Understanding Community Diversity on Coastal Defences; the Role of Key Drivers and Ecological Enhancements

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Dedication

This thesis is dedicated to my grandfathers, Peter Harris, and Frederick Hobbs.

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Abstract

Coastal defences have become prevalent in the marine environment in response to rising sea levels and increasingly frequent coastal storms. However, due to insufficient habitat heterogeneity and physical complexity such structures support lower biodiversity than natural rocky shores. As a result, a range of ecological enhancements have been developed to address the diversity deficit. This thesis monitored colonization of an ecologically enhanced rock armour defence at Runswick Bay, North Yorkshire. Artificial rock pools and sandstone boulder habitats were incorporated into the defence design to increase habitat heterogeneity and groove microhabitats were engineered to increase small-scale complexity of granite boulders. Fourteen months after construction, diversity of sessile and mobile assemblages was significantly higher in artificial pool and sandstone boulder habitats than in unmodified granite boulder habitats. The community which developed on engineered grooves was not different to that of substrates without grooves. This thesis also examined whether fine-scale complexity (rugosity) and substrate orientation act as drivers of diversity on coastal defences. At both mid and upper shore height, the most rugose substrate had the highest diversity of sessile and mobile species. Over a regional scale, the age of defence was more important in determining community structure than rugosity. In addition, diversity and structure of communities differed significantly between North, North-east and East orientations at mid and upper shore height. This thesis demonstrates that increasing the habitat heterogeneity and incorporating natural substrata into rock armour defences can improve biodiversity. This thesis also demonstrates the importance of fine-scale complexity across tidal heights, and that environmental factors determined by orientation affect community structure. These results can be used to inform how ecological enhancements are applied in future developments.

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Chapter 1 General Introduction

1.1 Changing Climate and Raging Seas

Anthropogenic forcing of the global climate through greenhouse gas emissions, coupled with changes in land use and surface albedo, is driving unprecedented change to climate systems worldwide (IPCC, 2013). Atmospheric Carbon Dioxide (CO_2) concentrations increased from 280 ppm at the beginning of the Industrial Revolution to 418.94 ppm in the present day (Showstack, 2013; Elias, 2018; Kalaitzi *et al.,* 2018; Tans and Keeling, 2021). Indeed, concentrations of atmospheric greenhouse gases including Nitrous Oxide (N_2O), Carbon Dioxide (CO_2) and Methane (CH_4) have increased 20%, 40% and 150% above pre-industrial levels, respectively (Hartmann *et al.,* 2018). Although Earth's responses to anthropogenic forcing are complex and further understanding is required, it is agreed that such increases in atmospheric greenhouse gasses have induced atmospheric warming and elevated Earth's global surface temperature (IPCC, 2013; Poppick *et al.,* 2017). The impacts of global warming, including the desertification of drylands (Burrell, Evans, and De Kauwe, 2020); glacial retreat and melting of polar ice (Fell, Carrivick, and Brown, 2017; Lee *et al.,* 2017; Overland *et al.,* 2019) and sea level rise (Slangen *et al.,* 2016), have been documented across every continent (Martin and Watson, 2016).

Global mean sea level rose by 0.19 m between 1901 and 2010 (IPCC, 2013), and is predicted to rise a further 0.24 – 0.30 m by 2065 as a result of increased precipitation, thermal expansion of the oceans and continued ice melt (Wright, Syvitski and Nichols, 2019; Frederikse *et al.,* 2020). Predictions indicate that by the end of the 21st century, global surface temperature will increase by 1.5 – 2 °C and global mean sea level will rise by a further 0.40 – 0.63 m (IPCC, 2013). Approximately 70% of the world's coastlines will experience sea level change however sea level rise will not be uniform across the globe (IPCC, 2013). In the UK, mean sea level has risen approximately 0.0014 m y^{-1} since 1901 (Woodworth *et al.,* 2009). Projections by the Marine Climate Change Impacts Partnership (MCCIP) indicate a continued rise in mean sea level, but show north-south spatial variation, with areas of southern England likely to experience sea levels rise potentially 0.4 m higher than parts of Scotland, by 2100 (Horsburgh, Rennie and Palmer, 2020). For example, mean sea levels in London and Cardiff in 2100 are likely to be 0.45 – 0.78 m and 0.43 – 0.76 m, respectively, above the 1981-2000 average whereas mean sea level estimates for Edinburgh and Belfast in 2100 will likely be 0.23 – 0.54 m and 0.26 – 0.58 m, respectively, above the 1981-2000 average (Horsburgh, Rennie and Palmer, 2020).

As a result of changing global weather systems and rising sea levels, numerous climate projections suggest that storms in the North Sea and north-east Atlantic may intensify during the 21st century (Lowe *et al.,* 2009; Quante and Colijn, 2016; Wolf, Woolf and Bricheno, 2020). Although the unprecedented series of winter storms in 2013-2014 were an extreme anomaly (Wolf, Woolf and Bricheno, 2020), studies have indicated that rising sea levels will likely increase wave height and shorten return period of extreme storm surge events around the UK coastline (Lowe *et al.*, 2001; Vousdoukas *et al.*, 2016). However, due to considerable inter-annual variability in wave climate data there is uncertainty in these projections (Wolf, Woolf and Bricheno, 2020). It is certain however that sea level rise will increase rates of erosion and deposition of coastal sediments in the UK. At present, approximately 17% of the UK's coastline is currently undergoing erosion with 28% of coastlines in England and Wales suffering erosion rates greater than 10 cm each year (Masselink *et al.,* 2020). Indeed, along the eastern coast of England, approximately 27% and 30.3% of the total length of the North-east and East England coastline is undergoing erosion, whereas over 56% of the Yorkshire and Humberside coastline is eroding (Masselink *et al.,* 2020). Rising sea levels and accompanied flooding of low-lying coastal regions pose substantial long-term economic considerations (Neumann *et al.*, 2015b), in addition to concerns for the health and livelihoods of coastal communities (Lane *et al.*, 2013).

1.2 Coastal Urbanisation and Climate Change

Globally, coastal regions provide essential ecosystem services and offer economic opportunities (Beaumont *et al.*, 2007), in addition to being recreationally and culturally valuable (Neumann *et al.*, 2015a). As a result, global population density is markedly higher along inhabited coastlines than more inland areas, and currently approximately half of the world population resides within 100 km of the coast (UNEP, 2002; Perkins *et al.,* 2015), leading to economic growth in coastal cities and driving expansion of infrastructure (Rumson and Hallett, 2018). Such areas are constantly undergoing development, improvement and expansion of industry and related infrastructure (Neumann *et al.*, 2015a), resulting in the continuous urbanisation of low-lying coastline (Rumson and Hallett, 2018). Increasing urbanisation of coastal areas as a result of population expansion has put increasing pressure on coastal ecosystems in recent years (Burt *et al.,* 2019). Development often results in the loss or degradation of coastal ecosystems including wetlands and salt marshes (Kermode *et al.,* 2016; Boorman and Hazelden, 2017) in addition to heavily impacting marine systems (Bishop *et al.,* 2017; Heery *et al.,* 2017). The term "*Ocean Sprawl*" has been given to the proliferation of man-made infrastructure in the marine environment (Firth *et al.*, 2016b); and includes structures built to facilitate aquaculture (McKindsey *et al.,* 2011; Dafforn *et al.*, 2015), ports and harbours necessary to support the shipping industry (Glasby *et al.*, 2007; Ruiz *et al.*, 2009) and defences intended to protect coastal communities from flooding and erosion of low-lying areas (Bulleri and Chapman, 2010; Cooper *et al.*, 2016).

