Marine Biological Association of the United Kingdom, 28: 9-19.

Reineck, H.-E. 1963. Sedimentgefuge im Bereich der sudlichen Nordsee. Abhandlungen der Senkenbergischen Naturforschen den Gesellschaft, 505: 1-138.

Reineck, H.-E. & Singh, I.B. 1980. Depositional Sedimentary Environments, 2nd edn.. Springer-Verlag, Berlin.

Reise, K. 1977. Predation pressure and community structure of an intertidal soft-bottom fauna. In: Biology of Benthic Organisms, (Eds.) Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 513- 519. Pergamon Press, Oxford.

Reise, K. 1978. Experiments on epibenthic predation in the Wadden Sea. Helgol Wiss Meeresunters, 31: 55-101.

Reise, K. 1981. High abundance of small zoobenthos around biogenic structures in tidal sediments of the Wadden Sea. Helgol Wiss Meeresunters, 34: 413-425.

Reise, K. 1983. Sewage, green algal mats anchored by lugworms, and the effects on Turbellaria and small polychaeta. Helgolander Meeresuntersuchungen, 36: 151-162.

Reise, K. 1985. Tidal Flat Ecology. An Experimental Approach to Species Interactions. Springer-Verlag, Berlin.

Reise, K. 1987. Spatial niches and long-term performance in meiobanthic plathelminthes of an intertidal lugworm flat. Marine Ecology Progress Series, 38: 1-11.

Remillard, M.M., Gruendling, G.K. & Bogucki, D.J. 1987. Disturbance by beaver (Castor canadensis Kuhl) and increased landscape heterogeneity. In: Landscape Heterogeneity and Disturbance (Ed.) Turner, M.G. pp. 103-122. Springer-Verlag, New York.

Renouf, L.P.W. 1920. A contribution to our knowledge of the fauna of the Clyde Sea Area. The Glasgow Naturalist, 8: 113-119.

Rescher, N. 1984. The Limits of Science. University of California Press, Berkeley.

Revsbeck, N.P. & Jorgensen, B.B. 1981. Primary production of microalgae in sediments measured by oxygen microprofile, $H^{14}CO_3$ fixation, and oxygen exchange methods. Limnology & Oceanography, 26: 717-730.

Revsbeck, N.P., Jorgensen, B.B. & Blackburn, T.H. 1983. Microelectrode studies of the photosynthesis and O_2, H_2S, and pH profiles of a microbial mat. Limnology & Oceanography, 28: 1062-1074.

Revsbech, N.P. & Ward, D.M. 1984. Microprofiles of dissolved substances and photosynthesis in microbial mats measured with microelectrodes. In: Microbial Mats: Stromatolites, (Eds.) Cohen, Y., Castenholz, R.W. & Halvorson, H.O. pp. 171-188. Alan R. Liss, New York.

Rhoads, D.C. 1967. Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. Journal of Geology, 75: 461-476.

Rhoads, D.C. 1974. Organism-sediment relations on the muddy sea floor. Oceanography and Marine Biology Annual Review, 12: 263-300.

Rhoads, D.C. & Boyer, L.F. 1982. The effects of marine benthos on physical properties of sediments: a successional perspective. In: Animal Sediment Relations, (Eds.) McCall, P.L. & Tevesz, M.J.S., pp. 3-52. Plenum Press, New York.

Rhoads, D.C. & Stanley, D.J. 1965. Biogenic graded bedding. Journal of Sedimentary Petrology, 35: 956-963.

Rhoads, D.C. & Young, D.K. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. II. Reworking by Molpadia oolitica (Holothuroidea). Marine Biology, 11: 255-261.

Riddell, J.F. 1979. Clyde Navigation: A History of the Development and deepening of the River Clyde. John Donald Publishers Ltd., Edinburgh.

Riemann, F. & Schrage, M. 1983. On a mass occurrence of a Thraustochytriod Protist (Fungi or Rhizopodan Protozoa) in an Antarctic anaerobic marine sediment. Veroffentlichungen des Instituts fur Meeresforschung in Bremerhaven, 19: 191-202.

Ritz, D.A., Lewis, M.E. & Shen, Ma. 1989. Response to organic enrichment of infaunal macrobenthic communities under salmonid seacages. Marine Biology, 103: 211-214.

Riznyk, R.Z. 1973. Interstitial diatoms from two tidal flats in Yaquina Estuary, Oregon, U.S.A. Botanica Marina, 16: 113-138.

