THE UNIVERSITY OF HULL

The role of macroalgal morphology and community structure on the accumulation of sediment and the subsequent effects on the dynamics of marine intertidal communities

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by

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Abstract

This study examines the influence of intertidal macroalgae on sediment accumulation, and the effect of sediment cover on intertidal community structure.

Three shores on the North Yorkshire coast, England, were used to investigate differences in the quantity of sediment trapped by ten morphologically different algal species, and the relationship between morphology and the quantity of sediment trapped. The quantity of sediment accumulated in quadrats of four different macroalgal communities (canopy, turf, canopy/turf and bare rock) was also examined. Differences in sediment cover and community structure were investigated on the intertidal rocky shore at Holbeck, North Yorkshire. The distribution and position of both were described using transects across three sites, whilst relationships were examined using 54 fixed quadrats in the mid shore.

Across three different shores the mass of dried sediment g^{-1} macroalgal dry mass was found to differ between macroalgal species. All measured aspects of macroalgal morphology correlated with the quantity of sediment trapped. Macroalgae with different morphologies trapped different grain size compositions but no differences were found in the quantity of sediment accumulated by turf, canopy, bare rock or unmanipulated algal communities. At three different sites at Holbeck, the site with the greatest sediment cover had lower macroalgal species diversity, richness and total abundance, patellid and littorinid abundance. Although differences were found in sediment cover between sites in the mid shore, no differences were found in community structure. Sediment cover had negative correlations with macroalgal richness and diversity in algal quadrats, but positive correlations with macroalgal abundance and diversity in bare rock quadrats

Within individual macroalgae morphology was found to affect the quantity of sediment trapped, however at quadrat level macroalgal morphology had no effect. At both the level of the quadrat and the whole shore sediment cover influenced community structure, whilst within the mid shore alone sediment cover did not affect community structure. This work suggests that relationships/interactions between sedimentation and intertidal community structure are scale dependent.

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Author's Declaration

The candidate confirms that the work submitted is her own work and that appropriate credit has been given where reference has been made to the work of others.

Chapter 1

General introduction

Factors affecting intertidal rocky shores

Intertidal rocky shores are dynamic environments subject to both terrestrial and marine influences. Inhabiting organisms are regarded as being fundamentally marine (Little & Kitching, 1996), but in temperate environments are exposed twice a day to terrestrial conditions. This difference in their environments results in them being subject to a variety of biotic and abiotic factors, not all of which are beneficial. Factors that detrimentally affect intertidal organisms as a result of the shore are generally regarded as either a stress or a disturbance. A stress on an organism causes a physiological response to a disturbance that is detrimental to productivity (Rykiel, 1985), in the case of macroalgae this would result in a restriction of photosynthetic production (Grime, 1979). Disturbance results in a decrease in biomass of the organism (Rykiel, 1985).

Stress and disturbance take a variety of forms, including occurring naturally during periods of emersion. The differing abilities of organisms to withstand emersion have resulted in well-studied patterns of zonation for both flora and fauna on the shore (Stephenson & Stephenson, 1949). Initially patterns of zonation were related solely to tidal height (reviewed in Underwood, 1998), and the affects of abiotic factors on organisms (Lubchenco, 1980; Little & Kitching, 1996). Whilst emersed there is a greater potential for both desiccation and freezing due to the wider range of temperatures to which they are exposed compared to when submersed (Dring, 1982). Upper limits of distribution are dependant upon tolerance to temperature and desiccation. In fucoids, drying out has been found to reduce their ability to photosynthesise (Schonbeck & Norton, 1978; Dring & Brown, 1982). *Fucus gardneri* Silva has also been found to become more brittle and subject to breakage when dry (Haring et al, 2002). Exposure to higher temperature also increases the mortality of fauna including trochids (Newell, 1979). However the effects of desiccation on fauna are also dependant on the morphology of the individual as bigger and steeper patellid shells retain more water and have a smaller relative circumference resulting in reduced water loss (Wallace, 1972). Emersion also alters the salinity of rockpools, either increasing salinity with water evaporation, or decreasing salinity with freshwater input. Therefore the most tolerant species are found in rockpools higher up the shore that are subject to the most extreme variations in salinity (Little & Kitching, 1996).

It was initially suggested that the lower distribution limits of macroalgae were purely determined by light availability for photosynthetic, as different wavelengths, which are utilised by different combinations of photosynthesis pigments occurring in the three macroalgal groups, have different penetration depths in water (Dring, 1982). Zonation in macroalgae was found to occur even in areas of no tidal change as a result of a gradient in light penetration (Stephenson & Stephenson, 1949). However lower limits of distribution are also affected by biotic factors including competition and predation, which also includes grazing on macroalgae. Where the dominant competitor was removed this can result in increased abundance of the outcompeted species. This occurs between macroalgal species (*e.g. Fucus spiralis* Linnaeus outcompetes *Pelvetia canaliculata* (Linnaeus) Decaisne & Thuret [Schonbeck & Norton, 1980] and *Laminaria hyperborea* (Gunnerus) Foslie outcompetes *Laminaria digitata* (Hudson) Lamouroux [Kain, 1979]), between faunal species (*e.g. Semibalanus balanoides* Linnaeus [as *Balanus balanoides*] overgrowing and undercutting *Chthamalus stellatus* [Connell, 1961b]), and also between macroalgae and fauna (*e.g. Cellana tramoserica* Holtenand *Siphonaria diemenensis* Quoy & Gaimard [as *Siphonaria denticulata*] occurs in areas of lower macroalgal cover [Underwood & Jernakoff, 1981]). The removal of predators from areas where they naturally occur reduces mortality of fauna (*e.g. Pisaster ochraceus* Brandt for *Mytilus californicus* Conr [Paine, 1974], and *Nucella lapillus* Linnaeus for barnacles [Connell, 1961a]), whilst the removal of grazers (*Strongylocentrotus* spp [Paine & Vardis, 1969], limpets [Cubit, 1984] and *Littorina littorea* Linnaeus [Lubchenco, 1982]) increases algal abundance, settlement and growth.

However, organisms inhabiting intertidal rocky shores are not just subject to the factors of temperature, desiccation, salinity, competition and predation that influence zonation patterns. Across sheltered shores, especially those with dense fucoid canopies, there are distinct patterns of zonation. However, as wave exposure increases, a mosaic pattern occurs (Wells, *et al.*, 2007), and the distribution of organism in zonation patterns becomes less clearly defined *(*Araújo, *et al.*, 2005). On temperate shores brown algal cover decreases on exposed shores, and is replaced by a community of *Mastocarpus stellatus* (Stackhouse) Guiry, red algal turfs, small mussels and limpets (Little & Kitching, 1996). In addition to normal wave exposure for a given shore, organisms are subject to sporadic storms. For example, this completely altered community structure in both New South Wales, Australia, where the canopy cover of *Hormosira banksii* (Turner) Decaisne was extensively damaged (Underwood, 1998; Underwood, 1999), and California where a first storm removed kelp canopy, allowing urchins to dominate, whilst a second storm removed the urchins allowing regrowth of the kelp canopy (Ebeling, *et al.*, 1985).

Anthropogenic factors also affect intertidal rocky shores, and are wide ranging in both type and extent. They include trampling (*e.g.* Keough & Quinn, 1998; Brown & Taylor, 1999), dredging (Gilkinson, *et al*, 2003), boating activity (Eriksson, *et al.*, 2004) and harvesting (Spencer, *et al.*, 1998). The effects are as wide ranging as the anthropogenic factors themselves, affecting different organisms on the shore in different ways and to different extents. The impacts of a variety of anthropogenic factors have been thoroughly reviewed in Crowe, *et al.*, 2000 and Thompson, *et al.*, 2002.

The nature of intertidal sediment

Sediment also influences rocky shore communities either by settlement on the shore or whilst particles are suspended in the water column. Sediment is defined as 'material derived from pre-existing rock, from biogenic sources, or precipitated by chemical processes, and deposited at or near the Earth's surface' (Allaby & Allaby, 1990). It incorporates grains ranging in size from minute specks to large boulders (Leeder, 1982) and includes material precipitated from solution, biological products, and particulate mineral matter (McLane, 1995).

Sediment in marine and intertidal areas is derived from a wide variety of sources (illustrated in figure 1.1). Sediment from natural coastal erosion inputs varying amounts of sediment into the water column depending upon the area of coastline

(Airoldi, 2003). Along the coast of Kiel Bay (Germany), coastal erosion accounts for approximately 7500m^3 yr^{-1} across a 35m stretch of cliff washed into the bay. The larger sediment fractions, course sand, gravel and stones are predominantly deposited near the shoreline, whilst finer material (approximately 60 - 65% of the total) is transported into deeper areas (Vogt & Schramm, 1991). In the UK, coastal erosion on the Holderness coast deposits 1.4 x 10^6 tonnes yr^{-1} into the North Sea, whilst the cliffs of Norfolk and Suffolk contribute 785 000 tonnes yr^{-1} (McCave, 1987). The erosion, and subsequent slumping or landslides, of subtidal areas also reintroduces sediment into the marine and intertidal system (discussed in Slattery & Bockus, 1997; Smith & Witman, 1999). Sediment released by landslips is subsequently redistributed by local current patterns (Slattery & Bockus, 1997).

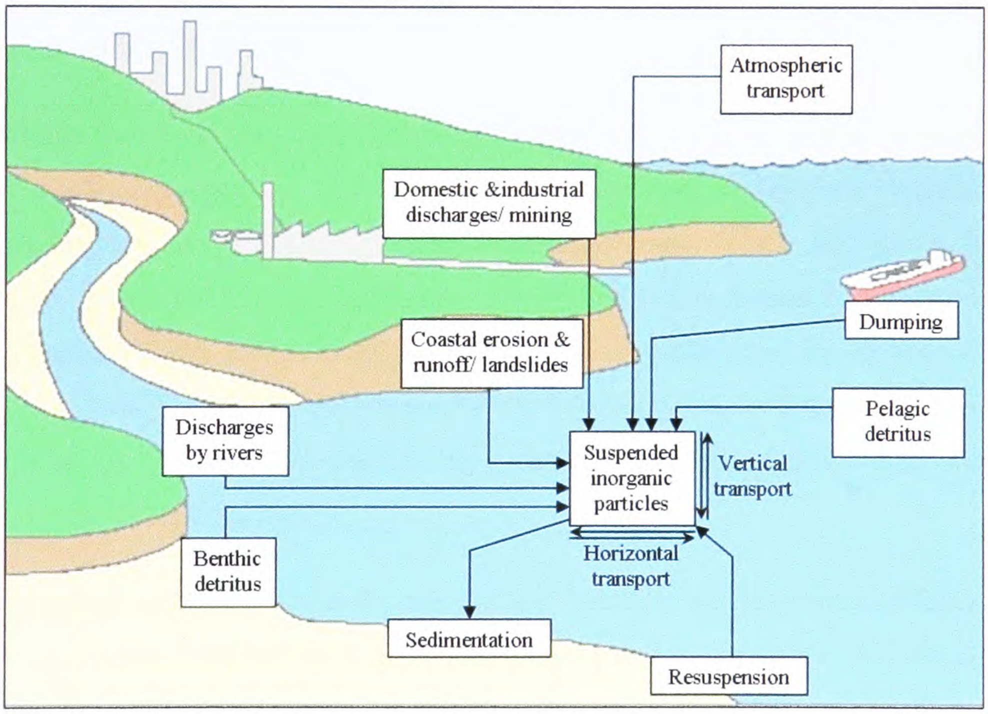


Figure 1.1: Schematic diagram of inputs, outputs and transport of sediment in intertidal environments (Airoldi, 2003).

Sediment is also carried into the marine environment from terrestrial sources such as rivers. The quantity of riverine sediment transported into the marine environment is dependent upon a variety of environmental factors, including the intensity of rainfall, soil type and vegetation cover along the length of the river and its tributaries (Airoldi, 2003). The quantity and type of sediment carried is dependent upon the river. Rivers in East Anglia yield about 5,500 tonnes yr^{-1} of sediment whilst those of the Wash contribute 100,000 tonnes yr^{-1} of sediment (McCave, 1987). Storms and intense rainfall can increase the quantity of sediment that is transported and this increased sediment load can last for hours to several days. As a result of a massive flood in March 1988 the Orange River, South Africa, 55 tonnes silts s^{-1} were transported out of the mouth of the river over several days (Branch, *et al.*, 1990).

Whilst coastal erosion and sediment discharge from rivers are the principle inputs of sediment into intertidal environments (Airoldi, 2003), whole or fragmented skeletal debris from a wide range of organisms (including red coralline algae, bivalves, foraminifers and gastropods) supply carbonate grains of sediment ranging in size from fine sand to gravel (Fornos, *et al.*, 1992). Fine grain sized sediment is also derived from volcanic debris and desert dust storms, through aeolian (wind) transport (reviewed in Moore, 1977).

In addition to natural sources of sediment, anthropogenic sources also input sediment into coastal environments. Sources of potential sediment deposits are suggested to include wind borne deposition (including nuclear bomb debris and petrol fumes [reviewed in Moore, 1977]), accidental spillage, coal refuse dumped off shore, china clay residues being pumped out of power stations (discussed in Boney, 1978), dumping of colliery waste directly onto shores (Hyslop, *et al.*, 1997), land reclamation (Bertin, *et al.*, 2005), and discharges from copper mine tailings (Castilla & Nealler, 1978; Farina & Castilla, 2001).

Movement of sediment within the marine and intertidal environments is dependent upon there being sufficient energy for movement either by traction (sediment rolling or sliding), saltation (the movement of sediment along the bed by a series of irregular bounces [Chanson, 1999]) or suspension (the movement of sediment in longer more irregular trajectories higher from the bed than saltation [Leeder, 1982]). The energy for sediment transport in intertidal areas can be provided by wind action or water movement. Aeolian transport by wind action starts as traction or surface creep. If wind velocity is sufficient then suspension of sediment can occur, however saltation is the most common mode of aeolian sediment transport (Haslett, 2000). Large quantities of sediment are transported by water movement by long shore currents (Davis & FitzGerald, 2004), again using a combination of traction, saltation and suspension. Sediment transport by long shore currents can be enhanced by wind action and results in a net lateral movement in one direction (Davis & FitzGerald, 2004).

It has been suggested that sediment transport and subsequent deposition in intertidal areas is primarily influenced by the local geographic structure (Storlazzi & Field, 2000). The geomorphology of shorelines can include a variety of features including coastal mountains, sea cliffs, small pocket beaches, river mouths and headlands. Dominant oceanic processes, including the direction of prevailing winds, waves, currents and tidal regimes and the interactions between these factors (Bird, 1984; Martin, *et al.*, 2005) provide a key secondary influence on sediment movement (Storlazzi & Field, 2000). Geomorphology has the potential to disrupt continuous sediment movement resulting in deposition; therefore most of sediment movement by long shore transport occurs in the low-energy surf zone restricting this method of sediment movement primarily to long sandy coastlines (Storlazzi & Field, 2000). For sediment movement to bypass geographic features, high-energy events such as storms are required to resuspend sediment and move it far enough off shore to bypass the obstruction and supply sediment to an area further down the shore or coast, and subsequently transport sediment from a greater depth (Storlazzi & Field, 2000). The combined wave-current interaction of more energetic oceanic conditions allow the generation of a higher bed shear stress to pump sediment high into the water column and initiate sediment suspension (Grant, *et al.*, 1984). Manmade coastal defences including groynes and sea walls can also simulate the effect of local geographic structures on sediment movement in intertidal areas. The use of groynes prevents long shore transport resulting in sediment accumulation, whilst seawalls prevent cliff erosion and the input of sediment into the water column (French, 2001).

Effects of sediment on macroalgae

Areas of rocky shore that are subject to comparatively higher sediment accumulation, whether through frequent sediment burial or generally greater sediment levels in the water column, have a lower macroalgal species diversity (Daly & Mathieson, 1977), and also a different species composition with a greater abundance of turf species (Gorgula & Connell, 2004; Balata, *et al.*, 2005). These differences can be attributed to the variations in sediment settlement as demonstrated by experimental manipulation of sediment accumulation, either through manual addition of sediment (*e.g.* Piazzi, *et al.*, 2005; Balata, *et al.*, 2007), removal by careful washing (*e.g.* Kendrick, 1991; Eriksson & Johansson, 2005), or reduction of settlement using Perspex sheets (Airoldi & Cinelli, 1997). In areas with comparatively higher sediment levels the abundance of macroalgal taxa (Balata, *et al.*, 2007) and macroalgal species diversity (Eriksson & Johansson, 2005) was lower. The abundance of turf species was greater in the higher sediment conditions (Airoldi & Cinelli, 1997; Gorgula & Connell, 2004), whilst species described as being erect (e.g. *Halimeda tuna* (Ellis et Solander) Lamouroux, *Flabellia petiolata* (Turra) Nizamuddin, *Tricleocarpa fragilis* (Linnaeus) Huisman & Townsendand *Dictyota dichotoma* (Hudson) Lamouroux) (Airoldi & Cinelli, 1997; Piazzi, *et al.*, 2005) and encrusting (Balata, *et al.*, 2005) had a greater abundance in lower sediment conditions.

The responses of macroalgae to sediment appear to be species specific. Where sediment deposition on the shore was comparatively higher, the abundance of the macroalgal species *Corallina vancouveriensis* Yendo (Taylor & Littler, 1982), *Dictyota dichotoma* and *Giffordia* sp (Airoldi & Cinelli, 1997), *Pilayella littoralis* (Linnaeus) Kjellman, *Sphacelaria arctica* Harvey and *Fucus vesiculosus* Linnaeus (Eriksson & Johansson, 2005), *Zanardinia typus* (Nardo) G. Furnari, *Dictyota dichotoma, Flabellia petiolata* and *Meredithia microphylla* (Agardh) Agardh (Balata, *et al.*, 2007) and *Halimeda tuna*, *Flabellia petiolata*, *Laurencia obtusa* (Hudson) Lamouroux and *Tricleocarpa fragilis* (Piazzi, *et al.*, 2005) was lower. Other macroalgal species showed no difference in abundance between areas with comparatively different levels of sediment accumulation (*Caulerpa racemosa* (Forsskål) Agardh, *Womersleyella setacea* (Hollenberg) Norris, *Sphacelaria radicans* (Dillwyn) Agardh (as *Sphacelaria cirrosa*), *Heterosiphonia crispella* (Agardh) Wynne, *Rodriguezella strafforelloi* Schmitz & Rodriguez, [Piazzi, *et al.*, 2005], *Cladophora* spp and *Enteromorpha* spp [Eriksson & Johansson, 2005]). *W. setacea* and *Pseudochlorodesmis furcellata* (Zanardini) Børgesen have been found in greater abundance in areas with comparatively higher sediment deposition off the Tuscan coast (Balata, *et al.*, 2007). It is, however, unclear if this increase in abundance is the result of higher sediment levels or the decrease in competition from other macroalgal species more adversely affected by sediment.

Sediment can affect macroalgae both whilst in the water column and whilst settled on the shore. Sediment in the water column reduces light penetration, and leads to a reduction in photosynthesis (Toohey, *et al.*, 2004). Smaller grain sizes (<63µm) decrease photosynthesis in *Hydrolithon reinboldii* (Weber-van Bosse & Foslie) Foslie, *Neogoniolithon brassica-florida* (Harvey) Setchell & Mason and *Hydrolithon onkodes* (Heydrich) Penrose & Woelkerling (as *Porolithon onkodes*) more than larger grain sizes (63-250µm) (Harrington, Fabricius, Eaglesham & Negri, 2005). The abrasive effect of larger grain sizes (500-2000µm) of sediment in moving water has been found on *Ulva lactuca* resulting in loss of mass (Hyslop & Davies, 1998). Coating of the macroalgal species *Cladophora rupestris* (Linnaeus) Kützing, *Plumaria plumosa* (Hudson) Kuntze (as *Plumaria elegans*), *Polysiphonia lanosa* (Linnaeus) Tandy, *Pelvetia canaliculata* (Boney, 1978) and *Ulva lactuca* (Hyslop & Davies, 1998) by fine grains of sediment in the water column has been found to occur. The coating varies between macroalgal species: a greater coating occurred on *C. rupestris* than *P. plumosa*, which was greater than both *P. lanosa* and *P. canaliculata*, but in all cases photosynthesis was reduced (Boney, 1978).

Sediment in the water column also adheres to the surface of *Eisenia bicyclis* (Kjellman) Setchell zoospores, which reduces their attachment ability (Arakawa, 2005). In laboratory studies sediment already settled on surfaces has also been found to decrease the attachment of *E. bicyclis* (Arakawa, 2005), the bull kelp *Durvillaea antarctica* (Chamisso) Hariot and the fucoid macroalga *Hormosira banksii* (Schiel, Wood, *et al.*, 2006) zoospores. In all cases the percentage attachment decreased as the quantity and area of coverage by sediment increased. A dense cover of sediment (7.3g cm^{-2} over 100% of the area) reduced attachment of both *D. antarctica* and *H. banksii* to a few individuals of each species (Schiel, *et al.*, 2006). Reduced survival of both *Macrocystis pyrifera* (Linnaeus) Agardh (Devinny & Volse, 1978) and *Fucus vesiculosus* (Berger, *et al.*, 2003) was also observed when sediment was added to the water column at the time of fertilisation. This has been suggested to be because the sediment settles faster than the zoospores, so covering the surface and preventing attachment (Devinny & Volse, 1978). For both *M. pyrifera* (Devinny & Volse, 1978) and *F. vesiculosus* (Berger, *et al.*, 2003) burial by sediment 24 and 48 hours after fertilisation respectively resulted in lower survival than when no sediment was added. Again, survival was reduced as the quantity of sediment added increased (Devinny & Volse, 1978; Berger, *et al.*, 2003). Similar patterns were found to occur in the growth of mature *Eisenia bicyclis* (Arakawa, 2005) and *Caulerpa taxifolia* (Vahl) Agardh (Glasby, *et al.*, 2005) when buried under different quantities of sediment. In both cases growth was measurably reduced when each species was buried in small quantities of sediment. Over seventeen days unburied *C. taxifolia* increased in length by 780%, whilst buried *C. taxifolia* only increased in length by 80% (Glasby, *et al.*, 2005). The addition of 30mg cm^{-2} of sediment to the water column to settle over *E. bicyclis* resulted in no observable growth (Arakawa, 2005).

Burial by sediment may alter the microclimate (Devinny & Volse, 1978). While this may be beneficial in some circumstances (*e.g.* increasing the available nutrients and so increasing the percentage of turf forming algal species [Gorgula & Connell, 2004]), it can also be detrimental (*e.g.* lower available oxygen and nitrogen or result in a hydrogen sulphate microclimate [Chapman & Fletcher, 2002]). Deoxygenated seawater with nitrogen gas bubbled through has been found to lower the percentage survivorship of *Fucus vesiculosus* embryos by 80-100% (Chapman & Fletcher, 2002). Light availability is also reduced by sediment burial. This reduced the photosynthetic yield of *Hydrolithon reinboldii, Neogoniolithon brassica-florida* and *Hydrolithon onkodes* (as *Porolithon onkodes*), although rapid recovery occurred when sediment was removed, with total recovery after 168 hours (Glasby, *et al.*, 2005). However Devinny & Volse (1978) were unable to separate the effects of light reduction on *Macrocystis pyrifera* zoospores from the other effects of sediment burial because survival was similar under both transparent and opaque trays that allowed differences in light penetration.

Effects of macroalgae on sediment

Whilst macroalgal species are affected by sediment deposition and accumulation, it also appears that they influence it. Sediment trapping by macroalgal species is generally associated with turf species. As a group, turf species exhibit a variety of morphologies, however sediment is accumulated and trapped in all cases (reviewed in Airoldi, 2003). Turf species have been defined as having tightly packed upright branches greater that 0.5cm in length (Hay, 1981). Filamentous algal turf (consisting mainly of *Polysiphonia fucoides* (Hudson) Greville) was found to trap significantly more sediment than the canopy *Fucus vesiculosus* under the natural sediment conditions of the Baltic Sea (Isaeus, *et al.*, 2004). Juvenile kelp species (Kennelly, 1989) and *Hormosira banksii* germlings (Schiel, *et al.*, 2006) have also been found to accumulate sediment. This has been attributed to their shorter, and hence more turf like, morphology (Kennelly, 1989). Kelp species (*Agarum fimbriatum* Harvey with some *Agarum cribrosum* Bory de Saint-Vincentand *Saccharina groenlandica* (Rosenvinge) Lane, Mayes, Druehl & Saunders [as *Laminaria groenlandica*]) have also been found to accumulate sediment. In all cases, the weight of sediment on kelp plates was between 2.4 and 4.8 times greater than on non-kelp plates (Eckman, *et al.*, 1989). However, canopy species have been associated with a decrease in the quantity of sediment trapped beneath them (Melville & Connell, 2001). The amount of sediment that accumulated under a canopy cover of *Cystophora* spp and *Ecklonia radiata* (C. Agardh) J. Agardh cover was found to be less than accumulated on open rock (Connell, 2003b).

Effects of sediment on fauna

Fauna on the shore show similar patterns to macroalgae in terms of both being affected by and affecting sediment accumulation on the shore. The diversity and number of individual encrusting faunal species (including bryozoans and ascidians) was higher in areas where the quantity of sediment was decreased (Maughan, 2001). Recruitment of spirobids (Connell, 2003b), *Pseudochitinopoma occidentalis* Bush, *Membranacea* sp and *Tubulipora* sp (Duggins, *et al.*, 1990) have lower recruitment in areas with comparatively higher sediment levels. However, as with the effect of sediment on macroalgae, the impact of increased sediment deposition appears to be species specific. Both serpulids and cheilostomata show no change in percentage cover when rates of sediment deposition are either increased or decreased compared to natural levels of sedimentation (Connell, 2003b). Sediment trapped by macroalgal turf species, however, appears to have a positive effect upon the inhabiting fauna. Statistically significant positive correlations are found between the quantity of sediment trapped in turf of predominantly *Corallina officinalis* and the number of families of polychaetes with sediment in mid shore and a significant positive correlation between the number of families of polychaetes of both and gastropods with sediment in the low shore (Kelaher, *et al.*, 2001). Similarly detritivores and herbivores show a strong correlation with the quantity of sediment in *Osmundea* *pinnatifida* (Hudson) Stackhouse (Prathep, *et al.*, 2003) and increased mass of sediment trapped within artificial algal mats showed a significant correlation with increased density of meiofauna (Gibbons, 1988). This positive relationship between faunal abundance and the quantity of sediment trapped has been attributed to increased water retention by the sediment reducing physical stress and the use of sediment as a food source (Prathep, *et al.*, 2003).

Fauna on the shore are also subject to periodic burial by sediment deposition. Fauna buried by deposited sediment have two approaches to surviving sediment burial: either, in the case of more mobile fauna, to move through the sediment and re-emerge on the surface (*e.g. Clinocardium nuttallii* Conrad and *Cancer magister* Dana [Chang & Levings, 1978]); or to remain buried until sediment is removed (*e.g. Patellagranularis* Linnaeus and *Siphonaria capensis* Quoy & Gaimard [Marshall & McQuaid, 1989]) and survive the adverse conditions associated with lower oxygen availability (Strommer & Smock, 1989) and nitrogen which result in a hydrogen sulphate microclimate (Chapman & Fletcher, 2002).

Re-emergence time is slower in deeper sediment. In one study *Clinocardium nuttallii* took one to ten minutes to emerge from 1-3mm of sediment compared to only half of the individuals buried re-emerging after 24 hours under 10cm of sediment (Chang & Levings, 1978). Re-emergence of *Cancer magister* look less than one minute in 1-3mm of sediment compared to six hours in 5cm of sediment (Chang & Levings, 1978). In both cases no re-emergence occurred in burial under 20cm of sediment after 24 hours, and some mortality was recorded in *C. magister* (Chang & Levings, 1978). Length of burial also affects mortality, with cumulative mortality of both *Perna perna* Linnaeus and *Mytilus galloprovincialis* Lamarck increased between one and nine days of burial (Zardi, *et al.*, 2006). However the length of survival is species specific with 100% mortality of *Littorina granularis* occurring within three days of burial (Marshall & McQuaid, 1989) compared with 100% of mortality in *Littorina littorea* in ten days (Chandrasekara & Frid, 1998). In contrast, *Hydrobia ulvae* Pennant had 100% survival after twenty-five days of burial (Chandrasekara & Frid, 1998). Sediment burial decreases oxygen concentration (Strommer & Smock, 1989) and increases the mass on organisms (Marshall & McQuaid, 1989). Experimental manipulation on *Patella granularis* showed that both of these factors decrease survival independently (Marshall & McQuaid, 1989).

Sediment also reduces feeding of fauna. The grazing of *Patella vulgata* Linnaeus was severely inhibited in the presence of a layer of sediment approximately 1mm thick but the reasons for the grazing inhibition have yet to be investigated (Airoldi & Hawkins, 2007). Suspended sediment can also clog the gills of suspension feeders, with the effects being greatest in less selective feeders (reviewed in Moore, 1977).

Effects of fauna on sediment

Fauna also have an influence on sediment movement; however they are generally responsible for its removal rather than its accumulation. The freshwater gastropod grazer, *Potamopyrgus antipodarum* Gray has been shown to reduce sediment levels in enhanced sediment environments to natural levels (James, *et al.*, 2000). Gastropods within intertidal environments also remove sediment. Significantly more sediment has been found to occur on areas of the shore where *Littorina littorea* had been removed compared to control areas (Bertness, 1984). Under laboratory conditions, the trochid *Melagraphia aethiops* Gmelin, and the turbid *Turbo smaragdus* Gmelin, were found to remove 70% and 80% of sediment respectively (Schiel, *et al.*, 2006). However, *Zeacumantus subcarinatus* Sowerby, although moving the sediment, had no significant effect on sediment removal (Schiel, *et al.*, 2006).

1.1. Rationale and Aims

The movement and input of sediment into marine and intertidal systems is a natural occurrence, however increases in sedimentation rates throughout the world are suggested to be occurring as a result of anthropogenic changes (reviewed in Airoldi, 2003). These not only increase sediment input, but also have the potential to change sediment movement patterns (*e.g.* groynes preventing long shore drift, [Davis & FitzGerald, 2004]). Differences in the quantity of sediment on the shore have resulted in observed variation in both the types and abundance of macroalgal species (*e.g.* Daly & Mathieson, 1977; Irving & Connell, 2002; Eriksson & Johansson, 2005). Although differences in sediment trapping are recognised to occur between macroalgal species, most previous research has been qualitative (reviewed in Airoldi, 2003) comparing community composition between areas of high or low sedimentation, whether that be naturally occurring (*e.g.* Taylor & Littler, 1982; Gorgula & Connell, 2004) or experimentally manipulated (*e.g.* Kendrick, 1991; Umar, *et al.*, 1998; Eriksson & Johansson, 2005; Piazzi, *et al.*, 2005). The limited quantitative studies have generally focused upon the effect of sediment on individual organisms, including both macroalgae (*e.g. Patellagranularis* Linnaeus and *Siphonaria capensis* Quoy & Gaimard [Devinny & Volse, 1978]; *Caulerpa taxifolia* [Glasby, *et al.*, 2005]) and fauna (*e.g. Patella granularis,* [Marshall & McQuaid, 1989] and *Cancer magister,* [Chang & Levings, 1978]). These studies have focused upon either the effects of burial and scour on individual organisms (*e.g.* Kendrick, 1991; Arakawa, 2005; Zardi, *et al.*, 2006), or the impacts that sediment has upon aspects of an individual organism's survival such as reproduction (*e.g.* Umar, *et al.*, 1998; Berger, *et al.*, 2003; Schiel, *et al.*, 2006) and feeding (Airoldi & Hawkins, 2007).

Although sediment deposition is recognised as occurring on intertidal rocky shores and affecting the species composition and life cycles of organisms, little research has been performed into the mechanisms of sediment deposition and movement. Faunal species have been found to move and remove sediment from their immediate vicinity (Bertness, 1984; Schiel, *et al.*, 2006). Sediment trapping and movement by macroalgal species has also been recognised. Many of these have been generalisations about sediment trapping by macroalgae (reviewed in Airoldi, 2003) although some quantitative measurements of sediment accumulations have been made into the quantity of sediment trapped by individual turf species (*e.g.* Gibbons, 1988; Prathep, *et al.*, 2003). A small number of quantitative studies have also been performed on sediment accumulation and removal beneath canopy species but these have been confined to subtidal areas and had conflicting results (Eckman, *et al.*, 1989; Kennelly, 1989; Melville & Connell, 2001; Connell, 2003b). These studies also focused on sediment movement in relatively small areas.

Increases in sediment in the water column as a result of anthroplogenic activities may result in changes in sediment settlement on intertidal rocky shores. It is, therefore, important to understand the factors that affect the quantity and position of sediment settlement on the shore, and the impact that sediment deposition has on the inhabiting community. This thesis considers the biological mechanisms that affect sediment deposition and movement on an intertidal rocky shore environment at a variety of different levels. Firstly, investigation of the morphological factors that influence sediment trapping by individual macroalgal species (Chapter 2). Secondly, investigation of the effect of the macroalgal community on sediment trapping and accumulation (Chapter 3). Thirdly, investigation of the effects of large scale movements and deposition of sediment across an intertidal rocky shore, using the rocky shore at Holbeck, North Yorkshire as a case study, including description of the general patterns of sediment accumulation and community composition across the shore (Chapter 4) and seasonal variation (Chapter 5). Finally, investigation of the relationship between sediment abundance and community structure (Chapter 5). The implications of all of these factors on sediment accumulation and movement on intertidal rocky shores are discussed in the final chapter (Chapter 6).

Chapter 2

The effect of morphology on the sediment trapping capacity of macroalgae.

2.1. Introduction

Within intertidal rocky shore communities many different macroalgal species have been found to trap sediment. These range from large canopy species, such as *Fucus serratus* Linnaeus (Isaeus, *et al.*, 2004) and *Agarum fimbriatum* (Eckman, *et al.*, 1989) through to small turf species such as *Osmundea pinnatifida* (Prathep, *et al.*, 2003) and *Corallina officinalis* Linnaeus (Kelaher, *et al.*, 2001). However, the amount and type of sediment varies with tidal height (Gibbons, 1988; Kelaher, *et al.*, 2001; Prathep, *et al.*, 2003), wave exposure (Dommasnes, 1969; Kelaher, *et al.*, 2001; Prathep, *et al.*, 2003), season (Stewart, 1983; Airoldi *et al.*, 1996; Fabiano & Cinelli, 1996; Prathep, *et al.*, 2003), and macroalgal species (Boney, 1978; Isaeus, *et al.*, 2004).

The total mass of sediment trapped in artificial algal mats with a basal area of 35cm^2 displayed variation with tidal height on Schaapen Island (West Coast of South Africa) (Gibbons, 1988). The greatest quantity of sediment was trapped at mean high water neap level, with the quantity of sediment being trapped decreasing down the shore to both mean tide level and mean low water spring (Gibbons, 1988). Differences in the mass of sediment down the shore have also been observed in natural macroalgae on the Isle of Man. The mass of sediment (g m^{-2}) trapped by *Osmundea pinnatifida* was statistically significantly greater at a height of 3.5m above compared to 2.0m above chart datum (Prathep, *et al.*, 2003). A greater mass of sediment (kg m^{-2}) was also found trapped by *Corallina officinalis* (with an occasional occurrence of *Jania* spp and *Amphora* spp) in the mid shore compared to the low shore (Kelaher, Underwood & Chapman, 2003). However, some studies have found conflicting results. *Corallina* turf cores of 50cm^2 were transplanted at Cape Banks Scientific Marine Research Area (Botany Bay, Australia) between the low and mid shore areas (Kelaher, *et al.*, 2003). After five months the mas of sediment trapped within the translanted algae was similar to the area in which they were transplanted to. A greater mass of sediment was trapped in the mid shore than the low shore (Kelaher, *et al.*, 2003). However at a second site there was no difference in the mass of sediment trapped between mid and low shore. At both sites the mass of sediment trapped varied greatly within each tidal height, but despite some general trends there were no interpretable statistical patterns amongst the different transplantation treatments (Kelaher, *et al.*, 2003). A previous study by Kelaher *et al.* (2001) in the same area (Cape Banks Scientific Marine Research Area, Botany Bay, Australia) showed no statistically significant difference in the mass of sediment trapped in *C. officinalis* turf between low and mid shore heights. Of the three sites studied two showed little difference in the mass (g) of sediment trapped whilst at the third site the amount trapped was greater at the low shore than the high shore (Kelaher, *et al.*, 2001).

The quantity of sediment trapped by macroalgae has also been found to be influenced by the wave exposure of the shore. Dommasnes (1969) observed that *Corallina officinalis* in areas of strong wave exposure did not trap any sediment, whilst more sheltered sites had a larger accumulation. However, in another study, greater sediment accumulation in *C. Officinalis* was found to occur in sites of medium to heavy wave exposure (Kelaher, *et al.*, 2001). On the lower part of the shore *Osmundea pinnatifida* also trapped sediment on both moderately exposed and exposed shores but the mass of trapped sediment (g m^{-2}) was found to be lower than on sheltered shores (Prathep, *et al.*, 2003). However on the higher part of the shore this only occurred during the winter; in the summer the mass of sediment (g m^{-2}) trapped on moderately exposed and exposed shores was greater than on the sheltered shore (Prathep, *et al.*, 2003). This highlights the seasonal differences that also occur in sediment trapping by macroalgae.

The mass of sediment (g m^{-2}) trapped by *Osmundea pinnatifida* on three different shores on the Isle of Man at both upper and lower tidal heights was significantly lower in summer than during winter (Prathep, *et al.*, 2003), with the exception of the upper shore level of the moderately exposed higher shore level. Here the mass of sediment (g m^{-2}) trapped was lower in winter than in summer. Lower levels of sediment trapping during summer months in winter were also found to occur in filamentous algal turf on the Liguria Sea, Italy (Airoldi, *et al.*, 1996) although the lowest levels were found to occur during autumn. However, the depth of sediment trapped within *Corallina officinalis* in San Diego, California was observed to be greater during summer-autumn than during winter-early spring (Stewart, 1983). Measurement of the dry mass of sediment trapped within a 12.5 x 12.5cm quadrat confirmed that there was a statistically significantly greater mass of sediment trapped by *C. officinalis* during summer than during winter (Stewart, 1983). However variations in the depth of sediment were observed throughout the year (Stewart, 1983).

The aforementioned studies into the effect of shore height, wave exposure, and season on sediment trapping have all focused on macroalgal species with turf like morphologies. As discussed in Chapter 1 sediment trapping by macroalgae is generally associated with turf species (reviewed in Airoldi, 2003). The shorter length, and hence more turf like composition of both juvenile kelp species (Kennelly, 1989) and *Hormosira banksii* (Schiel, *et al.*, 2006) have been used as an explanation for their capacity to trap sediment (Kennelly, 1989). However, it is not restricted to this morphological type. Both filamentous algal and canopy species have been found to trap sediment under natural sediment conditions in the Baltic Sea, although sediment trapping was greater in filamentous macroalgal species (Isaeus, *et al.*, 2004). Sediment accumulation of fine colliery sediment in the laboratory has also been found to occur in a range of morphologically different species (Boney, 1978). Sediment accumulation was studied in *Porphyra umbilicalis* Kützing (Membranaceous), *Plumaria plumosa* (as *Plumaria elegans*) (plumose branching), *Polysiphonia lanosa* (much branched), *Cladophora rupestris* (abundant branching, plant densely tufted) and *Pelvetia canaliculata* (a fucoid alga). Accumulation of sediment occurred in all cases due to the fine sediment sticking to the surface of the macroalgae with the greatest accumulation occurring in *C. rupestris* and the least in *P. lanosa* (Boney, 1978). Kelp species (*Agarum fimbriatum* with some *Agarum clathratum* Dumortier (as *Agarum cribrosum*) and *Saccharina groenlandica* [as *Laminaria groenlandica*]) have also been found to accumulate sediment (Eckman, *et al.*, 1989), as discussed in Chapter 1. However, as also discussed in Chapter 1, canopy species have also been found to have a reduced sediment trapping capacity compared to areas of open rock (Melville & Connell, 2001; Connell, 2003b) which has been related to the capacity of canopy species to sweep away the surrounding sediment (Kennelly, 1989).

Studies into the differences between the mass of sediment trapped by macroalgae have recognised that differences in the quantity can be related to both morphological groupings (*e.g.* Isaeus, *et al.*, 2004), and species (*e.g.* Boney, 1978). However all have relied upon qualitative assessments of the differences in morphology. The morphology of macroalgae has, however, been recognised to be made up of many measurable aspects including: wet weight, dry weight, epiphytic weight, surface area, texture, maximum length, maximum width, maximum width of final branch, maximum depth of final branch and degree of branching (Edgar, 1983). In practice, measurements of macroalgal morphology have considered surface area, biomass (Weiser, 1952; Dean & Connell, 1987; Bolam & Fernandes, 2002), height, width, stem width and number of branches (Chemello & Milazzo, 2002). Measurements of structural elements of morphology have also been combined to consider the arrangements of the structural elements within the macroalgae resulting in measurements of frond density (the density of fronds from the primary axis) (*e.g.* Grahame & Hanna, 1989; Hull, 1997; Kelaher, *et al.*, 2003), interstitial volume (the space available between the fronds) (Hacker & Steneck, 1990), and predominantly in the terrestrial environment order of branching and bifurcation ratio (describing branching patterns) (Steingraeber, *et al.*, 1979; Canham, 1988).

Measurement of macroalgal morphology is primarily used in considering its use as a habitat for intertidal epifauna. The acknowledged difficulties of quantifying habitat morphology on small scales (Attrill, *et al.*, 2000), may account for the predominant use of qualitative techniques when considering the morphology of macroalgae (*e.g.* Williamson & Creese, 1996; Bolam & Fernandes, 2002). However relationships have been found between measurements of general faunal abundance and diversity and some measurements of macroalgal morphology (Dean & Connell, 1987) and also the abundance of different taxa and measurements of macroalgal morphology. Generally the abundance of individuals of different taxa including ostracods (Hull, 1997), amphipods (Hacker & Steneck, 1990) and molluscs (Chemello & Milazzo, 2002) increased as branching density (measured as either frond density or degree of branching) increased. However there was a statistically significant inverse relationship between gastropod abundance and frond density (Kelaher, *et al.*, 2003). Other morphological measurements of macroalgae that have been shown to correlate with faunal abundance include degree of branching, algal width and the log of stem width; whilst there were no statistically significant associations between the number of branches, number of ramuli, number of leaves or number of vesicles and molluscan abundance (Chemello & Milazzo, 2002).

Whilst macroalgal morphology has been found to influence sediment trapping in macroalgae, morphological assessments have generally been qualitative comparing sediment trapping between different species (*e.g.* Boney, 1978; Isaeus, *et al.*, 2004). Quantitative studies comparing different morphologies have been limited to artificial macroalgae with different morphologies on the West coast of South Africa (Gibbons, 1988). In this case trapped sediment mass was found to be lowest in the most simple mats with trapped sediment mass increasing in more complex mats (Gibbons, 1988).

2.1.1. Rationale and Aims

As described above, differences in sediment trapped by macroalgae appears to be related to a number of different factors including species (*e.g.* Boney, 1978; Isaeus, *et al.*, 2004), seasons (*e.g.* Kelaher, *et al.*, 2001; Prathep, *et al.*, 2003), shore heights (*e.g.* Kelaher, *et al.*, 2001; Prathep, *et al.*, 2003) and wave exposure (*e.g.* Dommasnes, 1969; Prathep, *et al.*, 2003). Previous studies have generally been restricted to considering each of the factors affecting sediment trapping in isolation. However different patterns in sediment accumulation have been found to occur between site, season and shore height in *Osmundea pinnatifida* (Prathep, *et al.*, 2003). This would suggest the need to investigate combinations of these factors more thoroughly. Differences in faunal abundance have found to be affected by individual elements of macroalgal morphology (*e.g.* Hacker & Steneck, 1990; Chemello & Milazzo, 2002) and complexity (Gibbons, 1988), in addition to qualitative differences being found between different macroalgae species (*e.g.* Williamson & Creese, 1996; Bolam & Fernandes, 2002). Therefore investigation of associations between sediment trapping and quantifiable morphological characteristics may provide further insight into the processes taking place.

This chapter describes the investigation of associations between different species of macroalgae and their morphology and sediment trapping along three shores on the north east coast of England. Specific aims were:

1) To determine whether there is a statistically significant difference in the quantity of sediment trapped between ten species of macroalgae with different morphologies between three shores and in four different seasons of the year.

2) To determine whether there is a statistically significant relationship between six different measures of macroalgal morphology and the amount of sediment trapped.
3) To determine whether there is a statistically significant difference in the grain size composition of sediment trapped between three species of macroalgae with different qualitative morphologies.

2.2. Methodology

Three shores on the North East coast of England were selected for sampling, Crook Ness (National grid reference: TA 028 934), Holbeck (National grid reference: TA 050 870) and Black Rocks (National grid reference: TA 057 866) (figure 2.2.1). The shores were chosen as previous observations had noted the periodic movement of sediment onto and off the shores. All three shores had sediment entering the system which had the potential to be trapped by macroalgae. As differences in wave exposure have been found to affect the mass of sediment trapped within *Osmundea pinnatifida* (Prathep, *et al.*, 2003) the selected shores were chosen as they have similar aspects (North to North East) and moderate wave exposures. The close proximity of all the three shores to one another, within 10 miles (figure 2.2.1), ensured that all were subjected to similar weather conditions.

Within each shore, areas of similar shore height (based on biological zonation [Stephenson & Stephenson, 1949]) were selected for sampling. The sampling areas chosen consisted of flat bedrock, as topography influences sediment deposition (Jørgensen & Gulliksen, 2001; Littler *et al.*, 1983) and also had similar macroalgal community composition to minimise the effect of surrounding species.

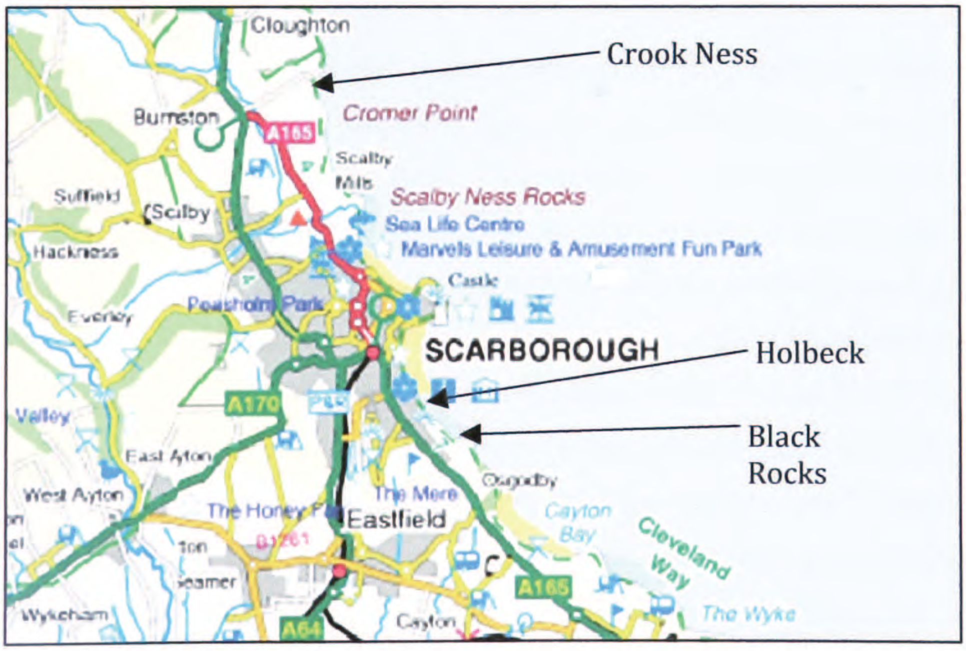


Figure 2.2.1: Position of the three sampling sites (Crook Ness, Holbeck and Black Rocks) in relation to Scarborough. North Yorkshire (Digimap, 2008).

2.2.1. Site descriptions

The rocky shore at Holbeck (plate 2 2.1) is situated to the southern end of Scarborough. The rocky platform lies to the south of a large sandy beach. The site had no biological upper shore (as defined by Stephenson & Stephenson, 1949) as the shore is terminated by a concrete sea wall to control cliff erosion (plate 2.2.1). The upper part of the shore contained an upper shore sediment zone that varied in length between approximately 20 and 60 meters. The rocky platform had an uneven topography with rocky ledges occurring throughout the shore resulting in a poorly defined macroalgal zonation pattern. A large depression of the shore occurs just inland of the sample collection site (plate 2.2.1). Several large rock pools also occur across the shore. The majority of the shore was covered by large fucoid beds, covering an understory of turf species dominated by *Osmundea pinnatifida* and *Corallina officinalis*. The lower part of the shore consisted of areas of *Laminaria digitata* and *Rhodothamniella floridula* (Dillwyn) Feldmann beds. In addition to the upper shore sediment zone, there was patchy sediment accumulation across the shore, with large areas of sediment accumulation occurring in the large depression on the shore, and also in the rockpool to the left of plate 2.2.1. The quantity of sediment accumulation throughout the shore, including the upper shore sediment zone, varied throughout the year (personal observation). The area in which samples were collected is indicated in plate 2.2.1.