In the United Kingdom, coastal and marine industries are a valuable component of the country's economy (Turner *et al.*, 1998); with tourism, energy, aggregate and fishing sectors generating a considerable annual revenue (Highley *et al.*, 2007; Lowe *et al.*, 2009). For example, the marine aggregate industry alone generated an estimate £250 million from extractions which supplied construction projects, beach nourishment contracts and exports abroad (Highley *et al.,* 2007), providing a substantial contribution to the East of England and Yorkshire and Humber regions where the majority of extraction licences were held. However, coastal flooding causes approximately £ 540 million of damage annually at present (Sayers *et al.,* 2015; Haigh *et al.,* 2020), and projections have estimated that coastal flooding could potentially cause £ 1.2 – 1.7 billion in damage by 2080 (Haigh *et al.,* 2020). Along the eastern coast of England, more than five million residential properties and a number of key energy infrastructure sites, including Bacton Energy terminal in Norfolk and Sizewell Nuclear Power Station in Suffolk, are at risk (Brown *et al.*, 2014; Thorne, 2014). Therefore, the need to ensure sufficient protection of coastally located industries and communities has generated much interest from local and national governments. Considerable attention has been afforded to the development of effective coastal protection strategies, of which coastal defences are a prominent example (Cooper *et al.*, 2016). Therefore use of the term 'coastal protection' typically refers to the protection of property and other assets through the installation of hard artificial defence structures, which vary considerably depending on the area and scale of their application (Cooper and McKenna, 2008; Cooper *et al.*, 2016). Often schemes which incorporate defence structures are undertaken on a case-by-case basis, with defences in different administrative regions often installed independently of each other and with only a limited consideration of their cumulative impact over larger geographic scales (Cooper *et al.*, 2016).

The result is the proliferation of hard artificial defence structures along the coast (Airoldi *et al.*, 2005; Firth and Hawkins, 2011; Firth *et al.*, 2016b). In the UK, the type of defence constructed, and the scale of its application is often determined using a cost-benefit framework, which weighs the expenditure of public funds against the value of assets in need of protection (Penning-Rosewell *et al.,* 2005; Turner *et al.,* 2007). For example, in a coastal town where homes and businesses are at risk of flooding, traditional sea defences, such as sea walls and rock groynes, designed to "*Hold-the-line*" may be implemented. This approach seeks to fix and maintain the position of the existing coastline to prevent assets from being lost (Turner *et al.,* 2007). In comparison, where sea level rise is encroaching on unpopulated land, such as coastal saltmarshes, the cost-benefit framework is unlikely to deem a multimillion-pound sea wall as a good investment. In this situation there may be "*No Active Intervention*" (Williams *et al.,* 2018). While the "*Hold-the-line*" approach has typically been historically favoured by coastal planners it has become apparent that hard, fixed shorelines do not adapt well to rising sea levels, and often valuable intertidal habitats are lost in a "*Coastal Squeeze*" as they are unable to migrate landwards as they would naturally (English Nature, 1992; Turner *et al.,* 2007). As a result of this, "*Managed Realignment*" approaches have been developed in which coastal defence structures are designed to be deliberately breached (Turner *et al.,* 2007; Luisetti *et al.,* 2011). In this way, intertidal habitats may extend beyond the defence, allowing valuable habitats such as saltmarshes and mudbanks to be conserved (Luisetti *et al.,* 2011; Williams *et al.,* 2018). The "*Managed Realignment*" approach has worked effectively at sites in the Humber and Blackwater Estuaries which adjoin the North Sea, but the level of success was found to vary with location (Luisetti *et al.,* 2011).

The importance of effective sea defences was illustrated during the winter of 2013 to 2014 when a series of extreme storm events occurred in Western Europe. During this period, 22 storm-induced wave events were identified between December 2013 and February 2014, with wave activity characterised by an average peak wave height of 8.1 m and peak wave periods of up to 22 seconds (Masselink *et al.,* 2015). Storms lasted for an average of 29 hours and were deemed the most energetic for nearly 65 years (Burvingt *et al.,* 2017). Their impact on the North Sea coastline and coastal communities was severe. On the 5th and 6th of December, thousands of people were evacuated from coastal communities in the East Anglian region and severe flooding was reported in Newcastle, Sunderland, Scarborough, Boston, Lowestoft and West Mersea to name only a few (Sibley, Cox and Titley, 2015). In Whitby alone, 200 properties were damaged including local energy infrastructure causing power outages (Sibley, Cox and Titley, 2015). There are no comprehensive studies of how different coastal management approaches performed during this extreme storm, however, as the North Sea-facing coast has a population density of approximately 250 people per km^2 (Gaslikova *et al.,* 2011), effective coastal defence mechanisms became a priority for many local authorities (Sibley, Cox and Titley, 2015).

The English coast is the most heavily defended in the UK with 44 – 45.6% of its coastline (or approximately 1947 km) fronted with hard sea defences or artificial beaches (UKMMAS, 2010; Masselink *et al.,* 2020). Comparatively, only 27.7%, 19.7% and 6.6% of the Welsh, Northern Irish and Scottish coastlines are defended (Masselink *et al.,* 2020). Masselink *et al.,* (2020) determined that approximately 68.9% coastlines in the East of England region (Norfolk, Suffolk and Essex) are fronted with some form of artificial beaches or defence works, as is 43.2% of coastlines in the Yorkshire and Humber region and 37.4% of coastlines in the North-east region. However, despite the proliferation of hard sea defences along the English east coast, very few studies have documented how coastal defences are implemented between different regions, or how the proportion of different types of coastal defence varies between East coast regions. For example, it is widely accepted that the English east coast is heavily defended (Masselink *et al.,* 2020), yet studies which examine coastal defences over a regional scale, or within a defined area of coast such as North Yorkshire, are limited.

1.3 Ecology of Rocky Shores

The North-east Atlantic stretches from the Strait of Gibraltar at its southern most boundary to the arctic and subarctic coasts of Scandinavia in the north (Hawkins *et al.,* 2019). It is a temperate but highly productive region with considerable biodiversity. The coastlines of most European countries including Norway, Sweden, the United Kingdom, Belgium, Denmark and Germany is encompassed by the North-east Atlantic, in addition to the northern coasts of France and Spain and the western coast of Portugal (Hawkins *et al.,* 2019; Reis *et al.,* 2021). The region also encircles Ireland, Iceland and the Portuguese Azores islands at its western edges (Hawkins *et al.,* 2019). Climatic conditions within the region are generally mild by the Gulf Stream and the North Atlantic Current (Rossby, 1996; Oziel *et al.,* 2020; Spooner *et al.,* 2020), with warm maritime air being released across Europe by South-westerly winds (Seager et al., 2002). As a result, North-east Atlantic coastlines experience a temperate oceanic climate with cool summers and mild winters (Claudino-Sales, 2019).

The coastal geography of the region is predominantly composed of hard rocky substrata (Emery and Kuhn, 1982), with areas of exposed sandy shore, enclosed shores of shingle and gravel (Ingólfsson, 2006) and sheltered areas of sand, mud and silt (Hawkins *et al.,* 2019). At northern latitudes, macroalgae, and brown algae in particular, dominate the midshore zone of rocky platforms (Marbà *et al.,* 2017; Jenkins *et al.,* 2008a). In northern Britain and Norway fucoid species often predominate, extending even into very exposed environments, whereas in southern Britain dense fucoid cover is restricted to sheltered shores, with only patches of cover in moderately exposed environments (Ballantine, 1961; Jenkins *et al.,* 2008a). Along more southerly British coastlines however, the diversity of grazing species increases and macroalgal cover decreases owing to greater grazing pressure (Franco *et al.,* 2015). In this area, space-occupying invertebrates, such barnacles (*Semibalanus balanoides* and *Chthamalus stellatus)* and mussels (*Mytilus edulis*), dominate the mid-shore (Crowe, Frost and Hawkins, 2011), and algal cover is contained mostly to low shore environments (Hawkins *et al.,* 2009).