Robertson, D. 1892a. Notes of thirteen Cumacea from the Firth of Clyde. Proceedings and Transactions of the Natural History Society of Glasgow, 3: 47-49.

Robertson, D. 1892b. A second contribution towards a catalogue of the amphipoda and isopoda of the Firth of Clyde and West of Scotland. Proceedings and Transactions of the Natural History Society of Glasgow, 3: 199-223.

Round, F.E. 1965. The epipsammon; a relatively unknown freshwater algal association. British Phycological Bulletin, 2: 456-462.

Round, F.E. 1968. The phytoplankton of the Gulf of California. Part II. The distribution of phytoplanktonic diatoms in cores. Journal of Experimental Marine Biology and Ecology, 2: 64-86.

Russell, R.D. & Taylor, R.E. 1937. Roundness and shape of Mississippi River sands. Journal of Geology, 45: 225-267.

Ryan, T.A. Jr., Joiner, B.L. & Ryan, B.F. 1976. Minitab Student Handbook. Duxbury Press, Massachusetts.

Saenger, P., Moverley, J. & Stephenson, W. 1988. Seasonal and longer term patterns in the macrobenthos versus benthic stability in a subtropical estuary. Proceedings. Ecological Society of Australia, 15: 229-237.

Saleh, I.M.S. 1990. Ecological and behavioural studies on harpacticoid copepoda in the intertidal zone at Ardmore Point, Clyde Estuary, with some observations on the anatomy of Tachidius discipes. Ph.D. Thesis, Glasgow University.

Salsman, G.C., Tolbert, W.H. & Villars, R.G. 1966. Sand ridge migration in St Andrews Bay, Florida. Marine Geology, 4: 11-19.

Sameoto, D.D. 1969a. Comparative ecology, life histories and behaviour of intertidal sand-burrowing amphipods (Crustacea: Haustoriidae) at Cape Cod. Journal of Fisheries Research Board of Canada, 26: 361-388.

Sameoto, D.D. 1969b. Some aspects of the ecology and life cycle of three species of subtidal sand-burrowing amphipods (Crustacea: Haustoriidae). Journal of Fisheries Research Board of Canada, 26: 1321-1345.

Sanders, H.L. 1968. Marine benthic diversity: a comparative study. American Naturalist, 102: 243-282.

Sanders, H.L. 1978. Florida oil spill impact on the Buzzards Bay benthic fauna: West Falmouth. Journal of Fisheries Research Board of Canada, 35: 717-730.

Sanders, H.L. & Hessler, R.R. 1969. Ecology of the deep-sea benthos. Science, 163: 1419-1424.

Santos, S.L. & Simon, J.L. 1974. Distribution and abundance of polychaetous annelids in a south Florida estuary. Bulletin of Marine Science, 24: 669-689.

Savidge, W.B. & Taghon, G.L. 1988. Passive and active components of colonization following two types of disturbance on an intertidal sandflat. Journal of Experimental Marine Biology and Ecology, 115: 137-155.

Schafer, W. 1972. Ecology and Palaeoecology of Marine Environments. Oliver and Boyd, Edinburgh.

Schaffner, L.C. 1990. Small-scale organism distributions and patterns of species diversity: evidence for positive interactions in an estuarine benthic community. Marine Ecology Progress Series, 61: 107-117.

Scheffe, H. 1959. The Analysis of Variance. Wiley, New York.

Scheltema, R.S. 1977. Dispersal of marine invertebrate organisms. In: Concepts and Methods of Biostratigraphy, (Eds.) Kauffman, E.G. & Hazel, J.E., pp. 73-108. Dowden, Hutchinson & Ross, Stroudsburg.

Schimel, J.P., Jackson, L.E. & Firestone, M.K. 1989. Spatial and temporal effects on plant-microbial competition for inorgainc nitrogen in a California annual grassland. Soil Biology Biochemistry, 21: 1059-1066.

Schimmelmann, A., Lange, C.B. & Berger, W.H. 1990. Climatically controlled marker layers in Santa Barbara Basin sediments and fine-scale core-to-core correlation. Limnology & Oceanography, 35: 165-173.

Schubel, J.R. 1984. Estuarine circulation and sedimentation: An overview. In: Marine Geology and Oceanography of Arabian Sea and Coastal Pakistan, Haq, B.U. & Milliman, J.D. (Eds.), pp. 113-136. Van Nostrand Reinhold Company Ltd., New York.

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.

Scott, T. 1900. Notes on some Crustacea from Fairlie and Hunterston. Transactions of the Natural History Society of Glasgow (Including the proceedings of the Society) (N.S.), 5: 346-355.