Crook Ness (plate 2.2.2) is situated approximately three miles north of Scarborough near the village of Burniston. The rocky flat scar is surrounded by a steep cliff with areas of boulders at the foot (plate 2.2.2). The upper part of the shore was dominated by fucoid communities, with two large rockpools, and a number of smaller ones (plate 2.2.2). Adjacent to the access point to the shore a freshwater inlet drained onto the shore, the upper part of which was surrounded by green algae, predominantly *Ulva* spp. The lower part of the shore had numerous small rockpools which were dominated by *Corallina officinalis*. The surrounding bedrock was covered by large patches of algal turf, predominantly *Osmundea pinnatifida* and *Cladostephus spongiosus* (Hudson) Agardh with some fucoid cover. There were a small number of large rockpools in the upper part of the shore (plate 2.2.2). There was limited settlement of sediment on areas of bare rock although sediment was observed to be trapped by macroalgal turf species on the lower parts of the shore. Samples were collected from the area indicated in plate 2.2.2.

Black Rocks (plate 2.2.3) is situated approximately 1000m south of Holbeck. The shore is surrounded by steep cliffs of Jurassic shale and sandstone (Scarborough Borough Council, 1997), which are vulnerable to regular slippage. At the base of the cliff was an area of sand, pebbles and boulders. The upper part of the shore was dominated by barnacles (predominantly *Semibalanus balanoides*) with some fucoid canopy cover, but was algal dominated in the mid to lower parts of the shore (plate 2.2.3). The mid part of the shore was covered by large fucoid beds covering small patches of algal turf species, predominantly *Osmundea pinnatifida* and *Corallina officinalis*. In the lower parts of the shore turf species became more dominant, with areas of *Laminaria digitata* and *Rhodothamniella floridula* beds. With the exception of the area at the base of the cliff, sediment accumulation was restricted to the mid and lower areas of the shore. The majority of sediment on the shore was observed trapped by macroalgal species; however large areas of sediment accumulation covered areas of macroalgae on occasion. The area in which sediment samples were collected is indicated in plate 2.2.3.

Plate 2.2.1: Position of the macroalgal sampling site at Holbeck.

Plate 2.2.2: Position of the macroalgal sampling site at Crook Ness.

Plate 2.2.3: Position of the macroalgal sampling site at Black Rocks.

2.2.2. Sampling

Ten different macroalgal species were selected for sampling (table 2.2.1). The species were chosen because they were generally abundant on all three shores and represented a variety of morphological types (Lobban & Harrison, 1997) reflecting the wide range of morphologies present on these intertidal rocky shores.

Samples were collected from each of the three shores over two consecutive days in October 2007, January 2008, April 2008 and July 2008 to represent all seasons. Although sediment movement can occur during a single tidal cycle (Stewart, 1983) the distance between shores made it impractical to sample during a single tidal cycle. Five random samples of each macroalgal species were collected from each shore. Collections were made in the lower mid to low shore using biological zonation (as described in Stephenson & Stephenson, 1949) to determine the collection areas. For macroalgal species that existed clearly as individuals (or small group of individuals where they existed very close together), single or small groups of individuals were collected by careful removal of the holdfast at the substrate. Where macroalgal species existed as a turf (indicated by * in table 2.2.1) a core of 3cm^2 area were scraped from the substrate. A preliminary study using the shore at Holbeck suggested that this collected sufficient sediment for subsequent analysis but prevented the sample being excessively large.

On returning to the laboratory the samples, with the exception of *Rhodothamniella floridula*, were carefully and thoroughly washed with fresh water (Gibbons, 1988) using a 38µm sieve to collect the sediment. The preliminary study at Holbeck revealed that the mass of sediment of grain sizes smaller than this was negligible. *R. floridula*, in the preliminary study, was the only species to trap large quantities of sediment less than 38µm. Therefore *R. floridula* was carefully washed in a bowl of freshwater to remove the sediment from the macroalgae. The water was then left to stand for a minimum of 72 hours for the sediment to settle before the water was carefully decanted off the top. The washed macroalgal samples were preserved in a freezer for future morphological analysis, as freezing has negligible effects on macroalgal morphology (Rice & Chapman, 1985). The collected sediment was stored in 70% ethanol prior to analysis.

Table 2.2.1: Species examined in this study and the external morphologies that they represent (modified from Lobban & Harrison, 1997; Stengel, Macken, Morrison & Morley, 2004).

Species	External morphology
Ulva lactuca Linnaeus	Thin, tubular and sheet like
Ulva intestinalis Linnaeus	Thin, tubular and sheet like
Fucus vesiculosus Linnaeus	Thick blades and branches (large)
Mastocarpus stellatus (Stackhouse) Guiry	Thick blades and branches (small)
Osmundea pinnatifida (Hudson) Stackhouse *	Turf, upright, coarsely branched
Corallina officinalis Linnaeus *	Turf, upright, articulated, calcareous
Cladophora rupestris (Linnaeus) Kützing	Delicately branched (filamentous)
Polysiphonia sp	Delicately branched (filamentous)
Cladostephus spongiosus (Hudson) C. Agardh	Delicately branched (filamentous)
Rhodothamniella floridula (Dillwyn) Feldmann*	Dense mat of hair like filaments

Macroalgal measurements

The morphology of each macroalgal sample was quantified using the measurements described below. Where samples consisted of more than one individual, measurements were taken on the longest axis to provide an assessment of the morphology of the whole sample (Churchill, 2006). In the case of filamentous macroalgae, individual fronds were separated and measurements were taken on the longest frond.

Frond density

The number of primary branches on the longest frond were counted. Frond density was calculated as the number of primary branches/ axis length (mm) (Grahame & Hanna, 1989; Hull, 1997).

Interstitial volume

Interstitial volume acts a measure of the space between the fronds. Samples were carefully floated into a naturally spread position on a very thin layer of water to prvent distortion to the image. Images of samples were produced using an hp 1250 scanner. The canopy volume (CV), (the potential volume the macroalga can occupy in the water), was calculated from the height (h) (cm) and width (w) (cm) of the scanned image (CV=hxw). The thallus volume (TV) (cm^3) of the sample was measured by water displacement of the thallus. Interstitial volume (IV) (cm^3) was calculated as IV=CV-TV (Hacker & Steneck, 1990). Interstitial volume was standardised for individual alga size by dividing by total axis length.

Branching arrangement

Measurements of branching in flora have previously been restricted to measurements of order of branching (Steingraeber, *et al.*, 1979) or bifurcation ratio (Steingraeber, *et al.*, 1979; Canham, 1988). Both these methodologies consider single structural elements of morphology. Bifurcation ratio considers the ratios of first to second order branches. Although order of branching considers branching throughout the individual, it is not entirely suitable for macroalgae as they are rarely branched with an even pattern. Therefore, branching arrangement was calculated as the number of tips divided by the previously calculated frond density to provide a measurement of the whole, rather than individual structural elements.

Axis length

The total length of the individual was measured from the base of the stipe to the tip (axis length) as sediment trapping has been associated with macroalgae of smaller sizes (Kennelly, 1989).

Longest branch and pre branching length

Sediment accumulation is the result of slowed water movement inhibiting sediment transport (Eckman, *et al.*, 1989). Longer branches have the potential to affect water movement over a greater area, whilst the position of branches may also affect water flow. Therefore the longest frond was measured from the point it divided from the main axis to the apex (mm). The length of axis before the first branch (pre branching length) was also measured (mm).

On completion of the morphological measurements samples were air dried at room temperature to a constant mass. The mass of sediment was standardised as sediment g^{-1} macroalgal dry mass to account for differences in the size of macroalgae. Dry mass was not used in any methods of quantifying macroalgal morphology to prevent spurious self-correlations. The dried mass of *Corallina officinalis* was divided by two to account for the calcium carbonate structure increasing its' mass disproportionately to its' size (Shears & Babcock, 2003).

Sediment analysis

As macroalgae act as a habitat for a variety of epifauna (*e.g.* Dean & Connell, 1987; Hacker & Steneck, 1990; Chemello & Milazzo, 2002), these needed to be removed to from the sediment samples prior to sorting and weighing to prevent them adding to the mass of sediment. Organic material can be removed from sediment by combustion, however this removes organic material indiscriminately. Combustion above 400°C causes decomposition of carbonates including shell fragments (Eleftheriou & McIntyre, 2005) that occur in marine sediment (Leeder, 1982). Sediments on the North East coast of England also contain a high proportion of coal (Buchanan & Longbottom, 1970). Although methods exist that attempt to minimise the decomposition of coal during the removal of organic matter (*e.g.* methods described in Buchanan & Longbottom, 1970), there would still be some removal of coal from the sediment. Therefore visual examination of the samples under a microscope and subsequent removal allowed the living fauna, especially gastropods, to be distinguished from shell fragments that naturally occur within marine sediment (Leeder, 1982). Samples were oven dried overnight at 70°C to a constant mass and the total dry mass of sediment recorded (g).

The composition of the sediment trapped by the macroalgal species *Corallina officinalis*, *Osmundea pinnatifida* and *Rhodothamniella floridula* was examined. These three species were selected because they reliably trap sufficient sediment to separate the sediment fractions using a sediment shaker. It is reasonable to assume sphericity with sand grains, and therefore it is recognised that good size distribution information can be obtained using a set of certified test sieves (Eleftheriou & McIntyre, 2005). Pre-weighed sediment samples were sieved using an Endecotts

Octagon 200 test sieve shaker for a fixed interval of 5 minutes at an amplitude of 8. Initial trials revealed that longer shaking times did not affect the final distribution of sediment. Sediment samples were separated using 1mm, 0.5mm, 250μm, 125μm 63μm and 0mm sieves (Eleftheriou & McIntyre, 2005). These corresponded with the Udden-Wentworth grade scale for grain sizes (Leeder, 1982), and allowed the classification of the different sediment fractions as very coarse sand (>1mm), coarse sand (0.5mm-1mm), medium sand (250μm-0.5mm), fine sand (125μm-250μm), very fine sand (63μm-125μm) and silt (<63μm) (Leeder, 1982). This made the findings readily comparable with previous work (Eleftheriou & McIntyre, 2005). After agitation the mass of sediment retained in each sieve was weighed. The relative proportion of the total mass for each grain size class was calculated (Eleftheriou & McIntyre, 2005).

2.2.3. Data analysis

The null hypothesis under test was that there was no statistically significant difference in the mass of sediment g^{-1} dried macroalgal mass between the ten different macroalgal species, between the three different sites (Crook Ness, Holbeck and Black Rocks) and between the four different sampling months (October, January, April and July). Neither the raw data, nor the Log10 transformed data (as the variances were greater than the mean [Fowler, *et al.*, 1998]) conformed to the assumptions of normal distribution (Kolmogorov-Smirnov, $p<0.05$ in all cases) or approximately equal variances (Levenes test, $p<0.05$ in all cases). Although the assumptions of normality and equal variances had been violated it was deemed appropriate to perform a three factor General linear model Analysis of Variance (GLM ANOVA) as current non-parametric equivalents only allow two-factor analysis in the form of the Scheirer-Ray-Hare test (Dytham, 2003). Repeated testing on the same experimental data increases the chance of a Type I error (Field, 2005) and so the use of a single test is more appropriate. ANOVA is also quite robust to heterogeneity of variances and which are not resolved by the use of non-parametric tests (Underwood, 1997). However, as heterogeneity of variances also increases the probability of a Type I error (Underwood, 1997), the level of significance was considered as 0.01 rather than 0.05 (Underwood, 1981). The use of ANOVA also allows the potential for post hoc testing to identify the source of any variation. A three factor GLM ANOVA was performed with MONTH as a fixed factor with four levels (October, January, April and July), SHORE as a fixed factor with three levels (Crook Ness, Holbeck and Black Rocks) and SPECIES as a fixed factor with ten levels (*Ulva lactuca, Ulva intestinalis, Fucus vesiculosus, Mastocarpus stellatus, Osmundea pinnatifida, Corallina officinalis, Cladophora rupestris, Polysiphonia* sp, *Cladostephus spongiosus* and *Rhodothamniella floridula*) (Underwood, 1997). MONTH, SHORE and SPECIES were all independent variables whilst mass of dried sediment g^{-1} dry macroalgal mass was the dependant variable (Pallant, 2001). *Post hoc* Tukey Honestly Significantly Different (HSD) tests, which are more appropriate for larger samples (SPSS, 1999), were used to determine where any statistically significant differences occurred.

The relationship between measurements of macroalgal morphology and the mass of dried sediment g^{-1} dry macroalgal mass trapped was also examined. Different morphological elements have the potential to influence the physical environment at different scales (Attrill, *et al.*, 2000). Measurements of the morphology of *C. spongiosus* included the whorles as branches, and initial analysis suggested that these were measured on a scale that was too fine to affect sediment trapping. As measurements of morphology of *C. spongiosus* appeared to be on a different scale to the other macroalgal species studied it was deemed appropriate to remove it from the analysis of the relationship between macroalgal morphology and mass of dried sediment g^{-1} dry macroalgal mass.

To test the null hypothesis that there was no statistically significant relationship on each measure of macroalgal morphology and the mass of dried sediment g^{-1} dry macroalgal mass a Spearman rank correlation was performed as the scales of macroalgal morphology measurements were not continuous (Dytham, 2003). As mentioned previously, repeated testing on the same experimental data increases the chance of a Type I error (Field, 2005). To limit the overall experimentwise error a Bonferroni correction was applied to the table of correlations (Sokal & Rohlf, 1995).

The sediment grain size composition trapped in the macroalgal species *Corallina officinalis*, *Osmundea pinnatifida* and *Rhodothamniella floridula* was considered. A Bray Curtis similarity matrix was generated from the raw percentage abundance of sediment grain size data which produced a stress value of 0.05 which has a good ordination and little prospect of a misleading interpretation (Clarke & Warwick, 2001). The Bray Curtis similarity matrix was used because it takes into account the rarity or dominance of grain sizes, allows further samples to be added without affecting the similarity of previous samples, and takes the values of 0 and 100 respectively when samples have no grain sizes in common or are identical (Clarke & Warwick, 2001). A graphical representation of the similarity between samples was produced using the Multi-dimensional scaling (MDS) routine in PRIMER with MONTH, SHORE and SPECIES as factors.

The same similarity matrix was then used to perform Analysis of Similarity (ANOSIM) to test the null hypothesis that there was no statistically significant difference in similarity in the overall grain size composition similarity between MONTH (across all shores and species), SHORE (across all months and species) and SPECIES (across all shores and months) (Clarke & Warwick, 2001). Each factor was analysed separately as currently PRIMER only allows two-way ANOSIMs to be performed (Clarke & Warwick, 2001). To examine which grain sizes contributed most to the overall similarity of samples within SITES (across all seasons and species), between MONTH (across all sites and species) and between SPECIES (across all sites and months) SIMPER routine in PRIMER was performed on each of MONTH, SHORE and SPECIES (Clarke & Warwick, 2001). This allows the grain sizes which contribute to both average within group similarity and average dissimilarity between groups to be identified (Clarke & Warwick, 2001).

2.3. Results

2.3.1. Differences in sediment trapping between macroalgal species.

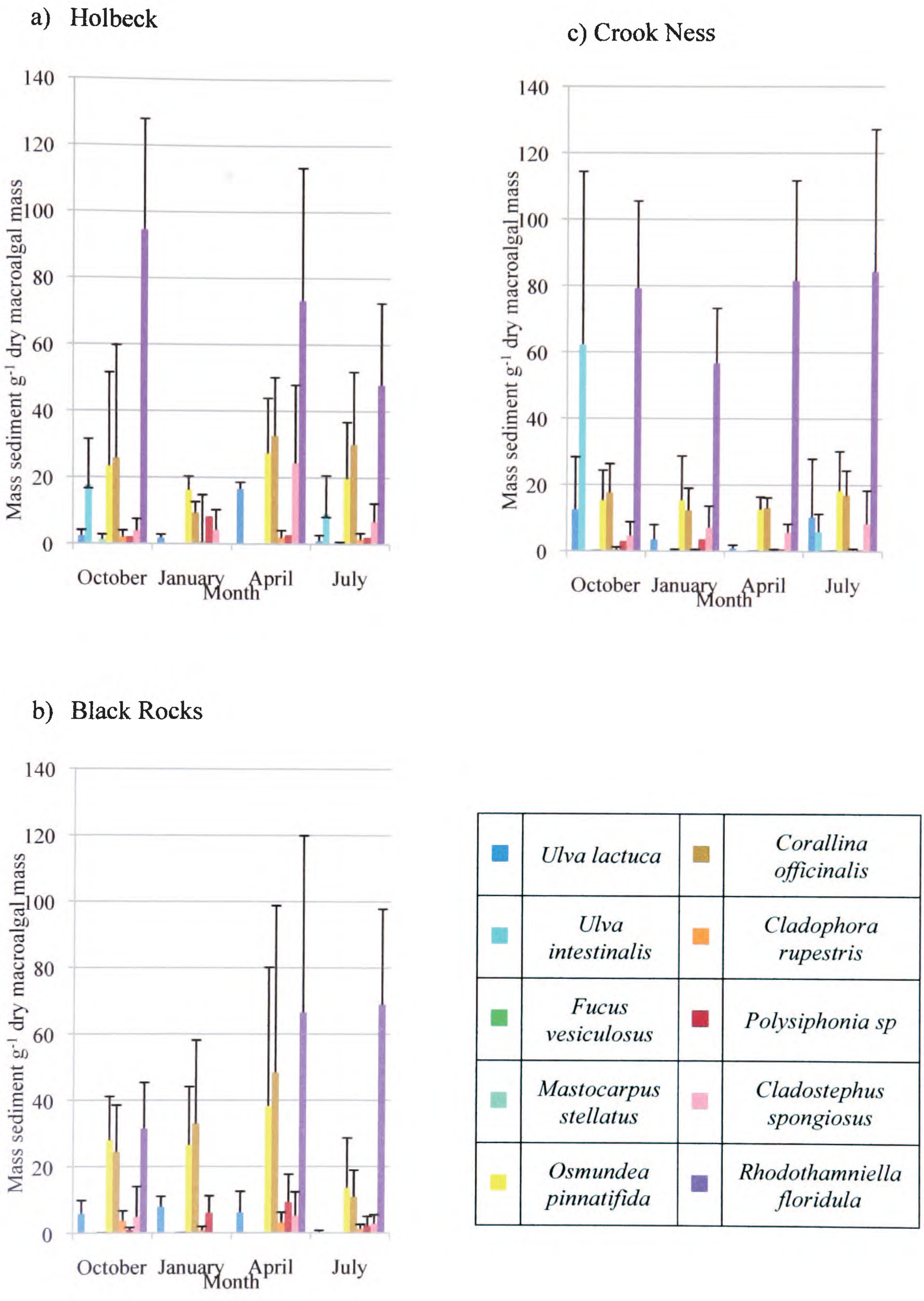
The results of the comparison of dried sediment g^{-1} macroalgal dry mass between shore, month and species are shown in figure 2.3.1. There was no statistically significant difference in the mass of dried sediment g^{-1} macroalgal dry mass between SHORE (table 2.3.1, figure 2.3.1). Statistically significant differences occurred in the mean mass of dried sediment g^{-1} macroalgal dry mass between different MONTHS and between different SPECIES (table 2.3.1, figure 2.3.1).

The mass of dried sediment g^{-1} macroalgal dry mass was lowest during January (figure 2.3.1): this was statistically significantly lower than the mean mass of dried sediment g^{-1} macroalgal dry mass trapped during both October and April (Tukey, $p<0.05$). The greatest mass of dried sediment g^{-1} macroalgal dry mass was trapped in *Rhodothamniella floridula* (Tukey, $p<0.05$). *Osmundea pinnatifida, Corallina officinalis* and *Ulva intestinalis* also trapped a greater mass of dried sediment g^{-1} macroalgal dry mass than other macroalgal species (Tukey, $p<0.05$) (figure 2.3.1). The statistically significant interaction between SHORE and SPECIES (table 2.3.1) indicates that this pattern does not occur at all three sites. Generally there was a large difference in mass of dried sediment g^{-1} macroalgal dry mass between *R. floridula* and all other macroalgal species (figure 2.3.1). However at Black Rocks in both October and April the difference in mass of dried sediment g^{-1} macroalgal dry mass was much smaller (figure 2.3.1b). The mass of dried sediment g^{-1} macroalgal dry mass trapped in both *C. officinalis* and *O. pinnatifida* was generally greater at Black Rocks compared to the two other shores (figure 2.3.1). The mass of dried sediment g^{-1} macroalgal dry mass trapped in *U. intestinalis* was also lower than *O. pinnatifida, C. officinalis* at both Holbeck and Black Rocks, but was greater at Crook Ness (figure 2.3.1)

However there was no statistically statistical interaction between MONTH and SPECIES (table 2.3.1), indicating that the greater sediment trapping of *R. floridula, C. officinalis* and *O. pinnatifida* and *U. intestinalis* occurred during all months, or between MONTH and SHORE (table 2.3.1), indicating that the lower abundance of sediment in January than both October and April occurred at all three sites. There was no statistically significant interaction between MONTH, SHORE and SPECIES (table 2.3.1). Although small variations were found in the mass of dried sediment g^{-1} macroalgal dry mass between most macroalgal species, *U. intestinalis* only trapped large quantities of sediment during October and July (figure 2.3.1), and this only occurred at Holbeck and Crook Ness. During October at Crook Ness the mass of dried sediment g^{-1} macroalgal dry mass in *U. intestinalis* was much greater than during any other month (figure 2.3.1c) or any other shore (figure 2.3.1), even compared to other macroalgal species (figure 2.3.1).

Table 2.3.1: Summary of the results of a three factor GLM ANOVA for dried sediment g^{-1} dry macroalgal mass using SPECIES, SHORE and MONTH as factors.

Source	**DF**	**Adj MS**	**F**	**p**
MONTH	3	976.114	4.116	0.007
SHORE	2	33.549	0.141	0.868
SPECIES	9	19552.157	82.438	<0.001
MONTH * SHORE	6	371.162	1.565	0.156
MONTH * SPECIES	25	332.79	1.403	0.95
SHORE * SPECIES	17	613.712	2.588	0.001
MONTH * SHORE * SPECIES	46	369.819	1.559	0.014
Error	436	237.174		



a) Holbeck

c) Crook Ness

b) Black Rocks

Figure 2.3.1: The mass of dried sediment g^{-1} dry macroalgal mass trapped in ten different macroalgal species with different morphologies on four sampling occasions at three shores (mean, + s.d.).

2.3.2. Relationships between macroalgal morphology and sediment trapping.

With the exception of frond density, all measures of macroalgal morphology were found to have a statistically significant negative correlation with the mass of dried sediment g^{-1} dry macroalgal mass, even after Bonferroni correction (table 2.3.2). Frond density showed a statistically significant positive correlation with the mass of dried sediment g^{-1} dry macroalgal mass, even after Bonferroni correction (table 2.3.2, figure 2.3.2).

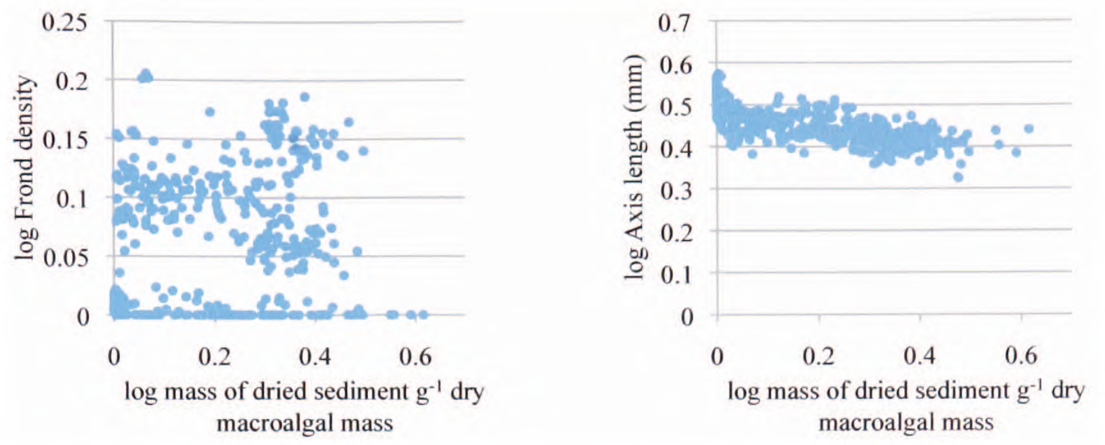
The negative correlation between the mass of dried sediment g^{-1} dry macroalgal mass and both interstitial volume (figure 2.3.2b) and axis length (figure 2.3.2d) are clearly evident. A large number of samples have low interstitial volume and also trap a low mass of dried sediment g^{-1} dry macroalgal mass (figure 2.3.2b). The negative correlation between longest branch and the mass of dried sediment g^{-1} dry macroalgal mass is also readily apparent. However, there was large variation in the mass of dried sediment g^{-1} dry macroalgal mass by samples with no branching. Examination of the individual samples revealed that all were *Ulva lactuca* and some *Ulva intestinalis*. These *U. lactuca* and *U. intestinalis* samples also accounted for the wide range of mass of dried sediment g^{-1} dry macroalgal mass trapped with branching arrangement, pre-branching length and frond density (figure 2.3.2a, c & f).

The negative correlations between the mass of dried sediment g^{-1} dry macroalgal mass and both branching arrangement and prebranching length are less obvious due to the wide variation of the data (figure c & f). In both cases a wide range of branching arrangement and prebranching length measurements trap small masses of dried sediment g^{-1} dry macroalgal mass.

Frond density displayed the only statistically significant positive correlation between macroalgal morphology and mass of dried sediment g^{-1} dry macroalgal mass (table 2.3.2, figure 2.3.2a). A large number of samples with a low frond density trapped a small mass of dried sediment g^{-1} dry macroalgal mass (figure 2.3.2a). However there was a large range in the mass of dried sediment g^{-1} dry macroalgal mass trapped between frond density (figure 2.3.2a).

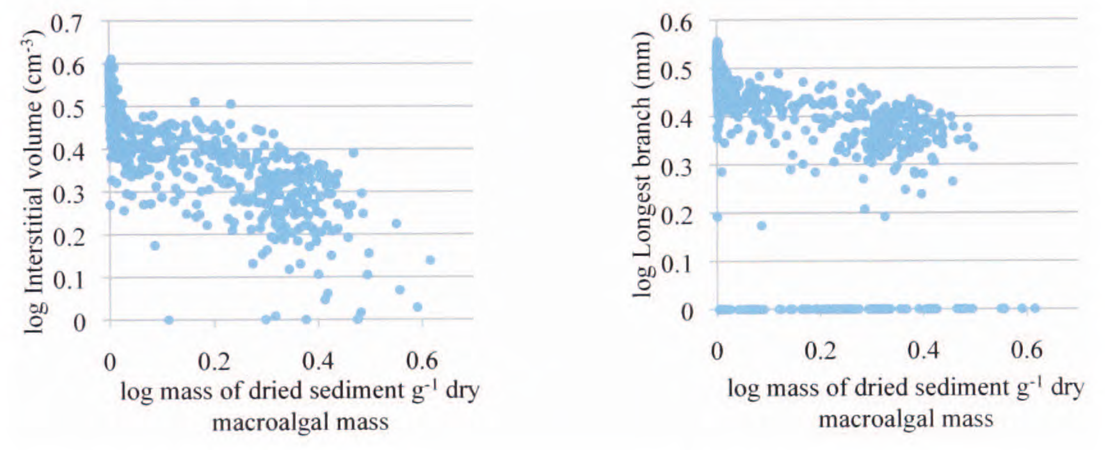
Table 2.3.2: Spearman rank-order correlation (r_s) for each measure of morphology and the mass of dried sediment g^{-1} dry macroalgal mass (* statistically significant at the 0.01 level after Bonferroni correction, ** statistically significant at the 0.001 level after Bonferroni correction) (d.f. = 438 in all cases).

	r_s
Interstitial volume	-0.817 **
Axis length	-0.806 *
Longest branch	-0.630 *
Pre branching length	-0.456 *
Branching arrangement	-0.324 *
Frond density	0.374 *



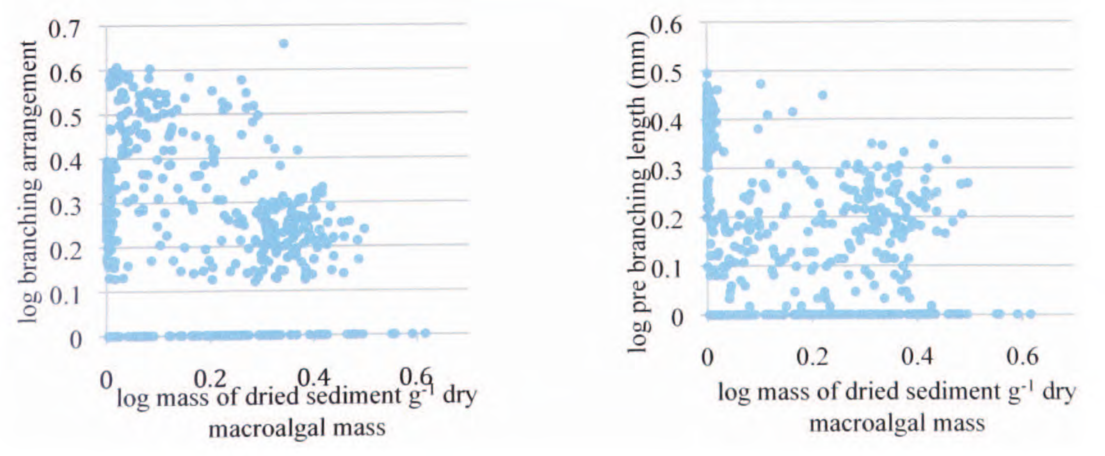
a) Frond density

d) Axis length



b) Interstitial volume

e) Longest branch



c) Branching arrangement

f) Pre branching length

Figure 2.3.2: Scatterplots showing the relationship between mass of dried sediment g^{-1} dry macroalgal mass and elements of macroalgal morphology using eight different species of macroalgae.

2.3.3. Differences in trapped grains size composition between macroalgal species.

The differences in sediment grain size composition between Crook Ness and both Holbeck and Black Rocks are evident in the MDS analysis on a Bray Curtis similarity Matrix (figure 2.3.3). Within the cluster of *Osmundea pinnatifida* and *Corallina officinalis*, to the left of the plot, samples from Crook Ness generally group together to the left of each cluster, whilst Holbeck and Black Rocks samples are interspersed with one another to the right of each cluster (figure 2.3.3).

The effect of MONTH, SHORE and SPECIES on the grain size composition of sediment trapped were each tested using a one-way ANOSIM. There was no statistically significant difference in the similarity of the grain size composition of sediment trapped by MONTH (ANOSIM, Global R = 0.008, p=19.1%). However there was a statistically significant difference in the similarity of grain size composition of sediment trapped by SHORE (ANOSIM, Global R = 0.108, p=0.1%). Pairwise comparisons revealed that there were statistically significant differences in the similarity of grain size composition of sediment trapped between Crook Ness and both Holbeck (p=0.1%) and Black Rocks (p=0.1%).

The similarity in sediment composition at each of the three sites was primarily determined by the percentage abundance of fine sand, which contributed over 40% to the overall similarity of samples at each of the three sites (table 2.3.3). To a lesser extent both very fine sand and medium sand also contribute to the similarity at each of the three sites (table 2.3.3).

The differences between Crook Ness and both Holbeck and Black Rocks were primarily attributable to the proportions of three grain size classes, fine sand, very fine sand and silt. The proportion of fine sand was lower at Crook Ness than either Holbeck or Black Rocks (table 2.3.3, figure 2.3.4), contributing 26.76% to the overall dissimilarity of 36.96% between Crook Ness and Holbeck, and 24.32% of the overall dissimilarity of 33.43% between Crook Ness and Black Rocks. The proportions of both very fine sand and silt were greater at Crook Ness than the other two sites (table 2.3.3, figure 2.3.4), contributing 26.21% and 19.16% respectively to the overall dissimilarity between Crook Ness and Holbeck, and contributing 25.95% and 19.19% respectively to the overall dissimilarity between Crook Ness and Black Rocks.

There was also a statistically significant difference in the similarity of the grain size composition of sediment trapped between SPECIES (ANOSIM, Global R = 0.633, p=0.1%). Pairwise comparisons revealed that there were statistically significant differences in the composition of trapped sediment between all three macroalgal species (p=0.1% in all cases). The MDS analysis on a Bray Curtis similarity matrix showed a clear cluster of *Rhodothamniella floridula* samples to the right of the plot (figure 2.3.3). *Corallina officinalis* samples and *Osmundea pinnatifida* samples display a more widely spread clustering, however the top of the cluster was dominated by *C. officinalis* (figure 2.3.3). The relatively low stress value of 0.05 (figure 2.3.3) highlights the very good repeatability of the plot.

The similarity between *C. officinalis* and *O. pinnatifida* clusters was primarily determined by the percentage abundance of fine sand grain sizes which contribute over 50% to the overall similarity of each of the species (table 2.3.4). The percentage abundance of grain sizes medium sand, very fine sand and very coarse sand also were important in determining the similarity within both the *C. officinalis* and *O. pinnatifida* samples (table 2.3.4). A total of 98.53% of the overall similarity of 84.48% of the *R. floridula* samples was determined by the proportion of smaller grain sizes. Very fine sand contributed 40.96% of the overall similarity, whilst fine sand and silt contributed 29.15% and 28.42% respectively to the overall similarity.

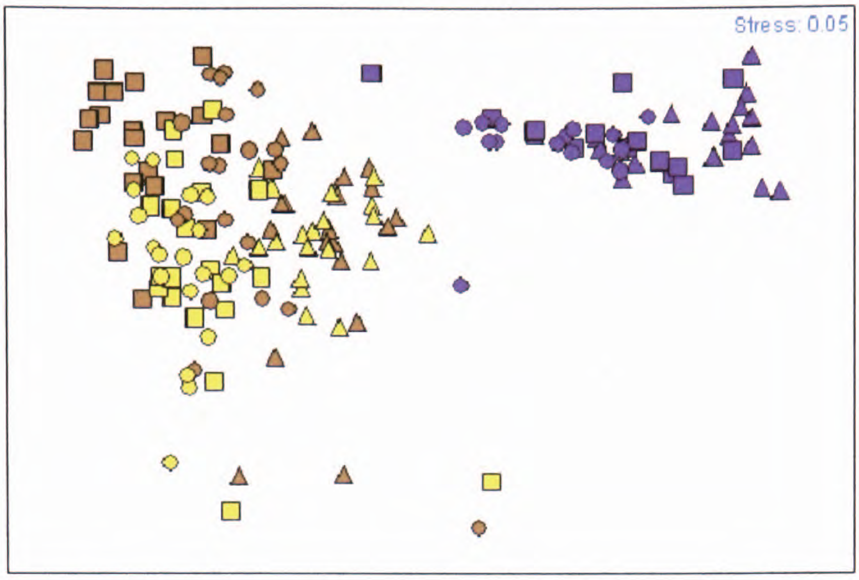
Differences in the grain size composition between *C. officinalis* and *O. pinnatifida* samples were primarily attributable to the greater abundance of fine sand trapped by *C. officinalis* which contributed 30.87% to the overall dissimilarity of 21.33%. The proportion of very fine sand was also greater in *C. officinalis* (contributing 19.67%), but the proportion of very coarse sand was greater (contributing 22.6%) (table 2.3.4, figure 2.3.4). The greater proportion of very fine sand was the most important in determining the differences between *R. floridula* and both *C. officinalis* (contributing 25.78% to the overall dissimilariy of 50.78%) and *O. pinnatifida* (contributing 25.84% to the overall dissimilariy of 51.91%). The proportion of silt was also greater in *R. floridula* than *C. officinalis* and *O. pinnatifida* (table 2.3.4, figure 2.3.4), contributing 23.96% and 23.91% to the overall dissimilarity respectively. Fine sand also contributed to the dissimilarity between *R. floridula* and both *C. officinalis* and *O. pinnatifida*, but the proportion was lower in *R. floridula* (table 2.3.4, figure 2.3.4) contributing 24.98% and 18.91% to the overall dissimilarity respectively.

Table 2.3.3: Grain size classes contributing to the sediment composition for each shore across all three macroalgal species and all four months.

	Holbeck 66.1% similarity		Black Rocks 70.87% similarity		Crook Ness 69.9% similarity	
Sediment grain size class	Percentage composition	Contribution	Percentage composition	Contribution	Percentage composition	Contribution
very coarse sand	9.11	6.05	9.93	7.05	8.08	5.57
coarse sand	2.89	2.33	3.24	2.63	3.38	2.58
medium sand	11.72	11.08	12.43	12.01	8.39	7.7
fine sand	50.53	63.53	48.14	58.93	37.11	43.55
very fine sand	15.76	12.53	16.26	10.09	28.36	30.52
silt	9.11	6.05	9.03	5.14	13.83	10.27

Table 2.3.4: Grain size classes contributing to the sediment composition for each macroalgal species across all three shores and all four months.

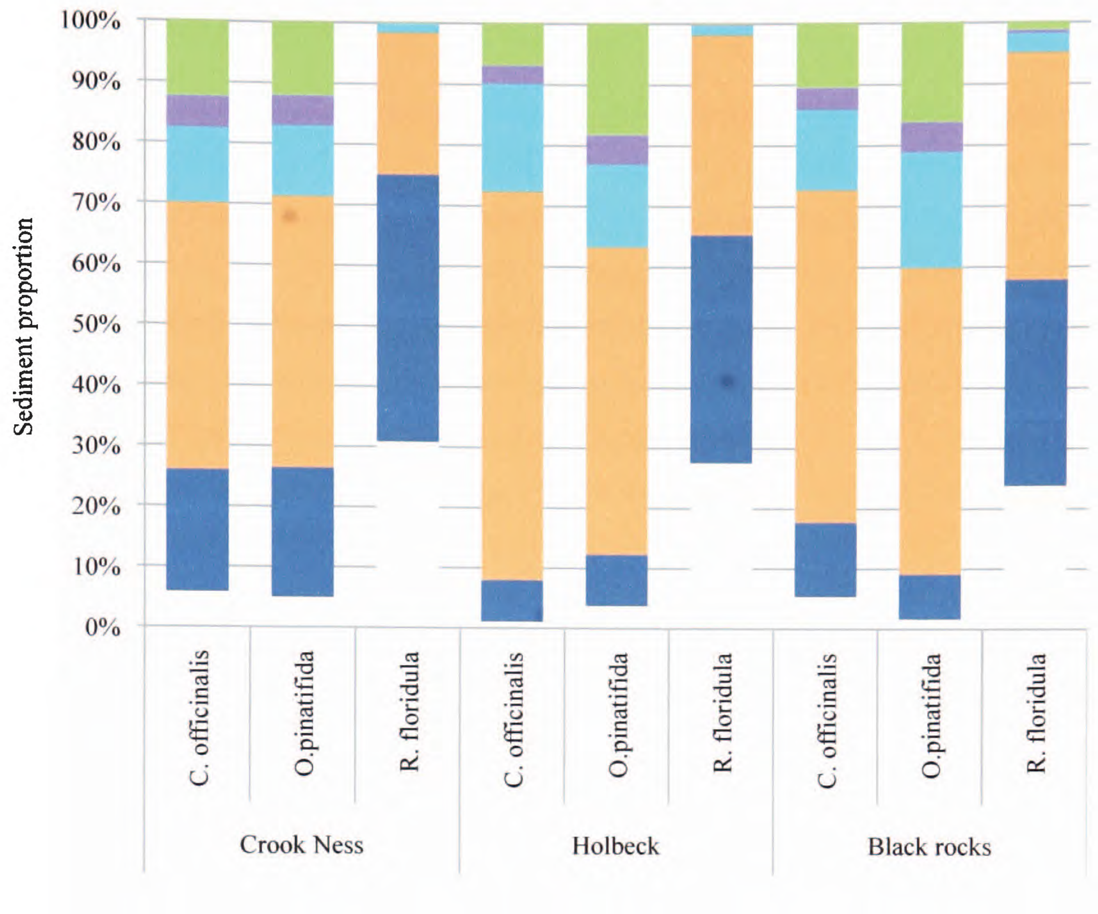
	Corallina officinalis **78.48% similarity**		***Osmundea pinnatifida*** **81.51% similarity**		***Rhodothamniella floridula*** **84.48% similarity**	
Sediment grain size class	**Percentage composition**	**Contribution**	**Percentage composition**	**Contribution**	**Percentage composition**	**Contribution**
very coarse sand	**9.81**	**7.49**	**15.53**	**13.92**	**0.44**	**0.04**
coarse sand	**3.91**	**3.55**	**4.88**	**4.66**	**0.26**	**0.11**
medium sand	**14.28**	**15.14**	**14.63**	**14.92**	**1.94**	**1.32**
fine sand	**53.96**	**60.06**	**48.48**	**54.20**	**30.15**	**29.15**
very fine sand	**12.97**	**11.20**	**12.32**	**10.19**	**38.91**	**40.96**
silt	**4.11**	**2.56**	**3.47**	**2.11**	**27.63**	**28.42**



Key:

■	*Corallina officinalis* Holbeck	■	*Osmundea pinnatifida* Holbeck	■	*Rhodothamniella floridula* Holbeck
▲	*Corallina officinalis* Crook Ness	▲	*Osmundea pinnatifida* Crook Ness	▲	*Rhodothamniella floridula* Crook Ness
●	*Corallina officinalis* Black Rocks	●	*Osmundea pinnatifida* Black Rocks	●	*Rhodothamniella floridula* Black Rocks

Figure 2.3.3: MDS plot of trapped sediment composition for three different macroalgal species (*Corallina officinalis, Osmundea pinnatifida, Rhodothamniella floridula)* on three shores (Crook Ness, Holbeck and Black Rocks) generated from a Bray Curtis similarity matrix of untransformed data.



Key:

🟩	very coarse sand (>1mm)	🟪	coarse sand (0.5mm-1mm)	🟦	medium sand (250μm -0.5mm)
🟧	fine sand (125μm-250μm)	🟦	very fine sand (63μm-125μm)		Silt (<63μm)

Figure 2.3.4: Grain size composition of sediment trapped by three different macroalgal species (*Corallina officinalis, Osmundea pinnatifida, Rhodothamniella floridula)* on three different shores (Crook Ness, Holbeck and Black Rocks) in North Yorkshire.

2.4.4. Summary of key findings

- Statistically significant differences were found in the mass of dried sediment g^{-1} macroalgal dry mass between the different algal species, and between the different months. *Rhodothamniella floridula* trapped significantly more sediment than all other species. *Corallina officinalis, Osmundea pinnatifida* and *Ulva intestinalis* trapped more sediment than the other macroalgal species. The interactions between month and species were not significant indicating that the differences in sediment trapping between species were found during all months.
- There was no significant difference in the mass of dried sediment g^{-1} macroalgal dry mass trapped between the three shores.
- Frond density showed a statistically significant positive relationship with mass of dried sediment g^{-1} macroalgal dry mass. All other measures of algal morphology (interstitial volume, axis length, longest branch, pre branching length and branching arrangement) showed a statistically significant negative relationship with mass of dried sediment g^{-1} macroalgal dry mass, however the strongest correlation was that between sediment mass and interstitial volume.
- The grain size composition trapped by *Rhodothamniella floridula* was statistically significantly different to both *Corallina officinalis* and *Osmundea pinnatifida* and consisted of a greater proportion of smaller grain sizes.

2.4. Discussion

Statistically significant differences were found in the quantity of sediment trapped between the different macroalgal species. The greatest quantity of sediment was trapped by *Rhodothamniella floridula*, and this may be due to its specialisation for trapping sediment. *R. floridula* is recognised as having sand binding properties as a result of the specialized interweaving filaments which are suggested to produce a complex network for particles to adhere to (Dixon & Irvine, 1995). In addition *R. floridula* occurs almost exclusively in sediment covered areas of the intertidal and subtidal areas of rocky shores (Stegenga, 1978). Although *R. floridula* is recognised for its capacity to trap sediment within its structure, there are currently no suggestions as to the potential benefits of trapping sediment of such action.

Osmundea pinnatifida, Corallina officinalis and *Ulva intestinalis* were also found to trap more sediment than the other macroalgal species studied. Possible explanations include greater sediment tolerance than other macroalgal species, thus allowing them to grow in areas with naturally greater sediment accumulation without the competition of other macroalgal species, or due to having a morphology that enhances sediment trapping, or a combination of factors.

All three species are tolerant of sediment inundation (Gorgula & Connell, 2004; Eriksson & Johansson, 2005). In the case of *U. intestinalis* this was related to a life history that has long periods of continuous spore dispersal and sediment tolerant dormancy stages (Eriksson & Johansson, 2005). The greatest quantity of sediment trapping of *U. intestinalis* occurred at Crook Ness during October. The wide standard deviation suggests that samples may have been collected from areas with a wide range of sediment impact. *O. pinnatifida* and *C. officinalis,* as turf species, have been suggested to have morphological attributes including apical meristems to keep dividing above the sediment, and a basal thallus that is resistant to burial and abrasion (Stewart, 1983) making them tolerant to sediment.

Macroalgal morphology also appears be influencing sediment trapping. Sediment trapping is usually associated with short turf species, whether these be species that are fundamentally regarded as turfs (Airoldi, 2003), or juvenile macroalgae which have turf like morphology for a short period of their life cycle (Kennelly, 1989). Both *O. pinnatifida* and *C. officinalis* are recognised as upright turf species (Lobban & Harrison, 1997), with *C. officinalis* reaching a maximum length of 12cm (Hiscock, 1986) and *O. pinnatifida* having an axis length of 2-8cm (Maggs & Hommersand, 2001). Negative correlations were found to occur between axis Length, length of the longest branch and pre-branching length, and this suggests that macroalgal height affects sediment trapping, with shorter turf plants trapping greater quantities of sediment. However *Cladostephus spongiosus* samples collected were not found to trap larger quantities of sediment, and this was a similar size to both *O. pinnatifida* and *C. officinalis*.

However in other aspects of morphology *C. spongiosus* is different to both *C. officinalis* and *O. pinnatifida*, and these may also influence sediment trapping. Whilst *C. officinalis* and *O. pinnatifida* both have an upright morphology, *C. spongiosus* is a delicately branched species, more closely resembling filamentous species such as *Polysiphonia* spp or *Cladophora rupestris* (Lobban & Harrison, 1997; Stengel, *et al.*, 2004). It is also described as having a 'soft' texture rather than being fleshy-wiry (*O. pinnatifida*) or stony (*C. officinalis*) (Lobban & Harrison, 1997). The more rigid structure of *C. officinalis* and *O. pinnatifida* may prevent water flow and inhibit sediment transport as sediment accumulation may be influenced by weak water circulation patterns around macroalgae that inhibit sediment transport rates (Eckman, *et al.*, 1989), and this may be enhanced by the shorter length. Larger species may sweep away surrounding sediment (Kennelly, 1989). Instead sediment trapping in filamentous species may to be the result of small grains sticking to the surface (Boney, 1978), and so would be limited by the available surface area.

Statistically significant correlations were also found to occur between the morphological measurements of frond density, interstitial volume, branching arrangement and pre-branching length with the quantity of sediment trapped. This suggests that these morphological features may also be important in determining sediment trapping by macroalgae. Frond density had the only statistically significant positive correlation with the quantity of sediment trapped. Water flow is reduced by the presence of algae compared with open water (Eckman, *et al.*, 1989). In a similar way, higher frond density may have smaller spaces between the branches, which could result in decreased water flow. Decreased water flow has been suggested to result in greater sediment accumulation (Schiel, *et al.*, 2006). However frond density does not fully describe space occupied by branches due to the different widths of macroalgal species, and this may explain the large variability between the results. Interstitial volume, however, allows the space between the fronds to be quantified. The negative correlation between interstitial volume and the quantity of sediment trapped suggests that the larger spaces between the fronds, which may have a greater water flow, result in less sediment being trapped.

Whilst statistically significant correlations were found to occur between all measurements of macroalgal morphology and the quantity of sediment trapped, the relationship is not readily apparent in some of the figures (*e.g.* figure 2.3.2c). The analysis was performed on a large number of samples (n = 440), and for each measure of complexity a wide range of values was obtained due to the different morphological structure of the algae. The morphology of species with limited branching like *Ulva lactuca* and *U. intestinalis* still accumulated sediment but may have low values of a given measure of algal morphology when compared to the other species, creating a noisy scatterplot. However, despite this, the significant correlations obtained still indicate that there is a relationship between the morphological trait and sediment accumulation. The inclusion of such morphologically simple species may mask the strength of the relationship between sediment trapping ability and algal morphology.

The wide range of sediment trapped by macroalgal species with limited branching highlights the fact that not all variation in sediment trapping can be entirely explained by macroalgal morphology. This is further highlighted by the greater quantity of sediment trapped by *U. intestinalis* compared to other macroalgal species. *U. intestinalis* has a simple morphology with little branching, and therefore morphological structure may not be playing a large role in the quantity of sediment it traps.

In this study measurements of morphology have been restricted to individuals, but this does not consider how individuals may interact together and the influence this has on sediment trapping. *U. intestinalis* form dense mats of individuals (Lobban & Harrison, 1997) and this may trap sediment in a similar way to *Rhodothamniella floridula*. *O. pinnatifida* and *C. officinalis* also occur in large patches. If sediment transport is limited by macroalgae reducing water flow (Eckman, *et al.*, 1989), then this may result in greater sediment accumulation where water movement has been slowed by macroalgae over a larger area.