Across rocky shore habitats, distributions of species show patterns of vertical zonation (Chappuis *et al.,* 2014). Algal species show vertical distribution patterns as physical and abiotic factors limit algal growth in upper shore environments, whereas in low shore environments biotic interactions, such as competition and grazing, become more important (Schonbeck and Norton, 1980). However, the effects of biological interactions, such as grazing and competition, have also been found to play a role in limiting algal distributions in upper shore environments due in part to the distribution of invertebrate species. The distribution of sessile invertebrates, such as barnacles, is often determined by the settlement behaviour of larvae (Crisp, 1955; Knights et al., 2006), whereas the distribution mobile invertebrates depend primarily on the responses of adult animals to both biotic and environmental stimuli (Newell, 1979). Distribution patterns also vary horizontally along rocky shores. This results from both environmental gradients and biological interactions as sheltered bays extend into more exposed shores or headlands (Hawkins *et al.,* 2019). For example, as limpets are the dominant grazer across the rocky intertidal mid-shore, they can prevent establishment of fucoids on both sheltered and exposed shores (Jenkins and Hartnoll, 2001). However, limpets are known to be sensitive to wave action and on very exposed shores where limpets are less common, wave action is a more impactful inhibitor of fucoid growth (Jonsson et al., 2006).

Temperate rocky intertidal habitats are dynamic and community composition varies not only spatially as discussed above, but also temporally as the community changes and incumbent species establish, are removed or perish, and re-establish. Rocky shores may experience primary succession, where colonisation of newly created substrata occurs for the first time (Frederiksen, Kraglund, and Ekelund, 2001). However, it is more likely that intertidal habitats will undergo secondary succession, where patches of biota are removed or partially removed on occupied substrata as a result of environmental or biological disturbances (Sousa and Connell, 1992; Laure *et al.,* 2009). Indeed, secondary succession of species within intertidal habitats is nearly continuously on going with different stages of succession under way at any one time due to variability in the location and level of disturbance (Benedetti-Cecchi, 2000a). Environmental or physical disturbances include the removal of biota by wave action or scouring by sand or cobbles (Dethier, 1984; Benedetti-Cecchi and Cinelli, 1996), Heat stress (Underwood and Jernakoff 1984) and smothering by sedimentation (Airoldi, 1998). Biological disturbances include over grazing, predation and removal of invertebrates through sweeping of macroalgal fronds (Hawkins and Hartnoll, 1985; Jenkins, Hawkins, and Norton, 1999).

Microbiota are the first colonise newly cleared substrates, being deposited within seconds of first submersion in sea water (Wahl, 1989). The community which develops forthwith is composed initially of bacteria and cyanobacteria, and subsequently by diatoms and more complex microorganisms (Frederiksen, Kraglund, and Ekelund, 2001; Laure *et al.,* 2009). This community creates a biofilm which is diverse and unstructured in the first week however after this initial colonisation period, a few species may begin to establish and predominate (Niell and Varela, 1984). The development and composition of biofilms at this stage can greatly influence the colonisation of successive macrobiota by interacting positively or negatively with settling larvae and algal propagules (Laure *et al.,* 2009). Biofilms can promote or inhibit growth of algal propagules on rocky shores. For example, species of the genus *Ulva* are known to be opportunistic and fast growing, however the establishment and growth of *Ulva sp.* on rocky shores has been shown to be accelerated by the presence of biofilms (Park, Kang and Choi, 2011). Similarly, biofilms are also capable of emitting surface-bound biochemical cues which act as a stimulant for invertebrate larvae to settle (Hadfield, 2011), such interactions have been observed in common space-occupying invertebrates including species from the genera *Balanus* and *Mytilus* (Satuito *et al.,* 1997).

Succession in rocky shore habitats is predominantly driven by the supply of invertebrate larvae and algal propagules, in addition to vegetative growth and the movement of mobile invertebrates through the habitat (Benedetti-Cecchi, and Cinelli, 1996; Laure *et al.,* 2009). Development of more complex macrobiotic communities on rocky shores may take between 1 and 10 months (Laure *et al.,* 2009; Park, Kang and Choi, 2011), depending on seasonal availability of larvae and algal propagules. Patterns of colonisation are also strongly influenced by a range of physical stresses, such as desiccation, heat stress and temperature fluctuations, and biological interactions, including grazing by invertebrates or shading or sweeping by existing algae (Benedetti-Cecchi, 2000b). Typically, opportunistic filamentous and foliose algae, such as species of the genus *Ulva*, are the first macroalgae to begin colonising, often monopolising the available space (Laure *et al.,* 2009). Following this, turf forming algae such as *Corallina spp*. and *Gelidium spp*., in addition to sessile invertebrates begin to colonise. Finally, larger macrophytes begin to establish, this including slower growing perennials and canopy forming species (Laure *et al.,* 2009). Late-stage colonists include fucoids and macroinvertebrates such as limpets and littorinids which have migrated from nearby habitats.

As succession commences, the mechanisms by which species compete to become dominant vary. For example, if environmental conditions allow, fucoids may appear earlier during colonisation and establish quickly (Benedetti-Cecchi, 2000a), creating a canopy which shades early colonising algal species inhibiting their growth (Jenkins, Hawkins and Norton, 1999). Grazing can also impact the rate of succession within a habitat by slowing or accelerating the establishment of algal species. For example, high densities of grazing limpets and snails may remove most newly settled algal spores thus inhibiting colonisation of a species by preventing establishment (Dethier, 1984). Similarly, by feeding preferentially on ephemeral algae, gastropods clear space for species less susceptible to grazing such as calcareous species (Benedetti-Cecchi, 2000b). Complex interactions between species within the assemblage can directly and indirectly impact the sequence of succession, making predicting the composition or structure of the community after colonisation difficult (Benedetti-Cecchi, 2000b).

Rocky shore habitats are dynamic and the composition of communities naturally changes as succession occurs. A number of studies have shown that with time, the richness and diversity of communities typically increases (Benedetti-Cecchi, 2000a; Foster *et al.,* 2003), but that as different species move into the habitat clear shifts in the composition of the community can occur (Hall *et al.,* 2019). Capturing the spatial and temporal variation in developing communities provides an insight into how the successional process is being played out. For example, examining how the Shannon-Wiener diversity (H') of a habitat differs over time or between locations can provide a valuable indication of where conditions for life may be most favourable. However, examining how the species richness (S) and total abundance (N) of sessile and mobile species changes over time and between habitats provides a more comprehensive picture of how the community changes. Examining species richness (S) total abundance (N) of sessile and mobile assemblages gives a better understanding of how species interact with their habitat and can provide an indication of how suitable or not a habitat is. Examining these metrics for mobile species, such as limpets and snails, and for sessile animals and algae separately can also highlight important interactions between organisms and their environment. For example, mobile species such as the limpet *Patella vulgata* have well documented migratory tendencies and are capable of moving away from areas where environmental and biological conditions are not optimal (Branch, 1975; Lewis and Bowman, 1975). In the same vein, it is important to assess how sessile flora and fauna persist in the areas into which they have settled, and how the community changed as the habitat underwent succession. For example, the occurrence of algal species on artificial coastal defences adjacent to natural rocky shores might indicate transfer of species between the habitats and patterns of connectivity which may become apparent over time (Liversage and Chapman, 2018). Similarly, the presence of key habitat forming species, such as *Semibalanus balanoides* and fucoids would indicate how well or how quickly succession of species through the habitat was occurring (Benedetti-Cecchi, 2000a).