Seed, R. & Boaden, P.J.S. 1977. Epifaunal ecology of intertidal algae. In: Biology of Benthic Organisms, (Eds.) Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 541-548. Pergamon Press, Oxford.

Segal, E. 1970. Light. Animals. Invertebrates. In: Marine Ecology, Vol. 1, Environmental Factors, Part 1, (Ed.) Kinne, O. pp. 159- 211. Wiley-Interscience, London.

Seitzinger, S.P. & Nixon, S.W. 1985. Eutrophication and the rate of denitrification and N_2O production in coastal marine sediments. Limnology & Oceanography, 30: 1332-1339.

Selley, R.C. 1982. An Introduction to Sedimentology, 2nd edn. Academic Press, London. 417 pp.

Serota, S. & Jangle, A. 1972. A direct reading pocket shear vane. Civil Engineering, A.S.C.E., 42: 73-74.

Sieburth, J. McN. 1975. Microbial Seascapes. University Park Press, Baltimore, Madison.

Siever, R. 1988. Sand. Scientific American Library, USA.

Simpson, E.H. 1949. Measurement of diversity. Nature, 163: 688.

Skoolmun, P. & Gerlach, S.A. 1971. Jahreszeitliche Fluktuationen der Nematodenfauna im Gezeitenbereich des Weser-Astuars (Deutsche Bucht). Veroffentlichungen des Instituts fur Meeresforschung in Bremerhaven, 13: 119-138.

Sleath, J.F.A. 1984. Sea Bed Mechanics. John Wiley, New York.

Smith, J.E. 1932. The shell gravel deposits, and the infauna of the Eddystone grounds. Journal of the Marine Biological Association of the United Kingdom, 18: 243-278.

Smith, M.J. 1981. Soil Mechanics, 4th edn. George Godwin, London.

Smith, R.L. & Klug, M.J. 1987. Flowthrough reacter flasks for study of microbial metabolism in sediments. Applied & Environmental Microbiology, 53: 371-374.

Smith, C.R. & Brumsickle, S.J. 1989. The effects of patch size and substrate isolation on colonization modes and rates in an intertidal sediment. Limnology & Oceanography, 34: 1263-1277.

Snedecor, G.W. & Cochran, W.G. 1967. Statistical Methods, 6th edn. The Iowa State University Press, Iowa.

Sokal, R.R. & Rohlf, F.J. 1981. Biometry. W.H. Freeman & Co. San Francisco.

Sorbe, J-C. 1989. Structural evolution of two suprabenthic soft-bottom communities of the South Gascogne continental shelf. Scientia Marina, 53: 335-342.

Spark, R. 1935. On the importance of quantitative investigation of the bottom fauna in marine biology. Journal du Conseil, 10: 3-19.

Sparrow, F.K. 1936. Biological observations on the marine fungi of Woods Hole waters. Biological Bulletin. Marine Biological Laboratory, Woods Hole, Mass., 70: 236-263.

Stal, L.J., Van Gemerden, H. & Krumbein, W.E. 1985. Structure and development of a benthic marine microbial mat. FEMS Microbial Ecology, 31: 111-125.

Stanley, D.J. & Taylor, P.T. 1977. Sediment transport down a seamount flank by a combined current and gravity process. Marine Geology, 23: 77-88.

Stanley, D.J. & Wear, M. 1978. The "mud-line": An erosion - deposition boundary on the upper continental slope. Marine Geology, 28: M19- M29.

Stanley, S.O., Leftley, J.W., Lightfoot, A., Robertson, N., Stanley, I.M. & Vance, I. 1981. The loch Eil project: Sediment chemistry, sedimentation, and the chemistry of the overlying water in Loch Eil. Journal of Experimental Marine Biology and Ecology, 55: 299- 313.

Stephen, A.C. 1929. Studies on the Scottish marine fauna: The fauna of the sandy and muddy areas of the tidal zone. Transactions of the Royal Society of Edinburgh, 56: 291-306.

Stephen, A.C. 1933. Studies on the Scottish marine fauna: The natural faunistic divisions of the North Sea as shown by the quantitative distribution of the molluscs. Transactions of the Royal Society of Edinburgh, 57: 601-616.

Stephenson, J. 1911a. The Nemertines of Millport and its vicinity. Transactions of the Royal Society of Edinburgh, 48: 1-29.

Stephenson, J. 1911b. On some littoral Oligochaeta of the Clyde. Transactions of the Royal Society of Edinburgh, 48: 31-65.