However, further work would be required to understand how individual macroalga interact together to influence sediment trapping.

In addition to an examination of the quantity of sediment trapped by macroalgae, the grain size composition trapped by *Rhodothamniella floridula, Osmundea pinnatifida* and *C. officinalis* was also examined. *C. officinalis* and *O. pinnatifida* trapped a similar grain size composition, but this was different to the sediment grain size composition trapped by *R. floridula*. *R. floridula* trapped a higher proportion of the smaller grain sizes, with the majority of the sample containing fine sand and smaller grain sizes. *R. floridula* was found occurring lower on the shore at all three sites than either *O. pinnatifida* or *C. officinalis* (personal observation). The grain size composition of *O. pinnatifida* has been found to consist of more larger grain sizes higher up the shore (Prathep, *et al.*, 2003). This was suggested to relate to differences in the sediment load in the water column (Prathep, *et al.*, 2003). However the difference in shore height between the samples of *R. floridula, C. officinalis* and *O. pinnatifida* was not as large as the differences in shore heights in the previous study of *O. pinnatifida*. Therefore it seems unlikely that the differences in grain size composition are related to shore height.

As discussed previously morphology appears to be affecting the quantity of sediment trapped, it may also, however, be affecting the grain sizes trapped. Morphologically the three species are different, although *C. officinalis* and *O. pinnatifida* are both turf species. *R. floridula* consists of very fine filaments (diameter of 20-30μm) that interweave to produce a complex network (Dixon & Irvine, 1995). This produces a matted morphology with only small spaces between the filaments. This may only allow fine particles to be trapped within the structure. The spaces between the fronds of both *C. officinalis* and *O. pinnatifida* are much larger. This has the potential for larger particles to be trapped within the structure. Sediment particles within turf species are also constantly being resuspended and moved (Stewart, 1983; Airoldi, *et al.*, 1996). Fine particles only require small amounts of energy to be resuspended, and therefore would be the most easily resuspended and removed particles from *C. officinalis* and *O. pinnatifida*, whereas the interweaving filaments of *R. floridula* trap sediment (Dixon & Irvine, 1995) and this may limit resuspension.

However differences in the composition of grain sizes trapped cannot be purely related to macroalgal morphology. Differences in trapped sediment grain size composition were found between Crook Ness and the two other sites. The difference occurred in all three macroalgal species. This suggests that the sediment trapped by the macroalgae was related to the composition of sediment entering the shore in addition to macroalgal morphology. Gibbons (1988) also suggested that sediment trapped by artificial macroalgae was similar to that found on the surrounding shore. The grain sizes being trapped at Crook Ness were finer than on the two other shores. Larger grain sizes require more energy for movement (Haslett, 2000); therefore they will be the first to be deposited. The sites at Holbeck and Black Rocks are close to two large sandy beaches, and therefore large grain sizes may be transported over this short distance, which could potentially be trapped by the macroalgae. Crook Ness is approximately 6.5 miles from a large sandy beach from which sediment could be transported. Due to the large amount of energy required to move the larger grain sizes, movement would be slower than for the smaller grain sizes. This potentially means that sediment in the water column would contain a higher proportion of the smaller grain sizes to be trapped by macroalgae, resulting in the differences between the sites.

The quantity of sediment trapped is also affected by factors other than the macroalgal species themselves. The quantity of sediment trapped was found to vary between the four different months sampled. The lowest quantities of sediment were found trapped in January whilst the greatest quantities of sediment were identified in October and April. A previous study into sediment trapping in *Corallina officinalis* also found that sediment trapping was lower in winter (Stewart, 1983) but there were no explanations for such differences. As there was no difference in the quantity of sediment trapped between the three shores, and the differences between months were found to occur on all three shores, this suggests that sediment trapping on the shore may be related to large scale changes in sediment dynamics.

It has been suggested that sediment accumulation is the result of increased sediment loads in the water column during stormy weather (Prathep, *et al.*, 2003). Heavy rainfall and wind induced wave action have also been used to explain the greater sediment accumulation during autumn (Airoldi, *et al.*, 1996). Storms influence sediment deposition and movement on intertidal rocky shores (*e.g.* Daly & Mathieson, 1977; Collinson & Thompson, 1982;

Prathep, *et al.*, 2003), and as storms occur during both autumn and spring this may result in the observed greater sediment trapping during October and April. However stormy weather also occurs during winter months and lower sediment trapping was found to occur during January.

Stewart (1983) suggested that sediment was continually being deposited, washed from, and moved through macroalgae. He found that considerable variations occurred in the quantity of sediment trapped between extreme conditions (Stewart, 1983). As sampling on each shore only took place on a single occasion within each season, the differences observed in the quantity of sediment trapped may be the result of fluctuations in the quantity of sediment rather than seasonal differences.

Alternatively the differences in sediment trapping between months may be the result of seasonal differences in the morphology of macroalgae. As previously discussed, macroalgal morphology appears to be having at least some influence on sediment trapping. Variations in macroalgal morphology in some species are very dramatic (*e.g.* the life stages of *Dumontia contorta* which exists as a crust during the summer months, with fronds growing during November until Spring, [Dixon & Irvine, 1977]) or can be smaller changes as a result of periods of growth (Lee, 1999; Lehvo, Back & Kiirikki, 2001), breakage from storm damage (Williams, 1996) or related to reproductive stages (Dethier, 1982). No regular seasonal changes have been observed in *Cladophora rupestris* (Burrows, 1991), *Polysiphonia* spp (Lee, 1999), *Ulva intestinalis* (Burrows, 1991). However *Ulva lactuca, Fucus vesiculosus, Mastocarpus stellatus, Osmundea pinnatifida,* and *Rhodothamniella floridula* all display some elements of seasonal growth. *U. lactuca* occurs at all times of year (Burrows, 1991) but growth is seasonal predominantly taking place during the summer (Lee, 1999). *R. floridula* also occurs throughout the year; however growth is most luxuriant during winter (Dixon & Irvine, 1995). The growth rates of *F. vesiculosus* peak during summer between May and June although growth continues throughout the year (Jormalainen, *et al.*, 2001). The reproductive tissue and parts of branches of *F. vesiculosus* are also shed during the late summer/ early autumn after the reproductive period (Berger, *et al.*, 2001). The changes in morphology of *O. pinnatifida* are also related to reproductive cycles with spermatangia being produced between February and June, Cystocarps between March and June and Tetraspoangia between October and December (Neto, 2000). Seasonal reproductive changes also occur in *M. stellatus* with tetrospores being formed during winter and maturing in spring (van den Hoek, *et al.*, 1995).

However, as changes in the morphology of the macroalgal species sampled occur at different times of the year, if these small changes in morphology were having a large affect on sediment trapping then a statistically significant interaction would be found to occur between species and month. This was not found to be the case. Therefore, as neither macroalgal morphology, nor seasonal differences in sediment in the water column provide a clear explanation as to the differences between months this suggests that a number of factors may be interacting together to influence sediment trapping.

The complexity of separating the factors affecting sediment trapping by macroalgae is further highlighted by the lack of statistically significant differences between shores, whilst statistically significant interactions were found to occur between shore and species, and also between month, shore and species. The three shores were chosen on the basis that they were close to one another and had similar aspects, wave exposure, topography and species composition. Therefore no differences between shores would be expected. However sediment movement has also been suggested to be affected by localised changes in topography (Littler, *et al.*, 1983). Localised sediment movement may also be affected by macroalgae changing patterns of water flow (Eckman, *et al.*, 1989). These localised differences may result in the large standard deviation observed within all species, at all sites and during all months. These large differences in an individual species are particularly evident in the sediment trapping of *Ulva* species, which had very large variations in sediment trapping between both months and sites with no clear pattern occurring. Therefore, although macroalgal morphology appears to influence sediment trapping the differences between months and sites show that other factors are also important.

Chapter 3

The effect of macroalgal community structure on sediment trapping

3.1. Introduction

Differences in sediment trapping have been found to occur between different species of macroalgae (Chapter 2.3; *e.g.* Iseaus *et al*, 2004; Boney, 1978). The differences in the quantity of sediment trapped have been found to relate to differences in macroalgal morphology (Chapter 2.3). However the sediment trapping by macroalgae may also be affecting by a variety of other factors including surrounding topography (Littler, *et al.*, 1983), sediment supply (Gibbons, 1988), shore height (Prathep, *et al.*, 2003), and season (*e.g.* Stewart, 1983; Airoldi, *et al.*, 1996). The surrounding macroalgae may also have an effect on sediment trapping.

Both Daly & Mathieson, 1977 and Littler *et al*, 1983 found that the areas inundated by sediment were characterised by opportunistic species including *Chaetomorpha linum* (Müller) Kützing, *Cladophora* spp, and *Ulva* spp. These opportunistic species have a number of characteristics that allow them to survive in sediment inundated areas including: high productivity, low biomass, opportunistic life histories, emphasis on the herbivore trophic levels and opportunistic reproductive strategies (Littler, *et al.*, 1983).

Not only do opportunistic species survive in areas of sediment inundation, but a variety of species also appear to be psammophytic, i.e. sand loving. Species including *Ahnfeltia plicata* (Hudson) Fries, *Ahnfeltiopsis linearis* (Agardh) Silva & DeCew (as *Gymnogongrus linearis*) and *Gigartina papillata* (Agardh) Agardh have been found to occur in areas with irregular sand inundation. It has been suggested that these have morphological and reproductive adaptations to sandy habitats which include being tough and wiry with the potential to regenerate from basal holdfasts (discussed in Daly & Mathieson, 1977). Although macroalgal species may occur in areas of sediment, these are not all sediment dependant: *Codium setchellii* Gardner appears to be sediment dependant but is able to survive in non-sediment inundated areas if protected from herbivoury (Trowbridge, 1992). This, and the suggested adaptations to survive sediment inundation suggest that, in the majority of macroalgal species, rather than being 'sediment loving', psammophytic species are just better adapted to surviving in areas of sediment.

Of those macroalgal species that have been proposed to be psammophilic, only *Rhodothamniella floridula* has specialised interweaving lateral filaments that produce a complex network to which sediment particles can adhere (Dixon & Irvine, 1995). However, the tightly packed fronds of filamentous turf may trap sediment, and filling the spaces between the fronds may prevent the settlement of other macroalgal species allowing the species to become dominant (Lobban & Harrison, 1997). A variety of macroalgal species can trap sediment within their structure. As discussed in Chapter 2.1, a variety of macroalgal species including *Fucus serratus* (Isaeus, *et al.*, 2004) *Agarum fimbriatum* (Eckman, *et al.*, 1989), *Osmundea pinnatifida* (Prathep, *et al.*, 2003) and *Corallina officinalis* (Kelaher, *et al.*, 2001) have been found to trap sediment.

Species on intertidal rocky shores do not live in isolation on the shore. Instead they live in a community consisting of a variety of macroalgae and animals (Lobban & Harrison, 1997). As discussed in Chapter 1, both macroalgae and fauna influence the organisms around them. In addition, physical differences including length of time exposed to terrestrial conditions, temperature, and wave exposure found down the shore, have a structuring affect on the community, influencing the areas in which particular macroalgal species are found. Whilst the species of macroalgae found in different areas of the shore may change (Stephenson & Stephenson, 1949; Little & Kitching, 1996), similar gross morphologies are often found (e.g. the canopy species *Fucus vesiculosus* is found in the mid shore, whilst *Fucus serratus* is found in the low shore and *Laminaria* sp occurs in the sublittoral, [Dring, 1982]).

It has been proposed that macroalgal species with similar morphological and anatomical features can be categorised into functional groups (Steneck & Watling, 1982; Padilla & Allen, 2000). These groups have similar functional attributes (Bonsdorff & Pearson, 1999) and can play equivalent roles within an ecosystem (Koehl, 1996). The traditional functional groups initially proposed by Littler and Littler (1980), were based on primary productivity (Littler & Littler, 1980) and ease of feeding by grazers (Steneck & Watling, 1982). Macroalgal species can, however, also be grouped into broader categories based on their morphology, such as turf, encrusting and canopy species. These more general groupings have been used in a variety of studies, especially where a number of different species with similar morphological types exist together (*e.g.* Connell, 2003a); Gorgula & Connell, 2004; Benedetti-Cecchi & Cinelli, 1992).

Whilst groups of species with similar morphologies may play equivalent roles within an ecosystem (Koehl, 1996), the different groups also have the potential to interact with each another. The canopy species *Ecklonia radiata* (Kennelly, 1989; Wernberg, *et al.*, 2005), *Pterygophora californica* Ruprecht (Reed & Foster, 1984; Clark, *et al.*, 2004) and *Macrocystis pyrifera* (Clark, *et al.*, 2004) have all be found to reduce light levels under their canopy cover. This reduction in light has an impact on the composition of the macroalgal community below. Experimental removal of *E. radiata* canopy cover in Marmion, Western Australia was found to double the number of understory macroalgal species (Wernberg, *et al.*, 2005). This was postulated to be related to increased light availability when canopy was removed, because where canopy was replaced by a dark Perspex sheet no differences in the number of macroalgal species was found compared to areas with *E. radiata* canopy cover (Wernberg, *et al.*, 2005). In contrast, studies in Port Jackson, Sydney, Australia found that species richness decreased with canopy removal (Kennelly, 1989). Canopy cover may provide protection from light as the removal of canopy cover resulted in the bleaching of the thallus of some turf species including *Corallina officinalis* and *Chondrus crispus* Stackhouse on the Isle of Man, UK, although there was little difference in community composition (Jenkins, *et al.*, 1999).

Canopy species also provide turf species with protection from desiccation (Dayton, 1975). On the Washington (USA) coastline, the removal of *Saccharina sessilis* (Agardh) Kuntze (as *Hedophyllum sessile*) resulted in a decline in understory macroalgal species which was attributed to a lack of protection from canopy (Dayton, 1975). This was further highlighted by the recovery of the understory as the canopy recovered (Dayton, 1975).

Turf species may also provide a level of protection for canopy species. In 20cm x 20cm plots where the turf species *Chondracanthus intermedius* (Suringar) Hommersand had been selectively removed, the percentage cover of the canopy species *Pterocladia capillacea* (Gmelin) Bornet was significantly lower than in undisturbed plots (Kim, *et al.*, 2004). The authors suggested that *C. intermedius* provided protection from desiccation, due to *C. intermedius* retaining water, and also buffering from wave action (Kim, *et al.*, 2004). Turf species may also provide protection for juvenile canopy species by preventing them from being scrapped away by mature canopy fronds (Black, 1974) as recruitment of juveniles has only been found to occur under canopy where turf species were also present (Brawley & Johnson, 1991; Benedetti-Cecchi & Cinelli, 1992). In addition, the algal turf provided the juveniles with protection from water displacement (Brawley & Johnson, 1991; Benedetti-Cecchi & Cinelli, 1992), wave action, and also acted as a refuge from grazers (Benedetti-Cecchi & Cinelli, 1992). The effects of canopy scour appear to be restricted to juvenile canopy species, with little affect to other understory species (Kennelly, 1989). However this may be related to the morphology of the canopy species, as abundance of articulated algae increased with increasing stipe length and width of canopy cover whilst encrusting algal cover decreased and there was no significant relationship with filamentous macroalgae (Fowler-Walker, *et al.*, 2005). This was postulated to be because a shorter stipe led to more severe abrasion of encrusting algae (Fowler-Walker, *et al.*, 2005).

As discussed in Chapter 2.1, sediment trapping is generally associated with turf species (Airoldi, 2003; Gorgula & Connell, 2004), whilst canopy species have been found to both enhance sediment accumulation, (Eckman, *et al.*, 1989) and decrease it (Kennelly, 1989; Melville & Connell, 2001). However, turf species do not live in isolation on the shore and, as discussed previously, turf and canopy species interact with one another to influence the conditions around them. Juvenile canopy species may act in a similar way to turf species, and Kennelly (1989) found that sediment trapping by juvenile *Ecklonia radiata* was lower when canopy cover was present than with just juveniles.

3.1.1. Rationale and Aims

As discussed previously (Chapter 2.4) different macroalgal species trap different quantities of sediment. Although differences are recognized to occur between individual species, generalisations have also been made into the similarities in the amount of sediment trapped with similar morphologies (Airoldi, 2003). Juvenile canopy species, which have been suggested to have a similar morphology to turf species, have been found to trap more sediment than canopy species (Kennelly, 1989). As discussed previously, functional groups have been created based on macroalgal species playing equivalent roles within an ecosystem (Koehl, 1996). As sediment trapping appears to be based on morphologically, this suggests the need to examine differences in sediment trapping between morphological groups.

Species on the shore also do not exist in isolation, instead they form part of a community. Within this community they have the potential to interact with one another influencing light (*e.g.* Clark, *et al.*, 2004; Wernberg, *et al.*, 2005), desiccation (Dayton, 1975; Kim, *et al.*, 2004) and scour (*e.g.* Black, 1974; Kennelly, 1989). There is therefore a need to explore sediment trapping in the context of interactions between different morphological groups. This chapter describes investigations:

1) To determine if there was a difference in the amount of sediment trapped by different macroalgal communities at four different times of the year and on three different shores.

3.2. Methods

The three shores described in Chapter 2, Crook Ness, Holbeck and Black Rocks, were chosen as sites for the experiment and the justification for their use and full site descriptions are outlined in section 2.2.1. A manipulative experiment was designed to examine the quantity of sediment trapped between the different morphological groups of macroalgae, across three different shores, and between four different times of year. Morphological groups of macroalgae were used rather than individual species because sediment accumulation has been related to generalised groupings of species *e.g.* turf species (Airoldi, 2003), although some work has also been done on individual canopy species (*e.g.* Kennelly, 1989; Connell, 2003b). Species with similar morphological and anatomical attributes have similar functional attributes (Bonsdorff & Pearson, 1999) and can play equivalent roles within an ecosystem (Koehl, 1996). Species were classified as either being canopy species (continuous vegetation in the uppermost layer of the community [Melville & Connell, 2001]) or turf species (tightly packed upright branching species [Hay, 1981] that are shorter than canopy species). This resulted in four different macroalgal treatments containing different combinations of the morphological groups; canopy species only (c), turf species only (t), both canopy and turf species (c/t), and bare rock (b). An orthogonal design was employed with each of the factors was present in combination with every other factor (Underwood, 1997). This not only allowed the determination of where differences occurred within a factor, but also where any interactions occurred (Underwood, 1997).

Within each shore an area of relatively flat bed rock was selected for manipulation, to minimise the influence of topography on sediment deposition (Jørgensen & Gulliksen, 2001; Littler *et al*, 1983), in the biological lower mid shore, characterised by the presence *Fucus vesiculosus, Fucus serratus* and *Semibalanus balanoides* (Stephenson & Stephenson, 1949). On each shore the area used was predominantly covered by the turf species *Osmundea pinnatifida* and *Corallina officinalis*, with a canopy cover of predominantly *F. vesiculosus* and *F. serratus*. On each shore, four plots were positioned to allow replication of each treatment (figure 3.2.1). These were positioned between approximately one and two meters apart both across and down the shore. This minimised the effect that the adjacent plots had on one another.

Each of the four plots on a shore consisted of a prepared 0.5m by 0.5m area of each of the four different treatments placed adjacently and arranged in a different order to the other plots on the shore (figure 3.2.1). This was to minimise any observed differences being the result of the surrounding treatments, rather than the studied treatment. Above and below the plot a 0.5m wide strip was cleared of all algae (figure 3.2.1). This minimised the effect of the surrounding algae upon sediment trapping within the treatments.

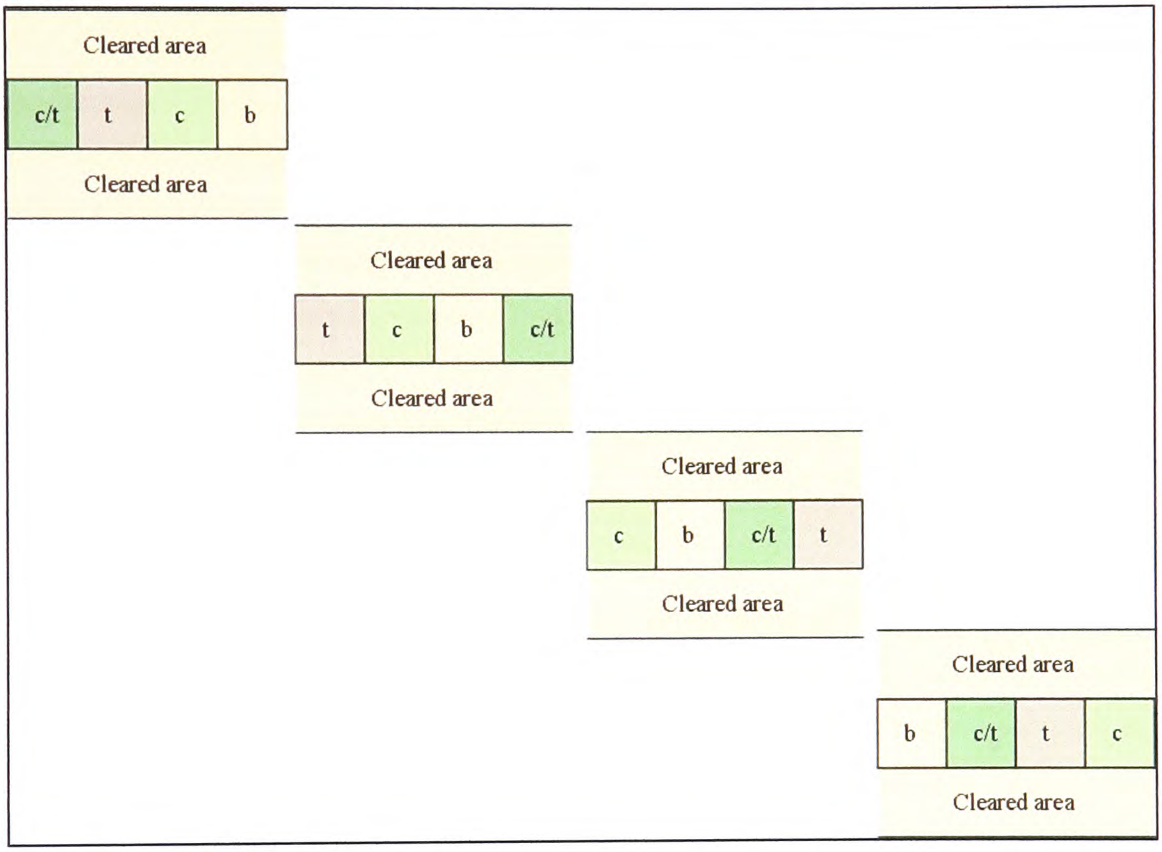


Figure 3.2.1: Arrangement of the plots and macroalgal treatments (canopy species only [c], turf species only [t], both canopy and turf species [c/t], and bare rock [b]) on each of the three shores (Crook Ness, Holbeck and Black rocks).

The removal of the macroalgae, was performed manually using a metal scraper (Lubchenco, 1980; Underwood, 1980), however this did not entirely remove encrusting algae. However the use of acids (Underwood, 1980) or burning with a propane torch (Lubchenco, 1980) to remove such species would have resulted in damage to the surrounding algae. Encrusting algae would only have to potential to trap sediment in the same way as a rock surface and therefore the complete removal deemed unnecessary. The careful manual removal of macroalgae within the treatments ensured only the required morphologies of macroalgae were removed whilst limiting damage to the other species. The plots were initially cleared during October 2007, however immediately prior to each sampling the plots were checked and any unwanted algae removed.

Plastic scouring pads have been used as a substitute for macroalgae (Gibbons, 1988). In addition to providing a habitat for fauna, they have also been shown to trap sediment within their structure (Gibbons, 1988). A pilot study was undertaken to determine which type of scourer would be an appropriate sediment trap for the experiment, four different types of scourers were attached to macroalgae at Holbeck using cable ties (to minimise the number of holes being drilled in the substrate). The scourers were collected after 24 hours and the sediment removed by washing in freshwater. All four types of scourer were found to trap sediment, however there was variation in the quantity and grain size of sediment trapped and ease with which sediment could be washed from the scourer. From the pilot study green, plastic meshed scourers were deemed most appropriate as they trapped a measurable quantity of sediment of all grain size classes. The sediment was also relatively easily removed by washing.

The sediment moving across each treatment was trapped using green plastic mesh scouring pads positioned in the centre of each of the treatments. The scouring pads were wrapped around cord and secured with a cable tie. The cord was then secured to screws at each end of the sample plot. Scourers were used instead of conventional sediment traps because breaking waves have the potential to wash sediment out of conventional sediment traps (Schiel, *et al.*, 2006). Schiel *et al.* (2006) compared a number of sediment traps for use in intertidal areas, however all the traps that they tried differed in the composition of sediment that they trapped. They also identified additional difficulties in ensuring sediment traps were securely attached and ensuring that the traps were sturdy enough to prevent wave damage. In addition to these considerations, all three shores, especially Holbeck, are frequently visited by members of the public, and so there was a need for sediment traps to be relatively inconspicuous.

Sampling took place during February 2008, May 2008, August 2008 and November 2008. The shores were sampled, where possible, over four consecutive days. This limited the effect of changing environmental conditions on the quantity of sediment trapped between shores. Although, as has been previously discussed in Chapter 2, sediment movement can occur during a single tidal cycle (Daly & Mathieson, 1977) sampling on a single day was impractical. The scourers were in position for 24 hours (two tidal cycles) before collection. On return to the laboratory the scourers were carefully washed in freshwater to remove the sediment. Sediment was dried at 70°C in a Leader oven over night (Stewart, 1983), and the scourers were air dried to a constant weight. The mass of sediment g^{-1} dry scourer mass was calculated.

3.2.1. Data Analysis

Due to adverse weather conditions, scourers were lost during February 2008 resulting in the retrieval of only one sample of each treatment at Black Rocks. Due to the lack of replication of one factor the data obtained was not orthogonal as originally planned. Therefore data were pooled by month to examine if there was a statistically significant difference in amount of trapped sediment between TREATMENT (c/t, c, t and b) or SHORE (Crook Ness, Holbeck and Black Rocks). Data was pooled by shore to examine if there was any statistically significant difference in the amount of trapped sediment between TREATMENT (c/t, c, t and b) or MONTH (February, May, August and November). The use of the data in multiple comparisons increases the chance of a Type I error occurring (Underwood, 1997). In addition, due to the experimental design, pooling the data by shore resulted in the samples not being independent which is an assumption for parametric tests (Dytham, 2003). Therefore the level of significance was considered to be 0.01 rather than 0.05 to counteract this (Underwood, 1981).

The null hypothesis under test was that there was no statistically significant difference in the mean mass of sediment g^{-1} dry scourer mass between the four different macroalgal TREATMENTS and between the three SHORES. Data were analysed for normality using Kolmogorov-Smirnov test and homogeneity of variances using Levenes test. The data did not conform to normal distribution (Kolmogorov-Smirnov test, $p<0.05$) nor could the variances be considered homogenous (Levenes test, $p<0.05$). Log10 transformation of the data, because the variances were greater than the mean (Fowler, *et al.*, 1998), did not result in the assumptions of normal distribution or equal variances in the data being met. It was deemed appropriate to carry out a 2-way two-way independent GLM ANOVA even though the assumptions of normality and homogeneity of variance had been violated. The Scheirer-Ray-Hare test provides a non-parametric equivalent to a 2-way independent GLM ANOVA, however there is considerable debate as to whether the Kruskal-Wallis test can be extended to two-way analysis in the form of the Scheirer-Ray-Hare test (Dytham, 2003). The use of a non-parametric test also limits the potential for *post hoc* testing. ANOVA is relatively robust to non-normality and heterogeneity of variances although it increases the probability of a Type I error (Underwood, 1997). The use of non-parametric tests also does not solve the problems of heterogeneity of variances (Underwood, 1997). However, due to the increased probability of a Type I error the results were interpreted with caution. A two-way independent GLM ANOVA was performed with TREATMENT as a fixed factor with four levels and SHORE as a fixed factor with three levels (Underwood, 1997). TREATMENT and SHORE were both independent variables, and mass of sediment g^{-1} dry scourer mass was the dependant variable (Pallant, 2001). *Post hoc* Games-Howell tests were used to determine where any statistically significant differences occurred. This test was appropriate as it was designed for use with unequal population variances and unequal sample sizes (Field, 2005). It is also a powerful test but is not affected by small sample sizes (Field, 2005), as was the case in this experiment.

The null hypothesis that there was no statistically significant difference in the mean mass of sediment g^{-1} dry scourer mass between the four different macroalgal TREATMENTS and between the four sampling MONTHS was also tested. The mass of sediment g^{-1} dry scourer mass data did not to conform to normal distribution (Kolmogorov-Smirnov test, $p<0.05$) but variances were homogenous (Levenes test, $p>0.05$) and Log10 transformation of the data, did not result in the assumption of normal distribution being met. However as the samples were not independent between months (as they were collected from the same site on the shore) a repeated measures approach was used for analysing the data. The data was tested for sphericity using Mauchly's test (Field, 2005) and were found to violate the assumption of sphericity (Mauchly's test, $W=0.007$, $p<0.001$). Transformation of the data did not result in the data conforming to sphericity. Although the assumptions of sphericity and normality had been violated, a mixed design GLM ANOVA was used in preference to MANOVA due to the greater power of the ANOVA test (Field, 2005). To account for the violation of the assumption of sphericity, a Greenhouse & Geisser correction was applied to produce a valid F-ratio (Field, 2005). This was more appropriate than the Huynh & Feldt correction due to being more conservative than the latter preventing a false null hypothesis being rejected (Field, 2005). A two factor mixed design GLM ANOVA was performed with TREATMENT as a fixed factor with four levels (c/t, c, t and b) and MONTH as a fixed factor with four levels (February, May, August and November). TEATMENT was an independent variable, MONTH was a repeated measure, mass of sediment g^{-1} dry scourer mass was the dependant variable (Pallant, 2001). *Post hoc* Bonferroni procedure tests, which are more appropriate for smaller sample sizes (Field, 2005), were used to determine where any statistically significant differences occurred between treatments. This test was selected due to the robust nature of the test when the assumption of sphericity has been violated in terms of the power and control of Type I errors (Field, 2005).

3.3. Results

The results of the comparison of mass of sediment g^{-1} dry scourer mass between treatment and shore are shown in figure 3.3.1. The two-way GLM ANOVA showed that there was no statistically significant difference in the mean mass of sediment g^{-1} dry scourer mass trapped between the four TREATMENTS (table 3.3.1: figure 3.3.1). There was little difference in the mean mass of sediment g^{-1} dry scourer trapped between the four treatments within a shore. The highest mass was trapped in the c/t samples (mean = 0.0571, s.d. = 0.116) and the lowest was trapped in the c treatment (mean = 0.0379, s.d. = 0.0929; Figure 3.3.1).

However, there was a statistically significant difference in mass of sediment g^{-1} dry scourer mass trapped between SHORES (table 3.3.1, figure 3.3.1). The *post hoc* test revealed that there was a statistically significant difference in the mean mass of sediment g^{-1} dry scourer mass between all three SHORES (Games-Howell, $p<0.05$). The greatest mass of sediment g^{-1} dry scourer mass was trapped at Black Rocks, (mean = 0.132, s.d. = 0.197) (figure 3.3.1), whilst the smallest mass of sediment g^{-1} dry scourer mass was trapped at Crook Ness (mean = 0.00438, s.d. = 0.00233) (figure 3.3.1) and this was consistent across all algal treatments (figure 3.3.1). At both Black Rocks and Crook Ness similar quantities of sediment were trapped compared to c/t and t, but the mass of sediment g^{-1} dry scourer mass in c was lower at Holbeck (figure 3.3.1). The mass of sediment g^{-1} dry scourer mass was greatest in b (mean = 0.0630, s.d. = 0.180). Again the mass of sediment g^{-1} dry scourer mass trapped at Crook Ness was similar to the other treatments (figure 3.3.1). The mass of sediment g^{-1} dry scourer mass trapped in b at Holbeck was less than c/t or t but greater than c, however b at Black Rocks trapped more than any other treatment although considerable variation occurred (figure 3.3.1).

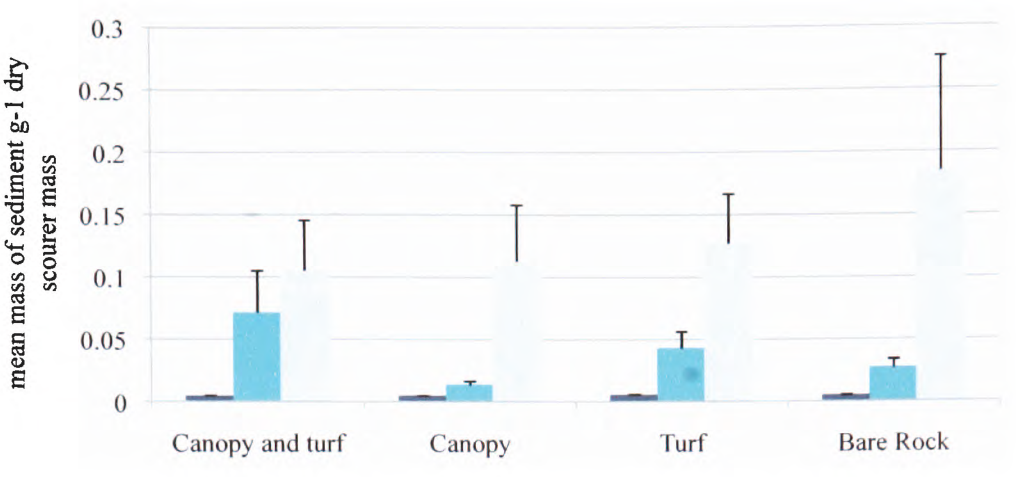
There was no statistically significant interaction occurring between TREATMENT and SHORE (table 3.3.1, figure 3.3.1) indicating that the same pattern of sediment accumulation with TREATMENT occurred across all three shores.

Table 3.3.1: Summary of results from a two-way independent GLM ANOVA for mass of sediment g^{-1} dry scourer using TREATMENT and SHORE as factors.

Source	**DF**	**Adj MS**	**F**	**p**
TREATMENT	3	0.006	0.438	0.726
SHORE	2	0.229	17.343	<0.001
TREATMENT * SHORE	6	0.01	0.772	0.593
Error	160			

The changes in the mean mass of sediment g^{-1} dry scourer mass trapped by the four different macroalgal treatments was assessed on four occasions during the year at three monthly intervals using a 2-way mixed design GLM ANOVA. No statistically significant difference was found in the mass of sediment g^{-1} dry scourer mass between TREATMENT ($F_{2.24}$ = 1.162, p > 0.345) or between MONTH ($F_{1.472,\ 35,331}$= 3.14, p = 0.07) (figure 3.3.2). The mean mass of sediment g^{-1} dry scourer mass was lowest in May (mean = 0.0189, s.d. = 0.613) (figure 3.3.2). The highest mean mass of sediment g^{-1} dry scourer mass was trapped during August (mean = 0.0884, s.d. = 0.156) (figure 3.3.2). There was also no statistically significant interaction between MONTH and TREATMENT ($F_{4.416,\ 35.331}$ = 0.519, p = 0.739), indicating that variations in the mean mass of sediment g^{-1} dry scourer mass between months showed similar patterns in all treatments.

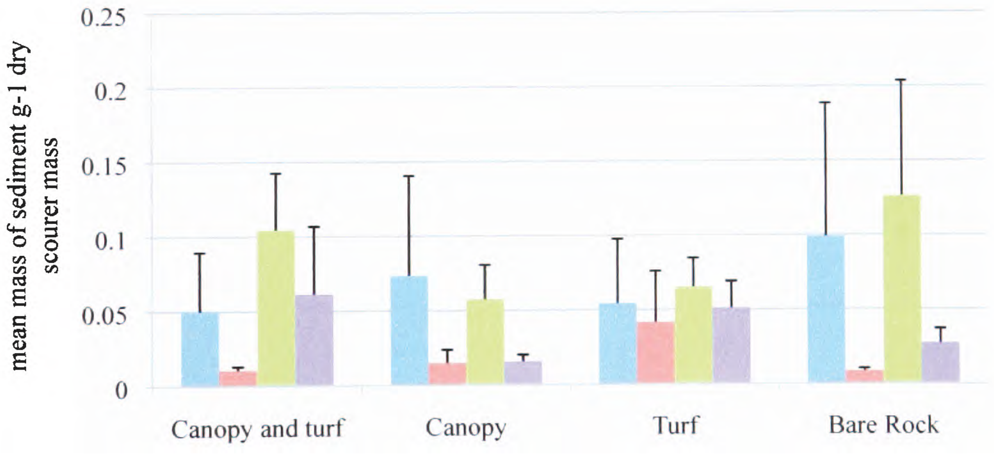
The mass of sediment g^{-1} dry scourer mass was lowest during May and November compared to February and August. Although this generally occurred in all treatments, except c/t where the mass of sediment g^{-1} dry scourer mass was slightly higher in November than February, the differences are most evident in the c and b treatments (figure 3.3.2). In t the mass of sediment g^{-1} dry scourer mass remained relatively consistent between months (figure 3.3.2). However, in all cases, there was a very large degree of variability in the mass of sediment g^{-1} dry scourer mass trapped between both treatment and month.



Key:

■	Crook Ness	🟦	Holbeck	□	Black Rocks

Figure 3.3.1: The mean mass of sediment g^{-1} dry scourer mass (+ s.e.) trapped by each macroalgal treatment (canopy species only, turf species only, both canopy and turf species, and bare rock) on each of the three shores (Crook Ness, Holbeck and Black rocks) (only positive s.e. error bars shown for clarity).



Key:

🟦	February	🟥	May	🟩	August	🟪	November

Figure 3.3.2: The mean mass of sediment g^{-1} dry scourer mass (+ s.e.) trapped in each treatment (canopy species only, turf species only, both canopy and turf species, and bare rock) on the four sampling occasions (February, May, August and November) (only positive s.e. error bars shown for clarity).

3.4.1. Summary of key findings

- No statistically significant differences were found mass of sediment g^{-1} dry scourer mass accumulated between the four different treatments of the macroalgal communities.
- No statistically significant differences was found in mass of sediment g^{-1} dry scourer mass between months.
- Statistically significant differences were found in mass of sediment g^{-1} dry scourer mass between shores with the greatest mass being trapped at Black Rocks and the least at Crook Ness, however no statistically significant interaction was found between treatment and shore indicating that the lack of differences in mass of sediment g^{-1} dry scourer mass between treatments occurred at all three sites.

3.4. Discussion

The quantity of sediment trapped showed no statistically significant difference between the four different macroalgal treatments. Previous work has suggested that different macroalgal morphological groups would trap different quantities of sediment. Generally sediment trapping has been found to occur in turf species which have a greater capacity to trap sediment within their structure (Seapy & Littler, 1982; Stewart, 1983; Airoldi, 2003). Some studies have shown greater levels of sediment accumulation under canopy species compared to bare rock due to the decreased water flow reducing sediment transport and hence increasing sediment accumulation and residence time (Eckman, *et al.*, 1989). However, other studies have reported a decreased quantity of sediment trapped beneath canopy species (Melville & Connell, 2001). This may be due to canopy species sweeping the away sediment surrounding them (Kennelly, 1989). However, there has been no research to indicate the size of area that individual macroalgae can influence in terms of sediment trapping. The dominant canopy species on all three shores were *Fucus vesiculosus* and *Fucus serratus,* which have the potential to grow to 150cm (Hiscock, 1979). This is greater than the width of the area cleared either side of each plot and also the size of each treatment area. Therefore the surrounding unmanipulated canopy could be influencing sediment trapping within the treatment areas, and adjacent treatments could also be influencing one another. Adjacent ecosystems experience flows of energy, nutrients and species across their mutual boundaries (Murcia, 1995). Therefore the boundary of a habitat is not just a line, but rather a zone, the width of which varies depending upon what is being measured (Meffe & Carroll, 1997). The edges of habitats differ to their interiors and where the patch is small this edge effect can penetrate through most of the patch (Pullin, 2002). The size of area in which algae can influence sediment trapping is unknown and therefore edge effects could be occurring throughout each of the macroalgal treatment areas and limiting the differences in the quantity of sediment trapped between different combinations of macroalgae.

Qualitative distinctions could be made between the macroalgal treatments at individual sites. At both Holbeck and Black Rocks in months where greater quantities of sediment were trapped there was greater distinction between the quantities trapped by the different macroalgal treatments. The pattern observed, however, was not identical between the sites.

Whilst the c/t treatment trapped the greatest quantities of sediment at Holbeck, it trapped the least sediment at Black Rocks. Similarly the greatest quantity of sediment was found on b at Black Rocks whilst at Holbeck sediment accumulation on b was lower than both c/t and t. This suggests that other factors may be influencing the quantity of sediment trapped by the different macroalgal treatments in addition to the macroalgal species present. The microtopography of a shore has been postulated to influence sediment trapping at a scale of meters (Airoldi & Virgilio, 1998). Sediment quantity has also been found to be mediated by the presence of the gastropod grazer *Littorina littorea* (Bertness, 1984). These additional factors may mask any differences that may occur between treatments and may be influential in creating the large degree of variability in the quantity of sediment trapped between the replicates of the different macroalgal treatments.

Distinctions in the quantity of sediment trapped between macroalgal treatments could only be made where greater quantities of sediment were trapped. This is especially apparent in the months with greater quantities of trapped sediment at both Holbeck and Black Rocks. The availability of suspended sediment has been suggested to be a significant controlling factor upon the trapping capacity of macroalgae (Stamski & Field, 2006). Thus macroalgal coverage may only be important in influencing where sediment accumulates when there is sufficient sediment in the water column.

There was a significant difference in the quantity of sediment trapped between the three different shores, Black Rocks, Holbeck, and Crook Ness. As previously mentioned, the availability of sediment has a significant control on sediment trapping (Stamski & Field, 2006). Crook Ness is situated approximately 6.5 miles from a large sandy shore whilst both Black Rocks and Holbeck are close to two large sandy beaches. This may limit the availability of sediment at Crook Ness hence accounting for the low levels of trapping observed. However, Holbeck is the site situated closest to a sandy shore. If proximity to a sandy shore was the only factor affecting differences in sediment trapping it would be expected that the greatest quantities of sediment would be trapped at Holbeck rather than Black Rocks. Sediment movement is, however, restricted by barriers such as coastal defences, as discussed in Chapter 1. These prevent natural long shore drift occurring and so greater quantities of energy are required to move sediment far enough offshore to bypass the barrier (Storlazzi & Field, 2000). The plots at Holbeck were situated at the end of the toe of the sea defences constructed after the Holbeck Hall landslip (see Chapter 4.1 for further details). Sediment movement would also be influenced by sea walls and other sea defences (Haslett, 2000) in the vicinity of the site, and therefore, the Victorian Swimming pool situated to the North of the Holbeck plots may be influencing sediment availability within the plots. Although Black Rocks is situated on a headland, due to the direction of sediment movement this would be unlikely to have any effect on sediment trapping. Hydrodynamic conditions can influence sediment accumulation even within differences of 100m (Airoldi & Virgilio, 1998), so although Holbeck and Black Rocks are only 1000m apart this may explain the significant differences between the two sites.

Differences in sediment accumulation have also been found to occur at different shore heights. Greater quantities of sediment accumulated in artificial algae at the top of the shore compare to lower down the shore (Gibbons, 1988). This was suggested to be related to the upward transport of sediment with each tide and also the increased agitation of water at the low shore. However no differences have been found in the quantity of sediment trapped by macroalgal turf between mid and low shore sites (Kelaher, *et al.*, 2001; Kelaher, *et al.*, 2003). Although all the plots were positioned in the biological mid shore based on the characteristic species identified by Stephenson & Stephenson (1949), they may not have been in identical positions in relation to chart datum which may influence the quantity of sediment trapped between sites.

The quantity of sediment trapped was not significantly different between months. Although seasonal differences have been found to influence the quantity of sediment trapped by macroalgae in other studies, the results have been inconclusive. Lower quantities of sediment have been found to be trapped in macroalgae during summer months in some cases (Littler, *et al.*, 1983; Airoldi, *et al.*, 1996; Airoldi & Virgilio, 1998; Prathep, *et al.*, 2003), whilst on other occasions the lowest quantities of sediment have been found to occur during the winter (Daly & Mathieson, 1977; Stewart, 1983). In other studies, seasonal patterns in sediment trapping have not been evident at all (Kendrick, 1991). However variations in sediment trapping have been found to occur between weeks and also over short periods of time as a result of storms (Stewart, 1983). Sediment accumulation on the shore has also been found to vary diurnally, and with spring and neap tides (Daly & Mathieson, 1977). The current study only provided a 'snapshot' of sediment movement at each site and also between the seasons and therefore may not be able to identify small scale movement occurring on shorter timescales.

Although a consistent pattern between months is not evident, sediment trapped in b and c treatments did show a pattern with less sediment being trapped during the samples from May and November. If sediment trapping was purely related to the quantity of sediment available in the water column then this pattern would be clearly seen in all combinations of algae. Turf species are recognised as trapping and retaining sediment (Seapy & Littler, 1982; Stewart, 1983; Airoldi, 2003), and this may prevent resuspension of the sediment from treatment t. The pattern may be less evident in c/t due to the interaction between the trapping of sediment by turf and the potential sweeping away of sediment by canopy. Sediment accumulating on the bare rock or in canopy areas would be more easily resuspended or deposited depending upon the quantity of sediment suspended in the water column.

Chapter 4

Sediment dynamics and community structure on an intertidal rocky shore

4.1. Introduction

Organisms on intertidal rocky shores are affected by a variety of factors, which are both biological (e.g. competition and predation) and physical (e.g. desiccation and wave exposure) (see Chapter 1 and reviewed in Connell, 1972). This results in organisms on the shore displaying patterns in their distribution. Patterns of zonation have been recognised to occur throughout the world (Stephenson & Stephenson, 1949). As discussed in Chapter 1, the upper limits are suggested to be determined by physical factors, whilst biological factors determine the lower limits (Connell, 1972). However, clear zonation patterns are not always evident as distribution is affected by other factors. Increased wave exposure results in a mosaic pattern occurring (Wells, *et al.*, 2007), whilst storms (Ebeling, *et al.*, 1985; Underwood, 1998) and ice scour (McCook & Chapman, 1997) can remove organisms from large areas of shore. Anthropogenic factors can also act at large scales (*e.g.* oil spills and pollution [Thompson, *et al.*, 2002]) or at smaller scales (*e.g.* trampling [Keough & Quinn, 1998; Brown & Taylor, 1999] and harvesting [Spencer *et al.*, 1998]) affecting the distribution of organisms.

The distribution of organisms does not stay constant throughout the year. Some species of fauna have seasonal patterns of migration (*e.g. Cancer irroratus* Say migrating off shore in Nova Scotia during winter [Hughes, 1972]), whilst the top shell *Osilinus lineatus* da Costa (as *Monodonta lineata*) migrate up the shore in Northern France [Littler & Kitching, 1996]). A variety of macroalgal species heteromorphic life cycles (*e.g. Dumontia contorta* (Gmelin) Ruprecht [Dixon & Irvine, 1977], *Porphyra umbilicalis* [South & Whittick, 1996]) are seasonally more abundant (*e.g. Ulva lactuca, Cladophora sericea* (Hudson) Kützing [Brodie *et al.*, 2007]) or have periods of seasonal growth (*e.g. Chondrus crispus* [Dixon & Irvine, 1977], *Fucus vesiculosus* [Stengel, *et al.*, 2004]) leading to changes in the macroalgal community structure. Seasonal storms can reduce algal biomass (Wernberg, *et* *al.*, 2001) and remove organisms (Ebeling, *et al.*, 1985; Underwood, 1999). Where areas have been cleared by disturbance, colonisation is by fast growing ephemeral algal species (Sousa, 1979; McCook & Chapman, 1997) or the barnacle species *Chthamalus dalli* Pilsbry (Farrell, 1991), before perennial macroalgal species become established at a later stage (Sousa, 1979; Farrell, 1991; McCook & Chapman, 1997). As disturbances can be both large (*e.g.* ice scour [McCook & Chapman, 1997]) or small (*e.g.* boulder movement [Sousa, 1979]), and can occur throughout the year, this can lead to a patchwork of different succession states across a shore.

As discussed in Chapter 1, sediment also acts as a disturbance on rocky shores. Burial by sediment reduces growth (Arakawa, 2005; Glasby, *et al.*, 2005), recruitment (*e.g.* Devinny & Volse, 1978; Arawaka, 2005) and limits the survival of macroalgal germlings (*e.g.* Berger, *et al.*, 2003; Schiel, *et al.*, 2006). Areas with higher sediment levels, either naturally or as a result of manipulation, have lower species diversity (Daly & Mathieson, 1977; Eriksson & Johansson, 2005) and different species composition with a greater abundance of turf species (*e.g.* Airoldi & Cinelli, 1997; Gorgula & Connell, 2004; Balata, *et al.*, 2005). Fauna are also affected by sediment, with mortality occurring in a variety of species (*e.g. Perna perna* [Zardi, *et al.*, 2006], *Littorina granularis* [Marshall & McQuaid, 1989], and *Littorina littorea* [Chandrasekara & Frid, 1998]) during periods of sediment burial.