Intertidal rocky shore habitats and biological communities also provide a number of valuable ecosystem services, including services which directly benefit human populations such as provision of food and raw materials, and disturbance prevention services (Beaumont *et al.,* 2007; Smale *et al.,* 2013). For example, in the North-east Atlantic, kelp forests and fucoid canopies provide essential habitat for molluscs and crustaceans which are preyed upon by the European Lobster, a fishery which is worth approximately £30 million annually to the UK economy (Elliott *et al.,* 2012). In addition, macroalgae has been used as livestock feed potentially as early as the first domesticated herds in the fifth millennia BC (Balasse *et al.,* 2005). Brown algae also high in alginates and other nutrients which have been used as soil conditioner and fertilizer in more modern times (Smale *et al.,* 2013). Rocky shores can also act to dampen the impact of coastal storms. Biogenic habitat forming species, such as phaeophytes, barnacles and mussels, modify the movement of water through the habitat, somewhat reducing the velocity of breaking waves (Løvås and Tørum, 2001; Smale *et al.,* 2013). In addition, rocky shores often hold a special significance to the communities which live nearby (Beaumont *et al.,* 2008). There are a number of cultural and recreational services provided by rocky shore habitats (Beaumont *et al.,* 2007; Smale *et al.,* 2013). For example, recreational diving, angling, bird watching, rock pooling and beach combing are all much enjoyed past times which provide cognitive stimulation and opportunities for mental wellness (Beaumont *et al.,* 2007). In the Scilly Isles alone, 85% of the revenue from tourism is generated through coastal and wildlife-oriented activities such as bird and seal watching tours, which would not be possible without healthy rocky shore habitats (Beaumont *et al.,* 2007).

1.4 Coastal Defence Structures as Habitats

Artificial coastal defences have become a more common feature on rocky shores and are built to be robust and long-lasting in order to withstand intense storms (Dafforn *et al.*, 2015) and act in various ways to reduce wave over-topping and prevent flooding and erosion (Salman *et al.*, 2004; Firth *et al.*, 2016b). Defence structures largely occur within the intertidal and shallow sub-tidal zones (Airoldi *et al.*, 2005) and may be constructed parallel to the shore; in the case of seawalls, breakwaters and rock armouring, or perpendicular to the shore; in the case of groynes and jetties (Bulleri and Chapman, 2010; Firth *et al.*, 2016b). Shore-parallel structures act to dissipate high-energy waves and reduce the impact of on-coming waves on the shoreline (Thomalla and Vincent, 2003; Bulleri and Chapman, 2010), whereas shore-perpendicular structures, are designed to modify sediment transport and current flow in order to limit or slow coastal erosion (Bulleri and Chapman, 2010; Firth *et al.*, 2014).

Coastal defences provide habitat for marine organisms and can facilitate ecological connectivity (Firth *et al.*, 2016b; Bishop *et al.,* 2017) although it has become apparent that such structures can also negatively impact existing ecological communities. When built, the construction and location of hard artificial structures can damage the shore onto which they are placed and disrupt associated ecosystem services (Cooper *et al.*, 2016). Installation of defences also often results in the permanent loss of substantial areas of mature intertidal habitat (Moschella *et al.,* 2005) and threatens the health and persistence of numerous habitat types, including macroalgal beds and sedimentary habitats through alteration to sediment transport regimes or water movement (Airoldi and Beck, 2007). Additionally, the introduction of hard artificial substrata where there previously was none has also been documented to facilitate range expansion of non-native invasive species (Bulleri and Chapman, 2010; Mineur *et al.*, 2012).

Coastal defences quickly become host to biological communities; however, the communities that develop often have a markedly poorer diversity comparative to native substrates (Bulleri *et al.*, 2006; Airoldi and Beck, 2007). This diversity deficit appears characteristic of coastal defence structures, regardless of style, size, geographic location or placement in sedimentary or rocky shore environments. There are number of explanations including that as defences are frequently installed in exposed or high-energy environments the development of naturally occurring biotopes may be inhibited due to exposure to intense wave action and sand scouring (Pister, 2009; Firth *et al.*, 2014).

Similarly, defences are often orientated to align with the assets being protected and may have a steeper vertical gradient than the gently-sloping sedimentary and intertidal shorelines where they are installed (Moschella *et al.,* 2005). This may cause prolonged periods of sun exposure and shading which can also inhibit development algal and faunal communities (Bulleri and Chapman, 2004; Mineur *et al.*, 2012; Firth *et al.*, 2016b). As Bulleri and Chapman (2004) noted, native rocky shores typically exhibit a range of slopes, which has been shown to be key in determining distribution patterns of intertidal fauna (Benedetti-Cecchi *et al.* 2000). Orientation of the substratum has also been identified as a key driver of structural differences between assemblages from native and artificial substrates (Whorff *et al.,* 1995; Benedetti-Cecchi *et al.* 2000; Glasby, 2000), with very different assemblages shown develop on the vertical and horizontal surfaces of artificial structures (Harris and Irons, 1982; Connell, 1999).

Closer examination showed defences present a very different physical environment to naturally-occurring rocky shores, a characteristic which is considered the primary cause of observed differences in community structure and functioning between coastal defences and natural substrates (Firth *et al.*, 2016a). In the past, artificial intertidal structures were looked on as a substitute rocky shore habitat (Thompson *et al.*, 2002; Bulleri and Chapman, 2004) but a growing body of work has indicated that artificial coastal defences lack sufficient variety and availability of habitats to successfully mimic native substrates and natural rocky shore environments (Aguilera, 2018). Defences are typically manufactured using hard wearing materials resistant to weathering (Coombes, 2014; Davis *et al.*, 2017), producing a homogenous environment which lacks many of the physical features present on rocky shores (Bulleri and Chapman, 2004; Mineur *et al.*, 2012; Firth *et al.*, 2016b). Thus, many of the vital microhabitats that exist within and around such physical features on natural rocky shores are absent from artificial defences (Firth *et al.*, 2013b; Hall *et al.*, 2018). Features such as overhangs, channels and pools provide essential refuges from biotic pressures, such as predation and competition (Mineur *et al.*, 2012) and act to retain water between tidal cycles offering protection from environmental stresses (Firth *et al.*, 2013a). In addition to lacking variety and heterogeneity in the range of habitats available, coastal defences are noted for having inadequate surface roughness (Coombes *et al.*, 2015). Concrete and granite are routinely favoured in the construction of coastal defences (Bulleri and Chapman, 2010), however both materials have a notably smoother and less textured surface, and create more uniformity over larger areas than rocky shore platforms (Coombes *et al.*, 2015; Firth *et al.*, 2016b).

1.5 Ecological Engineering and Habitat Enhancement on Coastal Defences

Given the necessity of using coastal defences to protect coastal communities in the future, the concept of sensitively engineering new structures and ecologically enhancing existing structures has gained momentum in recent years (Bulleri and Chapman, 2010; Firth *et al.,* 2016b). The term *ecological enhancement* refers to the action of modifying sites or structures to be more ecologically favourable by increasing or improving the extent and quality of available habitat (ITRC, 2004), and can be incorporated into the design of new structures or applied retrospectively by modifying existing structures (Hall *et al.*, 2018). Recent work in habitat enhancement on coastal defences has sought to improve the habitat structure of otherwise featureless substrata by improving either the heterogeneity of habitats available through the creation and incorporation of broader habitat types such as artificial rock pools and boulder rubble (Chapman & Blockley 2009; Firth *et al.*, 2016a; Liversage and Chapman, 2018), or through establishing greater physical complexity via the creation of pit, hole and overhang microhabitats (Evans *et al.*, 2016; Hall *et al.*, 2018; Waltham and Sheaves, 2018).