Steven, G.A. 1930. Bottom fauna and the food of fishes. Journal of the Marine Biological Association of the United Kingdom, 16: 677-706.

Stobie, R., Curtis, D.J., Gray, H. & Smyth, J.C. 1976. Intertidal invertebrates of the Clyde Estuary mudflats: 1974-1975 Survey. A Report to the Natural Conservancy Council

Stride, A.H. 1970. Shape and size trends for sand waves in a depositional zone of the North Sea. Geological Magazine, 107: 469-477.

Suchanek, T.H. 1983. Control of seagrass communities and sediment distribution by Callianassa (Crustacea, Thalassinidea) bioturbation. Journal of Marine Research, 41: 281-298.

Sundborg, A. 1956. The River Klaralven. A study of fluvial processes. Geografiska Annaler, 38: 127-316.

Sundby, B. 1974. Distribution and transport of suspended particulate matter in the Gulf of St. Lawrence. Canadian Journal of Earth Science, 11: 1517-1533.

Swan, D., Clayne, J.J. & Luternauer, J.L. 1979. Grain-size statistics II. Evaluation of grouped moment measures. Journal of Sediment Petrology, 49: 487-500.

Swift, D.J.P., Duane, D.B., & Pilkey, O.H. (Eds.). 1972. Shelf Sediment Transport. Hutchinson & Ross, Dowden.

Swift, D.J.P., Parker, G., Lanfredi, W., Perillo, G. & Figge, K. 1978. Shoreface - connected sand ridges on American and European Shelves: A Comparison. Estuarine and Coastal Marine Science, 7: 257-273.

Taylor, J.D. & Lewis, M.S. 1970. The flora, fauna and sediments of the marine grass beds of Mahe, Seychelles. Journal of Natural History, 4: 199-200.

Terwindt, J.H.J. 1967. Mud transport in the Dutch Delta area and along the adjacent coastline. Netherlands Journal of Sea Research, 3: 505-531.

Thayer, G.W., Adams, S.M. & LaCroix, M.W. 1975. Structural and functional aspects of a recently established Zostera marina community. In: Estuarine Research, Vol. 1 Chemistry, Biology and the Estuarine System. (Ed.) Cronin, L.E., pp. 518-540. Academic Press, New York.

Thode-Andersen, S. & Jorgensen, B.B. 1989. Sulfate reduction and the formation of ^{35}S-labeled FeS, FeS_2, and S in coastal marine sediments. Limnology & Oceanography, 34: 793-806.

Thorson, G. 1957. Bottom communities (sublittoral or shallow shelf). In: Treatise on Marine Ecology and Paleoecology, Ecolgy, 1. (Ed.) Hedgpeth, J.W. pp. 461-534. The Geological Society of America Memoir, 67.

Thornson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Netherlands Journal of Sea Research, 3:267-293.

Tufail, A. 1985. Microbial aggregates on sand grains in enrichment media. Botanica Marina, 28: 209-211.

Tufail, A. 1987. Microbial communities colonising nutrient-enriched marine sediment. Hydrobiologia, 148: 245-255.

Tufail, A., Meadows, P.S., & McLaughlin, P. 1989. Meso- and micro- scale heterogeneity in benthic community structure and the sedimentary environment on an intertidal muddy-sand beach. Proceedings of the 22nd European Marine Biology Symposium, Barcelona. Scientia Marina, 53: 319-327.

Tyler, P. 1977. Sub-littoral community structure of Oxwich Bay, South Wales in relation to sedimentological, physical oceanographic and biological parameters. In: Biology of Benthic Organisms, (Eds.) Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 559-566. Pergamon Press, Oxford.

Tyler, P.A. 1988. Seasonality in the deep sea. In: Oceanography and Marine Biology, Annual Review, 26: 227-258.

Tyler, P.A. & Banner, F.T. 1977. The effect of coastal hydrodynamics on the echinoderm distribution in the sublittoral of Oxwich Bay, Bristol Channel. Estuarine and Coastal Marine Science, 5: 293- 308.

Tyler, P.A. & Shackley, S.E. 1980. The benthic ecology of linear sandbanks: a modified Spisula sub-community. In: Industrialised Embayments and their Environmental Problems: a case study of Swansea Bay, (Eds.) Collins, M.B., Banner, F.T., Tyler, P.A., Wakefield, S.J., & James, A.E., pp. 539-551. Pergamon Press, Oxford.