Sediment on the shore is not static. Sediment movement and subsequent deposition is predominantly the result of water movement. Sediment movement is dependent upon there being sufficient energy for traction, saltation, or suspension (Leeder, 1982; Chanson, 1999). Wind action can enhance sediment movement by water (Davis & FitzGerald, 2004). High-energy events, such as storms, result in increased sediment movement and the transport of sediment from greater depths (Storlazzi & Field, 2000). Geographic features are also important, either at large scales, including coastal mountains, sea cliffs, small pocket beaches, river mouths and headlands (Storlazzi & Field, 2000), or as small scale features affecting the local depositional environment, such as increased sedimentation occurring on horizontal rather than vertical surfaces (Jørgensen & Gulliksen, 2001), and lower sediment deposition on areas raised above the surrounding substrata (Littler, *et al.*, 1983). As discussed in Chapter 1, biological factors also influence sediment movement and accumulation. Sediment trapping in macroalgae predominantly occurs in turf species (reviewed in Airoldi, 2003), but also occurs in filamentous species (Airoldi & Virgilio, 1998; Isaeus, *et al.*, 2004) and kelp species (Eckman, *et al.*, 1989). Kelp species (*Cystphora* spp & *Ecklonia radiata*) (Connell, 2003b) and faunal species (*Littorina littorea* [Bertness, 1984], *Melagraphia aethips* and *Turbo smaragolus* [Schiel *et al*, 2006]) have been found to remove sediment from the surrounding area.

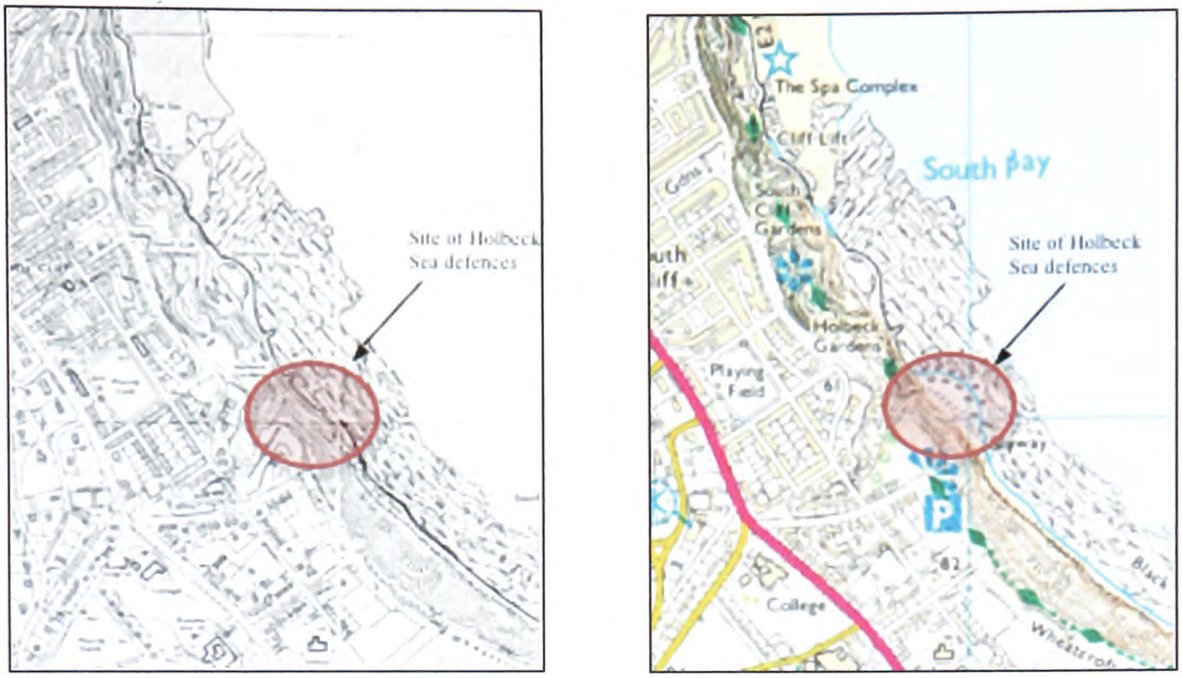
4.1.1. Rationale and Aims

A limited number of studies have investigated the distribution of sediment on intertidal rocky shores. Instead studies have focused upon the occurrence and abundance of organisms in areas where sediment with different levels of sediment inundation (*e.g.* Kendrick, 1991; Eriksson & Johansson, 2005; Balata, *et al.*, 2007). Most studies consider the distribution of sediment around local topographical features such as the slope of the surface (Jørgensen & Gulliksen, 2001) or areas of raised substrate (Littler, *et al.*, 1983). Littler *et al* (1983) and Daly & Mathieson (1977) undertook the few studies examining the distribution of sediment and macroalgae both along two transects in Southern California and New Hampshire respectively. Differences in the macroalgal species occurring between the two transects with different levels of sediment accumulation as a result of different profiles were described during each of the four seasons (Daly & Mathieson, 1977), whilst Littler *et al* (1983) described the where macroalgal species, fauna, and sediment occurred down two transects with similar sediment inundation during all four seasons.

This chapter aims to describe the dynamics of the intertidal distribution of both sediment and organisms at a local scale. The rocky shore chosen, Holbeck, Scarborough, North Yorkshire was subject to regular small-scale inundation of sediment that varied over time. Since the latter part of the 19th Century the shore has been protected by sea walls constructed at the base of the cliff (Department of the Environment and the Regions, 2006). However these have not totally prevented coastal erosion in the area. In June 1993 the cliffs surrounding the rocky shore at Holbeck caught media attention following the loss of the four-star Holbeck Hall hotel to a landslip (Girling, 2005). Although a number of landslips had occurred over the preceding years (Holbeck Hall Hotel ltd and Another v

Scarborough Borough Council, 2000) the 1993 landslip resulted in one million tonnes of debris falling onto the shore almost overnight (High-Point Rendal, 2006). The debris extended 100m across the rocky shore platform (Lee, 1999). Landslips of such a scale are not unusual for the area as the coast is subject to natural erosion (Holbeck Hall Hotel ltd and Another v Scarborough Borough Council, 2000). As a result of the landslip additional coastal defence works were undertaken to stabilise the area and prevent further landslips. The defence works consist of approximately 350m long barrier of rock armour around the base of the landslip as coastal protection as well as improved drainage of the cliffs (High-Point Rendal, 2006). The landslip and subsequent defence construction works required heavy vehicles to move across the shore and this resulted in the destruction of the rocky shore community in the local area.

Prior to the landslip the cliff line to the south of Scarborough was relatively straight (figure 4.1.1a), however the coastal defence works resulted in the construction of a rocky outcrop protruding seaward (figure 4.1.1b). The change in the shape of the shoreline at Holbeck has resulted in a shore that consists of distinct areas with observable differences in sediment accumulation pattern. Immediately to the North of the Holbeck sea defences, large areas of sediment were observed to accumulate throughout the shore, and a large upper shore sediment zone. To both the north and south of this area, smaller scale sediment accumulation has been observed, although the south also has some protection from sediment transport. This provided an ideal opportunity to describe patterns of sediment accumulation and deposition without the need to use a variety of sites with different local environmental conditions, which would potentially affect the sediment distribution and accumulation on the shore.



a) Pre 1993 (National grid 1969-1996)

b) Post 1993

Figure 4.1.1: Map of the coastline at the site at Holbeck displaying the changing shape since the construction of the sea defences (Digimap, 2009).

The aims of this chapter are:

1) To describe and compare large scale temporal changes in the distribution, volume, surface area and sediment composition of the upper shore sediment zones at each of the three sites at Holbeck.
2) To determine if the percentage cover of sediment on the shore varied between the three different sites (across seasons), between seasons (across the sites), or within each of the sites (across seasons).
3) To determine if total abundance, species diversity and species richness of the substrate covering species (macroalgae and barnicles) varied between the three different sites (across seasons), between seasons (across the sites), or down each of the sites (across seasons).
4) To determine if the substrate covering species (macroalgae and barnicles) community similarity varied between the three different sites (across seasons), between seasons (across the sites), or within each of the sites (across seasons).

5) To determine if the abundance of littorinids and patellids varied between the three different sites (across seasons), between seasons (across the sites), or within each of the sites (across seasons).

4.2. Methods

4.2.1. Site description

The rocky platform at Holbeck is situated at the southern end of Scarborough, UK (National grid reference TA 050 870) (as previously described in Chapter 2.2). The shore lies to the south of a large sandy shore and is within the Cayton, Cornelian and South Bays Site of Special Scientific Interest (SSSI), which is of geological and biological interest (Natural England, 1994). The shore consists of a moderately exposed wave cut platform (Hull, Winter & Scott, 2001) with a North East aspect. The shore was divided into three sites (figure 4.2.1), one between the old swimming pool and the groyne (North), another between the groyne and the Holbeck sea defences (Central), and one to the south of the Holbeck sea defences (South).

The North and Central sites appear superficially similar. The top of both sites is delineated by the concrete seawall that runs from the Spa complex to the Holbeck sea defences to control cliff erosion. The sea wall prevents either site displaying a biological upper shore community. Instead a mid shore community of *Fucus vesiculosus* and barnacles (as described in Stephenson & Stephenson, 1949) is present from the base of the sea wall. Both sites have an uneven topography, and therefore lack a defined pattern of macroalgal zonation running down the shore, but share a similar macroalgal species composition. The majority of the wave cut platform at both sites is covered by large fucoid beds and rockpools. The lower part of both sites consists of areas of *Laminaria digitata* and *Rhodothamniella floridula*.

However, unlike the North site, the Central site is subject to a greater abundance of sediment accumulation. A large upper shore sediment zone runs across the entirety of the Central site throughout most of the year. The upper shore sediment zone at the North site is much smaller, with a width of generally less than 10m. Large areas of sediment accumulation on the rocky platform of the Central site occur throughout the year. When this is uncovered areas of fast growing macroalgae develop.

The South site is to the south side of the Holbeck sea defences, beyond the extent of Scarborough's sea defences. Here, the upper part of the shore consists of large boulders, soil from the small landslips from the steep cliffs of Jurassic shale and sandstone cliffs behind the site, and some sediment accumulation. The upper and mid parts of the shore are predominantly covered by *Semibalanus balanoides* and *Patella vulgata.* Macroalgal cover is restricted to small patches of fucoids which were generally present along the edge to two large rockpools running down the majority of the site. The lower part of the shore is dominated by large turf beds predominantly of *Osmundea pinnatifida* with small fucoid patches, intersected by deep channels of water.

Sediment accumulation at the three sites is noted to differ. The South site is protected from sediment transported by longshore drift (Storlazzi & Field, 2000) by the Holbeck sea defences, whilst the Central site has large areas of sediment accumulation. However the close proximity of the three sites limits differences in environmental factors, such as storms, temperature and pollution, which may affect both sediment accumulation and community structure. This provides the opportunity to consider differences in sediment accumulation and movement at each of the sites, and also species composition and the interactions between these.

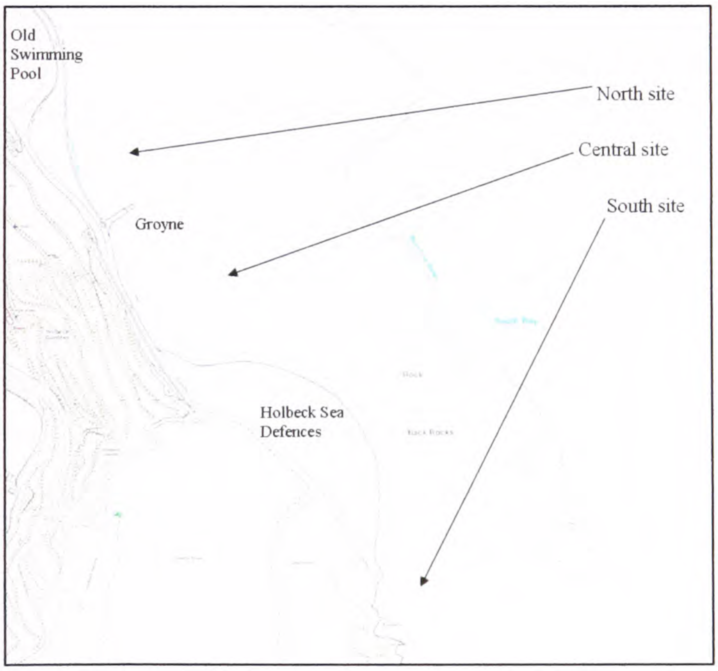


Figure 4.2.1: Map of the of the intertidal rocky shore at Holbeck showing the position of the three sites in relation to key anthropogenic features (Digimap, 2006).

4.2.2. Data collection

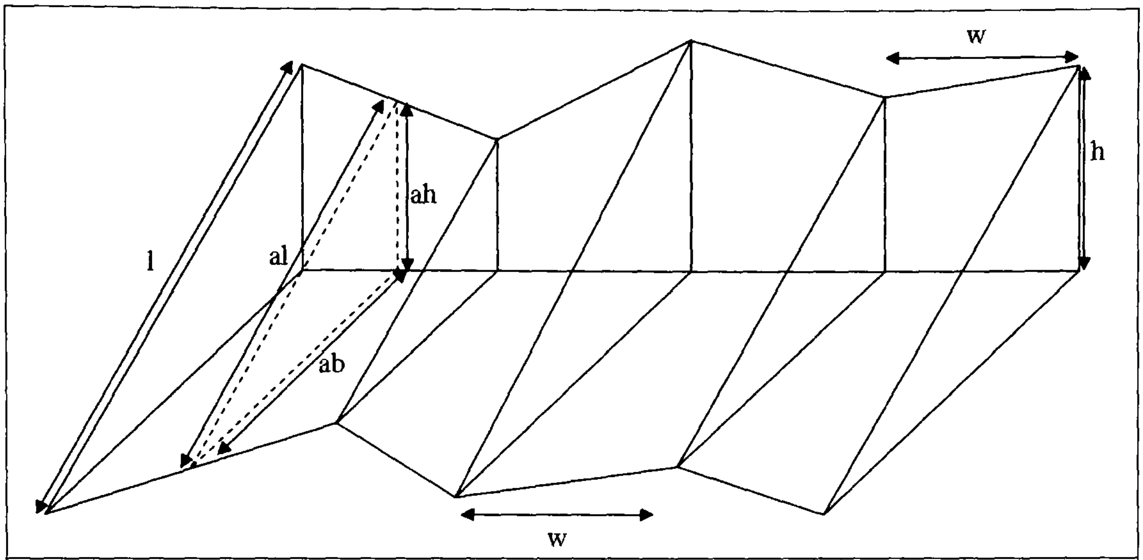
4.2.2.1. Temporal variation in the upper shore sediment zone

The area and position of the upper shore sediment zone at each site had been noted to vary over time. Frequent surveys of areas with rapid sediment movement allow the development and change to be measured and analysed (King, 1966). Measurements of the upper shore sediment zone were made on a weekly basis, tidal conditions permitting, for one year between June 2006 and May 2007. The assessment was continued on a monthly basis for a six-month period between June 2007 and November 2007.

To allow comparisons of sediment movement to occur over time, measurements are required to be made from fixed points (King, 1966). In the case of the Central and North sites measurements were made using the sea wall, and features within it such as steps and the groyne, as fixed points. The South site is not delineated by a sea wall therefore two large boulders, in line with one another, that were unlikely to be moved by environmental action, were selected and marked to act as a base line.

The volume and surface area of the upper shore sediment zone at each of the three sites was estimated using basic trigonometry (figure 4.2.2). Measurements of height (h) of the upper shore sediment zone were made using the sea wall (at the Central and North sites) and the boulders (at the South site) as fixed points with a known height (King, 1966). The sea wall was also used as a fixed point for measurements of length (l) at the Central and North sites. The length of the sediment zone was measured perpendicular to the sea wall until the point where bedrock became more dominant than sediment cover (figure 4.2.2). The marked boulders, and the base line between them at the South site were used as fixed points from which measurements were made. As the height and length of the sediment zone was known to vary across the width of each site measurements of height and length were taken every 5m at the Central and South sites and every 2m (due to the shorter width) at the North site (figure 4.2.2).

The volume of the sediment in an area has previously been estimated by trigonometry using the shape most similar to the sediment body (King, 1966). Due to the abrupt end of the sediment zone by the sea wall or cliffs each upper shore sediment zone broadly resembled a prism (figure 4.2.2). The measurements of height and length were used to calculate the volume and surface area of each of the blocks (figure 4.2.2). The sum of the blocks used to calculate both the volume and surface area of the upper shore sediment zone of each site.



Sediment base (b)	Average sediment base (ab)
Sediment height (h)	Average sediment height (ah)
Sediment length (l)	Average sediment length (al)
Block width of 5m (2m at North site) (w)	

Figure 4.2.2: A diagrammatic representation of sediment distribution in the sediment zone showing measurements used to calculated sediment volumes and surface area.

4.2.2.2. Sediment infauna

Preliminary sampling was undertaken to investigate the abundance of macrofauna inhabiting the upper shore sediment zone. Sediment cores were taken from the top, middle and bottom of the Central site at three points along the upper shore sediment zone. The sediment cores were sieved through a 1mm sieve. Within these nine samples, only 11 individual organisms were recorded, therefore it was determined that no further sampling would be undertaken during this study.

4.2.2.3. Photographic analysis of the position of the upper shore sediment zone

Measurement of the upper shore sediment zone provides information on changes in the total volume and surface area; however it provides limited information on how the sediment is distributed across the shore. Plane-table contour methods of field surveys have been used to map changes in sediment position of the spit at Gibraltar Point, Lincolnshire, however this is a time consuming method (King, 1966). Remote sensing also provides information for quantifying landform properties (Goudie, 1990). Remote sensing incorporates a wide range of imaging technology including satellite imaging, radio detection and thermo imaging (Goudie, 1990). It also includes the use of photography (Goudie, 1990). Aerial photographs can be a useful alternative to field surveys (King, 1966). However ground photographs can also be used to monitor geomorphological process, especially if there are fixed points of reference (Goudie, 1990). Cliff top photographs have been found to be suitable for mapping intertidal areas where the use of aerial photography is not practical. Previously the cover of macroalgal bed and bare rock have been analysed from such images (Ducrotoy & Simpson, 2001). Due to the large area of sediment and the large scale movement being considered any qualitative changes in the extent and distribution of the upper shore sediment zone would be apparent using this technique.

Photographs of the shore were taken within ten minutes of low tide to allow the greatest extent of the intertidal area to be exposed. Photographs were taken on a weekly basis, visibility permitting, for a 12-month period between June 2006 and June 2007 using a Pentax Option S30 digital camera. To allow coverage of all three sites, photographs were taken from two vantage points chosen primarily to ensure as greater photographic coverage of the sites as possible. In addition they were sufficiently close to one another to prevent a significant time interval between the two sets of photographs being taken and also accessible throughout the year without becoming obscured by vegetation. Previous use of aerial photographs in shore mapping (Ducrotoy & Simpson, 2001) used positioned visible markers on the shore to give static points of reference. However, due to the large number of static anthropogenic features at the sites these were used to ensure consistent positioning of the photographs.

4.2.2.4. Grain size composition

On one neap tide and one spring tide each month between June 2006 and May 2007 sediment samples were collected from the upper shore sediment zones. Sediment grain size composition varies across sandy shores (Blott & Pye, 2004). To allow sufficient replication across the width of the sediment zone samples were collected at 10m intervals across the width of the South and Central sites, and 2m intervals at the North site.

Sediment grain size composition can vary every 15m down the shore (Blott & Pye, 2004). Neither the South or North sites regularly extended down the shore beyond 10m and the maximum length down the shore of 25m only occurred on rare occasions during the year. Therefore spatial variability down the shore was unlikely and a single sample was collected in the middle of the upper shore sediment zone at each sampling position. The sediment length at the Central site was generally between 20m and 40m with regular increases to approximately 60m in length down the site. To examine the potential for spatial variability in the upper shore sediment zone at the Central site sediment samples were collected at the top (TP), and bottom (BM) of the upper shore sediment zone with a further, middle (ME), sample being collected approximately half-way between TP and BM (figure 4.2.3).

Sediment samples were collected from a depth of 0 to 15cm on the surface of the upper shore sediment zone (Blott & Pye, 2004). Sediment samples were oven dried overnight at 70^0C (Stewart, 1983) and each sample consisted of between 50g and 150g dry mass of sediment. Initial analysis of the sediment samples revealed that they were dominated by sand (grain sizes between 2mm and 0.062mm [Lewis & McConchie, 1994]). Sand grains can be assumed to have reasonable sphericity, and therefore good size distribution information can be obtained using certified test sieves (Eleftheriou & McIntyre, 2005). Pre-weighed sediment samples of between 50g and 150g were sieved using an Endecotts Octagon 200 test sieve shaker for a fixed interval of five minutes at an amplitude of 6. Initial trials revealed that longer shaking times did not affect the final distribution of sediment. Sediment samples were separated using 4mm, 2mm, 1mm, 0.5mm, 250μm and 0μm sieves. These corresponded with the Udden–Wentworth grain scale for grain sizes (Eleftheriou & McIntyre, 2005) and allowed the classification of the different sediment fractions as pebbles (>4mm), granules, (2mm-4mm), very coarse sand (1mm-2mm), coarse sand (0.5mm-1mm), medium sand (250μm-0.5mm) and fine/very fine sand (0μm-250μm)

(Lewis & McConchie, 1994). This makes the results more readily comparable with previous work (Eleftheriou & McIntyre, 2005). The amount of sediment within each sieve was weighed and the proportion of the total sediment mass calculated.

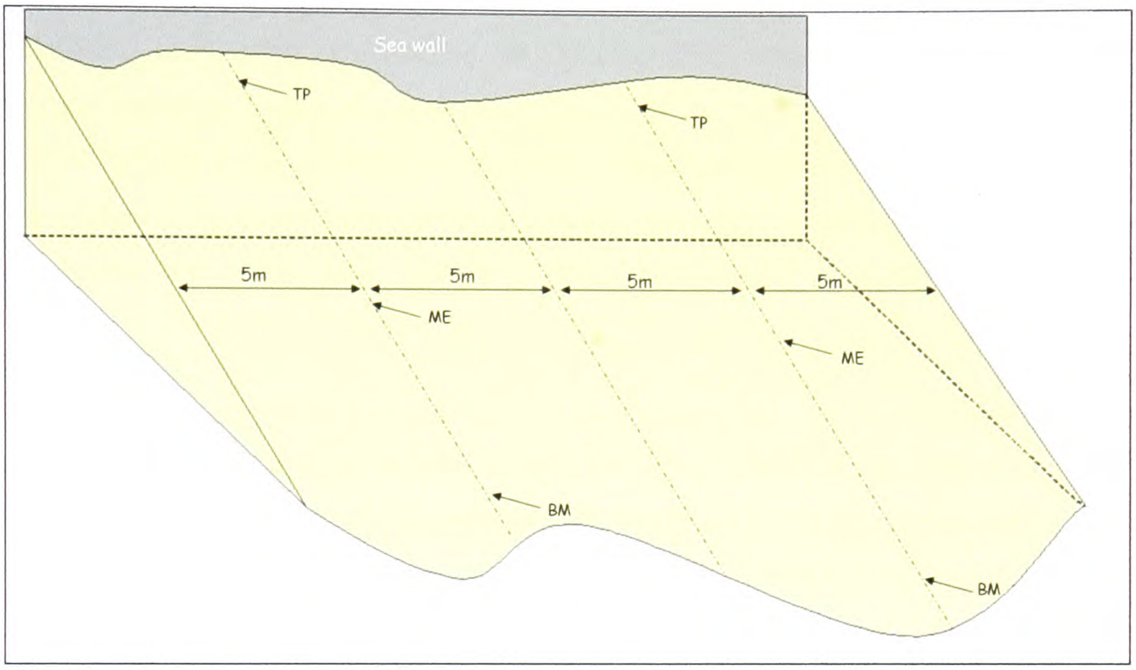


Figure 4.2.3: A diagrammatic representation of positions of sediment collections from the upper shore sediment zone at the Central site (top [TP], middle [ME], and bottom[BM]) in relation to the length measurements for calculating volume and surface area (indicated by the dotted line).

4.2.2.5. Zonation of sediment and biota

Three vertical transects were positioned on each of the three sites during October 2006 and marked for relocation using fixed anthropogenic features. Transects were equally spaced across each site and ran parallel to one another, perpendicular to the sea wall (Central and North sites) or the cliff line (South site) to low water level during a Spring tide (figure 2.2.3). Three randomly placed 50cm x 50cm quadrats were sampled every 10m along the transect. The use of transects allowed stratified random sampling to be carried out as a common method of sampling on intertidal rocky shores (Raffaelli & Hawkins, 1996). It allows sampling be performed at different shore heights of set intervals whilst maintaining the independence of samples for analysis purposes (Raffaelli & Hawkins, 1996). The use of transects down the sites ensured that patterns in the position of sediment and organisms down the site could be assessed.

Rockpools were not sampled as they are suggested to be unrepresentative anomalies of the surrounding community (Underwood & Skilleter, 1996; Ducrotoy & Simpson, 2001). Average sediment cover has also been found to be greater in rockpools than the surrounding rock surface (Littler, *et al.*, 1983). Therefore quadrats were positioned on the closest edge of the pool to the transect line where necessary. Where large rockpools were encountered and would have resulted in large repositioning of quadrats, no sampling occurred.

Within each quadrat the percentage cover of each macroalgal species, sediment cover and barnacle (predominantly *Semibalanus balanoides*) cover were visually estimated. Where macroalgal species could not be identified in the field their percentage cover was estimated and samples brought back to the laboratory for identification using appropriate keys (Hiscock, 1979; Hiscock, 1986; Burrows, 1991; Dixon & Irvine, 1995; Maggs & Hommersand, 2001). As *Fucus* juveniles could not be identified in the laboratory or the field they were recorded as the percentage cover of *Fucus* juveniles.

Visual estimation of the percentage cover of macroalgae, sediment and barnacles was used because it has been found to be equally as effective as using evenly spaced, random or stratified dots in assessing percentage cover (Meese & Tomich, 1992). It is also quicker than other methods and provides a three-dimensional view of the sampled area (Meese & Tomich, 1992). However, there is also the potential for variability in visual estimates between different observers (Meese & Tomich, 1992). In an attempt to minimise variations in visual estimates of percentage cover within a quadrat, gridded quadrats were used.

The abundance of the commonly occurring faunal groups, patellids and littorinids within each quadrat were also recorded. These faunal groups were recorded because *Patella vulgata*, the most common patellid on all three sites, is a key stone species responsible for structuring mid shore communities on moderately exposed and exposed shores, and its loss would have profound effects upon community structure (Raffaelli & Hawkins, 1996).

Littorinids on the three sites are predominantly *Littorina littorea* and *Littorina obtusata* Linnaeus. *L. littorea* are collected for economic purposes in the local area (Barry, 2001) and therefore information on their distribution and abundance is of importance.

Transects were sampled in October 2006 (Autumn), May 2007 (Spring), August 2007 (Summer) and January 2008 (Winter) (inclement weather prevented sampling winter 2006/7). All transects were sampled, where possible, over a period of two consecutive days to minimise sediment movement on the shore between sampling occasions. After the initial sampling the number of transects was reduced to two at each site due to time constraints. Transect lines B, C, D, E, G and H (figure 2.2.3) continued to be sampled because these were most easily relocated.

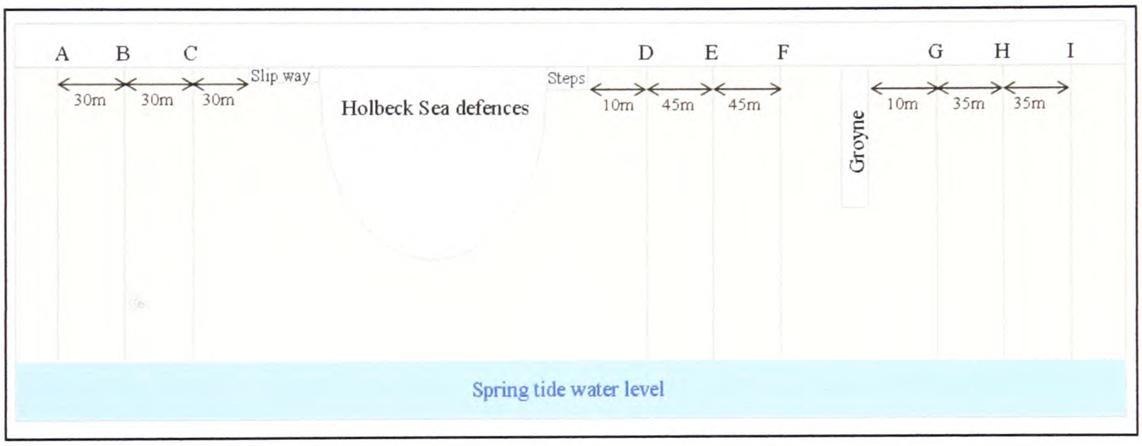


Figure 4.2.3: The relative positions of transect lines (A-I) across the three sites at Holbeck in relation to key anthroplogenic features.

4.2.3. Data analysis

4.2.3.1. Temporal variation in the upper shore sediment zone

Temporal changes in the volume and surface area of the upper shore sediment zone at each site over the 18 month period (June 2006 to November 2007) were described using line graphs and any patterns or differences in sediment accumulation in the upper shore sediment zone between the three sites were examined.

To examine differences in the extent of the upper shore sediment zone between site and season the calculations of sediment volume and surface area were classified as Winter (December, January and February), Spring (March, April and May), Summer (June, July and August) and Autumn (September, October and November) to provide replicates for statistical analysis. The null hypotheses under test was that there were no statistically significant differences in the average sediment volume or surface area between season or between site and that there was no statistically significant interaction between season and site. Both sediment volume and surface area were found to be normally distributed (Kolmogorov-Smirnov test, $p>0.05$ in both cases) and the variances could be considered homogenous (Levenes test, $p>0.05$ in both cases). Therefore two-factor GLM ANOVA was performed on both sediment volume and surface area with SEASON as a fixed factor with four levels (Winter, Spring, Summer and Autumn) and SITE as a fixed factor with three levels (North, Central and South) (Underwood, 1997). SEASON and SITE were independent variables; sediment volume and surface area were dependant variables (Pallant, 2001). *Post hoc* Tukey Honestly Significantly different (HSD) tests, which are more appropriate for larger samples (SPSS, 1999), were used to determine where any statistically significant differences occurred.

The images taken did not show sediment on the shore clearly enough due to the angle of the picture to allow accurate analysis using geographical information systems (GIS) software. However, changes in the shape and size of the sediment zone and large sediment patches on the shore were noted as was any evidence of the impact of the changes in sediment distribution on the shore over the sampling period, such as scouring. To illustrate the large scale changes in sediment accumulation and distribution on the shore a series of four photographs are presented. The photographs presented were clearest images of the extremes of sediment movement and changes in deposition that occurred on the shore during the sampling period.

The total proportion of sediment in each Udden- Wentworth grain size class for each site was calculated. Changes in the proportions of sediment in grain size classes over the 12-month period between June 2006 and May 2007 were described using bar charts. The total proportions of each grain size class at the top (TP), middle (ME) and bottom (BM) of the Central site were also calculated, and again changes in the proportions of sediment in grain size classes over the 12 month period were described using bar charts. Changes in the proportions of grain sediment in grain size classes between the three sites and also between TP, ME and BM of the Central site were examined.

4.2.3.2. Zonation of sediment and biota

The differences in position of sediment, the substrate covering species (macroalgae and barnicles), and the abundance of the patellid and littorinid faunal groups was examined between sites, seasons and stations within the shore. In all cases the total cover or abundance for each station on each transect was calculated using the three quadrats to provide a more representative sample of the community at each station due to the patchy nature of all three sites. Samples collected at stations below 210m at the Central site were removed from all statistical analysis as the tide only fell lower than this on one sampling occasion so no replication occurred, however the data is presented for comparison in graphical representations. Due to the differences in topography between the three sites the distances of the stations were not comparable. Therefore in each case the null hypothesis that there was no statistically significant difference between SITE and SEASON or any statistically significant interactions was examined separately to the null hypothesis that there was no statistically significant difference between STATIONS. Due to the differences in topography between the sites, differences between the stations were examined separately for each site with samples across the four seasons combined to provide sufficient replication.

The percentage cover of sediment on the shore did not approximate a normal distribution (Kolmogorov-Smirnov test, $p<0.05$) and the variances could not be considered equal

(Levenes test, $p<0.05$). Transformation of the data either by arc-sine transformation, which has the effect of 'spreading out' data towards the ends of the possible range and has the effect of potentially removing heterogeneity of variance (Underwood, 1997), or log10, due to the variance being greater than the mean (Fowler, *et al.*, 1998), did not result in the data conforming to the assumptions of normality or equal variances. Although the assumptions of normality and homogeneity of variances had been violated to was still deemed appropriate to perform a two factor GLM ANOVA. The non-parametric alternative, Schiner-Ray-Hare test, however, requires the samples to be identically distributed with the data in each sample being equi-probable in a combined ranking of the data (Underwood, 1997). The distribution of the sediment cover data did not show identical distribution and therefore the use of a non-parametric test was not deemed to be more valid than the parametric equivalent (Underwood, 1997). It is also very conservative and statisticians are unconvinced by the test and suggesting it is only used with caution (Dytham, 2003). ANOVA is also relatively robust to heterogeneity of variances and the use of non-parametric test does not solve the problems of heterogeneity of variances (Underwood, 1997). However, as heterogeneity of variances increases the probability of a Type I error (Underwood, 1997), the level of significance was considered as 0.01 rather than 0.05 to counteract this (Underwood, 1981). The use of ANOVA also allows the potential for *post hoc* testing to identify the source of any variation. A two factor GLM ANOVA was performed with SEASON as a fixed factor with three levels (Winter, Spring, Summer and Autumn) and SITE as a fixed factor with three levels (North, Central and South) (Underwood, 1997). *Post hoc* Tukey HSD tests were again used to determine where any statistically significant differences occurred.

Data on the percentage cover of sediment down the shore were found not to conform to normal distribution (Kolmogorov-Smirnov test, $p<0.05$) and the variances could not be considered equal (Levenes test, $p<0.05$). Transformation did not result in the assumptions being met, however as discussed previously ANOVA is very robust, however the level of significance was considered as 0.01 rather than 0.05 to counteract the increased probability of a Type I error (Underwood, 1981). A one factor GLM ANOVA was performed. *Post hoc* Tukey HSD tests were used to determine the source of any statistically significant differences between samples.

Using the combined macroalgal and barnacle data for each distance on each transect to provide a more representative sample of community structure at each distance due to the patchy nature of all three sites, the diversity indices, Shannon Wiener diversity index (H'), species richness (d) and total abundance was calculated using the DIVERSE routine in PRIMER. H' diversity index was used because it is the most commonly used diversity index (Clarke & Warwick, 2001), and considers the number of species present and how evenly the number of individuals is spread between the species (Fowler, *et al.*, 1998). Margalef's index (d) was used for species richness as opposed to the total number of species as it incorporates the total number of individuals as a measure of the total number of species for a given number of individuals (Clarke & Warwick, 2001). The cover of barnacles was included in the cover of species because barnacles are competitors with macroalgae for space on rocky intertidal shores (Dring, 1982).

The null hypothesis that there was no statistically significant difference in H', d or total abundance between SEASON or SITE, or interaction between site and season was examined. Neither H', d or total abundance approximated normal distribution (Kolmogorov-Smirnov test, $p<0.05$ in all cases) and the variances could not be considered equal (Levenes test, $p<0.05$ in all cases). Transformation of the data did not result in the data conforming to the assumptions of normality or homogeneity of variances. As ANOVA is a very robust test a two factor ANOVA was performed with SEASON as a fixed factor with three levels (Winter, Spring, Summer and Autumn) and SITE as a fixed factor with three levels (North, Central and South) (Underwood, 1997), but the level of significance was again considered as 0.01 (Underwood, 1981). *Post hoc* Tukey HSD tests were again used to determine where any statistically significant differences occurred.

A Bray Curtis similarity matrix was generated from the total abundance of each species at each station using the raw data as this produced the lowest stress level to examine the similarity of the community within each site and season (Clarke & Warwick, 2001). Bray Curtis similarity coefficient was used because it takes into account the rarity or dominance of species, allows further samples to be added without affecting the similarity of previous samples and takes the values of 0 and 100 respectively when samples have no species in common or are identical (Clarke & Warwick, 2001). The Bray Curtis similarity matrix was then used to perform a two-way Analysis of Similarity (ANOSIM) to test that there was no statistically significant difference in community similarity between SITES or SEASONS (Clarke & Warwick, 2001). SIMPER routine was also performed in PRIMER and used in conjunction with presence/ absence tables to examine which species contributed to the similarities and dissimilarities between SITE and SEASON separately. For clarity of results, due to the large number of samples, a second Bray Curtis similarity matrix was produces using the average abundance of each species on each transect (Boaventura, Re, Canacela da Fonseca & Hawkins, 2002). This was used to produce a graphical representation of the similarity between samples using Multi-dimentional Scaling (MDS) routine in PRIMER. The stress level was identical to the MDS plot produces using total species data from each station. However, due to the smaller number of point, the clusters were easier to identify.

For each site differences in H', d and total abundance at each station down the shore was also examined. In each case the data were found not to conform to normal distribution (Kolmogorov-Smirnov test, $p<0.05$ in each case) and the variances could not be considered equal (Levenes test, $p<0.05$ in each case). Transformation did not result in the assumptions being met, however as discussed previously ANOVA is a robust test. Therefore a one factor GLM ANOVA was performed, however the level of significance was again considered as 0.01 (Underwood, 1981). *Post hoc* Tukey HSD tests were used to determine the source of any statistically significant differences between samples. A Bray Curtis similarity matrix was also generated on the raw data of the total abundance of each species for each station as this produced the lowest stress level. However as the stress level of 0.2 was relatively high (Clarke & Warwick, 2001) a hierarchical agglomerative cluster diagram using group averages was produced using PRIMER as this has been suggested to be an effective way of determining groups (Clarke & Warwick, 2001). The similarity matrix was then used to perform an ANOSIM to test the null hypothesis that there was no statistically significant difference in community similarity with DISTANCE down each site. SIMPER analysis was performed to examine which species contributed to the similarity and dissimilarity between groups.

Although the abundance data collected was collected on fauna, the use of non parametric test was not deemed appropriate due to the high number of ties in the data. This violates the assumptions of both the non parametric Kruskal-Wallis and Scheirer-Ray-Hare tests

(Dytham, 2003). The additional difficulties with the Scheirer-Ray-Hare test are discussed previously, as has the robust nature of ANOVA. Therefore a two factor GLM ANOVA was performed with SEASON as a fixed factor with three levels (Winter, Spring, Summer and Autumn) and SITE as a fixed factor with three levels (North, Central and South) (Underwood, 1997) even though neither patellid and littorinid abundance were found to conform to normal distribution (Kolmogorov-Smirnov test, $p<0.05$ in both cases) or have approximately equal variance (Levenes test, $p<0.05$ in both cases), and transformation of the data could not resolve this. *Post hoc* Tukey HSD tests were again used to determine where any statistically significant differences occurred.

The abundance of both faunal groups, patellids and littorinids, at each station was also examined. For each site the abundance of patellids and littorinids were found not to conform to normal distribution (Kolmogorov-Smirnov test, $p<0.05$ in each case) and the variances could not be considered equal (Levenes test, $p<0.05$ in each case). Transformation did not result in the assumptions of normality and homogeneity of variances being met. A one factor GLM ANOVA was performed although the level of significance was again considered (Underwood, 1981). *Post hoc* Tukey HSD tests were used to determine the source of any statistically significant differences between samples.

4.3. Results

4.3.1. Temporal variation in the upper shore sediment zone

Upper shore sediment zone size

The volume and surface area of sediment in the upper shore sediment zone at each of the three sites (North, Central and South) was monitored for an 18-month period between June 2006 and November 2007 (figures 4.3.1a & 4.3.1b). Overall, both the volume and surface area of the sediment zone was greatest at the Central site (figures 4.3.1a & 4.3.1b).

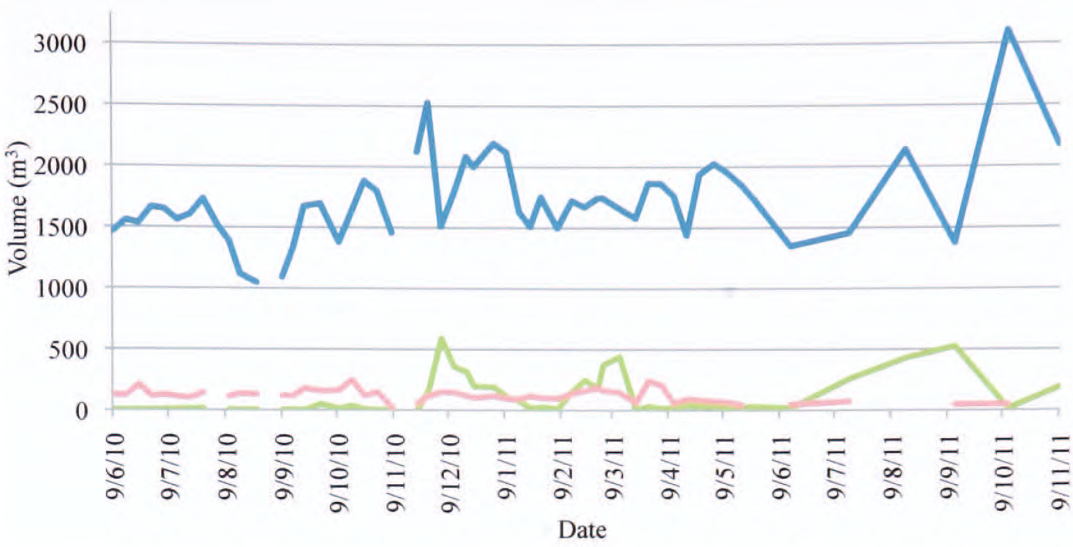
The volume of the sediment zone at the Central site varied between 1050m^3, (at the end of August 2006), and 3100m^3 (in October 2007) (figure 4.3.1a). Throughout the first 13 months the volume of sediment at the Central site generally fluctuated between 1500m^3 and 2000m^3 with a short decrease in volume between the middle of August 2006 and the middle of September 2006 (figure 4.3.1a). The volume of sediment gradually increased to above 2000m^3 by the end of November 2006 and then fluctuated between approximately 1400m^3 and 2200m^3. After September 2007 the volume of sediment continued to increase to the maximum volume in October 2007 before a slight decrease at the end of the sampling period (figure 4.3.1). The surface area of the Central sediment (figure 4.3.1b) followed a similar pattern to the volume of the sediment zone (figure 4.3.1a). For the first 12 months the surface area of the sediment zone at the Central site varied between approximately 1500m^2 and 2500m^2 with the lowest surface area of 1450m^2 occurring during mid August 2006 (figure 4.3.1b). The surface area of the sediment zone increased during early November 2006 to 3200m^2. After June 2007 there was a steady increase in surface area of the sediment zone of the Central site to a maximum value of 3100m^2 in October 2007 before a slight decrease at the end of the sampling period (figure 4.3.1b).

Sediment volume and surface area at the South site varied throughout the sampling period with little distinctive pattern (figures 4.3.1a & 4.3.1b). Sediment volume at the South site generally decreased throughout the 18 month time period, however larger fluctuations in the volume and surface area occurred throughout the time period (figure 4.3.1a & 4.3.1b). The largest change in sediment volume occurred between mid October 2006 and early

November 2006 where sediment volume decreased from a maximum level (250m^3) to a minimum of 20m^3 (figure 4.3.1a). Large but short-term changes in sediment volume also occurred at the end of June 2006 and at the end of March /early April 2007, (figure 4.3.1a). Larger changes in surface area occurred at the end of June 2006, at the end of March and in late May 2007 where sediment in the South site decreased from the maximum surface area during the sampling period (1100m^2) to a minimum surface area of 300m^2 (figure 4.3.1b).

The sediment zone at the North site was the most dynamic of the three sites, and displayed the lowest sediment volume and surface area for the majority of the sampling period (figure 4.3.2). Initially little difference was observed in the volume and surface area between sampling occasions (figures 4.3.1a and 4.3.1b), but between mid November 2006 and early December 2006 the volume of the sediment zone at the North site increased from 15m^3 to 520m^3 (figure 4.3.1a), whilst the surface area increases for 25m^2 to 970m^2 (figure 4.3.1b). Both sediment volume and surface area of the sediment zone decreased to their original low levels between early December 2006 and mid January 2007 (figures 4.3.1a & 4.3.1b). Increases in sediment volume and surface area at the North occurred between early February 2007 and early March 2007 before decreasing again to initial levels (figures 4.3.1a & 4.3.1b). Between mid March and early June the volume and surface area of sediment at the North site remained fairly constant (figures 4.3.1a & 4.3.1b). A gradual increase in both sediment volume, from 16m^3 to 523m^3 (figure 4.3.1a), and surface area, from 27m^2 to 965m^2 (figure 4.3.1b) occurred between early June 2007 and early September 2007. The volume and surface area of sediment then decreased again before starting to rise at the end of the sampling period (figures 4.3.1a & 4.3.1b).

a) Volume



a) Surface area

Key:

🟥	South	🟦	Central	🟩	North

Figure 4.3.1: Temporal changes in the upper shore sediment zone at each of the three sites (North, Central and South) on the rocky shore at Holbeck, North Yorkshire.

A two factor GLM ANOVA was used to test the effect of SEASON and SITE, and their interaction, upon sediment volume (table 4.3.1). SEASON had a statistically significant effect upon mean sediment volume (table 4.3.1), however *post hoc* Tukey tests were unable to resolve the source of the significance. The volume of sediment was greatest during Winter (mean = 677.02, s.d. = 797.0) and lowest during Spring (mean = 597.17, s.d. = 716.3) (figure 4.3.2a). SITE also had a statistically significant effect upon mean sediment volume (table 4.3.1). Sediment volume at the Central site (mean = 1717.14, s.d. = 349.15) was statistically significantly greater than both the North (mean = 98.45, s.d. = 150.88) and the South sites (mean = 117.58, s.d. = 49.19) (figure 4.3.2a). The interaction between SEASON and SITE was not statistically significantly different (table 4.3.1) indicating that variations in sediment volume at all three sites were similar between the different seasons. An increase in sediment volume was recorded in both the North and Central sites between Autumn and Winter, although this was most pronounced in the Central site. During the other seasons the volume of sediment remained relatively similar (figure 4.3.2a).

Table 4.3.1: Summary of results from a two factor GLM ANOVA for sediment volume using SEASON and SITE as factors.

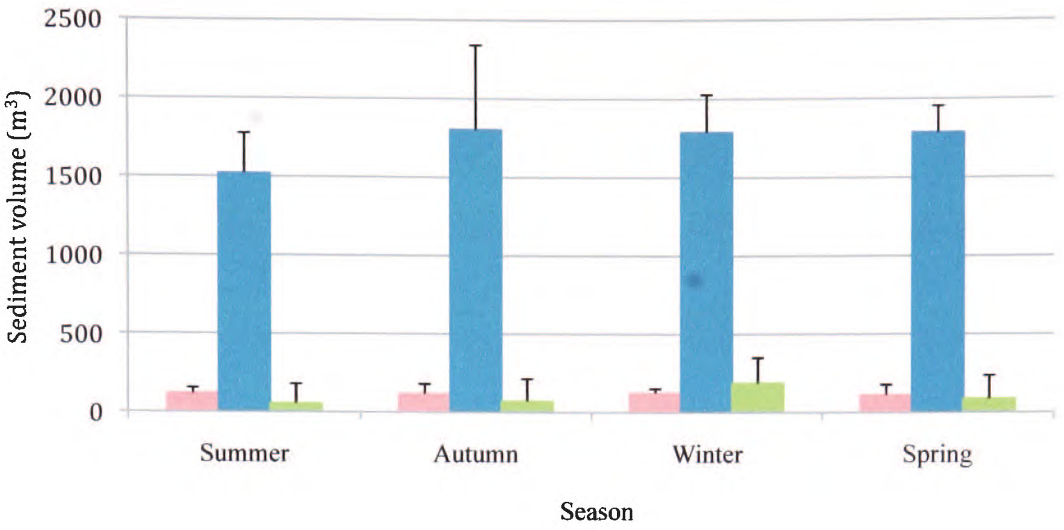
Source	**DF**	**Adj MS**	**F**	**P**
SEASON	3	138582.525	2.953	0.035
SITE	2	46003901.791	980.214	<0.001
SEASON*SITE	6	84404.172	1.798	0.103
Error	145	46932.527		

A two factor GLM ANOVA was used to test the effect of SEASON and SITE, and their interaction, upon sediment surface area (table 4.3.2) SEASON had no statistically significant effect upon the mean sediment surface area (table 4.3.2). However there was a statistically significant difference in the mean surface area between SITE (table 4.3.2). The mean surface area at the Central site (mean = 630.58, s.d. = 151.39) was significantly higher than that at the South site (mean = 630.58, s.d. = 151.39), which in turn was statistically significantly higher than the North site (mean = 169.11, s.d. = 246.63) (Tukey, p=0.05) (figure 4.3.2b). The interaction between SEASON and SITE was statistically significant (table 4.3.2) indicating that the mean surface area of sediment did not show the same change between seasons at the different SITES. At the Central site the mean surface area of sediment was higher in Autumn than both Summer and Winter, whilst at the North site the mean surface area of sediment was greater in Winter than Autumn (figure 4.3.2b).