Habitat structure is a key determinant of diversity in biological communities, and environments which have a greater range of habitats available typically have a higher diversity of species (Cramer and Willig, 2005; Carvalho, and Barros, 2017). As such, much of the work in this area has centred on either creating a wider range of large-scale habitats or improving physical complexity on a smaller spatial scale. The terms *habitat heterogeneity* and *complexity* have frequently been used synonymously in ecological studies to describe the availability and abundance of different habitat types on a range of spatial scales (Pickett *et al.,* 2010). In an ecological enhancement context, *habitat heterogeneity* is broadly defined as the relative abundance of different structural components within a habitat (McCoy and Bell, 1991). By contrast, *physical complexity* is used to describe relatively small-scale physical characteristics or structural components of a habitat (McCoy and Bell, 1991; Gee and Warwick, 1994). Physical complexity varies over a range of spatial scales, with *fine-scale (mm)* complexity often referring to the texture or roughness of a surface (Coombes *et al.,* 2015; MacArthur *et al.,* 2019) and *small-scale (cm)* complexity referring to small physical features such as grooves or pits (Evans *et al.*, 2016; Hall *et al.*, 2018).

Enhancement techniques vary widely, ranging in extremes from large pre-cast concrete units, such as the BIOBLOCK habitat enhancement unit (Firth *et al.*, 2014), to increasingly fine-resolution modifications for example increasing surface roughness at millimetre scale (Coombes *et al.*, 2015). Mechanisms to ecologically enhance defences have been trialled globally, including in Australia, Europe and the United States (Chapman, 2003a; Bulleri *et al.*, 2006; Sella and Perkol-Finkel, 2015), where mostly small-scale enhancement techniques have been integrated into existing intertidal defences, largely rock armour and concrete seawall style structures (Firth *et al.,* 2016b). Documented trials have included; the addition of drilled pits and holes, horizontal grooves and artificial pools as water retaining mechanisms (Firth *et al.*, 2013a; Evans *et al.*, 2016; Hall *et al.*, 2018), incorporation of natural boulder rubble (Liversage and Chapman, 2018), exaggerating surface roughness and texture (Coombes *et al.,* 2015) and the deployment of precast concrete units (Langhamer and Wilhelmsson, 2009; Firth *et al.*, 2014). These studies have largely shown that ecological enhancement of coastal defences positively impacts biodiversity by facilitating the natural succession (Thomsen *et al.*, 2016), providing opportunities for species to increase their vertical distribution (Chapman and Blockley, 2009) and for colonisation by rarer species (Liversage and Chapman, 2018).

The addition of water retaining features has proved an effective enhancement mechanism at various spatial scales and is widely agreed to be a simple and cost-efficient means of improving diversity (Firth *et al.*, 2016a). On natural rocky shores, pools are known to provide nursery habitat for grazing species, such as limpets, offering protection from temperature fluctuations and desiccation (Bowman and Lewis, 1977). Mobile fauna have particularly benefitted from the addition of water-retaining features. In trials conducted by Evans *et al.,* (2016) and Hall *et al.,* (2018) the use of small holes was shown to provide shelter for several gastropod snail species, which are known to actively seek select such crevices (Pardo and Johnson, 2004; Skov *et al.*, 2011). In both trials, the authors noted that mobile fauna were largely absent from the study area prior to commencement of the trials. The use of drilled holes notably improved both the richness and abundance of algal and invertebrate species observed in modified areas compared to unmodified areas (Hall *et al.*, 2018), in addition to hosting relatively rarer species or species more common to lower shore habitats (Evans *et al.*, 2016). Larger artificial basins and pools have also been found to increase richness and abundance of algal species, with many noting a greater abundance of macroalgal species (Browne and Chapman, 2014; Firth *et al.*, 2014; Firth *et al.*, 2016a) and the occurrence of typically low shore algal species (e.g. *Rhodophyta*) (Firth *et al.*, 2013a). However, the effectiveness of artificial pools depends considerably on their location. In a trial by Firth *et al.,* (2016a), a number of artificial pools were created on the sheltered and exposed sides of a causeway. Over time sheltered pools became inundated with sediment and thus failed to act as rock pools, whereas exposed pools showed less sedimentation and hosted a comparatively higher richness and diversity. However exposed pools which were immersed on every tidal cycle supported a greater functional richness than pools which were less regularly immersed.

It is well understood that the physical characteristics of a substrate affect its suitability for settlement (Salta *et al.*, 2013), with rough and textured surfaces being essential for the development of permanent and stable marine biofilms, which provide nutrition for many grazing species (Decho, 2000; Hutchinson *et al.*, 2006). Fine-scale surface texture also plays a key role in the recruitment and settlement of invertebrate larvae (Walters and Wethey, 1996), such as barnacle cyprids which, once settled, will facilitate the establishment of algal and other sessile species (Chabot and Bourget, 1988; Sueiro *et al.*, 2011). Surface texture can determine how closely barnacle larvae can settle to each other (Crisp, 1961, MacArthur *et al.,* 2019), in addition to influencing how strongly cyprids can attach to the substrate (Petersen, Gorb and Heepe, 2020). The barnacle *Semibalanus balanoides* has been found to display a preference for roughened surfaces (Holmes, Sturgess and Davies, 1997). A trial by MacArthur *et al.,* in 2019 examined a range of textured tiles in order to determine which texture would most improve barnacle cover and invertebrate richness. Tile designs mimicked natural rocky shore topography and varied in complexity from fine-resolution roughened surfaces (mm-scale) to more complex designs which featured small pit and groove microhabitats (all 1-3 cm in size). MacArthur *et al.,* (2019) found tiles with mm-scale grooved surface textures provided the optimum level of complexity for recruitment and settlement of barnacles, likely because the level of complexity was enough that barnacle cyprids could adequately adhere to the surface, but was not so great that cyprids were prevented from settling in close proximity (Crisp, 1961). In an earlier trial by Coombes *et al.,* (2015) precast concrete tiles with different mm-scale surface textures were deployed on horizontal rocky shores in south-west England. This study also found surfaces with a regular fine-scale grooved texture to be the most effective showing significantly greater barnacle cyprid settlement and recruitment after 6 months compared to tiles with smoother textures.

The use of grooves as a cost-effective habitat enhancement mechanism was trialled in 2018 by Hall *et al.*, in Runswick Bay, North Yorkshire and Bournemouth, Dorset. Hall *et al.*, intended to increase habitat heterogeneity by engineering deep, wide and roughly-hewn horizontal grooves to create areas of novel water retention and greater topographic complexity, in order to promote community establishment. Three grooves measuring 60 cm in length and 1 cm in depth were engineered into seven granite boulders. Each array consisted of two thin grooves which measured only 0.3 cm in width, and one thicker groove which measured 2 cm in width. After 12 months, grooves had a significantly higher barnacle count than unmodified controls and hosted 5 species previously absent from the defence. Given the success of engineered grooves in this context as a mechansim to improve biodiversity, the concept was carried forward and adapted into a newly built rock armour at Runswick Bay.

1.6 Habitat Enhancement Case Study: The Runswick Bay Coastal Protection Scheme

A key site in the field of ecological engineering is Runswick Bay, North Yorkshire (OS Reference: NZ 8217 1599). The Runswick Bay Coastal Protection Scheme is a multi-award winning scheme (Constructing Excellence, 2019), developed by Scarborough Borough Council and the Environment Agency in collaboration with stakeholders, to limit erosion of the cliffs surrounding Runswick Bay village and address deterioration of the Victorian seawall at the site (Environment Agency, 2015; JBA Consulting, 2017a). As part of the Runswick Bay Coastal Protection Scheme, a new rock armour was constructed in 2018 at the base of the existing seawall (Scarborough Borough Council, 2019) (See Figure 1.1 below, and Figure 2.1 for reference). The new rock armouring was constructed from approximately 9,500 tonnes of Norwegian granite boulders, each weighing between 5 and 10 tonnes, and measured 250 m in length, 8 m wide at the base and 2.5 m in height with a total footprint of roughly 2600 m^2 when completed (JBA Consulting, 2017a; Latham *et al.*, 2020) (Figure 1.1).