Uydess, I.L. & Vishniac, W.V. 1976. Electron microscopy of Antarctic soil bacteria. In:Extreme Environments, (Ed.) Heinrich, M.R. pp. 29-56. Academic Press, New York.

Underwood, A.J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology Annual Review, 19: 513-605.

Valiela, I. 1984. Marine Ecological Processes. Springer-Verlag, New York.

Vanderborght, J.P. & Billen, G. 1975. Vertical distribution of nitrate concentrations in interstitial water of marine sediment with nitrification and denitrification. Limnology & Oceanography, 20: 953-961.

Visher, G.S. 1969. Grain size distributions and depositional processes. Journal of Sedimentary Petrology, 39: 1074-1106.

Visher, G.S. & Howard, J.D. 1974. Dynamic relationship between hydraulics and sedimentation in the Altahama Estuary. Journal of Sedimentary Petrology, 44: 502-512.

Vosjan, J.H. & Olanczuk-Neyman, K.M. 1977. Vertical distribution of mineralization processes in a tidal sediment. Netherlands Journal of Sea Research, 11: 14-23.

Wade, B.A. 1972. A description of a highly diverse soft bottom community in Kingston Harbour, Jamaica. Marine Biology, 13: 57- 69.

Walker-Arnott, G.A. 1869. Notes on Cocconeis, Nitzschia, and some of the allied genera of Diatomaceae. Proceedings of the Natural History Society of Glasgow, 1: 211-223.

Walsh, J.J., Whitledge, T.E., Kelley, J.C., Huntsman, S.A. & Pillsbury, R.D. 1977. Further transition stages of the Baja California upwelling ecosystem. Limnology and Oceanography, 22: 264-280.

Ward, A.R. 1975. Studies on the sub-littoral free-living nematodes of Liverpool Bay. II. Influence of sediment composition on the distribution of marine nematodes. Marine Biology, 30: 217-225.

Warme, J.E. 1971. Paleoecological aspects of a modern coastal lagoon. University of California Publications in Geological Sciences, 87: 1-131.

Warwick, R.M. 1977. The structure and seasonal fluctuations of phytal marine nematode associations on the Isles of Scilly. In: Biology of Benthic Organisms, (Eds.) Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 577-585. Pergamon Press, Oxford.

Warwick, R.M. & Davies, J.R. 1977. The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to the substrate. Estuarine and Coastal Marine Science, 5: 267-288.

Warwick, R.M. & Uncles, R.J. 1980. Distribution of benthic macrofauna associations in the Bristol Channel in relation to tidal stress. Marine Ecology Progress Series, 3: 97-103.

Warwick, R.M. & Ruswahyuni. 1987. Comparative study of the structure of some tropical and temperate marine soft-bottom macrobenthic communities. Marine Biology, 95: 641-649.

Warwick, R.M. & Clark, K.R. 1991. A comparison of some methods for analysing changes in benthic community structure. Journal of the Marine Biological Association of the United Kingdom, 71: 225-244.

Watkin, E.E. 1942. The macrofauna of the intertidal sand of Kames Bay, Millport, Buteshire. Transactions of the Royal Society of Edinburgh, 60 : 543-561.

Watling, L. 1988. Small-scale features of marine sediments and their importance to the study of deposit-feeding. Marine Ecology Progress Series, 47: 135-144.

Watling, L., Kinner, P.C. & Maurer, D. 1978. The use of species abundance estimates in marine benthic studies. Journal of Experimental Marine Biology and Ecology, 35: 109-118.

Weise, W. & Rheinheimer, G. 1978. Scanning electron microscopy and epifluorescence investigation of bacterial colonization of marine sand sediments. Microbial Ecology, 4: 175-188.

Wethey, D.S. 1984. Spatial pattern in barnacle settlement: day to day changes during the settlement season. Journal of the Marine Biological Association of the United Kingdom, 64: 687-698.

Wiebe, P.H. 1970. Small-scale spatial distribution in oceanic zooplankton. Limnology and Oceanography, 15: 205-217.

Wieser, W. 1959. The effect of grain size on the distribution of small invertebrates inhabiting the benthos of Puget Sound. Limnology & Oceanography, 4: 181-194.

Wildish, D.J. 1985. Geographical distribution of macrofauna on sublittoral sediments of continental shelves: a modified trophic ratio concept. In: Proceedings of the 19th European Marine Biology Symposium, (Ed.) Gibbs, P.E., pp. 335-345. Cambridge University Press, Cambridge.