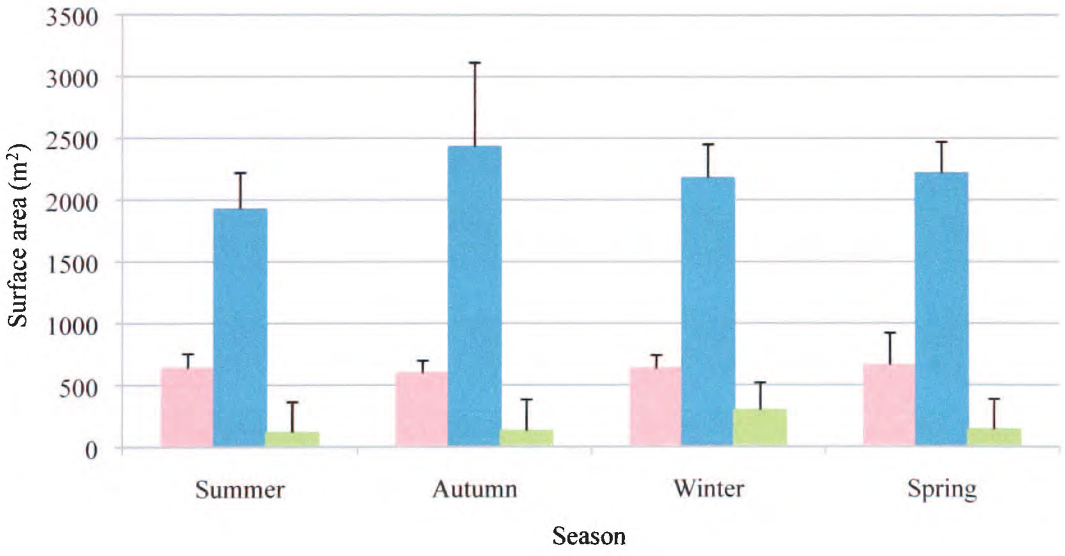
Table 4.3.2: Summary of the results from a two factor GLM ANOVA for sediment surface area using SEASON and SITE as factors.

Source	**DF**	**Adj MS**	**F**	**p**
SEASON	3	213605.184	2.403	0.07
SITE	2	59272416.904	666.684	<0.001
SEASON*SITE	6	245529.597	2.762	0.014
Error	145	88906.313		

a) Volume



a) Surface area



Key:

🟥	South	🟦	Central	🟩	North

Figure 4.3.2: Seasonal changes in the volume and surface area of the upper shore sediment zone at each of the three sites (North, Central and South) on the rocky shore at Holbeck, North Yorkshire (mean, + s.d.).

Upper shore sediment zone position

The position of the sediment zone on the shore was not consistent throughout the year. From the cliff top photographs this was most clearly evident at the Central site. During the period of minimum sediment deposition, no sediment can be seen in the upper shore sediment zone (plate 4.3.1). However limited algal growth was observed in the upper part of the shore suggesting that the area was subject to regular sediment burial and scouring. In contrast, during the period of maximum deposition, all of the previously clear, scoured areas, were covered with sediment. At this point the middle of the sediment zone expanded into the mid shore area (plate 4.3.2).

Between the two extremes, variation in the position of the sediment zone may also be observed (plates 4.3.3 & 4.3.4). During the observation period, sediment predominantly accumulated in the area of the sediment zone nearest to the Holbeck sea defences, which led to an increase in the length of the sediment zone (plate 4.3.3). Whilst sediment accumulated towards the sea defences, areas of bare rock are evident towards the groyne (plate 4.4.3). On other occasions sediment accumulated at the groyne end (plate 4.3.4). The height of accumulation at this end of the sediment zone was found, on occasion, to exceed the height of the groyne (plate 4.3.4). When sediment accumulation occurred towards the groyne end of the Central site, sediment accumulation and extent at the North site was also at its greatest (plate 4.3.4).

Sediment accumulation on the shore was not restricted to the upper shore sediment zone. Accumulation occurred throughout the shore (plates 4.3.1, 4.3.2 & 4.3.4). Although some areas of sediment accumulation were found to join with the sediment zone for short periods of time (plate 4.3.2), on the majority of occasions they were separated from the sediment zone (plate 4.3.4) and, therefore, not described in the previous measurements.

Plate 4.3.1: Position of the upper shore sediment zone on 25.08.06.

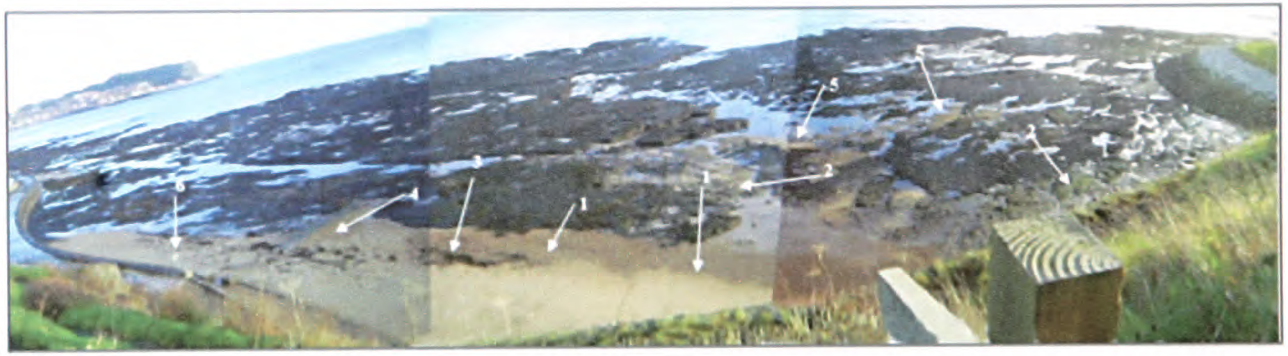
Plate 4.3.2: Position of the upper shore sediment zone on 07.11.06.

Key:

1	Sediment zone	2	Bare rock	3	Increase in sediment extent	4	Increase in sediment height	5	Areas of sediment on the shore	6	North site sediment zone

Plate 4.3.3: Position of the upper shore sediment zone on 06.02.07.

Plate 4.3.4: Position of the upper sore sediment zone on 04.12.06.



Key:

1	Sediment zone	2	Bare rock	3	Increase in sediment extent	4	Increase in sediment height	5	Areas of sediment on the shore	6	North site sediment zone

Upper shore sediment zone grain size composition

The proportions of Udden-Wentworth sediment grain sizes classes at each of the three sites were monitored for a 12-month period between June 2006 and May 2007 (figures 4.3.3 & 4.3.4). Although samples were collected on both spring and neap tides there was no observable difference in the proportions of the different grain size classes between the two tide states at any of the sites.

The three sites were dominated by different sediment grain size classes (figure 4.3.3). At the South site the sediment was dominated by pebbles (>4mm) (figure 4.3.3c). Between June 2006 and October 2006 pebbles constituted approximately 50% of the sediment samples, and from December onwards the proportion of pebbles increased to between 60 - 90% of the sample (figure 4.3.5c). Samples from the 18.05.07 showed a decrease in the proportion of pebbles to 50% accompanied by an increase in the proportion of medium sand (250µm-0.5mm) to approximately 40% (figure 4.3.3c). Throughout the 12 month sampling period the proportions of granules (2mm-4mm), very coarse sand (1mm-2mm) and coarse sand (0.5mm-1mm) were approximately equal (figure 4.3.5c). There was very little fine/ very fine sand (<250µm) observed throughout the sampling period (figure 4.3.5c).

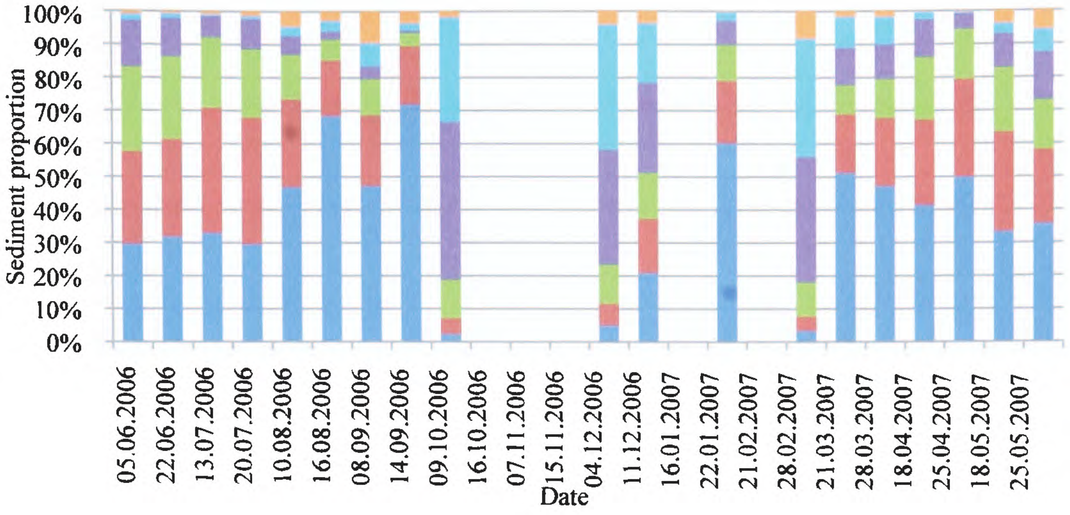
The North site also had a higher proportion of the larger sediment grain sizes, although the proportions of very coarse sand, granules and pebbles (>4mm) were very similar between June 2006 - September 2006 and between March 2007 - May 2007 (figure 4.3.3a). During these time periods, approximately 70% to 90% of the sediment consisted of these three grain size classes. Between October 2006 and February 2007, with the exception of late January 2007, the proportion of pebbles, granules, and very coarse sand decreased, and the samples were instead dominated by coarse sand and medium sand (figure 4.3.3a).

The Central (figure 4.3.3b) site had a smaller proportion of pebbles (contribution <11% throughout 12 month period) than either the North (figure 4.3.3a) or South (figure 4.3.3c) sites. Samples from the Central site were dominated by medium sand and coarse sand (figure 4.3.3b), which accounted for at least 50% of all the sample composition. The proportion of the grain size classes remained approximately constant throughout the 12 month sampling period (figure 4.3.3b) but during August 2006 - September 2006 proportions of very coarse sand, granules and pebbles increased, whilst in November 2006 and December 2006 the proportion of fine/ very fine sand increased (figure 4.3.3c).

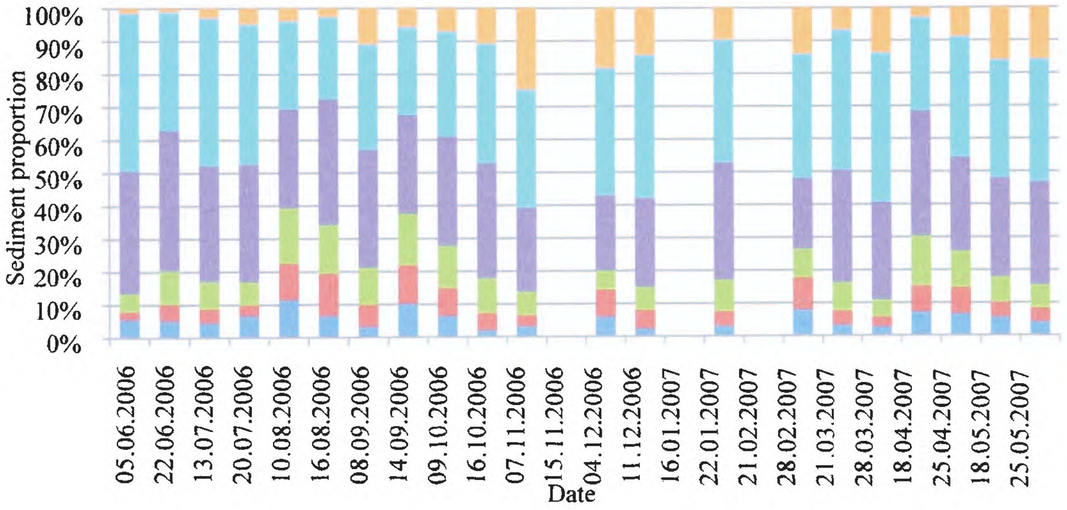
Due to the larger area and volume of the upper shore sediment zone at the Central site, the proportions of each sediment grain size class was examined at the top (TP), middle (ME) and bottom (BM) of the sediment zone (figure 4.3.4). At both TP (figure 4.3.4a) and ME (figure 4.3.4b) the samples were dominated by medium and coarse sand, although the ME had a higher proportion of very coarse sand, granules and pebbles. An increase in the larger sediment grain size classes of very coarse sand, granules and pebbles occurred during August 2006 at TP and at ME during both August 2006 and September 2006 (figures 4.3.4a & 4.3.4b). Increases in the proportion of fine/ very fine sand also occurred at TP and ME in November 2006 and the early part of December 2006 and at ME during November 2006 until January 2007 (figures 4.3.4a & 4.3.4b).

The proportion of each sediment grain size class were much more even in the BM samples across the seasons (figure 4.3.4c). However there was a higher proportion of fine/ very fine sand than either TP or ME (figures 4.3.4a & 4.3.4b) during November 2006 and December 2006. Unlike the pattern found at TP and ME, there was an increase in the proportion of the fine/ very fine sand towards the end of the sampling period from the end of April 2007 and during May 2007 (figure 4.3.4c). There was also an increase in the proportion of very course sand, granules and pebbles mirroring changes at TP and ME during August 2006 and September 2006 (figure 4.3.4).

a) North site



a) Central site



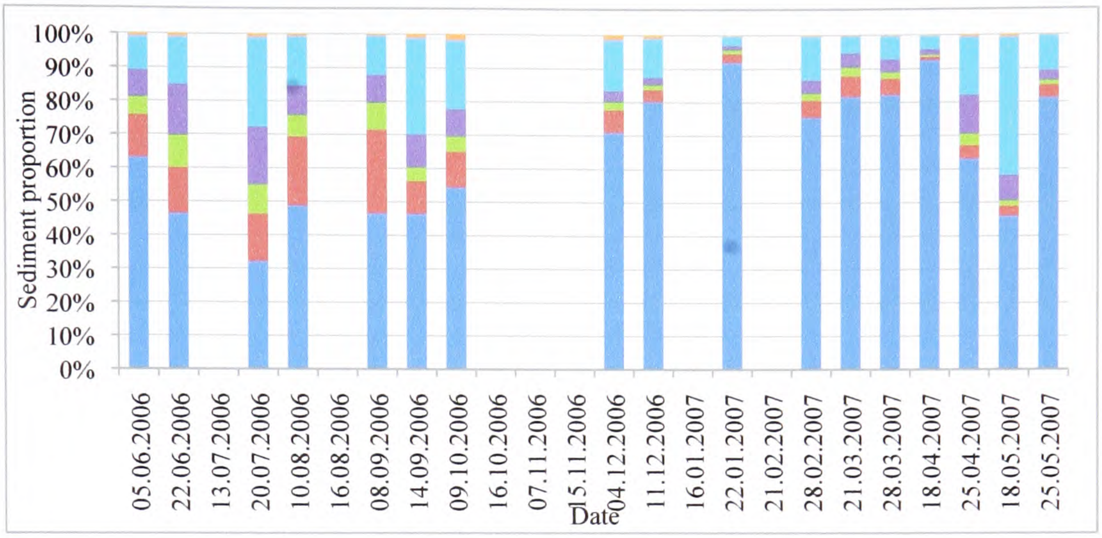
Key:

🟦	Pebbles (>4mm)	🟥	Granules (2mm-4mm)	🟩	Very coarse sand (1mm-2mm)
🟪	Coarse sand (0.5mm-1mm)	🟦	Medium sand (250µm-0.5mm)	🟨	Fine/ very fine sand (<250µm)

Figure 4.3.3: Temporal variation in grain size composition of the upper shore sediment zone at each of the three sites (North, Central and South) at Holbeck, North Yorkshire.

Figure 4.3.3 contd.

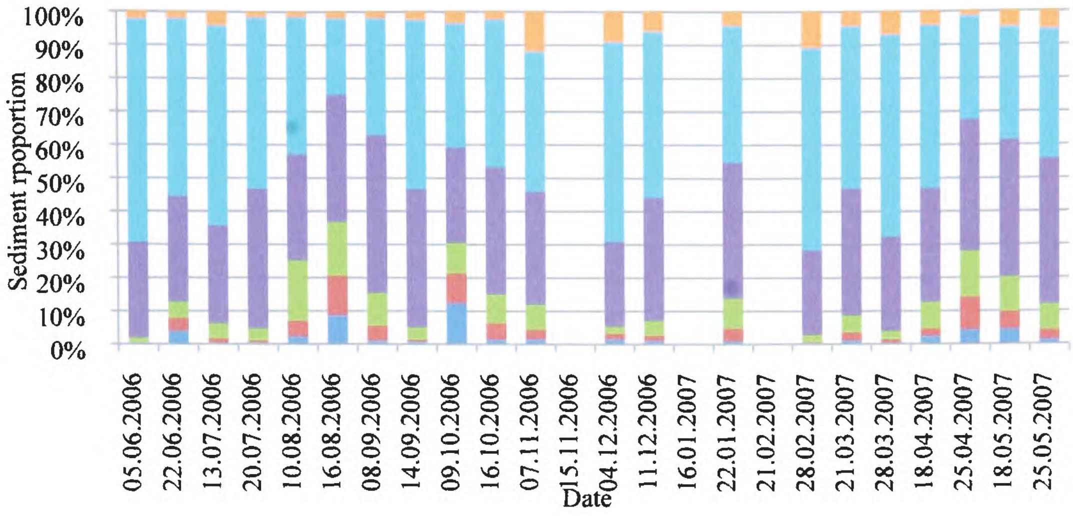
b) South site



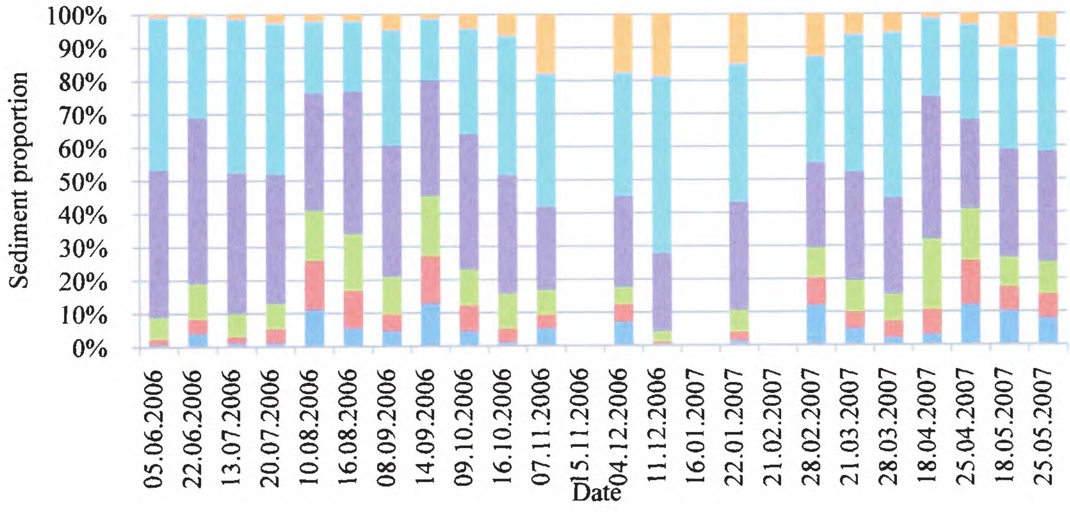
Key:

🟦	Pebbles (>4mm)	🟥	Granules (2mm-4mm)	🟩	Very coarse sand (1mm-2mm)
🟪	Coarse sand (0.5mm-1mm)	🟦	Medium sand (250µm-0.5mm)	🟧	Fine/ very fine sand (<250µm)

a) Top



a) Middle



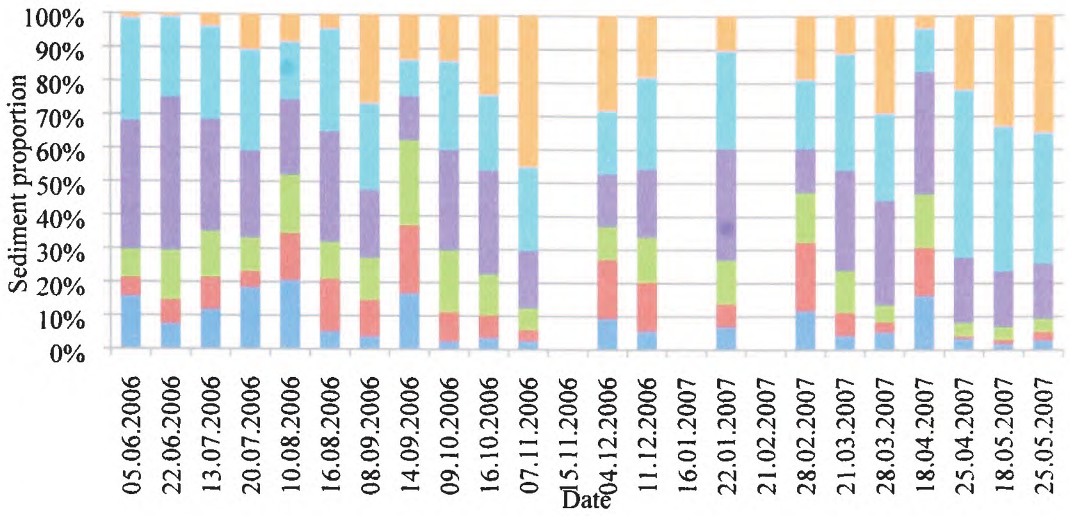
Key:

🟦	Pebbles (>4mm)	🟥	Granules (2mm-4mm)	🟩	Very coarse sand (1mm-2mm)
🟪	Coarse sand (0.5mm-1mm)	🟦	Medium sand (250µm-0.5mm)	🟧	Fine/ very fine sand (<250µm)

Figure 4.3.4: Temporal variation in grain size composition at the Top, Middle and Bottom of the Central site at Holbeck, North Yorkshire.

Figure 4.2.4 contd.

b) Bottom



Key:

🟦	Pebbles (>4mm)	🟥	Granules (2mm-4mm)	🟩	Very coarse sand (1mm-2mm)
🟪	Coarse sand (0.5mm-1mm)	🟦	Medium sand (250µm-0.5mm)	🟧	Fine/ very fine sand (<250µm)

4.3.2. Zonation of sediment and biota

4.3.2.1. Distribution of sediment on the shore

A two factor GLM ANOVA was used to test the effect of SEASON and SITE upon percentage sediment cover. Both SEASON and SITE had a statistically significant effect upon mean percentage sediment cover (table 4.3.3). Mean percentage sediment cover was statistically significantly lower in Winter (mean = 45.35, s.d. = 86.84) than Autumn (mean = 101.44, s.d. = 107.96) and Summer (mean = 107.14, s.d. = 116.95), whilst Summer had a statistically significantly higher mean percentage sediment cover than Spring (mean = 72.84, s.d. = 98.24) and Winter (Tukey, $p<0.05$) (figure 4.3.5). There was no statistically significant difference in the mean percentage sediment cover between the North (mean = 54.05, s.d. = 82.92) and South (mean = 62.96, s.d. = 87.19) sites, however both had a statistically significantly lower mean percentage sediment cover than the Central site (mean = 130.68, s.d. = 126.87) (Tukey, $p<0.05$) (figure 4.3.5). The interaction between SEASON and SITE was not statistically significant (table 4.3.3) indicating that the variations in sediment cover at all three sites were similar between seasons. Sediment cover was greatest during the Summer at both the Central and North sites and lowest in the Winter at all three sites (figure 4.3.5). Sediment cover at all three sites was also lower in Spring than Autumn (figure 4.3.3).

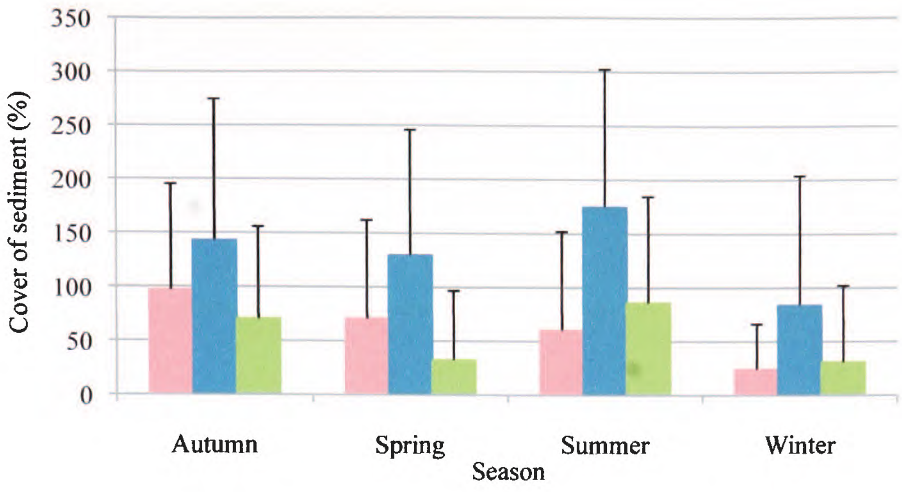
Table 4.3.3: Summary of results from a two factor GLM ANOVA for percentage sediment cover with SEASON and SITE as factors.

Source	**df**	**MS Adj**	**F**	**p**
SEASON	3	99825.238	10.625	<0.001
SITE	2	301888.578	32.131	<0.001
SEASON*SITE	6	15973.262	1.700	0.119
Error	495	9395.639		

The distribution of sediment down the transect varied between the three sites (figure 4.3.6). Mean sediment cover at the North site was relatively consistent down the entire transect. The mean percentage cover of sediment generally varied between 121.00 (s.d. = 163.42) at 210m and 6.25% (s.d. = 12.50) at 240m (figure 4.3.6). A one factor GLM ANOVA testing the effect of STATION on sediment cover revealed that there was a statistically significant difference in sediment cover at the North site (ANOVA, $F_{24, 160} = 1.943$, $p<0.01$). The only statistically significant difference in the mean percentage sediment cover occurred between the maximum at 10m (mean = 159.75, s.d. = 147.50) and the minimum at 40m (mean = 2.25, s.d. = 3.65) (Tukey, $p<0.05$), however there were no other significant differences between distances.

Mean percentage sediment cover at the Central site was greatest at either end of the transect (mean = 300.00, s.d. = 0.000 at 0m and 10m at the top of the transect and 210m, 230m and 240m at the bottom of the transect) (figure 4.3.6). Mean percentage sediment cover generally decreased between 0m and 70m then remained relatively consistent before increasing between 170m and 240m (figure 4.3.6). There was a statistically significant difference in the mean percentage sediment cover of the Central site (ANOVA, $F_{20, 133} = 3.866$, $p<0.001$). The mean percentage cover of sediment was statistically significantly greater at 0m and 10m than at 50m, 170m, 110m, 100m, 150m, 180m, 120m, and 190m (Tukey, $p<0.05$).

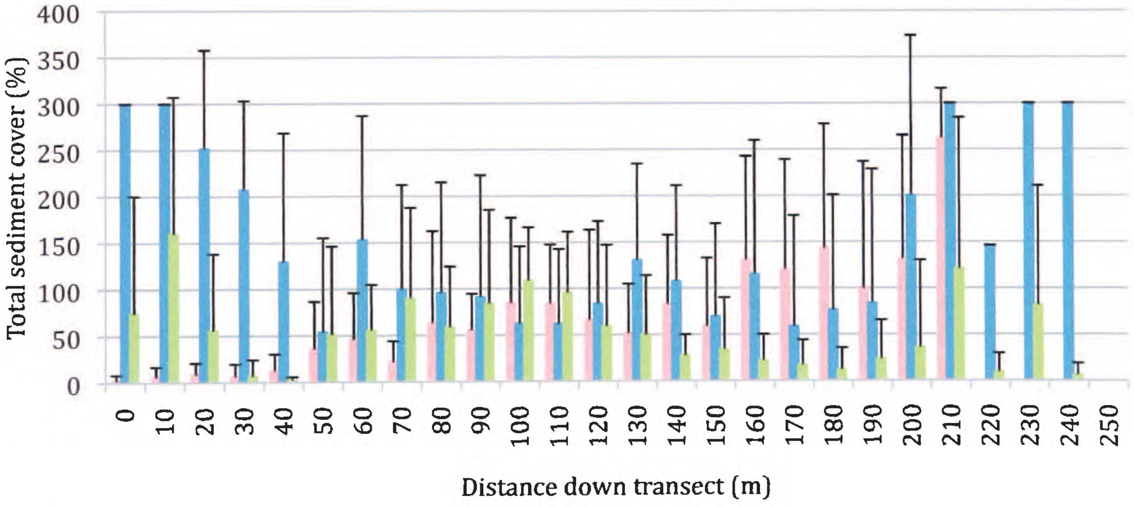
The mean percentage sediment cover at the South site generally increased from the top of the transect (0m, mean = 2.13, s.d. = 6.01) to the bottom of the transect (210m, mean = 262.00, s.d. = 53.74) (figure 4.2.6). There was a statistically significant difference in the mean percentage cover of the South site (ANOVA, $F_{21, 143} = 3.035$, $p<0.001$). Mean percentage cover between 0m and 150m, and at 190m was statistically significantly lower than sediment cover at 210m (Tukey, $p<0.05$).



Key:

🟥	South	🟦	Central	🟩	North

Figure 4.3.5: Seasonal changes in the mean percentage cover of sediment on the shore at each of the three sites (North, Central and South) on the rocky shore at Holbeck, North Yorkshire (+ s.d.).



Key:

🟥	South	🟦	Central	🟩	North

Figure 4.3.6: The mean percentage cover of sediment within the transect, across all four seasons, at each site (North, Central and South) on the rocky shore at Holbeck (+ s.d.).

4.3.2.2. Distribution of organisms on the shore

Differences in the macroalgal community between sites

The results of the comparisons for each of total abundance, species diversity (H') and species richness (d) and season and site are shown in figure 4.3.7.A two factor GLM ANOVA was used to test the effect of SEASON and SITE, and their interaction upon each of total abundance, species diversity (H') and species richness (d). In all cases there was a statistically significant difference between SITE (tables 4.3.4, 4.3.5 & 4.3.6). The total abundance, H' and d was lower at the Central site than the other two sites (figure 4.3.7). There was no statistically significant difference in mean total abundance between Central (mean = 217.711, s.d. = 180.9872) and South (mean = 230.733, s.d. = 171.332) sites, however both had a statistically significantly lower mean total abundance than the North site (mean = 326.668, s.d. = 167.784) (Tukey, $p<0.05$) (figure 4.3.7a). The d was statistically significantly lower at the Central site (mean = 0.798, s.d. = 0.675) than at both the North (mean = 1.014, s.d. = 0.572) and South (mean = 1.145, s.d. = 0.575) sites, although there was no statistically significant difference between the North and South sites (Tukey, $p<0.05$) (figure 4.3.7b). Mean H' was statistically significantly different between all three sites (Tukey, $p<0.05$). The lowest mean H' occurred at the Central site (mean = 0.815, s.d = 0.581), whilst the highest occurred at the South site (mean = 1.161, s.d. = 0.511) (figure 4.3.7c).

There was also a statistically significant difference in d between SEASON (table 4.3.5). Mean d was statistically significantly lower during Winter (mean = 0.811, s.d. = 0.532) than all other seasons (Autumn (mean = 1.030, s.d. = 0.618), Summer (mean = 1.104, s.d. = 0.654) and Spring (mean = 1.017, s.d = 0.638)) (Tukey, $p<0.05$), however all other comparisons between seasons were not statistically significant (figure 4.3.7b). However, no statistically significant differences occurred in total abundance or H' between SEASON (tables 4.3.4 and 4.3.6)

No statistically significant interaction occurred in total abundance, H' or d between SEASON and SITE (tables 4.3.4, 4.3.5 & 4.3.6). This indicated that in all cases variations at all three sites were similar between different seasons. The total abundance, H' and d were all generally lowest at all three sites in Winter (figure 4.2.7). Mean total abundance was greatest at all three sites during Summer (figure 4.3.7a). Mean H' remained relatively constant, especially in the South and Central sites, between the other three seasons (figure 4.3.7c).

Table 4.3.4: Summary of results from a two factor GLM ANOVA for total abundance with SEASON and SITE as factors.

Source	**df**	**MS Adj**	**F**	**p**
SEASON	3	92247.605	3.112	0.026
SITE	2	625193.058	21.090	<0.001
SEASON*SITE	6	14377.775	0.485	0.820
Error	496	29643.921		

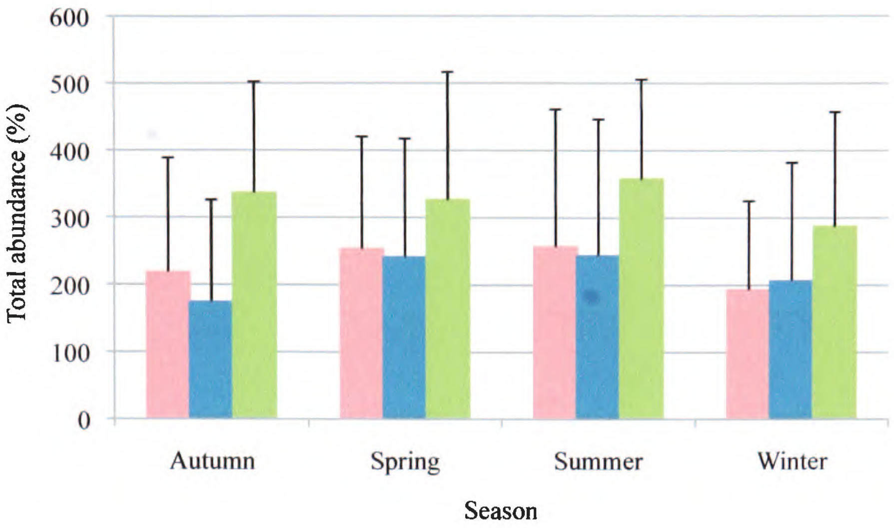
Table 4.3.5: Summary of results from a two factor GLM ANOVA for species richness (d) with SEASON and SITE as factors.

Source	**df**	**MS Adj**	**F**	**p**
SEASON	3	1.951	5.513	0.001
SITE	2	5.118	14.465	<0.001
SEASON*SITE	6	0.598	1.690	0.121
Error	496	0.354		

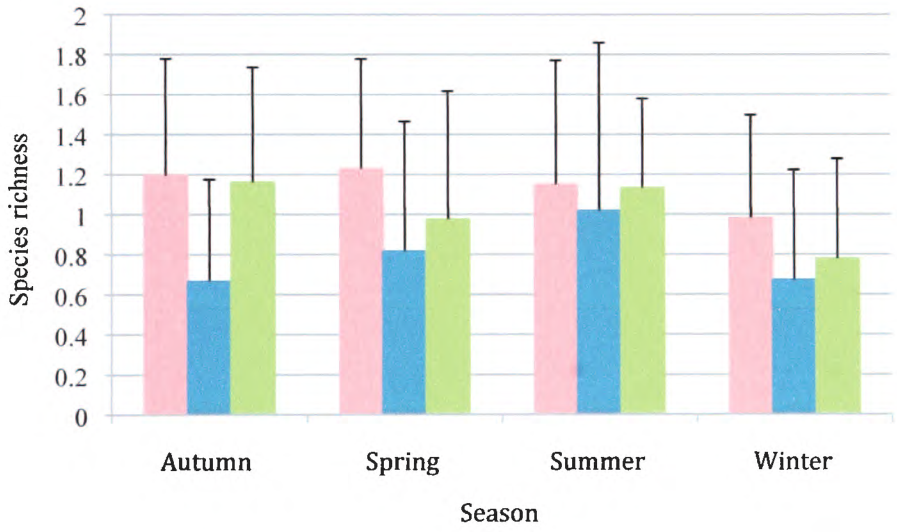
Table 4.3.6: Summary of results from a two factor GLM ANOVA for species diversity (H') with SEASON and SITE as factors.

Source	**df**	**MS Adj**	**F**	**p**
SEASON	3	0.819	2.989	0.031
SITE	2	4.945	18.040	<0.001
SEASON*SITE	6	0.305	1.114	0.353
Error	495	0.274		

a) Mean total abundance



b) Mean species richness



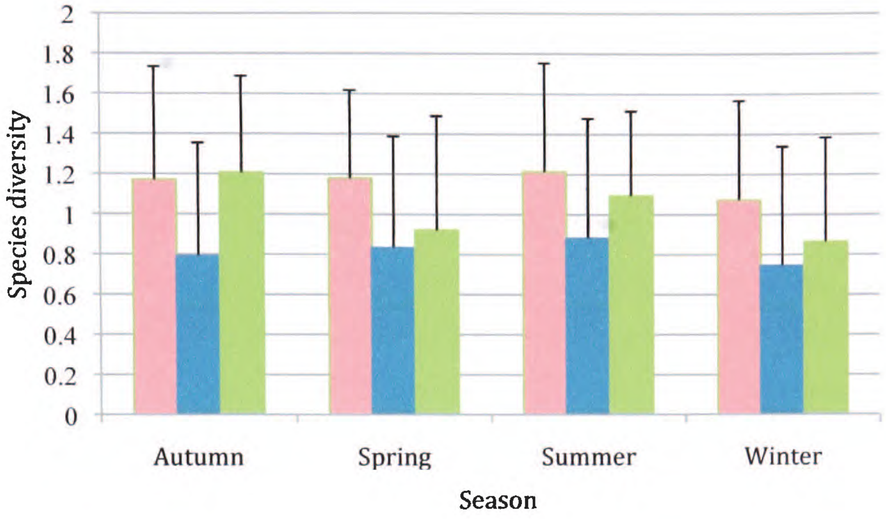
Key:

🟥	South	🟦	Central	🟩	North

Figure 4.3.7: Seasonal changes in the community composition of macroalgae and barnicles on the shore at each of the three sites (North, Central and South) on the rocky shore at Holbeck, North Yorkshire (+ s.d.).

Figure 4.3.7 contd.

c) Mean species diversity



Key:

🟥	South	🟦	Central	🟩	North

Differences in macroalgal community similarity between sites

Figure 4.3.8 shows an MDS plot generated from a Bray-Curtis similarity matrix of untransformed macroalgal community data. Whilst the relatively high stress value of 0.18 indicates some lack of repeatability of the clusters of samples in the MDS plot (Clarke & Warwick, 2001) the North and South site transects form two clusters with very little overlap (figure 4.3.8). The samples from the Central site lie between the North and South sites and display some overlap with both the other sites (figure 4.3.8). A two way ANOSIM was used to test the effect of SITE and SEASON upon the similarity of the communities. There was a statistically significant difference in the community similarity between the three sites (ANOSIM, Global R = 0.085, p = 0.1%). Pairwise comparisons of the sites revealed that the community similarity at all sites was statistically significantly different in all cases (p=0.01%). Clustering of the samples by season is less evident. Spring, Summer and Autumn of the North and Central sites are separated from the Autumn samples. Autumn samples form two small clusters at either side of the plot (figure 4.3.8). Although Autumn samples showed some clustering, there was no statistically significant difference in community similarity between the four seasons (ANOSIM, Global R = 0.111, p = 20.0%).

The majority of macroalgal species on the shore occurred throughout the year (table 4.3.7). However a few species were only identified during one or two seasons. *Laminaria saccharina* (Linnaeus) Lamouroux and *Cystoclonium purpureum* (Hudson) Batters only occurred during the Summer months, *Polysiphonia nigra* (Hudson) Batters and *Furcellaria lumbricalis* (Hudson) Lamouroux only occurred during Spring whilst *Ectocarpus* only occurred during Winter (table 4.3.7). Autumn had the most species that were only found during one season. *Chaetomorpha melagonium* (Weber & Mohr) Kützing, *Blidingia minima* (Nägeli & Kützing) Kylin, *Polyides rotundus* (Hudson) Gaillon, *Gelidium pusillum* (Stackhouse) Le Jolis, *Ceramium virgatum* Roth, *Ceramium gaditanum* (Clemente y Rubio) Cremades and *Halurus flosculosus* (Ellis) Maggs & Hommersand only occurred during Autumn (table 4.3.7).

Community similarity within each of the four seasons was primarily determined by three macroalgal species, *Fucus vesiculosus*, *Phymatolithon lenormandii* (Areschoug) Adey, and *Fucus serratus* (table 4.3.8). To a lesser extent *Osmundea pinnatifida* was also an important species in determining overall similarity within each of the seasons (table 4.3.8).

With the exception of Winter months *Fucus vesiculosus* was the most important species in determining overall community similarity (table 4.3.8).

The macroalgal community at all three sites consisted of similar species (table 4.3.7). The majority of species occurred at all three sites at some point throughout the year (table 4.3.7). *Fucus spiralis*, *Polysiphonia nigra* and *Furcellaria lumbricalis* were the only species restricted solely to the South site (table 4.3.7), whilst *Chaetomorpha melagonium*, *Saccharina latissima* (Linnaeus) Lane, Mayes, Druehl & Saunders, *Ectocarpus* and *Halurus flosculosus* only occurred on the North site (table 4.3.7). The only species found solely at the Central site was *Gelidium pusillum* (table 4.3.7).

The most important species in determining community similarity at both the Central and North sites was *Fucus vesiculosus* (table 4.3.9). *Phyomatolithon lenormandii* and *Fucus serratus* were also important species, with *Corallina officinalis* and *Osmundea pinnatifida* to a lesser extent (table 4.3.9). At the South site *Osmundea pinnatifida* was the most important species in determining community similarity (table 4.3.9) and, again, *Phyomatolithon lenormandii* and *Fucus serratus* were also important (table 4.3.9). The dissimilarity between the three sites was primarily attributable to the difference in abundance of *Fucus vesiculosus, Phyomatolithon lenormandii*, and *Fucus serratus*. The abundance of *Fucus vesiculosus* and *Phyomatolithon lenormandii* was greatest at the North site (table 4.3.9) as was that of *Corallina officinalis*, although this was only slightly greater than the abundance at the South site (table 4.3.9). The greatest abundance of *Rhodothamniella floridula* also occurred at the North site (25.68%) compared to the Central (15.16%) and South (9.48%) sites, as did the greatest abundance of *Fucus* juveniles (North = 11.73%, Central = 2.28%, South = 3.55%). The greatest abundance of *Fucus serratus* occurred at the Central site, whilst the South site had the greatest abundance of *Osmundea pinnatifida*.

Table 4.3.7: Species occurring at each of the three sites at Holbeck and the seasons in which they were identified.

	South				**Central**				**North**			
	A	**Sp**	**S**	**W**	**A**	**Sp**	**S**	**W**	**A**	**Sp**	**S**	**W**
Ahnfeltia plicata **(Hudson) Fries**		p	p			p	p	p	p	p	p	
Blidingia minima **(Nägeli & Kützing) Kylin**	p								p			
Ceramium botryocarpum **Griffiths & Harvey**		p	p	p		p	p			p	p	
Ceramium gaditanum **(Clemente y Rubio) Cremades**	p								p			
Ceramium nodulosum **(Lightfoot) Ducluzeau**	p								p			
Ceramium pallidum **(Nägeli & Kützing) Maggs & Hommersand**	p		p				p		p			p
Chaetomorpha ligustica **(Kützing) Kützing**	p		p				p				p	
Chaetomorpha melagonium **(Weber & Mohr) Kützing**									p			
Chondrus crispus **Stackhouse**	p	p	p	p	p	p	p	p	p	p	p	p
Cladophora rupestris **(Linnaeus) Kützing**	p	p	p	p	p	p	p	p	p	p	p	p
Cladophora sericea **(Hudson) Kützing**	p	p	p	p	p	p	p	p	p	p	p	p
Cladostephus spongiosus **(Hudson) Agardh**	p	p	p	p	p	p	p	p	p	p	p	p
Corallina officinalis **Linnaeus**	p	p	p	p	p	p	p	p	p	p	p	p
Cystoclonium purpureum **(Hudson) Batters**			p								p	
Dumontia contorta **(Gmelin) Ruprecht**	p	p	p	p	p	p	p			p	p	
Ectocarpus												p
Fucus **juveniles**	p	p	p	p	p	p	p	p	p	p	p	p
Fucus serratus **Linnaeus**	p	p	p	p	p	p	p	p	p	p	p	p
Fucus spiralis **Linnaeus**	p		p									
Fucus vesiculosus **Linnaeus**	p	p	p	p	p	p	p	p	p	p	p	p
Furcellaria lumbricalis **(Hudson) Lamouroux**		p										
Gelidium pusillum **(Stackhouse) Le Jolis**					p							
Halidrys siliquosa **(Linnaeus) Lyngbye**	p	p	p	p		p	p			p		

Table 4.3.7 contd.

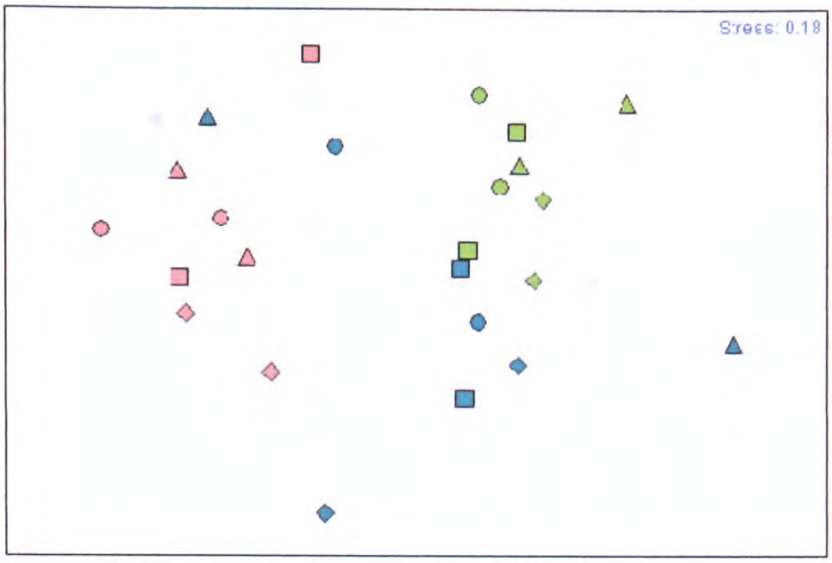
***Halurus flosculosus* (Ellis) Maggs & Hommersand**									p			
***Hildenbrandia rubra* (Sommerfelt) Meneghini**	p	p	p	p		p	p	p	p	p	p	p
***Laminaria digitata* (Hudson) Lamouroux**	p	p	p	p		p	p	p	p	p	p	p
***Lithothamnion glaciale* Kjellman**	p	p	p	p	p		p	p	p	p	p	p
***Lomentaria articulata* (Hudson) Lyngbye**	p	p	p			p			p	p	p	
***Mastocarpus stellatus* (Stackhouse) Guiry**	p	p	p	p	p	p	p	p	p	p	p	p
***Membranoptera alata* (Hudson) Stackhouse**	p	p	p	p			p		p	p	p	p
***Osmundea pinnatifida* (Hudson) Stackhouse**	p	p	p	p	p	p	p	p	p	p	p	p
***Phymatolithon lenormandii* (Areschoug) Adey**	p	p	p	p	p	p	p	p	p	p	p	p
***Plocamium cartilagineum* (Linnaeus) Dixon**	p	p	p	p	p	p	p			p	p	
***Polyides rotundus* (Hudson) Gaillon**	p								p			
***Polysiphonia atlantica* Kapraun & Norris**	p	p				p						
***Polysiphonia fucoides* (Hudson) Greville**	p	p	p	p	p	p	p	p	p	p	p	p
***Polysiphonia lanosa* (Linnaeus) Tandy**		p					p			p	p	p
***Polysiphonia nigra* (Hudson) Batters**		p										
Polysiphonia sp			p									
***Porphyra umbilicalis* Kützing**		p	p	p		p	p		p	p	p	
***Rhodomela confervoides* (Hudson) Silva**	p					p			p			
***Rhodothamniella floridula* (Dillwyn) Feldmann**	p	p	p	p		p	p		p	p	p	p
***Saccharina latissima* (Linnaeus) Lane, Mayes, Druehl & Saunders**											p	
***Ulva intestinalis* Linnaeus**	p	p	p	p	p	p	p		p	p	p	p
***Ulva lactuca* Linnaeus**	p	p	p	p	p	p	p	p	p	p	p	p
Ulva sp.	p											
***Verrucaria maura* Wahlenberg**	p	p	p	p	p	p	p	p	p	p	p	p

Table 4.3.8: Species contributing to the similarity in community for each season across all three sites at Holbeck.

	Autumn **27.00% similarity**		**Spring** **23.27% similarity**		**Summer** **20.99% similarity**		**Winter** **30.82% similarity**	
Species	**Average Percentage cover (%)**	**Contribution (%)**	**Average Percentage cover (%)**	**Contribution (%)**	**Average Percentage cover (%)**	**Contribution (%)**	**Average Percentage cover (%)**	**Contribution (%)**
Fucus vesiculosus	83.01	40.11	75.13	35.02	64.34	27.54	62.07	24.00
Phyomatolithon lenormandii	55.04	20.88	53.69	15.81	57.44	21.00	75.65	32.75
Corallina officinalis	19.40	12.01	16.45	6.90	18.19	7.50		
Fucus serratus	47.56	11.99	62.63	21.84	63.63	20.11	66.51	22.46
Osmundea pinnatifida	26.65	9.21	28.36	13.14	17.09	8.13	28.80	11.99

Table 4.3.9: Species contributing to the similarity in community for each site across all four seasons at Holbeck.