Following the successful trial by Hall *et al.,* (2018), on an older rock armour at the same site, plans were made during the planning and consultation process to incorporate enhancements into the proposed Runswick Bay rock armour, during its construction (Latham *et al.*, 2020). A number of habitat enhancement mechanisms were deployed which aimed to improve habitat heterogeneity and physical complexity of the rock armour by creating novel habitats and microhabitats and improving water retention. Improving the heterogeneity of habitats within the defence included the addition of;

A) Artificial rock pool habitats

Approximately 70 artificial basins were created on the upper surfaces of granite boulders. Each measured approximately 15 cm deep and 30 cm wide (JBA Consulting, 2017b) and were located in the intertidal and splash zones and above throughout the rock armour (Figure 1.2a)

B) Sandstone boulder habitats

Large sandstone boulders native to the site were set aside during construction and were later placed at the base of the new rock armour. These boulders were intended to act as “seed rocks” promoting colonisation of the granite once incorporated (Latham *et al.*, 2020) (Figure 1.2b). Although much of the macroalgal cover was lost as a result of disturbance during construction, sandstone boulders were covered in green filamentous algae and had some fucoid holdfast remnants still attached to them when added to the rock armour.

In addition, enhancements to improve physical complexity of the rock armour included the deployment of;

C) Grooves

Horizontal grooves, measuring approximately 40 – 80 cm in length, 1 cm in depth and 3 mm in width, were cut into granite boulder faces throughout the rock armour (JBA Consulting, 2017b) (Figure 1.2c). These grooves differed slightly from those used by Hall *et al.*, (2018) in that only narrow grooves were deployed, and no grooves were widened. Grooves were not added to sandstone boulders.

The Runswick Bay Coastal Protection Scheme is unique for a number of reasons, firstly because it is a rare example of a coastal defence structure with planned habitat enhancements incorporated throughout, and secondly because it represents the largest application of habitat enhancement mechanisms on a coastal defence structure in the UK at present (Latham *et al.*, 2020).

Figure 1.1 – Section of the rock armour created as part of the Runswick Bay Coastal Protection Scheme (taken at beginning of the study in February 2019).

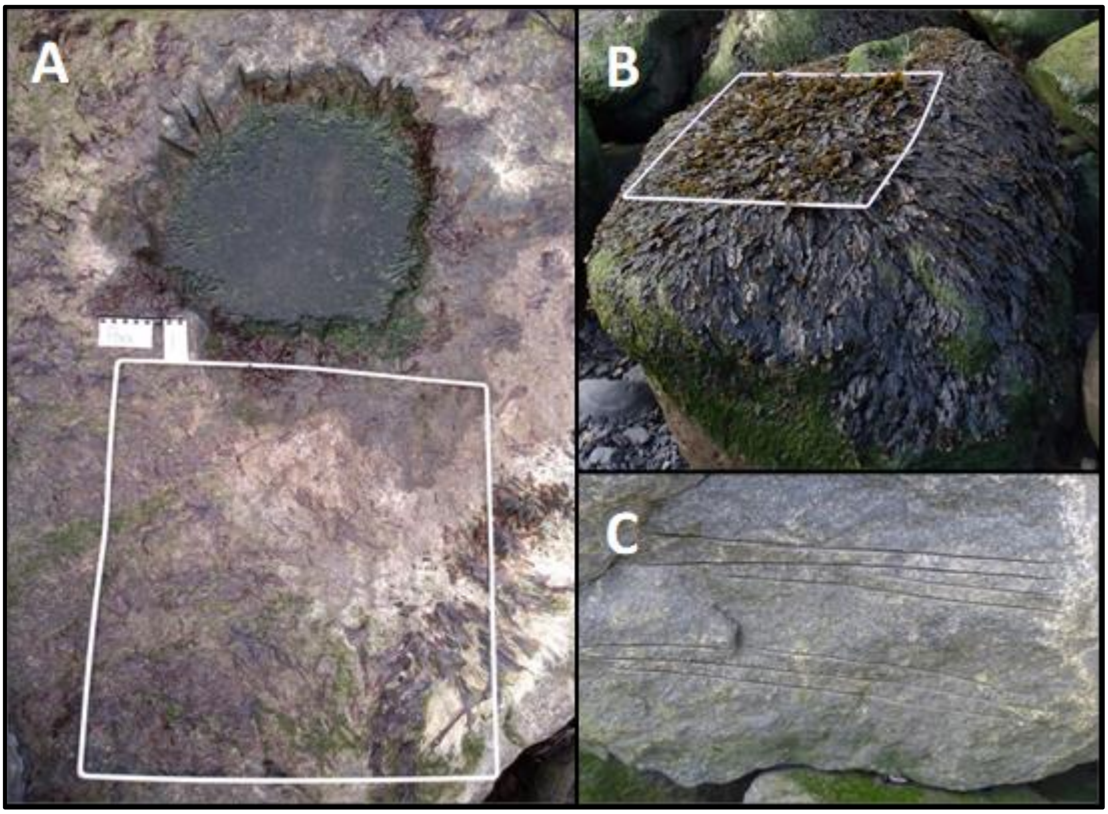


Figure 1.2 – Enhancements photographed at beginning of the current study; a) artificial pool (AP) above with unmodified granite boulder (GB) below, b) sandstone boulder (SB) and c) substrate treated with grooves (GS) with area of untreated substrate (US) between.

1.7 Aims of the Current Study

The current study investigated the colonisation and community development of the enhanced rock armour defence at Runswick Bay and examined how fine-scale complexity and substrate orientation affected community structure on unenhanced coastal defences at four locations in North and East Yorkshire.

Firstly, this study monitored colonisation in areas of increased habitat heterogeneity on the new rock armour at Runswick Bay to determine whether diversity and structure of sessile and mobile communities differed between habitat types (artificial pool, sandstone boulder and granite boulder habitats). Secondly this study monitored colonisation in areas of increased small-scale physical complexity on the new rock armour at Runswick Bay to determine whether diversity and structure of sessile and mobile communities differed between treatment types (substrates treated with grooves, and untreated substrates without grooves), over time. Thirdly, this study investigated whether fine-scale physical complexity of granite substrates affected diversity and community structure on one granite rock armour defence at North Bay, Scarborough where three types of substrates with differing levels of fine-scale complexity were present. Due to an absence of studies examining rock armour specifically within the North and East Yorkshire region, comparisons of fine-scale complexity between five granite rock armour defences at four locations in North and East Yorkshire were also made. And finally, this study investigated whether the orientation to compass-direction of granite substrates affected the diversity and structure of sessile and mobile communities at one site.

Chapter 2 aimed to determine whether there were differences in the diversity and composition of sessile and mobile communities between the three main habitat types (artificial pools, granite boulders and sandstone boulders) on the new rock armour at Runswick Bay; and how this varied over time.

Chapter 3 aimed to monitor colonisation of areas treated with and without added small-scale physical complexity (substrates treated with grooves and untreated substrates without grooves) to determine if diversity and composition of sessile and mobile communities differed between treatment types over time.