Wilson, W.H. 1981. Sediment-mediated interactions in a densely populated infaunal assemblage: the effects of the polychaete Abarenicola pacifica. Journal of Marine Research, 39: 735-748.

Wilson, J.B. 1982. Shelly faunas associated with temperate offshore tidal deposits. In: Offshore Tidal Sands, (Ed.) Stride, A.H. pp. 126-213. Chapman & Hall, London.

Wilson, J. & Noonan, M.J. 1984. Microbial activity in model aquifer systems. In: Groundwater Pollution Microbiology (Eds.) Bittan, G. & Gerbu C.P., pp. 117-133. John-Wiley & Sons, London.

Wilson, T.R.S., Thomson, J., Colley, S., Hydes, D.J. & Higgs, N.C. 1985. Early organic diagenesis: The significance of progressive subsurface oxidation fronts in pelagic sediments. Geochimica et Cosmochimica Acta, 49: 811-822.

Wimpenny, J.W.T. 1982. Responses of microorganisms to physical and chemical gradients. Philosophical Transactions of the Royal Society London, B, 297: 497-515.

Wimpenny, J.W.T, Coombs, J.P. & Lovitt, R.W. 1984. Growth and interactions of microorganisms in spatially heterogeneous ecosystems. In: Current Perspectivess in Microbial Ecology (Eds.) Klug, M.J. & Reddy, C.A. pp. 291-299. American Society for Microbiology, Washington, D.C.

Winer, B.J. 1971. Statistical Principles in Experimental Design, 2nd edn. McGraw-Hill, Tokyo.

Winogradsky, S. 1949. Microbiologie du Sol. Problems et Methodes. Masson et Cie Editurs, Paris.

Witte, F. & Wilde, P.A.W.J. de. 1979. On the ecological relation between Nereis diversicolor and juvenile Arenicola marina. Netherlands Journal of Sea Research, 13: 394-405.

Wood, E.J.F., Odum, W.E. & Zieman, J.C. 1969. Influence of seagrasses on the productivity of coastal lagoons. In: Lagunas Costeras Un Simposio Memoria Simposio Internacional sobre Lagunas Costeras, Castarares, A.A. & Phleger, F.B. (Eds.), pp. 495-502, UNAM- UNESCO, Mexico, Universidad Nacional Autonoma de Mexico.

Woodin, S.A. 1974. Polychaete abundance patterns in a marine soft sediment environment. The importance of biological interactions. Ecological Monographs, 44: 171-187.

Woodin, S.A. 1976. Adult larval interactions in dense faunal assemblages: patterns of abundance. Journal of Marine Research, 34: 25-41.

Wormald, A.P. & Stirling, H.P. 1979. A preliminary investigation of nutrient enrichment in experimental sand columns and its effect on tropical intertidal bacteria and meiofauna. Estuarine and Coastal Marine Science, 8: 441-453.

Wurzin, R.S. 1977. Predator-prey interactions between the crab Pilumnus hirtellus (Leach) and the brittle star Ophiothrix quinquemaculata on a mutual sponge substrate. In: Biology of Benthic Organisms, (Eds.) Keegan, B.F., Ceidigh, P.O. & Boaden, P.J.S., pp. 613-620. Pergamon Press, Oxford.

Yoder, J.A., McClain, C.R., Blanton, J.O. & Oey, L-Y. 1987. Spatial scales in CZCS - chlorophyll imagery of the southeastern U.S. continental shelf. Limnology & Oceanography, 32: 929-941.

Zieman, J.C. 1972. Origin of circular beds of Thalassia (Spermatophyta: Hydrocharitaceae) in South Biscayne Bay, Florida, and their relationship to mangrove hammocks. Bulletin of Marine Science, 22: 559-574.

ZoBell, C.E. 1946a. Marine microbiology: a monograph on hydrobacteriology. Waltham, Massachusetts.

ZoBell, C.E. 1946b. Studies on redox potential of marine sediments. Bulletin of the American Association of Petroleum Geologists, 30: 477-513.

ZoBell, C.E. & Anderson, D.Q. 1936. Vertical distribution of bacteria in marine sediments. Bulletin of the American Association of Petroleum Geologists, 20: 258-269.

ZoBell, C.E. & Feltham, C.B. 1938. Bacteria as food for certain marine invertebrates. Journal of Marine Research, 4: 312-327.

Zwarts, L. & Esselink, P. 1989. Versatility of male curlews Numerius arquata preying upon Nereis diversicolor: deploying contrasting capture modes dependent on prey availability. Marine Ecology Progress Series, 56: 255-269.