	South 21.02% similarity		**Central 25.26% similarity**		**North 32.45% similarity**	
Species	**Average Percentage cover (%)**	**Contribution (%)**	**Average Percentage cover (%)**	**Contribution (%)**	**Average Percentage cover (%)**	**Contribution (%)**
Fucus vesiculosus	27.11	12.74	79.96	36.03	103.99	45.47
Phyomatolithon lenormandii	47.37	25.14	52.13	17.34	77.83	22.47
Corallina officinalis	18.14	12.89	15.82	7.80	18.19	4.89
Fucus serratus	48.42	15.98	67.62	27.92	65.93	14.71
Osmundea pinnatifida	37.72	25.24	18.48	6.26	18.01	5.56



Key:

▲	North Autumn	■	North Spring	●	North Winter	◆	North Summer
▲	Central Autumn	■	Central Spring	●	Central Winter	◆	Central Summer
▲	South Autumn	■	South Spring	●	South Winter	◆	South Summer

Figure 4.3.8: MDS plot of community structure at each of the three sites (North Central and South) during each season (Autumn, Spring, Winter and Summer) generated from a Bray Curtis similarity matrix of untransformed data.

Differences in the macroalgal community within the North site

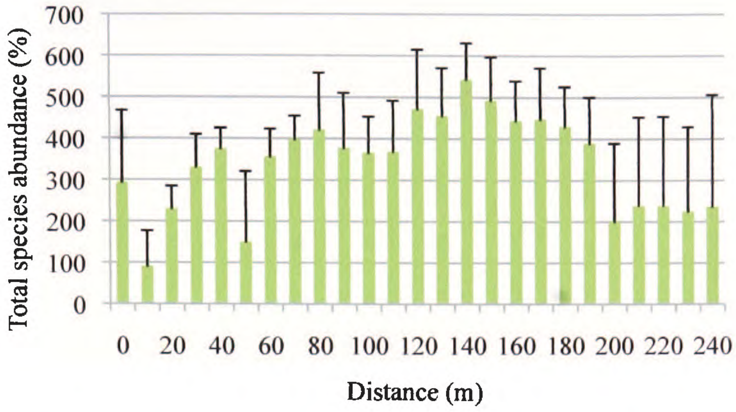
At the North site, the community structure showed a similar pattern down the transect in terms of total abundance, H' and d (figure 4.3.9). In all cases, there were low levels at 10m and 50m before a gradual increase down the transect until a further decrease at 200m (figure 4.3.9). The pattern was most notable in the mean total abundance (figure 4.3.9a) and mean d (figure 4.3.9c). There was a statistically significant difference in mean total abundance (ANOVA, $F_{24, 150}$ = 5.693, $p<0.001$) along the transect. The statistically significant differences in mean total abundance, in order of magnitude from lowest to highest, occurred between 10m < (50m = 60m = 100m = 110m = 40m = 90m = 190m = 70m) < (200m = 80m = 180m = 160m = 170m = 130m) < (230m = 20m = 120m) < (240m = 220m = 210m = 150m) < 140m. (Tukey, $p<0.05$) The mean d also varied statistically significantly along the transect (ANOVA, $F_{24, 150}$ = 2.734, $p<0.001$) in order of magnitude from lowest to highest, occurred between (10m = 240m) < (50m = 20m = 180m) < 170m. (Tukey, $p<0.05$) There were also statistically significant differences in mean species diversity (ANOVA, $F_{24, 150}$ = 4.159, $p<0.001$), in order of magnitude from lowest to highest, occurring between 10m < (210m = 190m = 80m = 170m = 150m = 110m) < (240m = 70m = 100m) < (180m =120m) (Tukey, $p<0.05$).

At the community level, there was a statistically significant difference in community similarity down the transect (ANOSIM, Global R = 0.453, P=0.1%). Figure 4.3.10 illustrates the results of a hierarchical agglomerative cluster diagram generated from a Bray-Curtis similarity matrix of untransformed community structure data using PRIMER. Cluster 1 predominantly comprised of samples collected from the low shore (200m - 240m) typified by *Rhodothamniella floridula* and *Laminaria digitata* as the dominant species (figure 4.3.10). Pairwise comparisons from the ANOSIM between samples from each station on the transect showed no statistically significant difference in community similarity between the low shore stations (200m – 240m) (P>0.05). However these samples were significantly different in terms of assemblage similarity to those stations higher on the shore (figure 4.3.10).

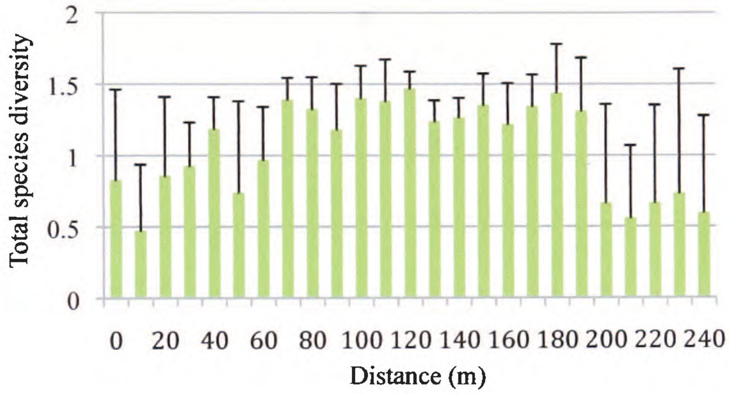
From a SIMPER analysis, at 200m *Rhodothamniella floridula* had an average total abundance of 149.3% cover, which contributed 58.8% of the average similarity between samples from that station. It was also the most important species in terms of defining the community structure between at 220m-240m. *Laminaria digitata* was also an important constituent of the community at the lower tidal levels (*e.g.* average total percent cover = 75.7%, contributing 17.7% of the average similarity between samples at 230m).

Cluster 2 represents samples collected from a predominantly mid shore community between 0m and 130m (figure 4.3.10). The samples collected from the stations at 0m-10m were dominated by *Fucus vesiculosus* which contributed at least 45% of the average similarity between samples (with the exception of 50m). *Phymatolithon lenormandii* also accounted for major proportion (13.0% -22.5%) of the average similarity between samples at these stations. At the lower end of this section pairwise comparisons revealed that there was no statistically significant difference in terms of assemblage similarity between samples at 70m – 130m within this cluster ($p<0.05$). Further down the transect (140m-200m) *Fucus serratus* replaced *Fucus vesiculosus* as the dominant fucoid species (cluster 3) (figure 4.3.10). *Fucus serratus* accounted for 21.0% - 65.7% of the average similarity between samples between 140m – 200m. *Phyomatolithon lenormandii* also accounted for a significant proportion of the average similarity between samples at these stations (8.55% - 53.9%). From the ANOSIM, *post hoc*, pairwise comparisons between the samples revealed that there was no statistically significant difference in terms of assemblage similarity between most samples at 130m – 170m within this cluster ($p>0.05$) (figure 4.3.10). Cluster 4 also represents a predominantly a mid shore community, however closer examination of the samples revealed that all samples were taken during spring and contained *Fucus* juveniles as part of the community structure (figure 4.3.10).

a) Mean total abundance



b) Mean species diversity



c) Mean species richness

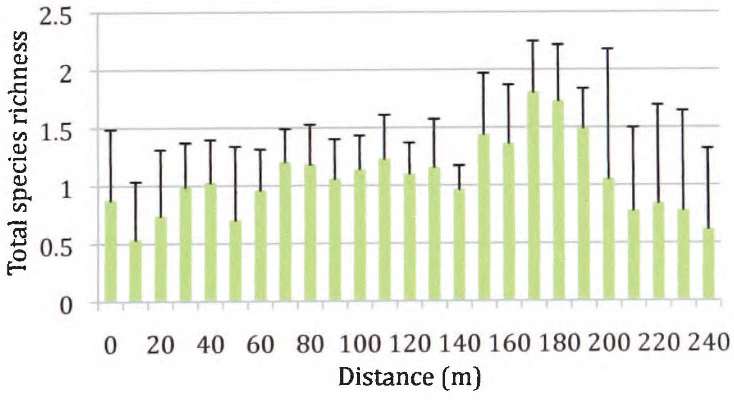


Figure 4.3.9: Species composition down the North site of Holbeck across all seasons (s.d.)

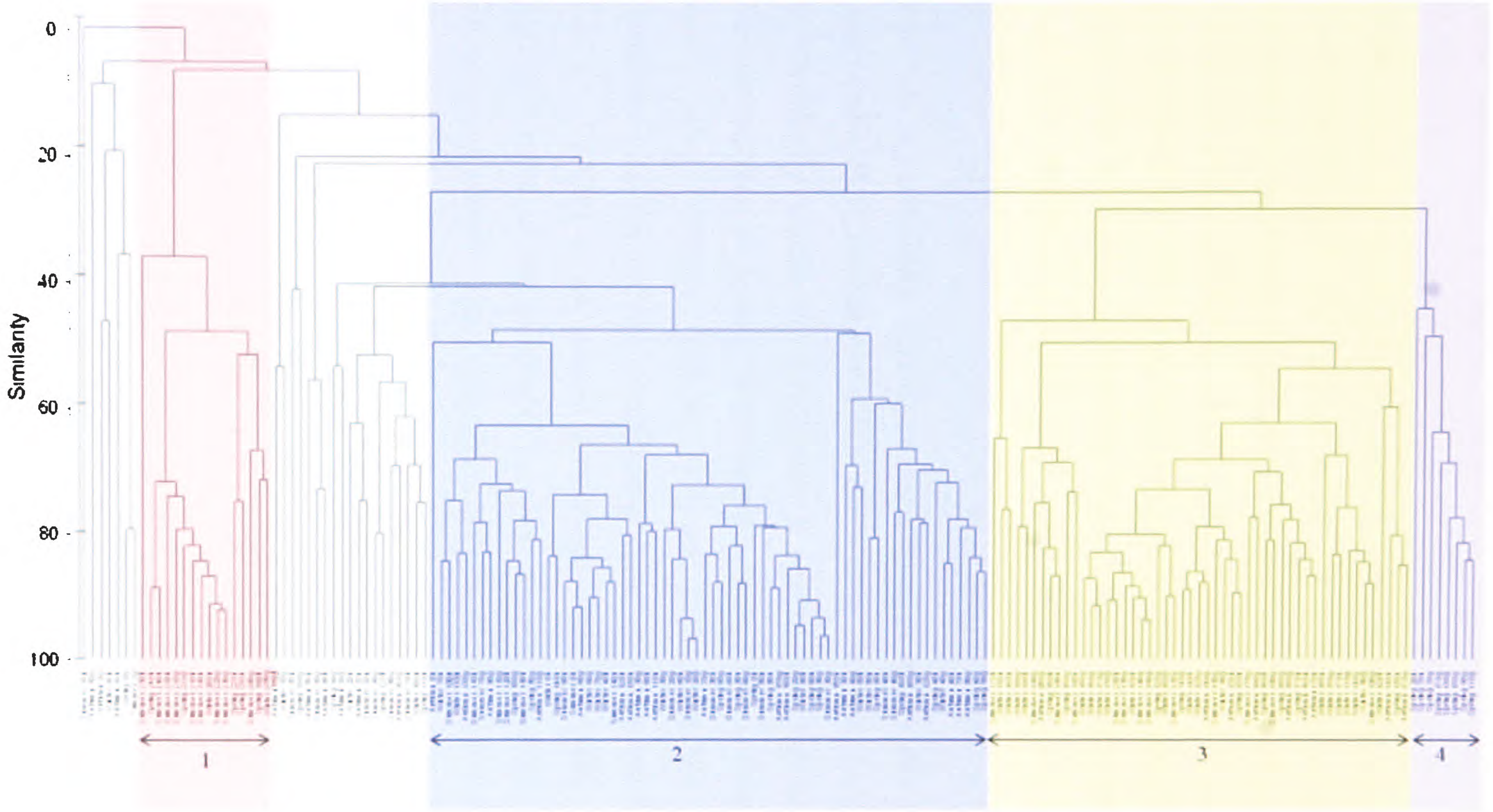


Figure 4.3.10: Dendrogram showing similarity of community structure at the North site of Holbeck (numbers and colour identify clusters).

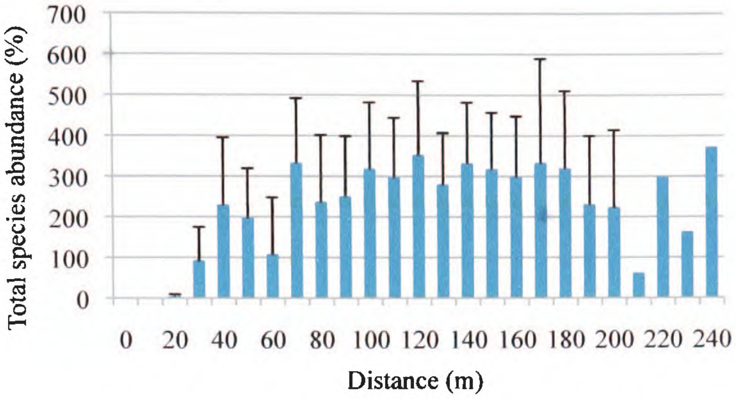
Differences in the macroalgal community within the Central site

Within the Central site community structure, showed a similar pattern of variation in terms of total abundance, H' and d. Statistically significant differences occurred between STATION for mean total abundance (ANOVA, $F_{20,\ 133}$ = 4.978, $p<0.001$), mean d (ANOVA, $F_{20,\ 133}$ = 3.848, $p<0.001$) and mean H' (ANOVA, $F_{20,\ 133}$ = 5.980, $p<0.001$). In all cases the lowest levels occurred at the top of the shore (figure 4.3.11). Mean total abundance was statistically significantly lower at 0m-20m than at 70m, 100m, 120m, 15m-180m, mean d was statistically significantly lower at 0m-10m than 20m, 120m, 140m and 180m, which in turn were statistically significantly lower than 90m, 150m and 190m, and mean H' was statistically significantly lower at 0m- 10m than 20m, 70m and 170m, which in turn were statistically significantly lower than 90m-150m and 180m-190m (Tukey, $p<0.05$ in all cases) (figure 4.3.11)

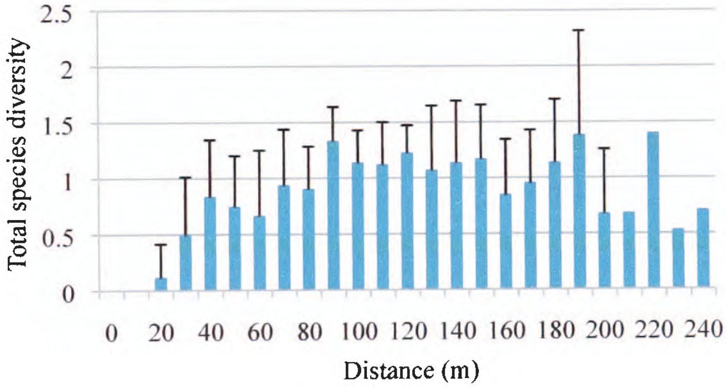
There was a statistically significant difference in the community similarity down the transect (ANOSIM, Global R = 0.176, P = 0.1%). Pairwise tests from ANOSIM revealed that statistically significant differences in community similarity were restricted to a difference between the middle of the transects (40m – 100m) from the lower mid part of the transect (140m – 200m). Between 40m and 110m, with the exception of 60m, *Fucus vesiculosus* was the species contributing most to the similarity between the samples (32.62% – 70.63% of the overall similarity). Between 140m and 180m Fucus serratus contributed most to the similarity between samples (24.62% - 60.81% of the overall similarity) and 100m – 160m *Osmundea pinnatifida* and *Phyomatolithon lenormandii* were important species in contributing to the overall similarity between samples (*Osmundea pinnatifida*, 6.81% - 16.84%; *Phyomatolithon lenormandii*, 5.64% - 32.63%).

Clusters 1 and 2 of the dendrogram primarily consist of samples between 30m – 150m with a mixed *Fucus* community, with a dominance of *Fucus vesiculosus* (figure 4.3.12). In addition to the *Fucus* community, cluster 2 also had a dominance of *Phyomatolithon lenormandii* (figure 4.3.12). Clusters 3 and 4 occur lower down the transect, primarily between 100m – 180m (figure 4.3.12). Both clusters consist of a mixed community of *Fucus serratus*, *Phyomatolithon lenormandii*, *Osmundea pinnatifida* and *Corallina officinalis*. However, within cluster 4 there was a dominance of *Phyomatolithon lenormandii* (figure 4.3.12). There was a cluster of samples from the lowest distances down (150m – 230m) the transect (cluster 5), although this is less well defined (figure 4.3.12) which was dominated by *Laminaria digitata* and *Fucus serratus*.

a) Mean total abundance



b) Mean species diversity



c) Mean species richness

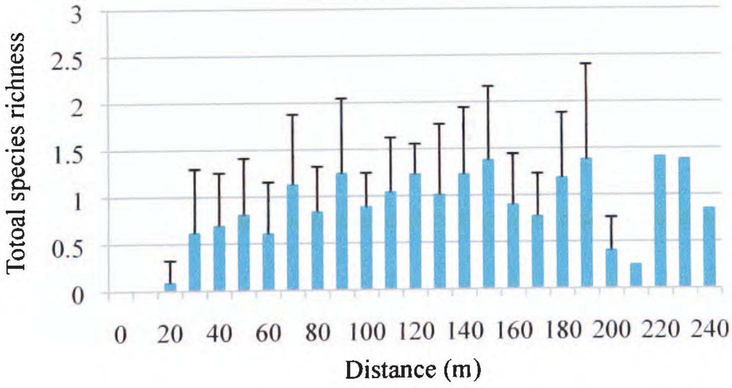


Figure 4.3.11: Species composition down the Central site at Holbeck across all seasons (+ s.d.).

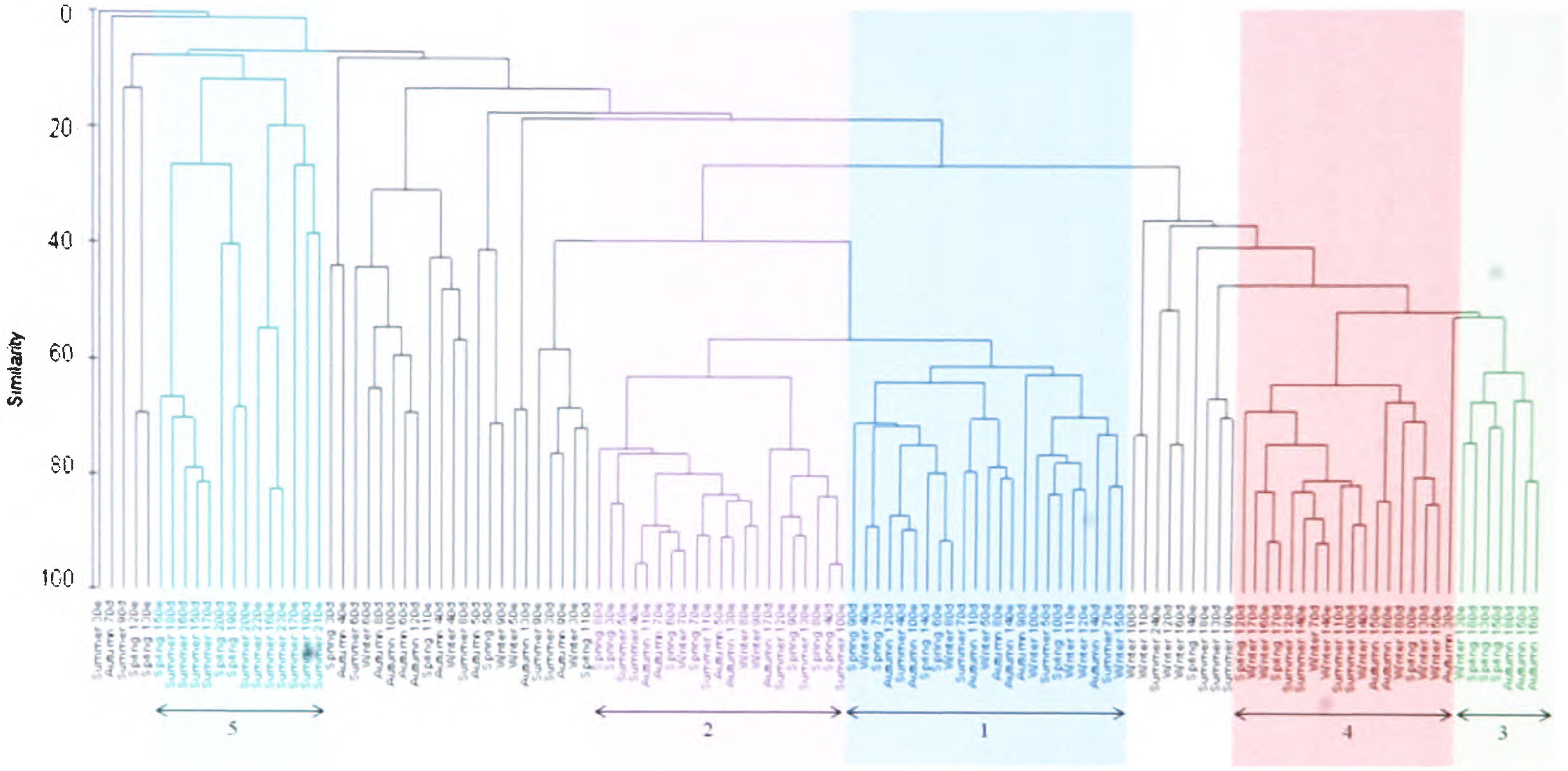


Figure 4.3.12: Dendrogram showing similarity of community structure at the Central site of Holbeck (numbers and colour identify clusters).

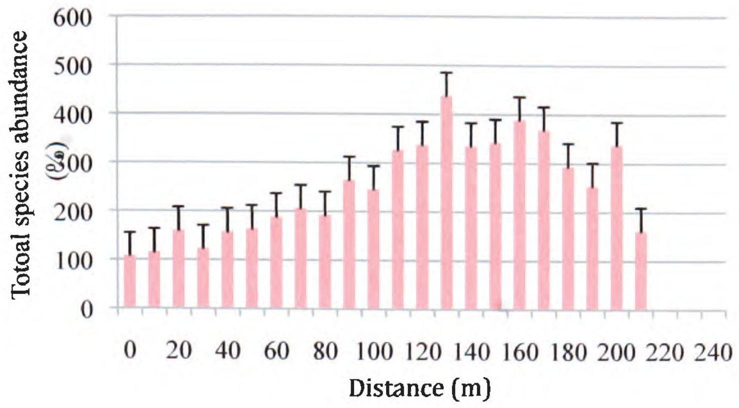
Differences in the macroalgal community within the North site

Statistically significant differences occurred between STATION at the South site in terms of the mean total abundance (ANOVA, $F_{21,143} = 3.711$, $p<0.001$), mean d (ANOVA, $F_{21,143} = 3.880$, $p<0.001$), and mean H' (ANOVA, $F_{21,143} = 3.504$, $p<0.001$). Mean total abundance increased gradually between stations to a maximum at 120m, before declining further down the shore (figure 4.3.12a). Differences in mean total abundance between the stations were small and statistically significant differences were only found between 0m which was lower than 10m, 30m and 160m, which were in turn lower than 120m (Tukey, $p<0.05$). Mean H' and d were also lowest at the top of the South site (figure 4.3.12). Mean H' at 0m was statistically significantly lower than at 10m, 40m and 50m at the top of the transect, and also 160m-180m and 210m lower down the transect (Tukey, $p<0.05$) (figure 4.3.12b). Mean d follows a similar pattern with 0m being statistically significantly lower than 10m-70m at the top of the transect and 100m, 130m, 160m-180m and 210m lower down the transect (Tukey, $p<0.05$) (figure 4.3.12c).

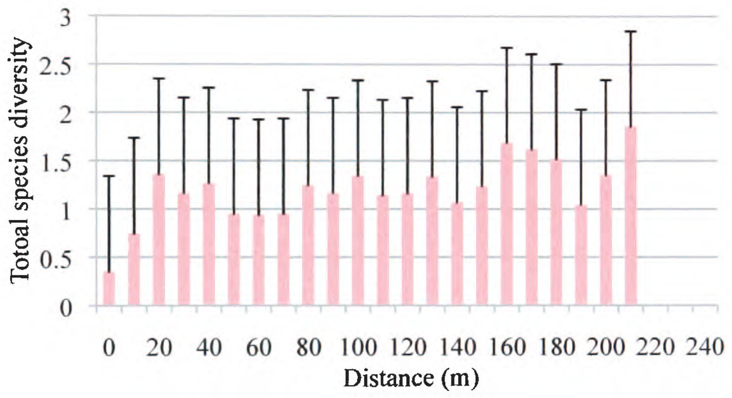
A statistically significant difference in community similarity occurred between STATIONS (ANOSIM, Global R = 0.423, P=0.1%). Pairwise comparisons from the ANOSIM showed four groups (0m-10m, 20m-90m, 110m-170m and 170m-210m) that were statistically significantly different from one another ($p<0.05$). These groups can be identified on the dendrogram created from the Bray Curtis similarity matrix. Cluster 1 was an upper shore community (samples from 0m – 20m) with algal cover limited to *Ulva intestinalis* and some *Fucus vesiculosus* (figure 4.3.14) with *U. intestinalis* being the most important species in determining similarity, followed by *F. vesiculosus.* Clusters 2 and 6 were both primarily low shore communities (170m onwards) (figure 4.3.14). Pairwise comparisons revealed that there was no statistically significant difference in assemblage similarity between low shore sites (180m onwards) ($p>0.05$). However, Cluster 2 was dominated by *Rhodothamniella floridula* and *Laminaria digitata* (figure 4.3.14), whilst Cluster 6 was also a low shore community but dominated by *Corallina officinalis* and *Polysiphonia fucoides* (figure 4.3.14).

Clusters 3, 4 and 5 were predominantly mid shore communities (figure 4.3.14). Cluster 3 consists of primarily of lower mid shore sites (100m – 170m) (figure 4.3.14). Although *Phymatolithon lenormandii* occurs throughout the site, especially in the mid shore, it is the dominant species occurring in samples in Cluster 3 whilst *Fucus serratus* also contributed to the overall similarity. Both Cluster 4 and 5 also consisted of upper mid shore samples, with a mix of *Fucus vesiculosus*, *Phymatolithon lenormandii*, *Osmundea pinnatifida* and Barnacles (figure 4.3.14). Cluster 4 was dominated by *Fucus vesiculosus*, whereas Cluster 5 is dominated by barnacles (figure 4.3.14).

a) Mean total abundance



b) Mean species diversity



c) Mean species richness

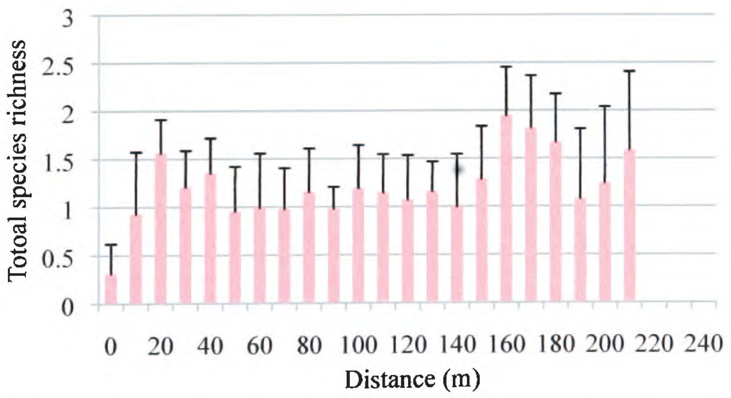


Figure 4.3.13: Species composition down the South site at Holbeck across all seasons (s.d.).

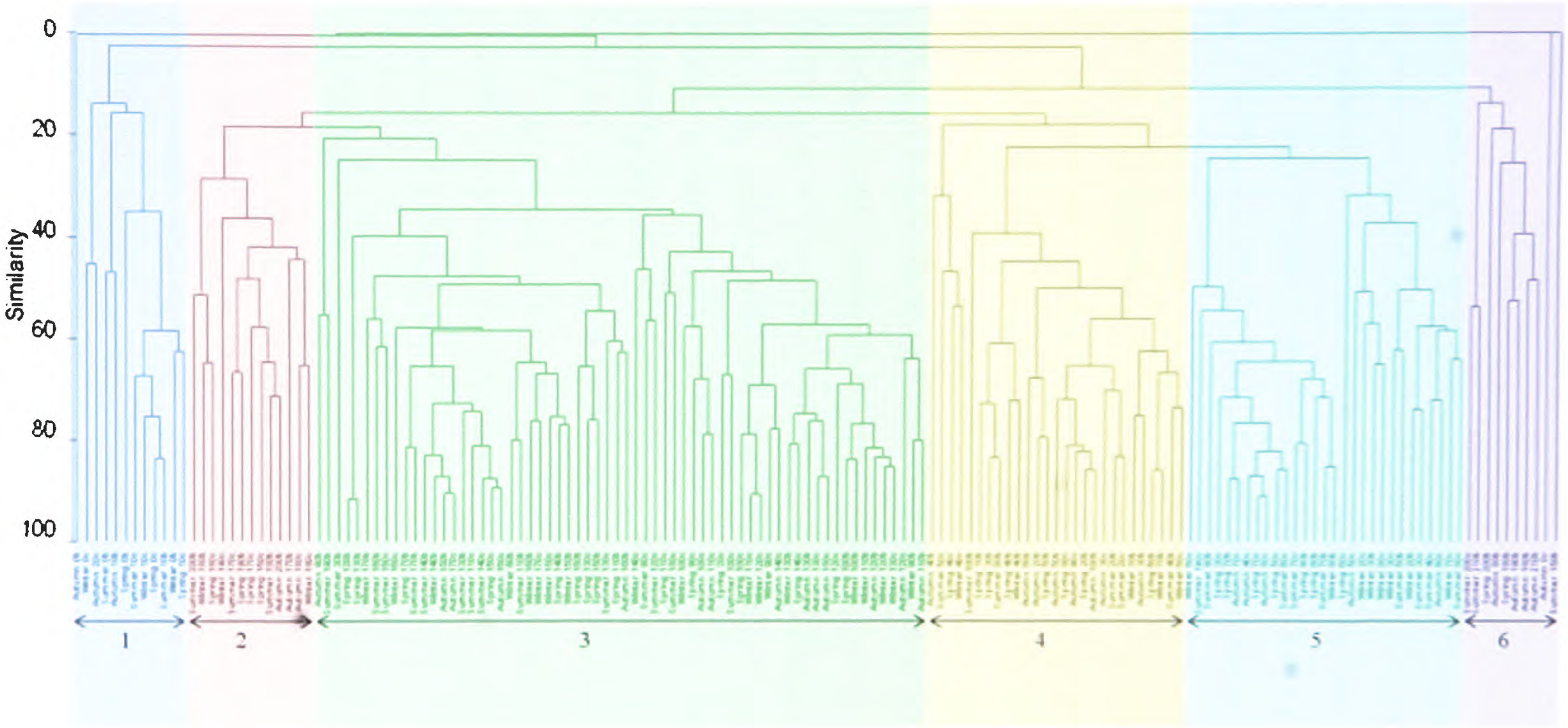


Figure 4.3.14: Dendrogram showing similarity of community structure at the South site of Holbeck (numbers and colour identify clusters)

Differences in faunal abundance

A two factor GLM ANOVA was used to test the effect of SEASON and SITE, and their interaction, on patellid abundance. There was no statistically significant difference in the mean patellid abundance between SEASON (table 4.3.10, figure 4.3.15), but there was a statistically significant difference between SITE (table 4.3.10, figure 4.3.15a). Mean patellid abundance was statistically significantly lower at the Central site (mean = 5.36, s.d. = 23.183) than at both the North (mean = 18.01, s.d. = 19.244) and South sites (mean = 18.75, s.d. = 23.183). There was no statistically significant interaction between SEASON and SITE (table 4.3.10) indicating that the lower abundance of patellids at the Central site occurred during all four seasons (figure 4.3.15a). There was no statistically significant difference in the mean abundance of patellids between different STATIONS at the Central site (ANOVA, $F_{20, 133} = 1.621$, $p = 0.056$), with low abundance compared to the other two sites occurring throughout the shore (figure 4.3.16a). Statistically significant differences between STATIONS occurred at both the North (ANOVA, $F_{24, 160} = 6.183$, $p<0.001$) and South sites (ANOVA, $F_{21, 143} = 5.774$, $p<0.001$). At the North site the abundance of patellids was statistically significantly lower at either end of the transect (10m and 210m-240m) than elsewhere on the transect, but statistically significantly greater at 30m and 40m (Tukey, $p<0.05$) (figure 4.3.16a). At the South site statistically significantly lower abundances of patellids again occurred at either end of the transect (0m, 190m and 210m) (Tukey, $p<0.05$) (figure 4.3.16a). Stations towards the upper part of the transect (30m, 70m and 90m) had the highest abundance of patellids, which were also statistically significantly greater than 120m and 150m-200m (Tukey, $p<0.05$) (figure 4.3.16a).

A two factor GLM ANOVA was also used to test the effect of SEASON and SITE, and their interactions, upon littorinid abundance. There was no statistically significant difference in mean littorinid abundance between SEASON (table 4.3.11). There was, however, a statistically significant difference in mean littorinid abundance between SITE (table 4.3.11), with a statistically significantly lower littorinid abundance at the Central site (mean = 7.51, s.d. = 23.402) than the North site (mean = 15.70, s.d. = 22.207) (Tukey, $p<0.05$) (figure 4.3.15b). The interaction between SEASON and SITE was not statistically significant (table 4.3.11) indicating that the lower abundance of littorinids at the Central site compared to the North site occurred during all four seasons (figure 4.3.15b). The low abundance of littorinids occurred throughout the Central site with no statistically significant differences between STATIONS (ANOVA, $F_{20, 133} =$

1.621, p=0.056). However there was a greater mean abundance of littorinids at 120m, although this had a large standard deviation (figure 4.3.14b). Differences in the distribution of littorinids on the shore occurred at both the North (ANOVA, $F_{24, 160}$ = 4.315, p<0.001) and South sites (ANOVA, $F_{21, 143}$ = 4.510, p<0.001). At the North site the greatest abundance of littorinids occurred at 70m-80m (figure 4.3.16b), which was statistically significantly higher than the abundance of littorinids found on the lower part of the shore (170m-240m) (Tukey, p<0.05) (figure 4.3.16b). The South site showed a similar pattern although the greatest abundance of littorinids was found higher up the shore at 20m and 40m, which was statistically significantly higher than the abundance of littorinids found at either end of the transect (0m and 140m-210m) (Tukey, p<0.05) (figure 4.3.16b).

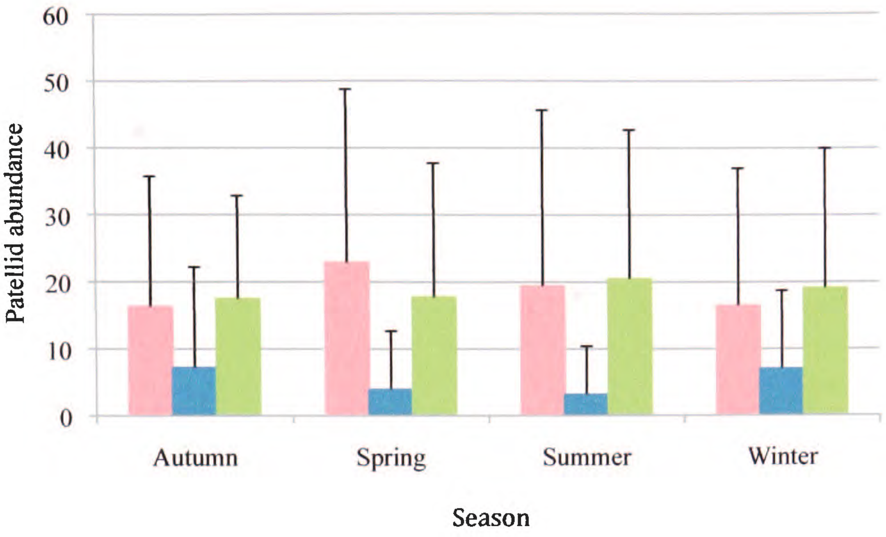
Table 4.3.10: Summary of results from a two factor GLM ANOVA for patellid abundance with SEASON and SITE as factors.

Source	**df**	**MS Adj**	**F**	**p**
SEASON	3	11.836	0.034	0.992
SITE	2	9242.895	26.554	0.001
SEASON*SITE	6	402.725	1.157	0.328
Error	496	348.079		

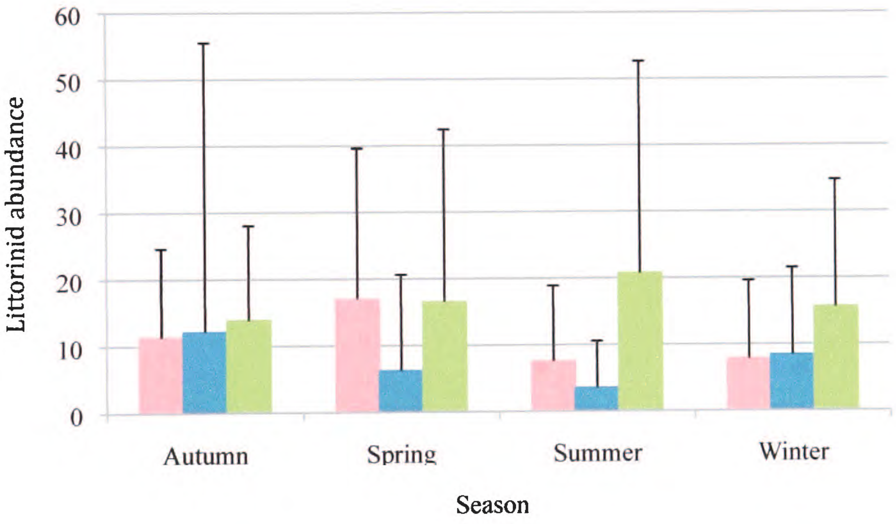
Table 4.3.11: Summary of results from a two factor GLM ANOVA for littorinid abundance with SEASON and SITE as factors.

Source	**df**	**MS Adj**	**F**	**p**
SEASON	3	108.329	0.257	0.857
SITE	2	2831.016	6.704	<0.01
SEASON*SITE	6	936.281	2.224	0.04
Error	496	422.277		

a) Patellids



b) Littorinids

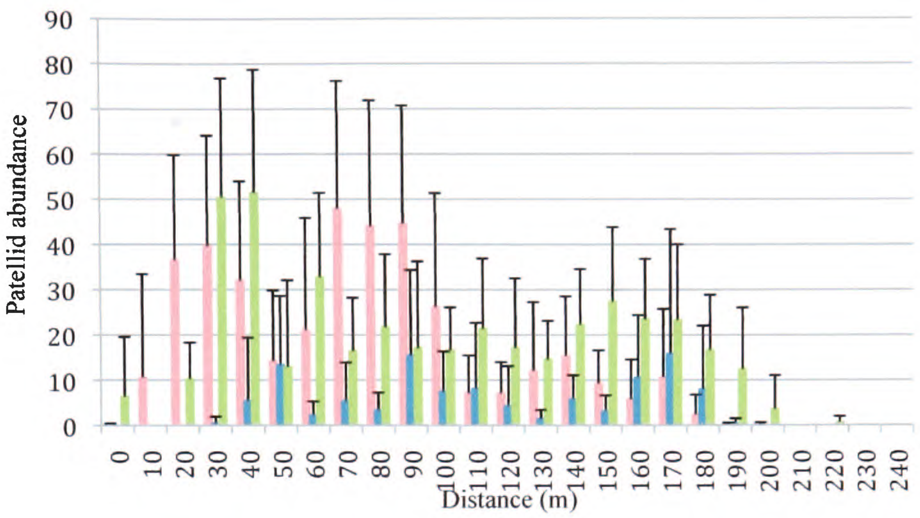


Key:

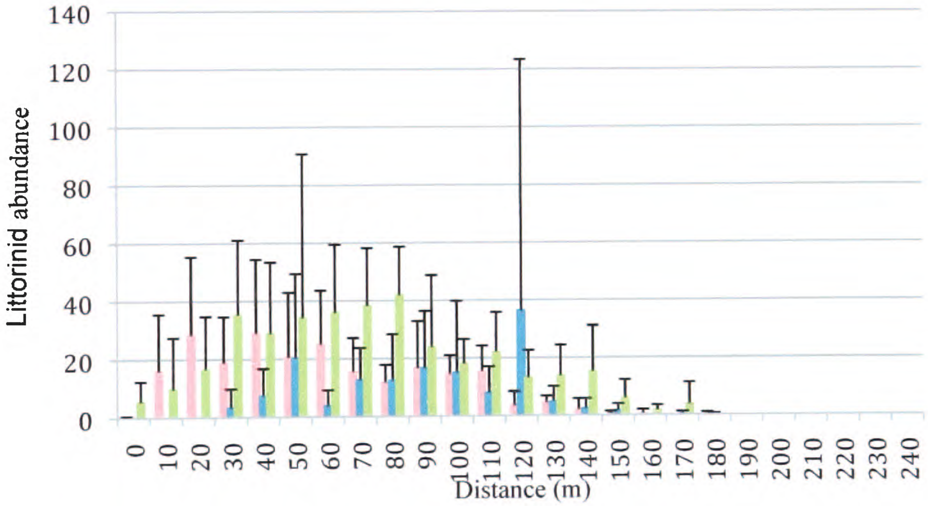
🟥	South	🟦	Central	🟩	North

Figure 4.3.15: Seasonal changes in the abundance of littornids and patellids on the shore at each of the three sites (North, Central and South) on the rocky shore at Holbeck, North Yorkshire (+ s.d.).

a) Patellids



a) Littorinids



Key:

🟥	South	🟦	Central	🟩	North

Figure 4.3.16: Mean species abundance down each of the three sites (North, Central and South) at Holbeck across all seasons (+ s.d.).

4.3.3. Summary of key findings

- The upper shore sediment zone at all three sites showed variation in volume, surface area, position and grain size composition throughout the year. The volume of the upper shore sediment zone was statistically significantly higher during winter than spring but there was no statistically significant difference in surface area between seasons.
- The Central site had the largest upper shore sediment zone both in terms of volume and surface area compared to both the North and South sites. The percentage cover of sediment on the shore was also greatest at the Central site.
- The Central site was found to have statistically significantly lower species diversity, richness and total abundance, and patellid and littorinid abundance than both the North and South sites. Community structure was also different between the three sites although this was the result of differences in the proportions of species rather than different species occurring at the three sites.
- Statistically significant differences were found in the percentage cover of sediment down each of the sites although the sites did not show the same patterns sediment accumulation within the shore.
- Statistically significant differences in species diversity, richness, total abundance within the transect occurred at all three sites. These differences did not reflect differences in the percentage cover of sediment within the shore.
- Statistically significant differences in patellid and littorinid abundance occurred at the North and South sites. These differences did not reflect differences in the percentage cover of sediment within the shore.

4.4. Discussion

All three sites at Holbeck varied in the surface area, volume, sediment grain size composition of their upper shore sediment zones. The lack of infauna found in the Central site sediment zone also suggested it was a dynamic environment as infauna is very susceptible to sediment disturbance, with recovery times being dependent upon the severity of the disturbance (Dernie, *et al.*, 2003). The changes observed in sediment volume, surface area and grain size composition suggest that sediment is moving in and out of all three sediment zones, rather than just sediment movement occurring within each zone.

Sediment surface area and volume fluctuated between sampling occasions throughout the eighteen-month sampling period at all three sites. These regular changes were most evident at the Central site as a greater quantity of sediment was involved. Whilst general trends in sediment accumulation may occur, previous studies have observed unpredictable fluctuations and also periodic inundations (Daly & Mathieson, 1977; Taylor & Littler, 1982; Trowbridge, 1996). Where more detailed observations were made, such variation could be related to spring-neap tides or and diurnal fluctuations. Additionally storm activity (Daly & Mathieson, 1977) could result in sediment movement occurring over a single tidal cycle (Stewart, 1983), therefore weekly sampling of the sediment zones may not describe all sediment movement across the shore.

The differences in surface area and volume of the upper shore sediment zone were most pronounced at the Central and North sites. Both of these sites are contained by sea defences: the groyne to the south of the North site, and Holbeck sea defences to the south of the Central site. Greater energy in the water column is required to move sediment far enough from the shore to be transported around obstructions like sea defences (Storlazzi & Field, 2000), therefore sediment may not be removed from the upper shore as frequently, resulting in greater accumulation of sediment before removal, but also greater quantities being removed when this occurs.

At both the Central and North sites increases in sediment surface area and volume occurred during Winter 2006/ 2007 and Summer 2007. There was also a change in the grain size composition recorded during Winter 2006/ 2007 with a greater proportion of smaller grain sizes. The difference in grain size composition was most evident at the North site and the bottom of the Central site. Rainfall is generally greater and temperatures lower during winter than summer months. However during Summer 2007 Yorkshire experienced rainfall 300% above average, and lower than average temperatures (Met Office, 2008), which may have had a similar effect to the stormy weather in the winter months. Rain and storms can increase sediment supply through erosion and increased terrestrial run off (Davis, 1994; French, 2001; Airoldi, 2003), and therefore increase the sediment available for deposition in the water column. Lower temperatures would also increase the energy required for sediment movement (Perkins, 1974) and therefore material would have accumulated in the sediment zone.

Sediment deposition at the South site did not always follow the same pattern as the other two sites, and the sediment also differed in grain size composition. This suggests that the sediment may come from a different source. The South site terminates in cliffs of Jurassic clay and sandstone overlaid by boulder clay, which are vulnerable to regular slippage (Scarborough Borough Council, 1997). Erosion can be enhanced by wave action (Davis, 1994) and rainfall (French, 2001). Therefore sediment accumulation at the South site may not only be the result of differences in marine sediment, and more complex interactions may be affecting sediment accumulation, resulting in less clearly defined changes.

Previous observations of the shore at Holbeck suggested that the greatest quantity of sediment was accumulating at the Central site, compared to the North and South sites, hence the use of the shore for this study. This was confirmed with the greatest percentage cover of sediment occurring on transects on the Central site. The greater sediment accumulation here may be related to the sea defences preventing transport from the site (Storlazzi & Field, 2000). The Central site also has a lower topography than the other two sites, with a ledge occurring between the North and Central sites. Littler *et al*, 1983 found reduced sediment accumulation in raised compared to surrounding lower areas, which may account for the increased sedimentation at this site.

The mean total abundance, species diversity (H'), species richness (d) of macroalgae and barnicles and the abundance of patellids and littorinids were all lower at the Central site. With the exception of total abundance and littorinid abundance this difference was always statistically significant compared to both other sites. This is consistent with previous studies which have also found lower diversity and abundance of macroalgae in areas with greater sediment accumulation (Daly & Mathieson, 1977; Eriksson & Johansson, 2005; Balata, *et al.*, 2007). They related this to the absence of species, which were sediment intolerant. Both *Littorina littorea* (Chandrasekara & Frid, 1998) and patellid species (Marshall & McQuaid, 1989; Brown, 1996) have a low tolerance to sediment burial. Periodic sedimentation may also have indirect effects on the fauna. *Patella vulgata* is the dominant patellid at Holbeck. The presence of sediment has been found to reduce grazing in *P. vulgata* (Airoldi & Hawkins, 2007). As *P. vulgata* graze upon a microscopic film of macroalgae covering rocks (Tait, 1981), and they may also be indirectly affected as sediment may remove the microscopic film by scour, or cover it. As *L. littorea* are versatile opportunists, feeding on both macroalgae and microphagously (reviewed in Norton, *et al.*, 1990), the indirect effects of sediment may be less influential.

In contrast, there was no significant difference in the percentage cover of sediment, d and H' or the abundance of patellids and littorinids between the North and South sites. Total abundance was, however, found to be lower at the South site than the North possibly the result of the limited abundance on the shore of canopy species (*Fucus vesiculosus* and *Fucus serratus*) except around the two large rockpools running down the shore (personal observation). Canopy species make a large contribution to total abundance of macroalgae due to the large coverage of individuals. As all three sites were subjected to the same physical conditions, this suggests that the differences compared to the Central site may, at least in part, be attributable to differences in sediment accumulation.

Differences in macroalgal community structure occurred between all three sites. The Central site is dominated by *Fucus vesiculosus* and *Fucus serratus*. Sites with high sediment levels are generally associated with a greater abundance of turf species (Airoldi & Cinelli, 1997; Gorgula & Connell, 2004), however at the Central site the contribution of the dominant turf species (*Corallina officinalis* and *Osmundea pinnatifida*) was much lower than canopy species. This suggests that species composition may not just be attributable to sediment settlement and burial. Turf species are tolerant of sediment burial because of their growth (Stewart, 1983) and reproductive strategies (Airoldi, 1998). However, due to the greater sedimentation at the Central site macroalgal species would have to be tolerant to increased sediment loads in the water column. This would lead to reduced light penetration and reduction of photosynthetic rate (Toohey, *et al.*, 2004), and also reduced settlement by juveniles (Arakawa, 2005). Canopy species (including fucoids) float in the water column when submersed, and therefore the effect of reduced light penetration (Toohey, *et al.*, 2004) may be lower than for turf species on the bedrock. Fucoids are leathery macrophytes and their fronds are relatively tough to deter grazers (Steneck & Watling, 1982). This toughness may reduce the effect of scour from sediment in the water column. Branching of fucoids does not occur from the holdfast, but after a thin stipe (Rajan, 2002), therefore sediment moving along the surface by traction would have less opportunity to come into contact with the algae and cause damage. Artificial scour has also been found to reduce the biomass of turf species and the percentage cover of filamentous species (Kendrick, 1991). Therefore scour by sediment movement may be having a greater effect on the macroalgal community structure at Holbeck than sediment burial. However, if macroalgal species composition was purely related to sediment movement through the water column, the North site would have a similar species composition, total abundance, H' and d to the Central site, as sediment movement at Holbeck is from the north to south. The North site is dominated by *F. vesiculosus*, but also by *Phymatolithon lenormandii*. The quantities of turf species are small suggesting that scour had an influence on macroalgal community structure, but total abundance, d and H' were statistically significantly greater than at the Central site, which suggests that sediment settlement may be influencing the macroalgal community at the Central site. The community structure at the South site is different to the other two, with *O. pinnatifida, Phymatolithon lenormandii, Fucus vesiculosus, Fucus serratus* and *Corallina officinalis* all making similar contributions to the community structure. Although sediment accumulation at the South site was not statistically significantly lower than at the North site, sediment may move through the area more quickly due to the lack of sea defences and hence have little effect on the community.