Chapter 4 aimed to determine whether diversity and structure of sessile and mobile communities differed between granite and sandstone substrates with different levels of fine-scale physical complexity at one site in Scarborough North Bay, North Yorkshire. Fine-scale complexity of five granite rock armour defences across North and East Yorkshire was also examined to determine whether fine-scale physical complexity impacted diversity and community structure over a regional scale.

Chapter 5 aimed to determine whether diversity and structure of sessile and mobile communities were different between granite substrates with different compass orientations at one site in Scarborough South Bay, North Yorkshire.

Finally, Chapter 6 discussed the key findings of Chapters 2 – 5, examined the wider implications of this research and makes recommendations for future ecological engineering work.

Chapter 2 Colonisation in areas of increased habitat heterogeneity on an ecologically enhanced rock armour defence in Runswick Bay, North Yorkshire.

2.1 Introduction

Planning and designing coastal defences requires a balance to be struck between ensuring maximum asset protection, defence longevitey and economic and aethetic specifications (Troch *et al.,* 2014). In many instances, habitat enhancement work has been limited by cost and site access, resulting in the development of mostly small-scale enhancement techniques which can be retro-fitted to existing defences (see Chapter 1 Section 1.5, see also Firth *et al.*, 2016b for a comprehensive review). However, considering potential enhancement opportunities during the design and planning of new defences can ensure that sufficient funding is provided (Hall *et al.*, 2018) and that conservation of diversity is maximised (Firth *et al.*, 2016b). Indeed, exploring opportunities for enhancement in the earliest stages of planning can make the ecological suitability of the defence a greater priority for both developers and stakeholders (Naylor *et al.*, 2012). Planning ecological enhancments into the design of an artificial structure can also increase the spatial scale over which enhancments are applied. For example, a trial in 2009 by Langhamer and Wilhelmsson incorporated holes into the concrete foundations of wave-energy generators to promote colonisation by fish and crustacean species. Enhancements had to be implemented during the design stage as the concrete foundations had to be cast as single units, either with or without holes. In this way Langhamer and Wilhelmsson were able to deploy an equivalent number of foundations with and without holes. The study showed that concrete units with pre-planned holes supported a greater abundance of commercially important crab and lobster species, and proved that synthesis of ecologically intelligent design with coastal and marine infrastructure can have a wide range of industrial and societal benefits (Kidd 2007; Jay *et al.*, 2012; Firth *et al.*, 2016b).

However, examples of enhancement mechanisms pre-planned into artificial coastal defences are scarce. The Runswick Bay Coastal Protection Scheme is a rare example of a variety of habitat enhancement techniques being planned into the design of a large coastal defence. In this instance, considering enhancement opportunities early in the development process created scope to incorporate more varied habitat types, by creating artificial rock pool and sandstone boulder habitats, and to improve the small-scale (cm) physical complexity of the imported granite boulders by adding engineered grooves, as described in Chapter 1 Section 1.5. Both artificial rock pools and sandstone boulders present valuable habitats engineered into the defence, and the addition of grooves created areas of valuable small-scale physical complexity. It is well documented that rock pools provide important shelter from abiotic stresses between tidal cycles (Newell, 1979; Underwood and Jernakoff, 1984; Martins *et al.,* 2007), act as nursery habitats (Bowman and Lewis, 1977) and provide more plentiful and varied foraging than emergent rock (Mendonça *et al.*, 2019). As a sedimentary rock, sandstone is highly porous and therefore able to retain water within itself which would similarly offer protection to floral and faunal assemblages from desiccation (McGuinness, 1984; Jackson *et al.*, 2013). Extensive macroalgal canopies would also act to shade the substrate, mitigate moisture loss and provide a refuge to animals from thermal stresses (Scrosati and Ellrich, 2018). There was also potential that artificial pool and sandstone boulder habitats could promote colonisation of the granite boulders of the new rock armour (Latham *et al.*, 2020). Indeed, Liversage and Chapman (2018) noted that species common to sandstone boulder habitats had the potential to colonise artificial habitats. Therefore, colonisation of the granite boulders may be positively influenced by the presence of artificial pool habitats and sandstone boulder habitats, which hosted algal communities when incorporated into the rock armour.

The Runswick Bay Coastal Protection Scheme provides an ideal opportunity to determine if planned ecological enhancements installed during construction have a positive effect on biodiversity. The aim of this chapter was to determine whether there was a difference in the species richness (S), total abundance (N), Shannon-Wiener diversity (H’) and community similarity of sessile and mobile communities between the three main habitat types on the new coastal defence (artificial pool (AP), sandstone boulder (SB) and granite boulder (GB) habitats), and how this varied over time (over a 14-month sampling period). The specific hypotheses to be tested were;

1. S, N, H’ and community similarity of sessile and mobile communities was significantly different between habitats and over time.
2. Within each habitat, S, N, and H’ of sessile and mobile communities was significantly different over time.
3. S, N and H’ of sessile and mobile communities in each habitat was significantly higher at the end of the study than at the start.

2.2 Method

2.2.1 Site Description

Located 7 km to the north of Whitby and 3 km south of Staithes in North Yorkshire, Runswick Bay consists of a sand beach approximately 2 km in length with a rocky intertidal platform and the settlement of Runswick Bay village situated at the northern end. A Marine Conservation Zone (MCZ) extending approximately 3 nautical miles out to sea and covering an area of approximately 68 km^2 was designated at the site in 2016 to preserve a number of key biotopes in the area, including high, moderate and low energy intertidal rock and moderate energy infralittoral and circalittoral rock biotopes (Natural England, 2018a). The site is also as a Site of Special Scientific Interest (SSSI) due to unique fossil formations present (Natural England, 2018b). Runswick Bay village is a popular tourist destination and consists of 96 residential properties in addition to 17 non-residential buildings (Environment Agency, 2015). The village is skirted by cliffs comprised of soft Jurassic bedrock, overlain by glacial sediment which are prone to landslides and at particular risk of rapid erosion (Environment Agency, 2015).

The enhancements described in Chapter 1 Section 1.6 were installed throughout the new defence (Figure 2.1). Sample stations where all habitat types, artificial pool (AP), granite boulder (GB) and sandstone boulder (SB), were situated in close proximity and at the same height were selected for monthly sampling (N = 14), (Figure 2.1 and Figure 2.2). Only stations located in the intertidal and where all habitat types could be replicated were selected for sampling. All stations were moderately exposed. Care was taken to ensure sample stations were located at the same tidal height and that boulder orientation was consistent between stations (Kim and DeWreede, 1996). All samples were taken from the upper-shore, which was determined using biological indicator *Fucus spiralis*, a species indicative of upper-shore environments (White, 2008a).