There was variation in sediment distribution down the shore at all three sites. Sediment cover at the South site increased down the shore. This may be due to the Holbeck sea defences directly north of the site providing greater protection from sediment movement at the top of the shore. The lower part of the shore, including the lower mid shore, had a greater abundance of turf species (*Corallina officinalis* and *Osmundea pinnatifida*). As turf species trap sediment (reviewed in Airoldi, 2003) this may account for the increased sediment cover down the shore. Sediment at the Central site was greatest at either end of the shore, whilst the North site had greatest percentage cover of sediment at either end, and also the middle of the transect. Total abundance, H' and d were all found to be lower at either end of the Central transects where sediment cover was 300%, due to the poolong of the three quadrat samples. However, in all other areas on the transects the abundance of macroalgal and fauna didn't follow an identical pattern to sediment cover. As sediment levels fluctuate on a variety of cycles (Daly & Mathieson, 1977; Taylor & Littler, 1982; Trowbridge, 1996), the 'snapshot' measurements made using the transects may not fully describe sediment distribution patterns at each site, and their relationship with community structure (this is further investigated in Chapter 5). General zonation patterns of both macroalgae and fauna (as described by Stephenson & Stephenson, 1949; Lubchenco, 1980; Little & Kitching, 1996) were apparent at all three sites although local topography, and the mosaic distribution of species that occurs on moderately exposed shores (Wells, *et al.*, 2007) prevented them being clearly defined.

No difference was found in total abundance or species diversity (H') between seasons, nor was there a difference in community similarity. Throughout the year the macroalgal community was dominated by perennial species (*Fucus vesiculosus, Fucus serratus, Phymatolithon lenormandii* and *Osmundea pinnatifida*), with only small changes in their percentage contribution to community composition. Whilst the majority of species on the shore (see table 4.3.7 for complete species list) were perennial (Burrows, 1991; Irvine & Chamberlain, 1994; Dixon & Irvine, 1995; van den Hoek, *et al.*, 1995; Lee, 1999; Jormalainen, *et al.*, 2001; Maggs & Hommersand, 2001; Wernberg, *et al.*, 2001; Brodie & Irvine, 2003; Brodie, *et al.*, 2007) they experience periods of seasonal growth. However these occur at different times of the year, for example *Ulva lactuca, Cladophora sericea, Chaetomorpha mediterranea* experience maximum growth during the summer (Brodie, *et al.*, 2007) *Ulva intestinalis, Cladophora rupestris* [Burrows, 1991] and *Porphyra umbilicalis* (Brodie & Irvine, 2003), whilst *Dumontia contorta* (Maggs & Hommersand, 2001) and *Chaetomorpha melagonium* (Brodie *et al*, 2007) growth is greatest during the autumn and winter.

Species richness (d) was lower during the winter. This was the only sampling period where no unique species were found. Storms also have the potential to remove individuals during this period (Williams, 1996). Fewer species experience maximum periods of growth during the winter (Burrows, 1991; Irvine & Chamberlain, 1994; Dixon & Irvine, 1995; van den Hoek, *et al.*, 1995; Lee, 1999; Jormalainen, *et al.*, 2001; Maggs & Hommersand, 2001; Wernberg, *et al.*, 2001; Brodie & Irvine, 2003; Brodie, *et al.*, 2007). Therefore the differences in d may be the result of natural small changes in the seasonal composition on a shore that is dominated by perennial species rather.

There was no significant difference in the abundance of either littorinids or patellids between the different seasons. *Littorina littorea*, the predominant species found at all three sites, has been found to display seasonal cycles in abundance which were postulated to be related to predation and desiccation patterns (Saier, 2000) and may not be influential at Holbeck. Differences in patellid abundance have been related to food availability (Jenkins & Hartnoll, 2001) rather than seasonality. However, the differences in patellid abundance were small as *post hoc* tests were unable to resolve the source of the variation, and may, therefore be the result of normal mortality and recruitment.

Whilst differences in sediment cover were found between seasons, these did not demonstrate the same pattern as the changes in sediment accumulation in the upper shore sediment zones. As sediment moved across the shore in and out of the sediment zones, and the amount of sedimentation reflects the available sediment in the water column (Schiel, *et al.*, 2006), similarities may be expected. However, as discussed previously sediment deposition on the shore can fluctuate markedly (Daly & Mathieson, 1977; Taylor & Littler, 1982; Trowbridge, 1996). The transect sampling was performed on one occasion in each season, and this may not have coincided with the measurement of the upper shore sediment zone due to the suitability of the tides for sampling. However seasonal differences in sediment accumulation at the three sites will be examined in more detail in Chapter 5.

Chapter 5

The effect of variations in sediment accumulation on the community structure of an intertidal rocky shore.

5.1. Introduction

The abundance and distribution of organisms on intertidal rocky shores can vary during the year, as discussed in Chapter 4.1. Some faunal species migrate up and down the shore (Hughes, 1972; Little & Kitching, 1996). Macroalgal abundance on the shore can be fluctuate seasonally (*e.g.* Brodie, *et al.*, 2007) due to seasonal growth patterns (*e.g.* Dixon & Irvine, 1995; Stengel, *et al.*, 2004) or heteromorphic life cycles (*e.g.* South & Whittick, 1987; Dixon & Irvine, 1995).

In addition to natural temporal changes on the shore, organisms are subject to a wide range of stresses and disturbances (described in chapter 1). This can be the result of natural pressures such as desiccation (Schonbeck & Norton, 1978; Dring & Brown, 1982), grazing (Lubchenco, 1980; Cubit, 1984), wave action and storms (*e.g.* Dayton & Tegner, 1984). Alternatively they can be the result of anthropogenic activities, such as dredging (Gilkinson, *et al.*, 2003), pollution (Crowe, *et al.*, 2000), trampling (*e.g.* Keough & Quinn, 1998; Brown & Taylor, 1999), boating activity (Eriksson, *et al.*, 2004) and harvesting (Spencer, *et al.*, 1998).

Three mechanisms have been proposed by which recolonisation and succession may occur: firstly the facilitation model in which later species are dependent upon other species 'preparing the way' for them; secondly, the tolerance model in which later species have evolved to tolerate lower levels of resources than previous ones; and thirdly the inhibition model in which species resist invasions by competitors until they are damaged or die (Connell & Slatyer, 1977). Research has demonstrated that patterns occur during macroalgal succession. Generally ephemeral algae including *Ulva, Ulothrix* and *Porphyra* are the first colonising species (Sousa, 1979; Sousa, 1984; Buschmann, 1990; McCook & Chapman, 1997). Where these species do not colonise, initial bare substrate colonisation is by barnacles (Lubchenco & Menge, 1978; Farrell, 1991). Although not all studies exhibit a middle stage of succession, perennial algae (*e.g. Chondrus crispus, Chondracanthus canaliculatus* (Harvey) Guiry [as *Gigartina* *canaliculata*] and *Fucus* species) occur in the last recorded stages of succession (Lubchenco & Menge, 1978; Sousa, 1979; Sousa, 1984; Buschmann, 1990; Farrell, 1991; McCook & Chapman, 1997).

As discussed in Chapter 1, sediment acts as a stress and a disturbance to intertidal organisms. Suspended sediment in the water column can reduce light penetration resulting in decreased photosynthetic rates in macroalgae (Toohey, *et al.*, 2004; Harrington, *et al.*, 2005), and can clog the gills of non-selective suspension feeding fauna (reviewed in Moore, 1977). Scour by sediment can also reduce the biomass of macroalgae (Hyslop & Davies, 1998) and the movement of larger sediment sizes including pebbles and rocks can result in the removal of individuals (described in Underwood, 1998).

Within intertidal rocky shore environments the quantity and distribution of sediment is not consistent throughout the year. Large seasonal differences in the quantity and quality of sediment occur in the Baltic Sea, with maximum rates occurring during late spring (Berger, *et al.*, 2004), and large depositions of sediment in late spring also occurring on the coast of British Columbia (Mathieson, 1982). Sediment levels have been found to fluctuate on the basis of neap-spring and diurnal cycles (Daly & Mathieson, 1977; Airoldi, 2003). Irregular fluctuations have also been found to occur as a result of storms (Daly & Mathieson, 1977; Renaud, *et al.*, 1996). As discussed in Chapter 2, the quantity of sediment trapped by macroalgae on the shore also varies during the year. Sediment trapping has been found to be lower in summer than winter amongst both *Osmundea pinnatifida* (Prathep, *et al.*, 2003) and filamentous macroalgae, although the lowest levels of sediment trapping in filamentous macroalgae occurs during autumn (Airoldi, *et al.*, 1996). However the depth of sediment trapped in *Corallina officinalis* was greater during summer/ autumn than winter/ early spring, but variations in depth occurred throughout the year (Stewart, 1983).

Differences in the macroalgal community have been found to occur between areas of relatively higher and lower sediment levels (discussed in Chapter 1). Areas with greater sediment levels have generally been found to have lower macroalgal species abundance (*e.g.* Taylor & Littler, 1982; Balata, *et al.*, 2007) and diversity (Daly & Mathieson, 1977; Eriksson & Johansson, 2005), with a greater abundance of turf and filamentous species (Gorgula & Connell, 2004; Balata, *et al.*, 2005; Balata, *et al.*, 2007), but a lower abundance of erect (Airoldi & Cinelli, 1997; Balata, *et al.*, 2005; Piazzi, *et al.*, 2005), encrusting (Balata, *et al.*, 2005; Balata, *et al.*, 2007), articulated and foliose macroalgal species (Balata, *et al.* 2007). The effects of sediment appear to be species specific (e.g. the percentage cover of *Pilayella littoralis, Sphacelaria arctica* and *Fucus vesiculosus* was lower in areas with higher sediment levels, whilst *Cladophora glomerata* (Linnaeus) Kützing and *Enteromorpha* spp was greater [Eriksson & Johansson, 2005]). Sediment also reduces recruitment of macroalgae, either by sticking to the zygotes and reducing attachment (Arakawa, 2005), surface sediment preventing attachment (Arakawa, 2005; Schiel, *et al.*, 2006), or reducing survival (Devinny & Volse, 1978; Berger, *et al.*, 2003) (reviewed in Chapter 1).

5.1.1. Rationale and Aims

Studies into the effects of sedimentation have generally focused on differences in the community composition between areas with comparatively higher and lower sedimentation levels, whether as a result of naturally occurring differences between sites (*e.g.* Gorgula & Connell, 2004; Balata, *et al.*, 2005) or manipulation of sediment loads (*e.g.* Kendrick, 1991; Airoldi & Cinelli, 1997; Connell, 2003b). Daly & Mathieson (1977) provided one of the few studies at a site where the changes in sediment and the macroalgal community were monitored. This study only compared two transects which were qualitatively assessed as having high and low levels of sediment accumulation. In all cases differences were noted in the macroalgal community between the areas. Different shores would also be subject to other factors in addition to sediment accumulation. However manipulation of sediment levels within quadrats at a single site does not provide a realistic simulation of the sediment patterns organisms are subject to, with sediment levels fluctuating within a single tidal cycle, on the basis of neap-spring and diurnal cycles (Daly & Mathieson, 1977) and also as the result of irregular storms (Daly & Mathieson, 1977; Renaud, *et al.*, 1996). In addition, although the quantity of sediment used in experimental manipulations may be known, differences in the community structure have only been compared on the basis of qualitative sediment levels, i.e., higher, natural and lower.

As described in Chapter 4.1, the shore at Holbeck has large areas within a single site that are subject to different levels of sediment accumulation. The three sites were situated within an area of approximately 500m and are subject to similar environmental conditions, spore dispersal in the water column, and natural variation in sediment accumulation. Even within sites, variation in sediment was found to occur down the site (see Chapter 4.3).

This chapter aims to examine temporal changes in community structure and sediment settlement at the three sites at Holbeck, and also to investigate the relationship between sediment settlement and community structure within different types of habitat. Specifically this chapter aims:

1) To determine if the percentage cover of sediment varied between the three different sites, between months, or between habitats.
2) To determine if total macroalgal abundance, macroalgal species diversity and macroalgal species richness varied between the three different sites, between months, or between habitats.
3) To determine if community similarity varied between the three different sites, between months, or between habitats.
4) To determine if the abundance of littorinids, patellids and percentage cover of barnacles varied between the three different sites, between months, or between habitats.
5) To determine if there was a relationship between the percentage cover of sediment and total macroalgal abundance, macroalgal species diversity, macroalgal species richness, littorinid abundance, patellid abundance and percentage cover of barnacles in either algal or bare rock habitats.

5.2. Methods

The three sites at Holbeck, previously described in detail in chapter 4 were chosen for this investigation. Within each site, eighteen 50cm x 50cm fixed quadrats were marked during May 2006 (see figure 5.2.1 for arrangement of quadrats). The use of 50cm x 50cm quadrats was considered to be appropriate for both macroalgae and the larger fauna found in intertidal areas, e.g. limpets (Little & Kitching, 1996). There was no characteristic upper shore at the sites and clear zonation patterns were not always apparent (see Chapter 4.2) and therefore to ensure that sampling at all three sites was performed consistently within the same region of the shore, quadrats were positioned where *Fucus vesiculosus* and *Semibalanus balanoides* were abundant. This ensured that all samples were collected from a mid shore community. Quadrats were not positioned in areas where low shore species were found, as these areas were not accessible during neap tides and winter storms,

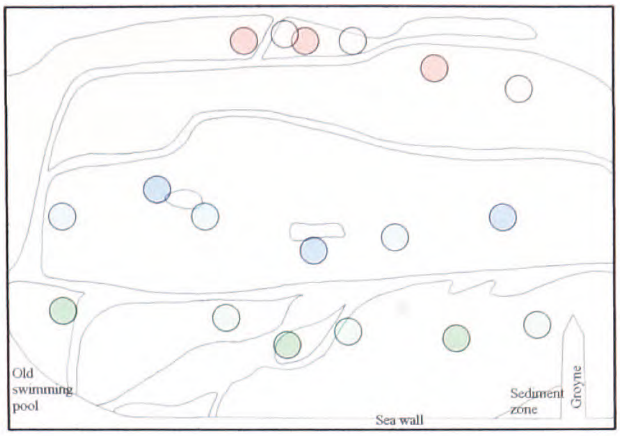
To ensure coverage of the entire mid shore zone, the area was divided into upper, mid and lower levels. These levels did not have any biological or physical determinants, but merely ensured samples were collected from throughout the mid shore zone (figure 5.2.1). At each level, six quadrats were marked using screws and brightly coloured plastic cable ties. Three quadrats were marked within an algal bed (ALGAL) and three in areas that were predominantly bare rock (BARE) at the start of the sampling period (figure 5.2.1). This allowed the interaction of sediment and the shore to be investigated within the two different intertidal habitats.

The percentage cover of each macroalgal species was visually estimated within each quadrat (for justification of methodology and sampling technique applied see section 4.2). Where macroalgae could not be identified to species in the field their percentage cover was estimated and samples collected and identified back in the laboratory using a microscope and appropriate keys (Rhodophyceae [Hiscock, 1986; Maggs & Hommersand, 2001; Dixon & Irvine, 1995]; Chlorophyceae [Burrows, 1991]; Phaeophyceae [Hiscock, 1979]). *Fucus* juveniles could not be identified to species either in the field or the laboratory and were therefore recorded as percentage cover of *Fucus* juveniles.

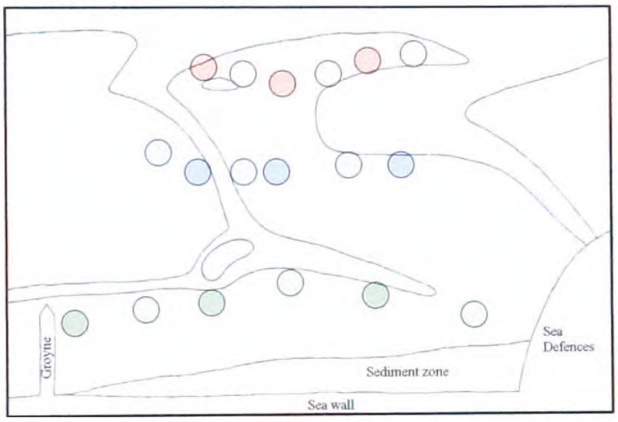
The percentage cover of sediment within each quadrat was also estimated visually. The percentage cover of sediment has been found to positively correlate with the amount of sediment collected within sediment traps (Schiel, *et al.*, 2006). This therefore provided an indication of the amount of sediment within the area. Percentage cover of barnacles (predominantly *Semibalanus balanoides*) was also visually estimated. Barnacles are passive filter feeders (Bertness, *et al.*, 1999), and were sampled as they may be affected by sediment build-up. The abundance of patellids and littorinids within each quadrat was also recorded. As discussed in Chapter 4.2, *Patella vulgata* (which dominated the patellid group on the shore) is a key stone species (Raffaelli & Hawkins, 1996), and *Littorina littorea* (which dominated the littorinid group) is collected for economic purposes (Barry, 2001).

Quadrats were investigated for an eighteen-month period between June 2006 and November 2007, tides and light permitting. For the initial twelve months, sampling was performed on one spring tide and one neap tide each month. However preliminary analysis revealed no statistically significant difference in the diversity, total macroalgal abundance or macroalgal species richness, percentage sediment cover, or the abundance of patellids between tidal states (Wilcoxon Signed ranks, $p<0.05$ in all cases). The only statistically significant difference occurred in the abundance of littorinids, with a greater abundance occurring during neap tides (Wilcoxon Signed ranks, $z = -2.608$, $p<0.01$). As no significant differences were observed between tidal states, and samples were sometimes not obtainable on neap tides during winter months, sampling was reduced to one spring tide each month. Sampling usually took place over two consecutive days as, although sediment movement can occur during a single tidal cycle (Daly & Mathieson, 1977), it was impractical to sample the three sites in a single tide.

a) North site



b) Central site



c) South site

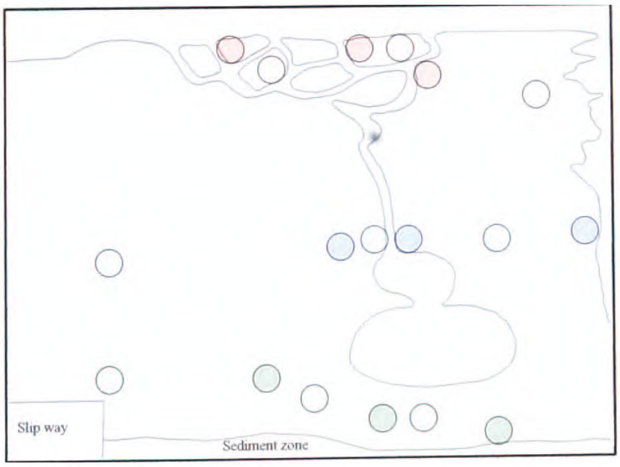


Figure 5.2.1: Site maps of the intertidal rocky shore at Holbeck illustrating the approximate positioning of the fixed quadrats at each of the three sites (quadrat classification - ● Lower Algae, Lower Bare, ● Mid Algae, ● Mid Bare, Upper Algae, Upper Bare).

5.2.1. Data analysis

The null hypothesis under test was that there was no statistically significant difference in the mean percentage cover of sediment between the three different sites (North, Central and South), two initial habitats (Algal and Bare rock) and eighteen sampling occasions (once each month between June 2006 and November 2007). Data were found not to be spherical (Mauchly's test, $p<0.001$), nor conform to normal distribution (Kolmogrov-Smirnov test, $p<0.05$) and variances could not be considered equal (Levenes test, $p<0.05$). Log10 transformation of the data, because the variances were greater than the mean (Fowler, *et al.*, 1998), did not result in the assumptions of sphericity, normal distribution or approximately equal variances in the data being met. Although the assumption of sphericity had been violated, three factor mixed design ANOVA was used in preference to MANOVA due to the greater power of the ANOVA test (Field, 2005). As discussed in Chapter 3.2, ANOVA is also relatively robust to non-normality and heterogeneity of variances although it increases the probability of a Type I error (Underwood, 1997). However, to minimise errors due to the violation of the assumption of sphericity, a Greenhouse & Geisser correction was applied to produce a valid F-ratio. This was deemed more appropriate than the Huynh & Feldt correction due to it being more conservative than the latter so preventing false null hypotheses being rejected (Field, 2005). Due to the application of the Greenhouse & Geisser correction the level of significance was set at 0.05, however, results between 0.05 and 0.01 were interpreted with caution. *Post hoc* Games-Howell tests were used to determine where any statistically significant differences occurred in each of the two independent variables, SITE and HABITAT. This test was designed for use with unequal population variances and is also accurate with unequal sample sizes (Field, 2005). It is also a powerful test but can be liberal with small sample sizes (Field, 2005), as was the case in this experiment. *Post hoc* Bonferroni tests were carried on the repeated measures variable MONTH. Bonferroni tests were considered to be the most robust method to use when assumptions of sphericity have been violated in terms of the power of the test and the control of the Type I error rate (Field, 2005).

To examine the macroalgal community structure a Bray Curtis similarity matrix was produced on the untransformed data as this produced the lowest stress value (Clarke & Warwick, 2001). The benefits of the use of the Bray Curtis similarity coefficient are discussed in Chapter 4.2. This similarity matrix was then used to perform a two-way Analysis of Similarity (ANOSIM) to test that there was no statistically significant difference in community similarity between each of MONTH or SITE and then MONTH and HABITAT (Clarke & Warwick, 2001). Although repeated testing increases the chance of a Type I error, only a maximum of two factors can be analysed in an ANOSIM, therefore results between 0.05 and 0.01 were interpreted with caution. To examine which species contributed most to the overall similarity within and dissimilarity between the factors SITE, HABITAT and MONTH the SIMPER routine was performed in PRIMER on each of the factors (Clarke & Warwick, 2001) and used in conjunction with a presence absence table.

Shannon Wiener species diversity (H'), macroalgal species richness (d) and total abundance of macroalgae were calculated using the DIVERSE routine in PRIMER. The use of H' and Margalef's index as species richness (d) as opposed to the total number of species in describing the macroalgal community is discussed in Chapter 4.2. The null hypotheses under test were that there were no statistically significant differences in mean H', d and total abundance and also between the mean percentage cover of barnacles, mean abundance of patellids and mean abundance of littorinids between the three different sites (North, Central and South), two initial habitats (Algal and Bare rock) and eighteen sampling occasions (once each month between June 2006 and November 2007). Only d was found to conform to normal distribution (Kolmogrov-Smirnov test, $p>0.05$), all other variables were not normally distributed (Kolmogrov-Smirnov test, $p<0.05$). In all cases the data did not conform of assumptions of sphericity (Mauchly's test, $p<0.001$). Approximately homogenous variances were found to occur on, H', total abundance, and the abundance of patellids (Levenes test, $p>0.05$ in all cases). However both the percentage cover of barnacles and the abundance of littorinids variances could not be considered approximately equal (Levenes test, $p<0.05$ in both cases). In all cases Log10 transformation of the data did not result in the assumptions of sphericity, normal distribution or approximately equal variances in the data being met. For the reasons outlined previously a three factor mixed design ANOVA was deemed most appropriate, with the application of a Greenhouse & Geisser correction. Results between 0.05 and 0.01 were interpreted with caution. *Post hoc* Bonferroni tests were again carried on the repeated measures variable MONTH. *Post hoc* Games-Howell tests were used to determine where any statistically significant differences occurred in each of the two independent variables, SITE and HABITAT for differences in both the percentage cover of barnacles and the abundance of littorinids as variances could not be considered equal. However Gabriel's procedure was used as a *post hoc* test for the two independent variables (Field, 2005), SITE and HABITAT for d, H', total abundance and the abundance of patellids because, whilst the variances were equal there were slight variations in sample size, and Gabriel's procedure was designed to cope with these whilst still providing a test with good power (Field, 2005).

To determine if there was a correlation between the percentage cover of sediment and each of d, H', total abundance, the abundance of patellids the percentage cover of barnacles and the abundance of littorinids a Spearman Rank Correlation coefficient was applied to the data. Although no difference was found in the mass of sediment trapped between the different macroalgae present in Chapter 3, Chapter 2 showed clear differences in the quantity of sediment trapped between different macroalgal species. Differences in sediment cover have also been suggested to have an impact upon recruitment (*e.g.* Umar, *et al.*, 1998; Arakawa, 2005; Schiel, *et al.*, 2006), in addition to resulting in differences in community structure (*e.g.* Gorgula & Connell, 2004; Balata, *et al.*, 2005; Balata, *et al.*, 2007). Therefore the relationship between the percentage cover of sediment and the inhabiting community were examined in algal and bare rock quadrats separately. Due to the patchy nature of each of the sites (as discussed in Chapter 4.2) averages were calculated of each of the three levels, upper, mid and lower, on the shore (see figure 5.2.1) in an attempt to reduce variability between samples. As repeated testing on the same experimental data increases the chance of a Type I error (Field, 2005), a Bonferroni correction was applied (Sokal & Rohlf, 1995).

5.3. Results

5.3.1. Temporal changes in sediment accumulation

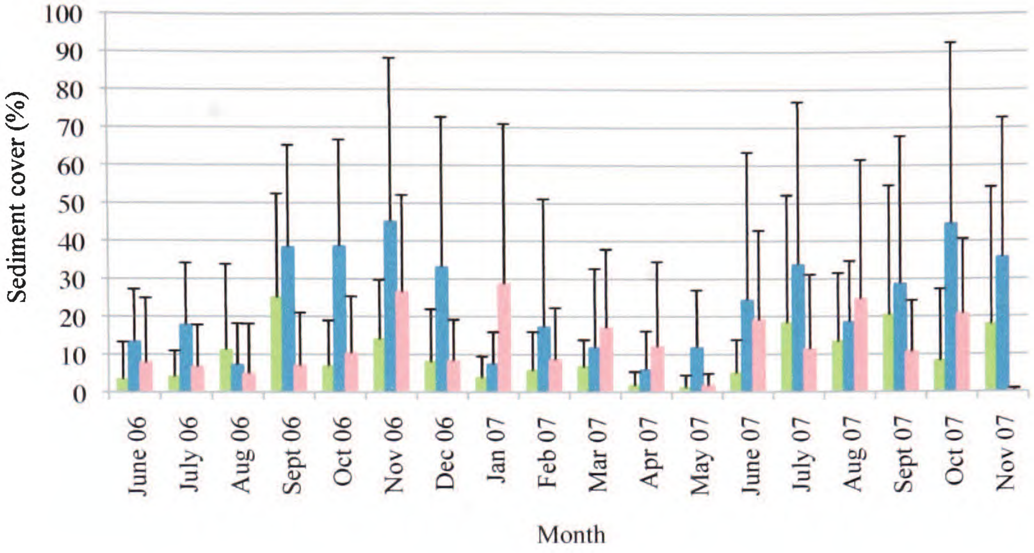
The results of the comparison of the percentage cover of sediment between habitat, site and month are shown in figure 5.3.1. There was no statistically significant difference in the mean percentage cover of sediment between HABITAT (table 5.3.1, figure 5.3.1). There was, however a statistically significant difference in the mean percentage cover of sediment between SITE (table 5.3.1). The mean percentage cover of sediment was statistically significantly lower at the South site (mean = 8.089, s.d. = 19.400) than the Central site (mean = 26.349, s.d. = 32.502) (Games-Howell, $p<0.05$) (figure 5.3.1). There was also a statistically significant difference in the mean percentage cover of sediment between MONTH (table 5.3.1). There was a statistically significantly greater mean percentage cover of sediment in September 2006 (mean = 27.000, s.d. = 31.910) than June 2006 (mean =15.574, s.d. = 23.5176), April 2007 (mean = 6.632, s.d. = 16.818) and May 2007 (mean = 11.000, s.d. = 24.743). There were no statistically significant interactions between MONTH*SITE, MONTH*HABITAT, HABITAT*SITE or MONTH*HABITAT*SITE (table 5.3.1) indicating that the lower mean percentage cover occurs at the South site compared to the Central site occurs in both algal and bare rock habitats and during all months, and the lower cover of sediment in July 2006 than September 2006 also occurs at all three site in both algal and bare rock habitats (figure 5.3.1).

Although statistically significant differences in sediment deposition only occurred between July 2006 and September 2006, in both algal and bare rock habitats, percentage sediment cover over the eighteen month period showed a general increase during late summer and autumn (approximately July – November) whilst falling to lower percentage sediment cover during later winter and spring (approximately January – May) (figure 5.3.1). Percentage sediment cover in the South site was also greater in algal quadrats than bare rock, although this was not statistically significant.

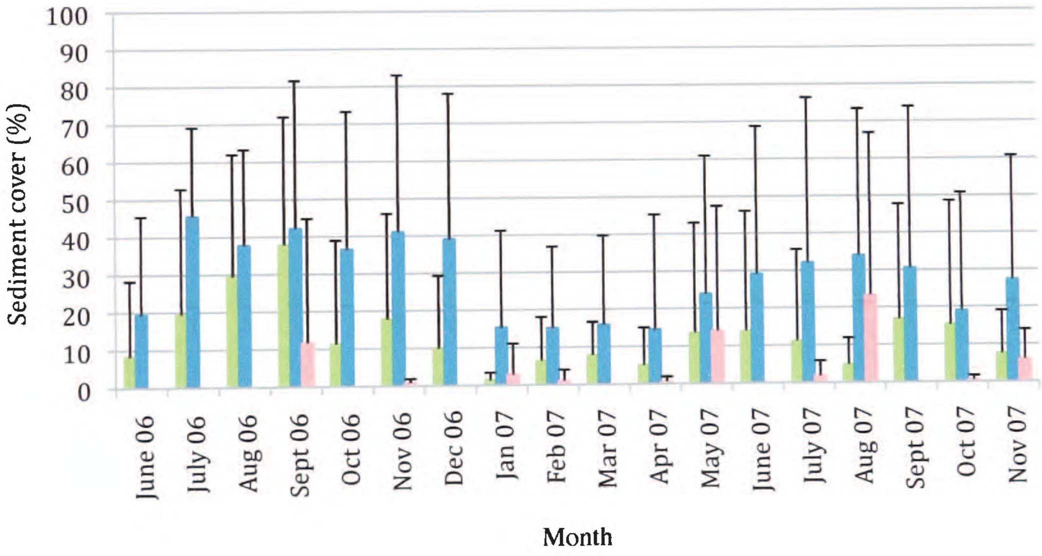
Table 5.3.1: Summary of a three-way mixed design GLM ANOVA for percentage cover of sediment with SITE and HABITAT as independent factors and MONTH as a repeated measures factor.

Source	**DF**	**Adj MS**	**F**	**p**
SITE	2	30747.511	4.975	0.014
HABITAT	1	583.619	0.094	0.761
SITE*HABITAT	2	295.586	0.48	0.953
Error	30	6180.036		
MONTH	5.356	2978.242	2.402	0.036
MONTH*SITE	10.713	1416.925	1.143	0.332
MONTH*HABITAT	5.356	884.421	0.713	0.624
MONTH*SITE*HABITAT	10.713	892.506	0.720	0.715
Error	160.691	1239.737		

a) Algal quadrats



b) Bare rock quadrats



Key:

🟩	North	🟦	Central	🟥	South

Figure 5.3.1: Monthly changes in the mean percentage cover of sediment at each of the three sites (North, Central and South) at Holbeck (+s.d.).

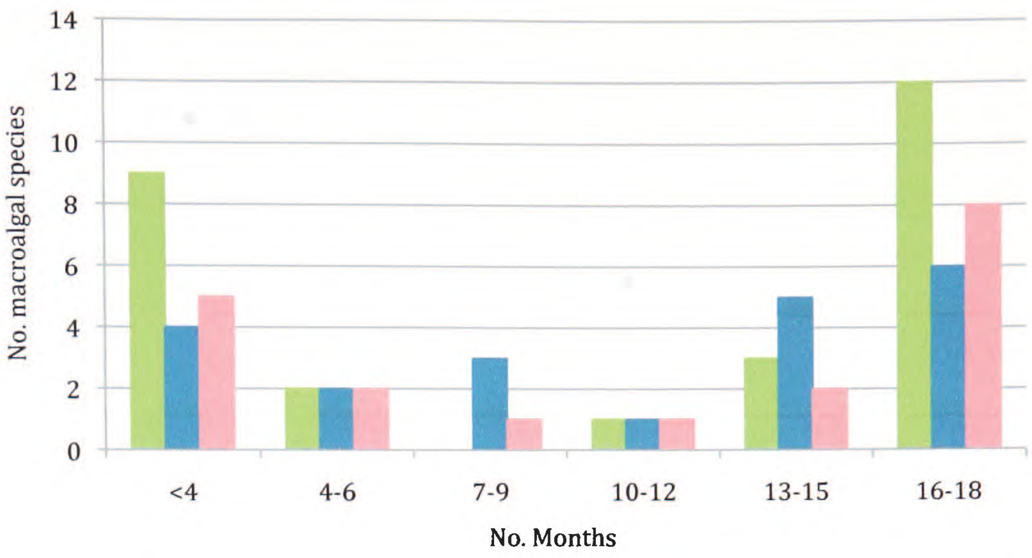
5.3.2. Temporal changes in community structure.

Differences in macroalgae

The greatest species richness (27 species) was found to occur at the North site, whilst the lowest occurred at the South site (19 species) (table 5.3.2). Seventeen of the macroalgal species were found to occur at all three sites (table 5.3.2), and nine of the macroalgal species were only found to occur exclusively on the North site (table 5.3.3). The majority of macroalgal species at all three sites were found to occur frequently, occurring in 16-18 of the months (figure 5.3.2). These included the *Fucus* species, *Phymatolithon lenormandii*, *Osmundea pinnatifida*, *Corallina officinalis* and *Mastocarpus stellatus*. A small number of macroalgal species were found to occur for between 4 and 15 of the months (figure 5.3.2). However, a large number of species occurred infrequently (for less than four months) (figure 5.3.2). These included *Ceramium nodulosum*, *Lithothamnion glaciale* Kjellman, *Polysiphonia lanosa*, *Ahnfeltia plicata*, *Ectocarpus* sp and *Lomentaria articulata* (Hudson) Lyngbye. The majority of these infrequently occurring species occurred during the winter and early spring months. Where species occurred infrequently at a site the abundance was generally less that 1%. Although some macroalgal species occurred infrequently at one site, they occurred more frequently at others. Both *Ulva lactuca* and *Cladostephus spongiosus* occurred in less than four of the months at the South site but during more than 15 of the months at the North site.

Table 5.3.2: Species found to occur at each site through the sampling period on the shore at Holbeck (p indicates presence of species).

	North	**Central**	**South**
Ahnfeltia plicata **(Hudson) Fries**	p	p	
Catenella caespitosa **(Withering) Irvine**	p		
Ceramium nodulosum **(Lightfoot) Ducluzeau**	p		
Ceramium pallidum **(Nägeli & Kützing) Maggs & Hommersand**	p		
Ceramium **sp**	p		
Chondrus crispus **Stackhouse**	p	p	p
Cladophora rupestris **(Linnaeus) Kützing**	p	p	p
Cladophora sericea **(Hudson) Kützing**	p	p	p
Cladostephus spongiosus **(Hudson) Agardh**	p	p	p
Corallina officinalis **Linnaeus**	p	p	p
Dumontia contorta **(Gmelin) Ruprecht**	p	p	p
Ectocarpus **sp**		p	p
Fucus **juveniles**	p	p	p
Fucus serratus **Linnaeus**	p	p	p
Fucus vesiculosus **Linnaeus**	p	p	p
Hildenbrandia rubra **(Sommerfelt) Meneghini**	p	p	p
Laminaria digitata **(Hudson) Lamouroux**	p		
Lithothamnion glaciale **Kjellman**	p	p	p
Lomentaria articulata **(Hudson) Lyngbye**	p		p
Mastocarpus stellatus **(Stackhouse) Guiry**	p	p	p
Osmundea pinnatifida **(Hudson) Stackhouse**	p	p	p
Phymatolithon lenormandii **(Areschoug) Adey**	p	p	p
Polysiphonia fucoides **(Hudson) Greville**	p	p	
Polysiphonia lanosa **(Linnaeus) Tandy**		p	
Rhodomela confervoides **(Hudson) Silva**	p		
Rhodothamniella floridula **(Dillwyn) Feldmann**	p		
Ulva intestinalis **Linnaeus**	p	p	p
Ulva lactuca **Linnaeus**	p	p	p
Verrucaria mucosa **Wahlenberg**	p	p	p



Key:

🟩	North	🟦	Central	🟥	South

Figure 5.3.2: The number of months during the 18 month sampling period that individual macroalgal species were recorded within quadrats at all three sites at Holbeck.

There was a statistically significant difference in the community similarity between MONTH (ANOSIM, Global R = 0.011, p = 2.9%). June 2006 was different from October 2006, November 2006, January 2007, May 2007 and July 2007 to November 2007 (p<5% in all cases), whilst August 2006 was different from October 2006, November 2006, January 2007 to May 2007, July 2007 to November 2007 (p<5% in all cases). There was also a statistically significant difference in community similarity between SITE (ANOSIM, Global R = 0.043, p = 0.1%). The macroalgal community at the South site was statistically significantly different from both the Central and North sites (p = 0.1% in both cases), however there was no statistically significant difference in the community between North and Central sites (p>5%)

The same three species, *Fucus vesiculosus*, *Phymatolithon lenormandii* and *Osmundea pinnatifida*, were found to be the most important in determining community similarity at all three sites (table 5.3.3). *Fucus serratus* also was important in determining community similarity, but to a lesser extent at the North site (table 5.3.3). The community dissimilarity between all three sites (Central and North = 70.65%, Central and South = 75.09%, North and South = 77.46%) was attributable to the differences in the abundance of *F. vesiculosus* (table 5.3.3). The greatest abundance of *F. vesiculosus* occurred at the Central site, whilst the lowest occurred at the South site (table 5.3.3). The greatest abundance of *Phymatolithon lenormandii* occurred at the Central site, whilst the lowest occurred at the North site (table 5.3.3). In addition, the abundance of *O. pinnatifida* contributed to the dissimilarity between all the sites with the greatest abundance occurring at the South site and the least at the Central site (table 5.3.3). *F. serratus* also contributed to the dissimilarity between the South site (6.35%) which was lower than both the North site (12.98%) and Central site (9.34%).

Table 5.3.3: Species contributing to the similarity in the macroalgal community between the three sites at Holbeck.

	South 22.05% similarity		**Central 32.29% similarity**		**North 28.00% similarity**	
Species	**Average Percentage cover (%)**	**Contribution (%)**	**Average Percentage cover (%)**	**Contribution (%)**	**Average Percentage cover (%)**	**Contribution (%)**
Fucus vesiculosus	27.58	45.95	41.38	66.78	37.00	62.18
Phymatolithon lenormandii	17.90	27.94	18.54	18.37	16.54	15.84
Osmundea pinnatifida	9.34	13.33	4.51	7.58	6.06	7.33
Fucus serratus					12.98	5.81

A two way ANOSIM was used to test the effect of habitat and month on community similarity. There was a statistically significant difference in the community similarity between MONTH (ANOSIM, Global R = 0.028, p = 0.1%). Generally community similarity between June 2006 and October 2006 was statistically significantly different from July 2007 to September 2007 (p<5% in all cases). There was a statistically significant difference in community similarity between HABITAT (ANOSIM, Global R = 0.315, p = 0.01%).

The abundance of *F. vesiculosus*, *Phymatolithon lenormandii* and *O. pinnatifida* were again found to be important in determining the similarity in both algal and bare rock quadrats (table 5.3.4). Of these *F. vesiculosus* was the most important species in determining community similarity in both algae and bare rock quadrats (table 5.3.4). Community dissimilarity between the two initial habitat types (80.45%) was again primarily determined by differences in the cover of *F. vesiculosus* and *Phymatolithon lenormandii*, both of which had a greater abundance in algal than bare rock quadrats (table 5.3.4). The abundance of *O. pinnatifida* and *F. serratus* also contributed to the dissimilarity between initial habitats (table 5.3.4). In both cases the cover was greater in algal than bare rock quadrats (*F. serratus* algae = 16.68%, bare rock = 2.61%). The only species contributing to the dissimilarity between algae and bare rock quadrats that was greater in bare rock was *Fucus* juveniles (algae = 0.75%, bare rock = 5.30%)

Table 5.3.4: Species contributing to the similarity in the macroalgal community between bare and algal habitats at Holbeck.

	Algae 47.66% similarity		**Bare rock 18.27% similarity**	
Species	**Average Percentage cover (%)**	**Contribution (%)**	**Average Percentage cover (%)**	**Contribution (%)**
Fucus vesiculosus	56.72	66.16	14.01	46.48
Phymatolithon lenormandii	29.27	20.96	5.91	16.77
Osmundea pinnatifida	10.35	5.79	2.81	15.40

The similarity of the macroalgal community between months was primarily determined by the abundance of *Fucus vesiculosus*, and to lesser extent the cover of *Phymatolithon lenormandii* (table 5.3.5). With the exception of June 2006, July 2006, August 2006, September 2006, and December 2006 *Osmundea pinnatifida* was the next most important species in determining assemblage similarity. However, during these months *Fucus serratus* was the next most important species (table 5.3.5). Between September 2006 and February 2006 and March 2006 the abundance of *Fucus* juveniles also contributed to the community similarity within each month. Dissimilarity between months was also dependant, primarily, on the abundance of the same macroalgal species as determine the similarity (table 5.3.5). In all cases the abundance of *F. vesiculosus* was greater during July 2007 to September 2007 compared to June 2006 to October 2006 whilst the abundance of *P. lenormandii* was lower (table 5.3.5). June 2006 had a lower abundance of *F. vesiculosus* compared to the other months, and with the exception of November 2006 and January 2007, when the abundance of *P. lenormandii* was greater. However there was no apparent difference in the abundance of *O. pinnatifida* between the months (table 5.3.5). No consistent difference in the abundance of *F. vesiculosus* was found in August 2006 compared to the other months but the abundance of *P. lenormandii* and *O. pinnatifida* was greater (table 5.3.5).

Table 5.3.5: Species contributing to the similarity in community assemblage between the eighteen months at Holbeck.

	June 06 22.41% similarity		**July 06 22.79% similarity**		**Aug 06 22.15% similarity**		**Sept 06 23.66% similarity**		**Oct 06 25.41% similarity**	
Species	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**
Fucus vesiculosus	29.45	44.80	33.19	59.72	33.78	48.57	33.60	53.86	37.63	58.78
Phymatolithon lenormandii	20.72	26.06	17.73	19.20	21.12	23.65	17.64	21.20	19.04	16.65
Osmundea pinnatifida	7.52	15.79	6.35	10.82	8.70	14.52	5.63	6.10	7.01	6.60
Fucus serratus	12.51	6.15	12.54	7.08	13.00	6.09	9.57	4.31		
***Fucus* juveniles**							4.88	7.74	7.63	10.67

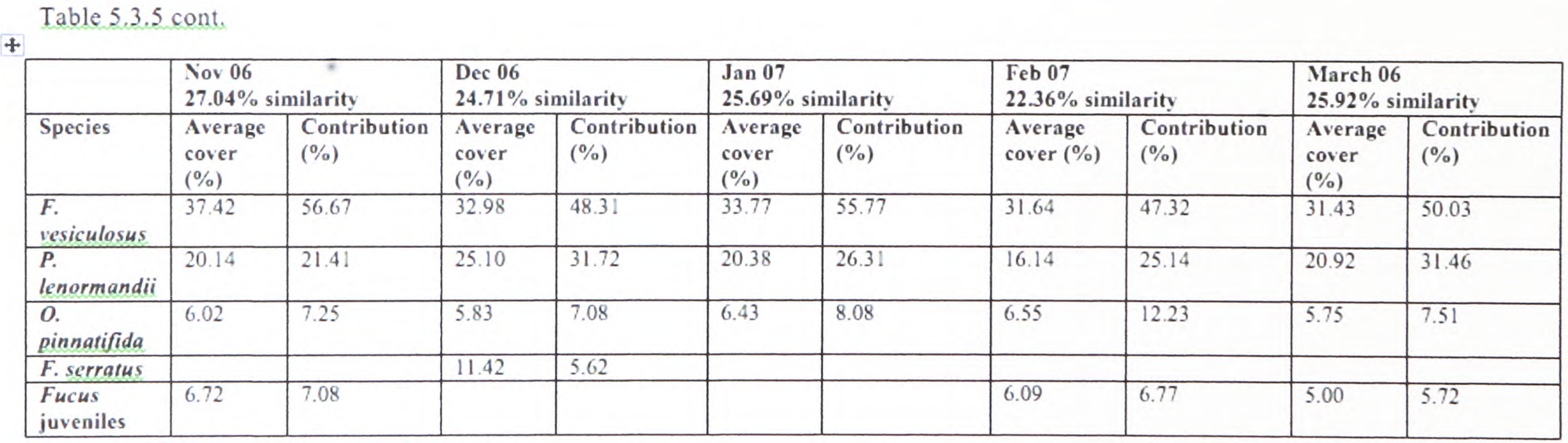


Table 5.3.5 cont.

	Nov 06 27.04% similarity		Dec 06 24.71% similarity		Jan 07 25.69% similarity		Feb 07 22.36% similarity		March 06 25.92% similarity	
Species	Average cover (%)	Contribution (%)	Average cover (%)	Contribution (%)	Average cover (%)	Contribution (%)	Average cover (%)	Contribution (%)	Average cover (%)	Contribution (%)
F. vesiculosus	37.42	56.67	32.98	48.31	33.77	55.77	31.64	47.32	31.43	50.03
P. lenormandii	20.14	21.41	25.10	31.72	20.38	26.31	16.14	25.14	20.92	31.46
O. pinnatifida	6.02	7.25	5.83	7.08	6.43	8.08	6.55	12.23	5.75	7.51
F. serratus			11.42	5.62						
Fucus juveniles	6.72	7.08					6.09	6.77	5.00	5.72

Table 5.3.5 cont.

	April 07 26.11% similarity		**May 07 29.56% similarity**		**June 07 32.82% similarity**		**July 07 29.68% similarity**	
Species	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**
F. vesiculosus	32.65	57.92	39.45	68.90	40.56	68.18	43.40	78.66
P. lenormandii	16.06	20.06	14.95	14.42	18.88	18.45	13.71	9.21
O. pinnatifida	7.66	12.88	7.92	9.84	8.09	6.89	6.23	6.91
F. serratus								
***Fucus* juveniles**								

Table 5.3.5. cont.

	Aug 07 30.57% similarity		**Sept 07 27.76% similarity**		**Oct 07 34.47% similarity**		**Nov 07 30.30% similarity**	
Species	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**	**Average cover (%)**	**Contribution (%)**
F. vesiculosus	37.67	70.79	35.08	68.73	39.96	69.68	36.79	75.85
P. lenormandii	14.81	16.31	9.63	12.24	13.85	19.75	14.19	13.72
O. pinnatifida	5.59	6.44	7.22	9.74	5.44	5.74	3.72	6.25
F. serratus								
***Fucus* juveniles**								

The results of the three-factor mixed design GLM ANOVA showed that there was no statistically significant difference in the mean macroalgal species richness (d) between SITE, between HABITAT or between MONTH ($p>0.05$ in all cases). There were no statistically significant interactions between MONTH*SITE, MONTH*HABITAT, HABITAT*SITE or MONTH*SITE*HABITAT ($p>0.05$ in all cases) indicating that at all three sites, in both algal and bare rock quadrats, mean d remained relatively consistent throughout the eighteen month sampling period.

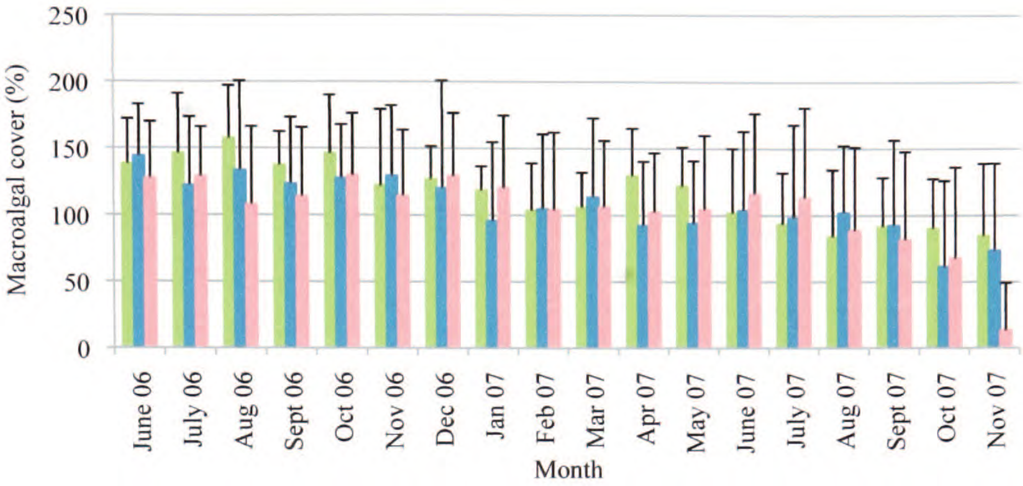
Similarly, there was no statistically significant difference in the mean macroalgal species diversity (H') between SITE, between HABITAT or between MONTH ($p>0.05$ in all cases). Again, no statistically significant interactions were found to occur between MONTH*SITE, MONTH*HABITAT, HABITAT*SITE or MONTH*SITE*HABITAT ($p>0.05$ in all cases). This indicates that mean H' did not vary significantly over the eighteen month sampling period at all three sites, or between algal and bare rock quadrats.

No statistically significant difference was also found to occur in mean total abundance between MONTH (table 5.3.6). However a statistically significant difference in mean total abundance occurred between SITE (table 5.3.6) but *post hoc* Gabriel's test were unable to resolve the source of the variation. A statistically significant difference was also found to occur in the mean total abundance between HABITAT (table 5.3.6). The mean total abundance was statistically significantly greater in algal quadrats (mean = 166.664, s.d. = 47.995) than bare rock quadrats (mean = 33.559, s.d. =3 3.373) (Gabriel's, $p<0.05$). A statistically significant interaction was found to occur between MONTH*SITE (table 5.3.6). Whilst mean total abundance remained relatively consistent at both the Central and North sites throughout the eighteen-month period, total abundance at the South site decreased (figure 5.3.3). A statistically significant interaction also occurred between MONTH*HABITAT (table 5.3.6). The total abundance in algal quadrats decreased over the eighteen-month sampling period, whilst it increased in bare rock quadrats (figure 5.3.3). This pattern occurred at all three sites as no statistically significant interaction occurred between SITE*HABITAT (table 5.3.6). There was also no statistically significant interaction between MONTH*SITE*HABITAT (table 5.3.6) indicating that at all three sites the same pattern of greater mean total abundance occurring in algal quadrats than bare rock quadrats occurred, and this continued throughout the eighteen month sampling period (figure 5.3.3).

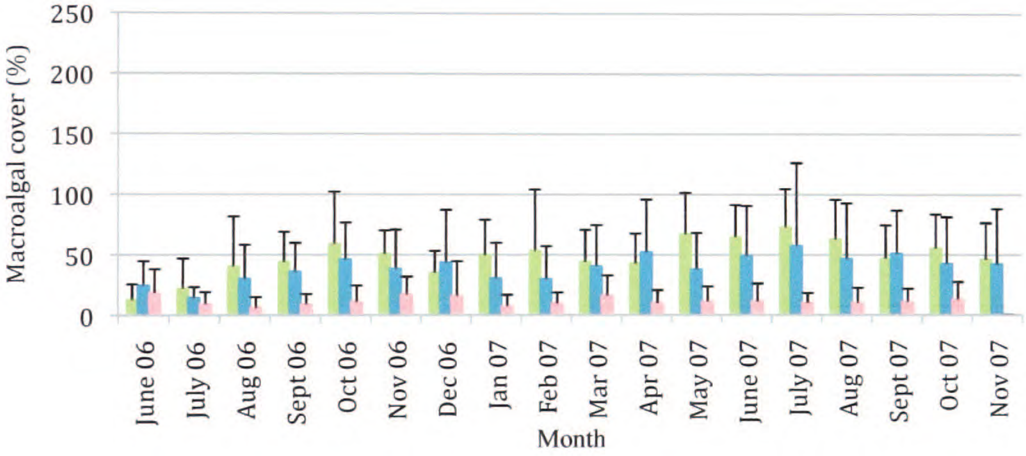
Table 5.3.6: Summary of a three-way mixed design GLM ANOVA for total abundance of macroalgae with SITE and HABITAT as independent factors and MONTH as a repeated measures factor.

Source	**DF**	**Adj MS**	**F**	**p**
SITE	2	48448.236	3.305	0.05
HABITAT	1	748806.046	51.079	0.001
SITE*HABITAT	2	1662.276	0.113	0.893
Error	30	14659.839		
MONTH	7.765	2346.371	1.888	0.065
MONTH*SITE	15.529	2119.776	1.705	0.049
MONTH*HABITAT	7.765	5387.264	4.334	0.001
MONTH*SITE*HABITAT	15.529	1031.552	0.830	0.648
Error	232.938	1243.054		

a) Algal quadrats



a) Bare rock quadrats



Key:

🟩	North	🟦	Central	🟥	South

Figure 5.3.3: Monthly changes in the mean percentage cover of macroalgae at each of the sites (North, Central and South) at Holbeck (+ s.d.).

Differences in fauna

A three factor mixed design ANOVA was also used to test the effect of MONTH, HABITAT and SITE, and their interactions upon the abundance of each of the faunal groups, patellids, littorinids and barnacles. There was no statistically significant difference in the abundance of patellids between SITE or HABITAT ($p>0.05$ in all cases). However, there was a statistically significant difference in the mean abundance of patellids between MONTH ($F_{5.476,\ 164.281} = 2.255$, $p<0.05$) but *post hoc* Bonferroni tests were unable to resolve the source of the variation. There were found to be no statistically significant interactions between MONTH*SITE, MONTH*HABITAT, HABITAT*SITE or MONTH*SITE*HABITAT ($p>0.05$ in all cases), indicating the there was no difference in the mean abundance of patellids at all three sites and between both algal and bare rock habitats, and although differences occurred in the number of patellids throughout the year there was no clear pattern of change.

There was also no statistically significant difference in the abundance of littorinids between SITE (table 5.3.7). However there was a statistically significant difference in the abundance of littorinids between HABITAT (table 5.3.7), with statistically significantly more littorinids occurring in algal quadrats (mean = 6.49, s.d. = 7.428) than bare rock quadrats (mean = 2.76, s.d. = 4.197). There was also a statistically significant difference in the mean abundance of littorinids between MONTH (table 5.3.7). There was a statistically significantly greater abundance of littorinids in April 2007 (mean = 6.85, s.d. = 5.503) than July 2006 (mean = 3.06, s.d. = 4.341) or August 2006 (mean = 3.94, s.d. = 6.132) (Bonferroni, $p<0.05$). No significant interactions were found between SITE*HABITAT (table 5.3.7) indicating that the lower abundance of littorinids found in bare rock quadrats occurred at all three sites throughout the year (figure 5.3.4). There was also no significant interaction between MONTH*SITE, or MONTH*HABITAT (table 5.3.7), indicating that the greater abundance of littorinids occurring in April 2007 compared to July 2006 and August 2006 occurred in all three sites and in both initial habitats (figure 5.3.4). There was no significant interaction between SITE*MONTH*HABITAT (table 5.3.7) indicating that the differences between habitats and months occur at all three sites (figure 5.3.4).

Table 5.3.7: Summary of a three-way mixed design GLM ANOVA for littorinid abundance with SITE and HABITAT as independent factors and MONTH as a repeated measures factor.

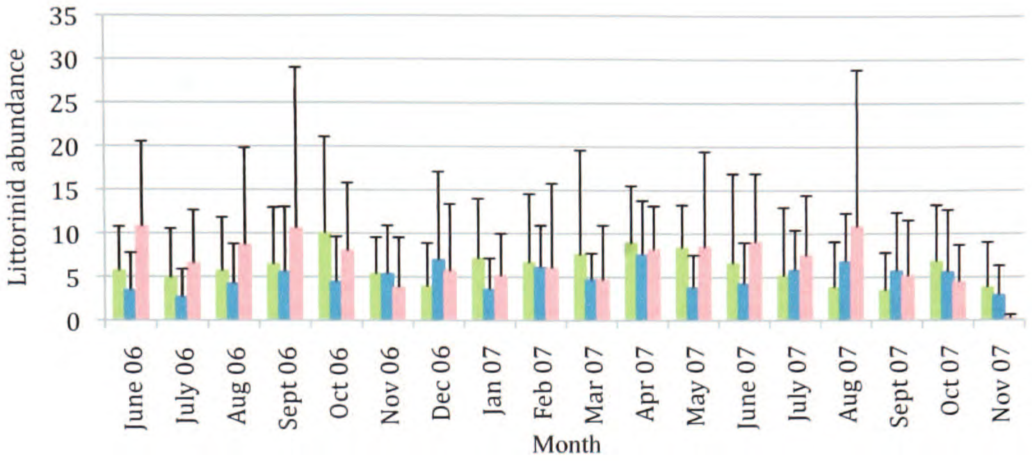
Source	**DF**	**Adj MS**	**F**	**p**
SITE	2	12.435	0.090	0.914
HABITAT	1	2199.041	14.725	0.001
SITE*HABITAT	2	85.169	0.570	0.570
Error	30	149.343		
MONTH	8.119	93.039	2.427	0.015
MONTH*SITE	16.239	50.799	1.325	0.181
MONTH*HABITAT	8.119	56.789	1.481	0.163
MONTH*SITE*HABITAT	16.239	46.796	1.221	0.252
Error	243.584	38.338		

Statistically significant differences were found to occur in the mean percentage cover of barnacles between HABITAT (table 5.3.8), SITE (table 5.3.8) and MONTH (table 5.3.8) (table 5.3.8). There was a statistically significantly greater mean percentage cover of barnacles in bare rock quadrats (mean = 22.150, s.d. = 28.475) than algal quadrats (mean = 2.673, s.d. = 6.786) (Games-Howell, $p<0.05$). The mean percentage cover of barnacles was also statistically significantly greater at the North site (mean = 21.635, s.d. = 26.5205) than at the Central (mean = 3.553, s.d. = 10.272) or South (mean = 12.619, s.d. = 24.9763) sites (Games-Howell, $p<0.05$), and statistically significantly fewer barnacles were found to occur during October 2007 than July 2006 (Bonferroni, $p<0.05$). Statistically significant interactions occurred between MONTH*SITE (table 5.3.8), indicating that the abundance of barnacles at the South site remained fairly consistent throughout the 18 months whereas both the Central and especially the North Site showed large variations in the abundance of barnacles throughout the 18 months (figure 5.3.5). Statistically significant interactions also occurred between HABITAT*SITE (table 5.3.8), indicating that the abundance of barnacles at the within bare rock and algal quadrats was different between the three sites. At both the North and South sites the abundance of barnacles was much lower in algal quadrats than bare rock. However at the Central site the abundance of barnacles was similar in both quadrat types (figure 5.3.5). There was no statistically significant interaction between MONTH*HABITAT (table 5.3.8) indicating that the greater percentage cover of barnacles at the north site was observed throughout the year, and that the lower abundance of barnacles in October 2007 than July 2006 occurred at all three sites (figure 5.3.5). There were also no significant interactions between MONTH*SITE*HABITAT (table 5.3.8) indicating that the greater abundance of barnacles on bare rock than algal quadrats occurred throughout the eighteen-month sampling period, and that this pattern occurred at all three sites (figure 5.3.5).

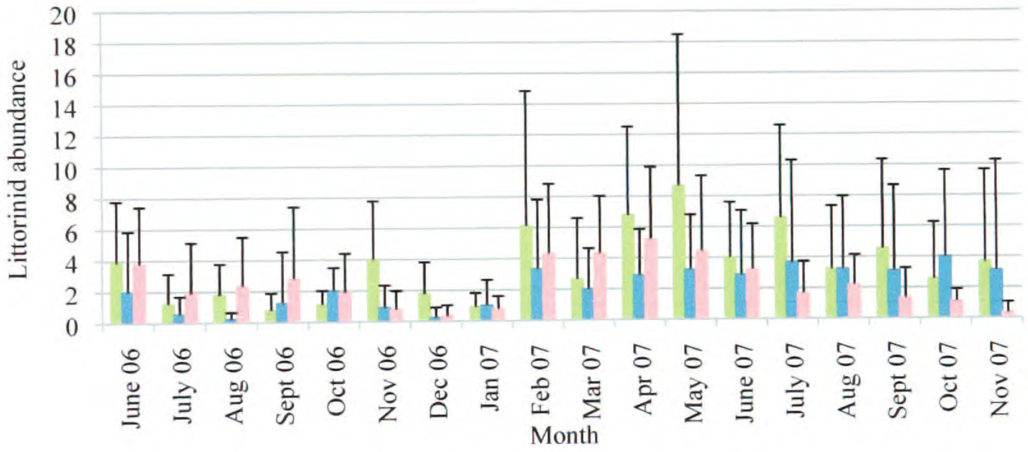
Table 5.3.8: Summary of a three-way mixed design GLM ANOVA for percentage barnacle cover with SITE and HABITAT as independent factors and MONTH as a repeated measures factor.

Source	**DF**	**Adj MS**	**F**	**p**
SITE	2	24582.553	9.100	0.001
HABITAT	1	23849.321	8.828	0.006
SITE*HABITAT	1	12971.682	4.802	0.016
Error	30	2701.492		
MONTH	5.425	1436.819	4.653	0.001
MONTH*SITE	10.850	867.726	2.810	0.002
MONTH*HABITAT	5.425	439.991	1.425	0.214
MONTH*SITE*HABITAT	10.850	479.328	1.552	0.119
Error	162.753	308.777		

a) Algal quadrats



a) Bare rock quadrats

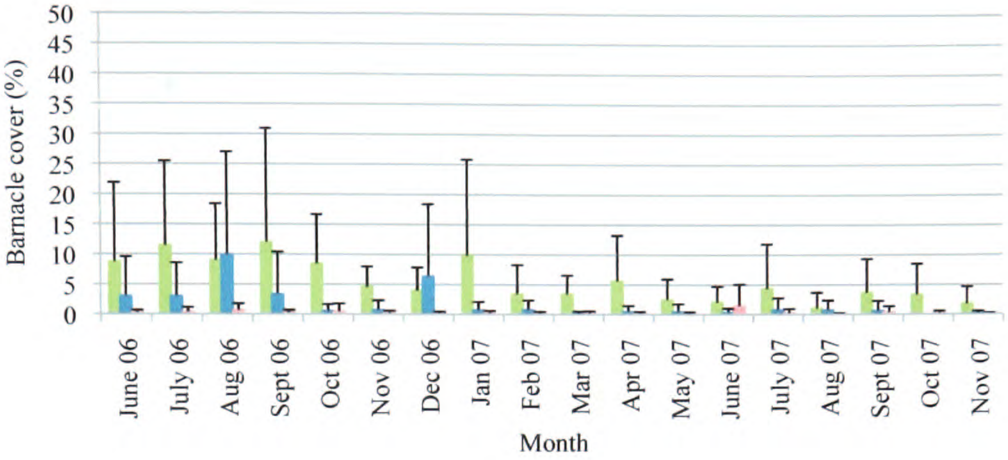


Key:

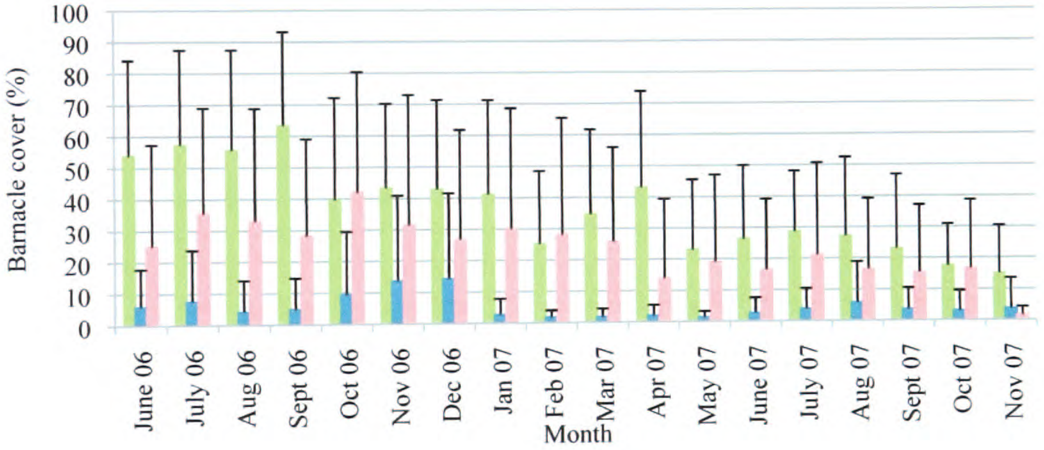
🟩	North	🟦	Central	🟥	South

Figure 5.3.4: Monthly changes in the mean abundance of littorinids at each of the sites (Norht, Central and South) at Holbeck (+ s.d.). Note scales on graphs differ.

a) Algal quadrats



b) Bare rock quadrats



Key:

🟩	North	🟦	Central	🟪	South

Figure 5.3.5: Monthly changes in the mean percentage cover of barnacles at each of the sites (North, Central and South) at Holbeck (+ s.d.). Note scales on graphs differ.

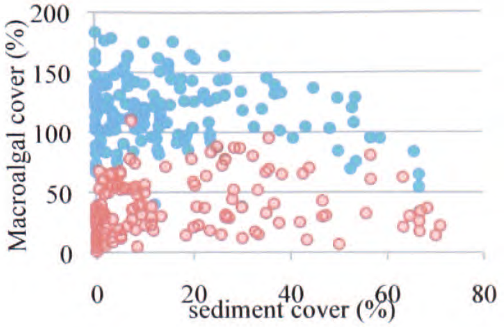
5.3.3. Relationships between sediment accumulation and community structure.

Correlations were performed on the average percentage cover with each of the total abundance, d H', percentage cover of barnacles, abundance of patellids and abundance of littorinids within both algal and bare rock quadrats (figure 5.3.6). Within algal quadrats, statistically significant negative correlations were found to occur between average percentage cover of sediment and average d (table 5.3.5, figure 5.3.6b), H' (table 5.3.5, figure 5.3.6c) and abundance of patellids (table 5.3.5, figure 5.3.6e). Within bare rock quadrats statistically significant negative correlations were found to occur between average percentage sediment cover and the average percentage cover of barnacles (table 5.3.5, figure 5.3.6d) and abundance of patellids (table 5.3.5, figure 5.3.6e). However, statistically significant positive correlations were found to occur between average percentage cover of sediment and average total abundance (table 5.3.5, figure 5.3.5a) and H' (table 5.3.5, figure 5.3.6c). Neither in algal nor bare rock quadrats did the average percentage cover of sediment display a relationship with the average abundance of littorinids (table 5.3.5, figure 5.3.6f).

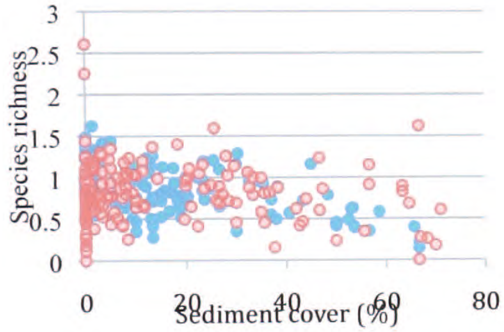
Table 5.3.5: Spearman rank order correlations (r_s) examining the relationship between average percentage cover of sediment and community structure on the intertidal rocky shore at Holbeck in both algal and bare rock quadrats (ns = not significant at the 0.05 level after Bonferroni correction, * statistically significant at the 0.05 level after Bonferroni correction, ** statistically significant at the 0.01 level after Bonferroni correction).

	Algal quadrats	Bare rock quadrats
Average total macroalgal abundance	-0.85 (ns)	0.496**
Average macroalgal species richness	-0.333**	0.088 (ns)
Average macroalgal diversity	-0.174*	0.242**
Average percentage cover of barnacles	-0.081 (ns)	-0.296**
Average abundance of patellids	-0.246**	-0.610**
Average abundance of littorinids	0.031 (ns)	0.005 (ns)

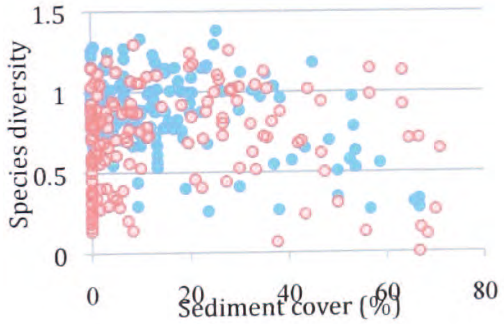
a) Macroalgal cover



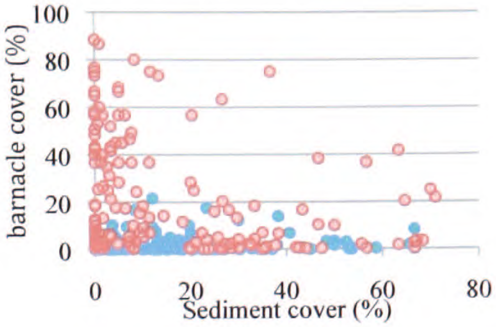
b) Macroalgal species richness



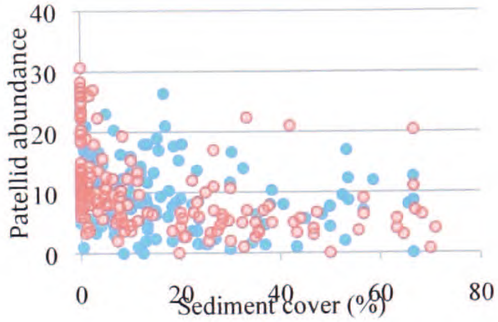
c) Macroalgal species diversity



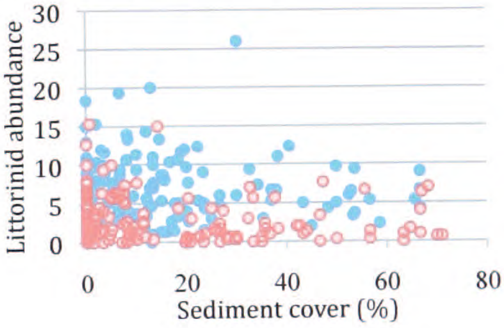
d) Barnacle cover



e) Patellid abundance



f) Littorinid abundance



Key:

🟦	Algal quadrats	🟥	Bare rock quadrats

Figure 5.3.6: Scatter plots examining the relationship between average percentage cover of sediment and community structure on the intertidal rocky shore at Holbeck in both algal and bare rock quadrats.

5.3.4. Summary of key findings

- The percentage cover of sediment was statistically significantly greater at the Central site than the South site.
- There was no statistically significant difference in macroalgal diversity, richness and total abundance or the abundance of patellids or littorinids between the sites. Differences in the macroalgal community were found between the three sites, but these were the result of differences in the proportions of species rather than different species.
- Statistically significant differences were found in percentage sediment cover between months. The percentage cover of sediment was found to increase between July and November and decrease between January and May.
- No statistically significant differences were found in macroalgal diversity, richness and total abundance between months. Statistically significant differences were found in the abundance of patellids and littorinids and the percentage cover of barnacles, but these did not follow the same patterns as the differences in sediment accumulation. Differences were found in macroalgal community structure between months, but were the result of differences in the proportions of species rather than different species.
- The percentage cover of sediment was not statistically significantly different between algal and bare rock quadrats.
- No statistically significant differences were found in macroalgal diversity or richness or patellid abundance. Total macroalgal abundance and littorinid abundance was statistically significantly greater in algal quadrats, whilst the percentage cover of barnacles was greater in bare rock quadrats.
- In algal quadrats statistically significant negative correlations were found between macroalgal species richness, macroalgal diversity and the abundance of patellids and the percentage cover of sediment. In bare rock quadrats the percentage cover of barnacles and the abundance of patellids had a negative relationship with the percentage cover of sediment. Statistically significant positive correlations were found between the percentage cover of sediment and total macroalgal abundance and macroalgal diversity.

5.4. Discussion

The greater sediment accumulation at the Central site previously reported in Chapter 4.3 was also evident within the fixed quadrats at the three sites. Again, this greater sediment accumulation was attributed to the lower topography of the site (Littler, *et al.*, 1983) and also the presence of the Holbeck sea defences to the south of the site disrupting sediment movement (Storlazzi & Field, 2000). Lower sediment accumulation was found to occur at the South site. The South site has some protection from sediment transport due to the Holbeck sea defences, and as sediment is also being trapped at the Central site this may also limit sediment supply to the South site.

There was no significant difference in either littorinid or patellid abundance, or in macroalgal diversity (H') and macroalgal species richness (d) between the three sites. Although a significant difference in macroalgal total abundance was recorded between the three sites, the level of significance was very low (p=0.05). The interpretation of this observed difference should therefore be treated with caution due to the increased chance of a Type I error, particularly as the data were not normally distributed and had unequal variances (Underwood, 1997). However, as discussed in Chapter 4, areas with higher sedimentation levels have previously been found to have a lower macroalgal abundance and H' (Daly & Mathieson, 1977; Eriksson & Johansson, 2005; Balata, *et al.*, 2007). Patellids and littorinids are also both affected by sediment burial as their movement is restricted (Brown & Trueman, 1996; Chandrasekara & Frid, 1998).

The lack of observed differences in H', d total abundance and patellid and littorinid abundance between the three sites may be the result of the large variability in within site sediment accumulation, which may allow species that are less tolerant of sedimentation to occur on some areas of the shore at all three sites. Previous studies found macroalgal species richness and diversity to be negatively affected by increased sediment loads (*e.g.* Daly & Mathieson, 1977; Balata, *et al.*, 2007), but also had consistent increases in sediment over long periods of time. At all three sites at Holbeck, although sedimentation occurs throughout the year, the quantity of sediment within individual patches was very variable. Lack of consistent sediment cover across the whole of all three sites may result in similar macroalgal communities that are tolerant to periodic inundation by sediment. Both littorinids and patellids are only able to survive short-term burial (Marshall & McQuaid, 1989; Chandrasekara & Frid, 1998), and therefore frequent sediment accumulation and removal at all three sites may not limit abundance.

As discussed in Chapter 4, the macroalgal community may be influenced by scour as well as sediment burial (Kendrick, 1991). As sediment moves from north to south across all three sites at Holbeck, the effect of sediment movement would be similar at all three sites and may account for the lack of differences.

Community structure varied between the three sites. Whilst the dominant macroalgal species were the same at all, the abundance of these species varied between them. Previous studies have found the abundance of turf species has been found to be greater in areas with higher sediment levels (Airoldi & Cinelli, 1997; Gorgula & Connell, 2004). However, as discussed in Chapter 4, the effects of sediment movement rather than sediment burial may be influencing community structure at the three sites. The lower abundance of *Fucus vesiculosus* at the South site may be related to interactions between species, rather than the effects of sediment. At this site the quantity of *F. vesiculosus* across the shore was much lower than the other two sites, and primarily being restricted to the edge of the large rock pools running down the shore (figure 5.2.1c). The rest of the shore is covered almost exclusively by barnacles and limpets. Barnacles out compete *Fucus* species by 'cutting through' the holdfast of the macroalgae as the barnacles increase in size (Dring, 1982). The lower density of *Fucus* within the South site would also retain less moisture possibly increasing the effects of desiccation, reducing their ability to photosynthesise (Schonbeck & Norton, 1978; Dring & Brown, 1982) and strength (Harrington, *et al.*, 2005) and may thus make them more susceptible to the breakage by barnacles and also from storm damage. The effects of desiccation may be more influential at the South site because of the small patches of macroalgae, where as the greater abundance of macroalgae at the North and Central sites would provide protection from desiccation (Bertness, *et al.*, 1999) and the subsequent effects.

The percentage cover of barnacles was lower at the Central site. Filter feeders are suggested to have their feeding mechanisms clogged by sediment in the water column (Moore, 1977). Alternatively sediment scour and cover at the Central site may be preventing settlement and colonization in the same way the whiplash effect of fucus can prevent barnacle larvae settlement (Dring, 1982).

No difference was found in sediment cover between algal and bare rock habitats. Although individual macroalgal species have been found to trap sediment (Chapter 2.3), these differences are not as apparent at community level (Chapter 3.3). This may be due to the influence of the surrounding community or interactions between different macroalgal species. However, as no differences were found in sediment accumulation between algal and bare rock quadrats at all three sites and during all months, this suggests that sediment accumulation on the shore is the result of large scale processes that affect the whole shore. Increased terrestrial runoff (*e.g.* Airoldi, 2003) and storms (*e.g.* Collinson & Thompson, 1982; Prathep, *et al.*, 2003) have both been postulated to influence sediment availability and accumulation on the shore. These would occur across all three sites and may be more influential than either the macroalgae or fauna on the shore.

There was also no difference in H', d or patellid abundance between algal and bare rock quadrats. This may be related to the lack of differences in sediment accumulation between the two quadrats types, but as no differences were observed in H', d or patellid abundance between sites with different levels of sediment accumulation, other factors may be important. The differences in total abundance and macroalgal community structure between algal and bare rock quadrats are attributable to their initial habitat classification.

Statistically significant differences were found in the abundance of littorinids and the percentage cover of barnacles between algal and bare rock quadrats. A greater abundance of littorinids were found in algal than bare rock quadrats, whilst a greater percentage cover of barnacles were found in bare rock than algal quadrats. In both cases these may relate to interactions between fauna and macroalgae rather than sediment. Barnacle settlement in areas of canopy may be low due to the 'whiplash' effect of macroalgae preventing barnacle larvae settlement (Dring, 1982), whilst littorinids use macroalgae as a source of food (Norton, *et al.*, 1990).

The percentage cover of sediment varied during the year, with a greater cover in late Summer/ Autumn, and less during Winter. A similar pattern was found in the quantity of sediment trapped in *Corallina* (Stewart, 1983), but no explanation was offered for this observation. Increased sediment loads are generally related to winter storms (Collinson & Thompson, 1982; Prathep, *et al.*, 2003), but this could also increase sediment movement away from an area, reducing residence time and preventing continuous accumulation.

There were no differences in H', d, total abundance, or abundance of patellids during the year, suggesting that the temporal changes in sediment were not having a significant influence. The majority of the macroalgal species (see table 5.3.1), which occurred at all three sites are perennial (Burrows, 1991; Dixon & Irvine, 1995; van den Hoek, *et al.*, 1995; Lee, 1999; Maggs & Hommersand, 2001) and occurred throughout most of the eighteen-month sampling period. Even those only found during one or two months at Holbeck and are not regarded as perennial can occur throughout the year (*e.g. Polysiphonia lanosa* and *Ceramium* sp [Maggs & Hommersand, 2001]; *Ahnfelta plicata* and *Catenella caespitosa* [Dixon & Irvine, 1995]). Differences occurred in the macroalgal community structure during the eighteen-month sampling period, but these were once again related to changes in the abundance of the dominant macroalgal species rather than macroalgae occurring seasonally. The differences between June 2006 - October 2006 and July 2007 - September 2007 appear to be attributable to the growth of *Fucus vesiculosus*, whilst the abundance of the other dominant species remained similar. Although growth of *F. vesiculosus* occurs throughout the year, it peaks during May - June (Jormalainen, *et al.*, 2001), and therefore the abundance would be greater between the two years. The abundance of the species that occurred sporadically was generally less than 2%. As the quantities were very small they would have little effect on the total abundance, d or H'. There were no identifiable patterns in the growth of sporadic occurrence of macroalgal species, but this may due to the small quantities found.

Whilst there was no overall difference in total abundance between months, there was a statistically significant interaction between month and habitat. During the eighteen-month sampling period the total abundance of macroalgae decreased in algal quadrats, but increased in bare rock quadrats. This suggests, that even on sediment inundated shores, natural succession occurs with the growth and recruitment to macroalgae. Recruitment of Fucus juveniles was noted twice during the eighteen-month sampling period (starting September 2006 and February 2007), which corresponds with the suggested reproductive peaks in spring and fall (Serrao, *et al.*, 1999). The abundance of barnacles also fell in bare rock quadrats. Decreases in abundance of barnacles have been found to occur in later sucessional stages (Benedetti-Cecchi, 2000), also suggesting that succession was occurring.

Within each site sediment accumulation did not appear to be directly affecting the macroalgal community, with differences in sediment accumulation between sites and months not being reflected in differences in H', d or total abundance. Similarly, the patterns of abundance of patellids and littorinids, and the cover of barnacles did not appear to be directly related to differences in sediment. However the lack of differences in the intertidal community in relation to differences in sediment accumulation may be due to the wide variability found in sediment accumulation at all threes sites as statistically significant correlations between sediment accumulation and both the macroalgal and faunal communities.

Within algal quadrats there was a negative relationship between percentage sediment cover and both d and H' which may be the result of species which are less tolerant of sediment (*e.g.* Eriksson & Johansson, 2005; Balata, *et al.*, 2007) not occurring in those areas. However there was no difference in total abundance which may be the result of increased growth of more tolerant macroalgal species taking advantage of the reduced competition by other macroalgal species. The lack of a relationship between sediment and barnacles in algal quadrats may be the result of canopy species providing some protection from sediment as they remove sediment from the surrounding area (Kennelly, 1989)

Whilst sediment appeared to have a negative effect in algal quadrats, on bare rock positive relationships were observed between percentage sediment cover and total abundance and H' of macroalgae. Sediment may act as a disturbance on bare rock surfaces, clearing small areas and allowing colonisation of macroalgae to occur. However increased algae cover may trap greater sediment loads. During growth of the *Fucus* juveniles, increased quantities of sediment were observed to be trapped in areas with high densities of juveniles. This has been suggested enhance survival by providing protection from desiccation (Schiel, *et al.*, 2006), whilst turf species have generally been associated with sediment trapping (reviewed in Airoldi, 2003).

Patellids have a negative relationship with the percentage cover of sediment in both algal and bare rock quadrats. They may be responding directly to higher levels of sediment, as patellid species are intolerant to sediment (Brown, 1996), which is possibly due to an inability to withstand burial (Marshall & McQuaid, 1989). Alternatively sediment may be covering or removing food sources (Tait, 1981). Both of these could occur in both algal and bare rock quadrats. Littorinids, however, showed no relationship with sediment in either algal or bare rock quadrats, suggesting that whilst sediment may affect macroalgae and some fauna species at a local level, not all faunal species are affected.

Chapter 6

General discussion

As outlined in Chapter 1, the presence and amount of sediment in marine and intertidal systems is determined by a variety of factors including both natural ecological and anthropogenic influences (reviewed in Airoldi, 2003). The changes in sediment levels impact on macroalgal community composition and abundance to varying degrees (*e.g.* Gorgula & Connell, 2004; Eriksson & Johansson, 2005; Balata, *et al.*, 2007), and macroalgae can influence sediment accumulation (*e.g.* Kennelly, 1989; Prathep, *et al.*, 2003; Isaeus, *et al.*, 2004). Individual macroalgal species vary in both sediment trapping ability (*e.g.* Boney, 1978; Isaeus, *et al.*, 2004) and their tolerance to sediment loads (*e.g.* Eriksson & Johansson, 2005; Piazzi, *et al.*, 2005; Balata, *et al.*, 2007). The effect of sediment deposition on a shore is not solely restricted to the macroalgal community, faunal species can be negatively affected by sediment burial, and again the responses appear to be species specific (*e.g.* Chang & Levings, 1978; Chandrasekara & Frid, 1998). The relationship between sediment accumulation and rocky shore community structure is therefore complex and dynamic, and the purpose of the current research has been to explore some of these interactions in greater detail. In light of the potential influence that increased sediment levels could have on intertidal communities, the current study investigated the influence that macroalgae had upon sediment trapping and accumulation (Chapters 2 and 3), patterns in sediment accumulation and movement in relation to community structure (Chapters 4 and 5) and the relationships between sediment accumulation and community structure (Chapter 5).

The relationship between individual macroalgal species and sediment trapping was described in Chapter 2. The mass of dried sediment g^{-1} macroalgal dry mass was found to be greater in the macroalgal species with turf like morphologies such as *Corallina officinalis* and *Osmundea pinnatifida*, whilst the filamentous turf *Rhodothamniella floridula*, which has sediment trapping filaments (Dixon & Irvine, 1995), trapped the greatest quantity of sediment. The current research took a novel approach by attempting to relate differences in the amount of sediment trapped by a given species to specific quantifiable aspects of macroalgal morphology. All measurements of macroalgae had a relationship with the quantity of sediment trapped, suggesting the size of macroalgae is important in determining the quantity of sediment trapped. With the exception of frond density, all correlations were negative (Chapter 2.3.2). The strongest correlation found was between the quantity of sediment trapped and interstitial volume. As discussed in Chapter 4.4, the larger spaces between fronds described by interstitial volume would result in less reduction in water flow. Lower water flow has been found to inhibit sediment transport rates (Eckman, *et al.*, 1989) and so increase sediment deposition. This suggests it is the effects that macroalgal morphology has on water movement and sediment transport that is important in sediment trapping rather than the size of the macroalgae itself.

The grain size composition trapped by *C. officinalis* and *O. pinnatifida* trapped consisted of smaller proportion of small grain sizes than *R. floridula*. As discussed in Chapter 2.4, this may be related to the differences in morphology between the species. However further research would be required to determine which aspects of morphology influence the grain sizes trapped. Sediment grain size has been found to influence the abundance of specific inhabiting meiofauna (Prathep, *et al.*, 2003) therefore the morphology of macroalgae may also be indirectly affecting the inhabiting meiofauna.

In Chapter 2, significant differences occurred in the amount of sediment trapped between the different algal species, however the experimental approach used in Chapter 3 demonstrated no significant difference in the amount of sediment trapped at the community level between shores and seasons. This suggests that sediment accumulation may be scale dependent. Different structural features, including the arrangement of structural elements of macroalgae and the arrangement of organisms on the shore, have been postulated be influential at different scales (Attrill, *et al.*, 2000). The relationship between macroalgal morphology and amount of sediment accumulated suggests that macroalgae have an influence on sediment trapping at a small scale of centimetres. However the lack of difference in the amount of sediment trapped between different macroalgal communities (Chapter 3), and in sediment cover between algal and bare rock quadrats (Chapter 5), suggests that within the area of a 50cm x 50cm quadrat macroalgae did not appear to influence sediment accumulation.

Within the area of a 50cm x 50cm quadrat sediment cover appears to influence the macroalgal community. As found in Chapter 5, the effects of sediment cover differ between algal and bare rock quadrats. In algal quadrats negative relationships were found between sediment cover and both macroalgal species richness and diversity, whilst in bare rock quadrats positive relationships were found between sediment cover and both macroalgal abundance and diversity. This may be the result of natural colonisation of bare rock by macroalgae. However, within the mid shore there was no significant difference in macroalgal richness, diversity or abundance between the three different sites (which differed in sediment cover see Chapter 5.3). Whilst when the entire shore was compared at the three sites, the Central site, which had the highest sediment cover (see Chapter 4.3.2), had a significantly lower macroalgal richness, diversity and total abundance. This suggests that the effect of sediment on macroalgal communities may also scale dependent.

Sedimentation can affect the abundance and distribution of organisms on the shore by two mechanisms, sediment burial and sediment scour (Kendrick, 1991). Different mechanisms may act on different scales (Thrush, *et al.*, 1997). The cliff top photographs (Chapter 4, plates 4.3.2- 4.3.4) showed that the upper part of the Central site was frequently subjected to periods of sediment burial. These events appeared to occur on a small scale in localised areas, but the effects appear severe, as the removal of the sediment revealed large areas of bare rock and restricted algal growth consisting of the ephemeral macroalgal species *Ulva lactuca* and *Ulva intestinalis*. Studies that simulated sediment burial by the addition of sediment in localised areas have found lower macroalgal diversity and richness in areas with greater sediment loads (*e.g.* Eriksson & Johansson, 2005; Piazzi, *et al.*, 2005; Balata, *et al.*, 2007). This supports the idea that the effects of sediment burial are both detrimental and localised. It may also suggest that the severity of the effect may be dependent upon the duration of buried by sediment (Kendrick, 1991). The upper part of the Central site where algal growth was restricted to ephemeral species, was subject to frequent, long periods of burial, whilst the upper part of the North site was subject to very occasional, short burial periods of generally a few days (personal observation) and in this area some perennial species survived.

Whilst the effects of sediment burial appeared to be localised but relatively severe, (as discussed in Chapters 4.4 and 5.4) sediment movement may have a generalised negative effect across the whole of the shore at Holbeck. In addition to sediment movement resulting in scour (Hyslop & Davies, 1998), sediment movement in the water column would reduce light penetration (Toohey, *et al.*, 2004). The macroalgal species observed across all three sites were not restricted to the ephemeral species (*e.g. Ulva lactuca* and *Ulva intestinalis*) that were found in areas with frequent sediment burial suggesting that the effects of sediment movement may be less severe than sediment burial. Kendrick (1991) compared the effects of simulated scour and sediment addition on the percentage cover of filamentous macroalgae, and found that percentage cover was greater in scoured areas than where the sediment was added. This again suggested that the effects of sediment burial may have a greater impact than sediment scour.

In the biological mid shore of all three sites the same dominant species occurred, Fucoids, *Osmundea pinnatifida* and *Phymatolithon lenormandii.* All three species have aspects of their life cycles that suggest some tolerance to sediment movement and accumulation on the shore. Turf species have been postulated to have life cycles that are tolerant to sediment due to their growth (Stewart, 1983) and reproductive strategies (Airoldi, 2003). *Fucus vesiculosus* has two reproductive cycles during the year (Serrao, *et al.*, 1999), whilst species with very short reproductive periods have been suggested to be more sensitive to high sediment loads (Eriksson & Johansson, 2005) and they are relatively tough and so would be resilient to scour (See Chapter 4.4). Mature fucoids can reach a maximum length of 150cm (Hiscock, 1979), and may lie above sediment cover hence burial by sediment and also float in the water column and so sediment may have less of an effect on photosynthesis. P. *lenormandii* is resistant to grazing (Steneck & Watling, 1982), and has a calcareous structure (Irvine & Chamberlain, 1994), both of which provide it with the potential to be resistant to scour. The low growth form and lack of branching (Irvine & Chamberlain, 1994) may provide resilience to sediment burial. This suggests that all three sites had a mid shore community that has the potential to be relatively tolerant to sediment movement and burial.

Although sediment cover was found to be greater at the Central site in the mid shore as well as across the whole site, differences in community composition were only found in the transect based sampling of the whole shore, (see Chapter 4.3.2) not when just sampling mid shore communities (see Chapter 5.3). Sampling of the mid shore included both algal and bare rock habitats, but no significant difference was found in percentage sediment cover between the mid-shore algal and bare rock quadrats, nor were there differences in macroalgal species richness, diversity or total abundance. However, the transect based sampling of the entire shore would have included the sampling of a wider range of microhabitats potentially including areas of reduced sediment accumulation containing species that were less tolerant to sediment inundation. The lower part of the shore at the Central site had larger beds of *Rhodothamniella floridula* than the North and South sites. As *R. floridula* is associated with sediment trapping (Dixon & Irvine, 1995), interactions between sediment and community structure in the low shore of the three sites may be different. Rock pool habitats were not also examined as part of this study due to the natural differences in their communities compared to the surrounding rock (Underwood & Skilleter, 1996; Ducrotoy & Simpson, 2001), but their lower topography has the potential for greater sediment accumulation (Littler, *et al.*, 1983). As the affects of sediment may differ between habitats, generalisations of the effects of sediment may not be appropriate between habitats. Instead further work may be required to investigate the different affects that sediment accumulation may be having in microhabitats.

These studies have focused primarily upon the relationship between sediment accumulation and macroalgal communities. However, as discussed in Chapter 1, fauna will be affected by sediment accumulation and also have the potential to influence sediment accumulation. As with macroalgae the effects of sediment on fauna will be species specific, as differences have been found in re-emergence time between species (Chang & Levings, 1978) and mortality during burial (*e.g.* Marshall & McQuaid, 1989; Zardi, *et al.*, 2006). Both littorinid and patellid abundance were lower on the Central site where sediment accumulation was the greatest. Patellid abundance had a statistically significant negative relationship with sediment cover, however there was no relationship between littorinids and sediment cover, and the negative relationship between barnacles and sediment cover only occurred in bare rock quadrats (discussed in Chapter 5.4). Sediment trapped within macroalgae has been suggested to have a positive effect on the inhabiting fauna by providing protection against desiccation (Gibbons, 1988). However, larger fauna may be directly affected by sediment through burial (*e.g.* Chang & Levings, 1978; Chandrasekara & Frid, 1998) and the clogging of feeding apparatus (Moore, 1977). As discussed in Chapter 5.4, fauna may also be indirectly affected the effects of sediment on macroalgae, therefore the effects of sediment cover on macroalgae described previously may also affect the faunal community.

Increased sedimentation levels are generally related to anthropogenic activity (Airoldi, 2003; Gorgula & Connell, 2004). Areas with higher sediment loads were found to have a different species composition when compared to areas with lower anthropogenic activities, and lower sediment levels (Gorgula & Connell, 2004). However, in addition to increased sediment levels, areas would also be subject to other factors that may influence the intertidal community including boating activity (Eriksson, *et al.*, 2004), and collection and trampling on the shore (*e.g.* Keough & Quinn, 1998; Brown & Taylor, 1999) and increased nutrient levels (Eriksson, Johansson & Snoeijs, 2002; Gorgula & Connell, 2004). Each of these factors has been found to influence community structure, but were also related to increased anthropogenic activity and therefore may occur in the same area. Both sediment load and increased nutrient levels (using the herbicide duron) have been found to negatively affect crustose coralline algae independently. However the combination of the two resulted in irreversible damage (Harrington, *et al.*, 2005). In contrast, in South Australia both increased sediment and increased nutrient loads positively affected the percentage cover of turf forming algae but increased nutrient levels resulted in the greatest increase in turf forming algae (Gorgula & Connell, 2004). This highlights the need to examine the effects of sediment on community structure within the context of other anthropogenic activities within the area. The rapid expansion of Scarborough during the latter end of the 19th Century resulted in much of the area being protected by sea walls around the bottom of the cliffs (Department of the Environment Transport and the Regions, 2006). More recent coastal planning has focused on understanding coastal processes as a whole with current coastal defences in Scarborough focusing on 'holding the line' (Scarborough Borough Council, 2006). Within this, sediment in South bay, directly to the north of Holbeck, is mechanically moved once a year in early spring to the West Pier from the Spa approach road to keep the upper levels of the shore relatively high and provide a natural toe protection to the sea wall (N. Corrie, personal communication). The manual movement of sediment by heavy machinery can compact the surrounding sediment, altering sediment runoff patterns and so increase sediment removal patterns (French, 2001). Manual sediment movement also alters the beach profile after which sediment movement occurs to adjust the beach to a 'stable' profile (French, 2001) and this may result in the resuspension of sediment into the water column which could influence community the intertidal community at Holbeck.

The community structure at Holbeck was not compared with other shores on the North Yorkshire Coast as part of this study. In a previous study when macroalgal species richness at Holbeck was compared with five other sites, Holbeck was found to have similar macroalgal species richness to the rocky shores at Boggle Hole, Ravenscar and Scalby (Tobin, 2000). Species richness as part of this study was found to be slightly higher than the study by Tobin (2000) during 1996/ 1997, but small differences were found in species richness between the 1996 and 1997 samples so natural variation may also account for the small differences between the two studies. Comparison of the species lists for all sampling occasions between the two studies found a similar number of species occurred although there were some differences in the actual species found. As species richness at Holbeck was found to be similar to those found in 1996/ 1997, which were similar to those found on other shores, this suggests that the sediment loads are not driving changes in species richness. Changes in species richness only occur when there is a major impact on the shore (Wells, *et al.*, 2007), suggesting that at the current levels of sedimentation are not causing a major impact at any point during the year. Instead the macroalgal community appears to be relatively tolerant to the current levels of sediment both on the shore and in the water column. However, the presence of sediment across the shore may construct an inhabiting community that is relatively stable in the current sediment conditions. Patterns of succession and recruitment appear to be occurring at Holbeck, although longer term monitoring and comparison with other shores would be required to establish if the patterns were consistent with those found on other shores. It is also unclear how the community would respond if sediment levels increased significantly.

However whilst there was no difference in macroalgal diversity, richness and abundance in the mid shore between sites with different sediment levels, nor were there differences in the dominant species, the proportions of the dominant species differed. As discussed in both chapters 4 and 5, the proportion of turf species was lower, whilst the proportion of canopy species was greater at the with greater sediment accumulation. Therefore, whilst species richness may be of Holbeck may be similar to other shore on the North Yorkshire coast the community structure may differ.

The results of these studies suggest that scale is important in determining both the affect of macroalgae on sediment accumulation and *vice versa*. Whilst the quantity of sediment trapping by individual macroalgal species may be of importance to fauna inhabiting the macroalgae (Gibbons, 1988; Prathep, *et al.*, 2003), it appeared to be less relevant to the quantity of sediment trapped at a larger scale, and therefore would have limited relevance when considering sediment accumulation on a shore, and or down a stretch of coast within a biogeographic area. Levin (1992) suggested that whilst measurement can be made on a variety of different scales, not all serve a purpose equally well. This appears to be the case when considering both the affects the interactions between sediment accumulation and macroalgal communities, and suggests care must be taken to ensure measurement of the impacts of sediment are made at a relevant and appropriate scale.

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