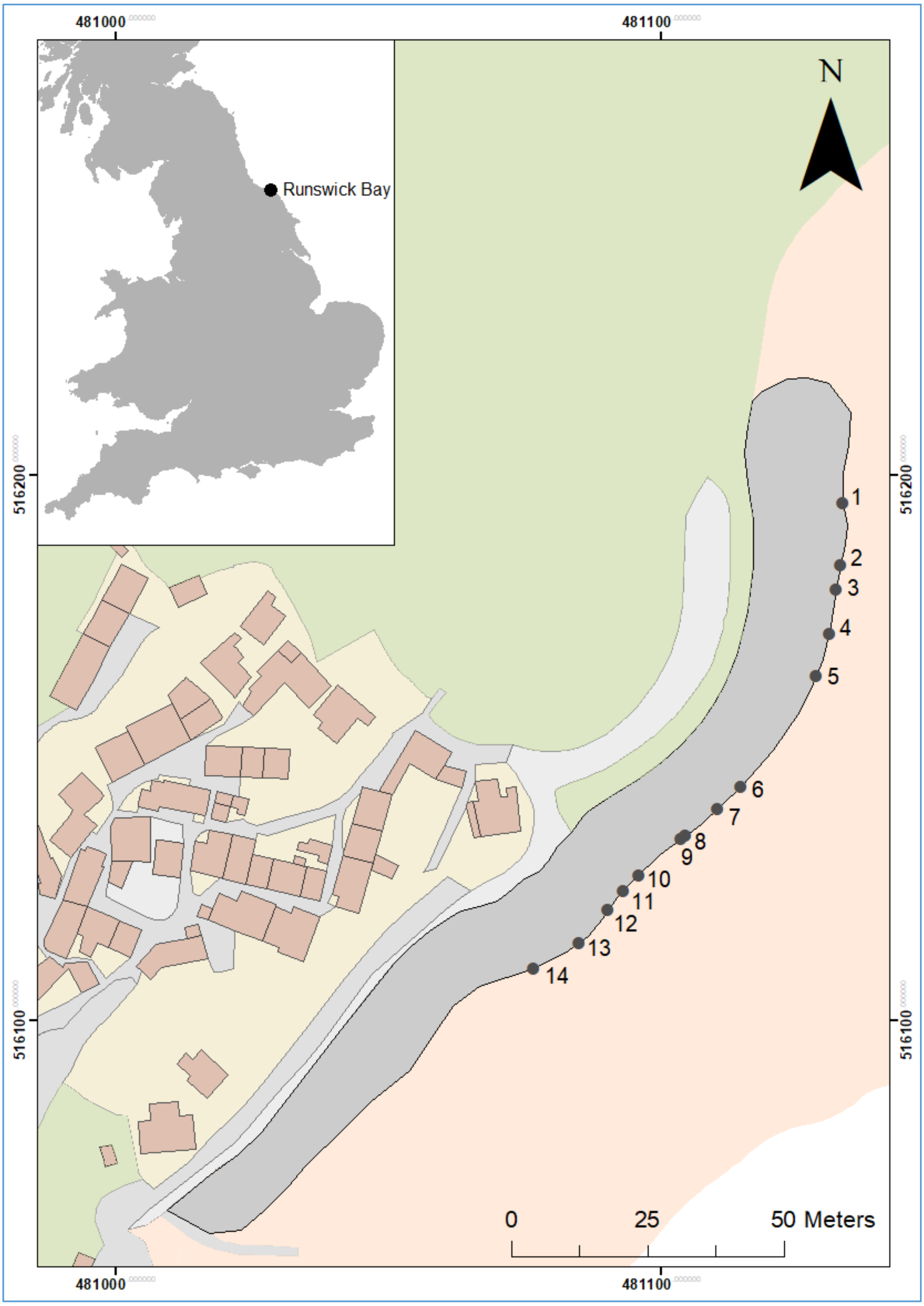


Figure 2.1 – Study site at Runswick Bay, North Yorkshire. Numbered sample stations (N=14) are where all habitat types: artificial pool (AP), granite boulder (GB) and sandstone boulder (SB), were present. The grey area indicates the footprint of the new rock armour defence.

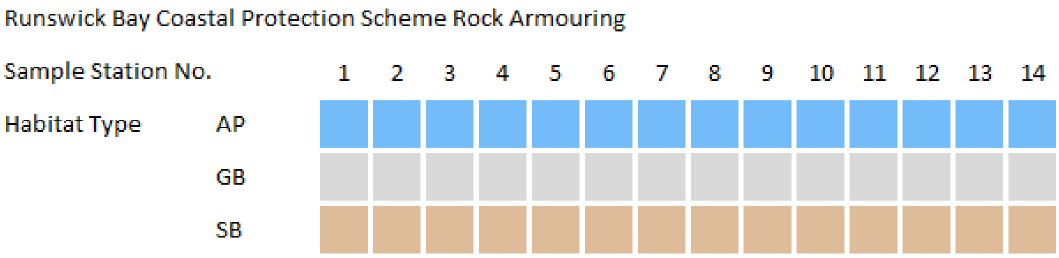


Figure 2.2 – The experimental design where 14 sample stations were selected, and the three habitat types were present at each station: artificial pool (AP), granite boulder (GB) and sandstone boulder (SB).

2.2.2 Method

GPS coordinates of each sample station were logged using a Garmin eTrex10 Handheld GPS, and photographs of each sample station were taken to facilitate visual relocation during subsequent visits (Ducrotoy and Simpson, 2001). In order to monitor changes in floral and faunal communities in each habitat type (AP, GB and SB) over time, a 50 x 50 cm quadrat was used to estimate the percentage cover of sessile species and a count of all mobile species was also made (Chapman, 2006).

Sessile species data included all algal and encrusting animal species, such as the acorn barnacle *Semibalanus balanoides*, which are fixed to the substrate (Bulleri and Chapman, 2004). The term “algal species” was used where encrusting animal species were absent from the sample or where algal species only were examined. Mobile species refers to organisms capable of moving or migrating into and out of the habitat (Chapman, 2006). A subset count of common grazing species; *Patella vulgata, Littorina littorea, Littorina obtusata* and *Littorina saxatilis* was taken from the overall mobile species data, as these species are common on both natural and artificial rocky shores and perform key roles in succession in intertidal habitats (Benedetti-Cecchi, 2000b; Laure *et al.,* 2009).

Identification of species was facilitated using Bunker *et al.,* 2017 for algae and Cremona, Simms and Ward, 2001 for fauna.

2.2.3 Statistical Analyses

Percentage cover data of sessile flora and sessile faunal species, and count per unit area (number of individuals per 50cm^2) of mobile species was split and analysed separately.

The DIVERSE routine in PRIMER was used to calculate S, N and H’. The Shannon-Wiener Diversity Index was used as it is representative of both the richness and the evenness of species in a sample (Spellerberg and Fedor, 2003).

To answer the first hypothesis that S, N, H’ and community similarity of sessile and mobile communities was significantly different between habitats and over time, sessile S, N and H’ data was tested for conformation to a normal distribution and homogeneity of variances using Kolmogorov-Smirnov test and Levene’s test, respectively (Dytham, 2011). Sessile S, N and H’ data was found to be normally distributed (Kolmogorov-Smirnov test, $P > 0.05$) with equal variances (Levene’s test, $P > 0.05$) and was fitted into a General Linear Model (GLM) to determine the importance of habitat, time and the interaction between habitat and time on colonisation of habitat types. Mobile species S, N and H’ data did not conform to normality (Kolmogorov-Smirnov test, $P > 0.05$) or have equal variances (Levene’s test, $P > 0.05$) and so was examined descriptively using the median and range of S, N and H’ data to identify differences between habitat types and over time.

To examine sessile community similarity between habitats and over time, a square root transformation was applied to the raw percentage cover algal species data to down-weight the influence of very abundant species (Clarke *et al.,* 2006a). A Bray-Curtis Similarity Matrix was generated from the transformed data and a visual representation of similarity between sessile communities from each habitat type (habitat types from different sample stations were pooled) for each month, was produced using non-metric multidimensional scaling (nMDS) of the similarity matrix (Legendre and Gallagher, 2001). A Two-Way Crossed ANOSIM with replicates was used to test for significant differences in community similarity between both time (month sampled) and habitat type factors (AP, GB and SB), using the similarity matrix. This was followed by Similarity of Percentages (SIMPER) analysis in order to identify species responsible for producing changes in the structure of sessile communities over time. Relative abundance of key algal species each month was then plotted to show changes to community structure during sampling (Menge and Farrell, 1989).

To determine diversity of animal communities between habitat types and over time, S, N and H’ of grazing fauna was compared between habitats at the start and end of the sampling period. Here grazing species refers to common grazing species; *Patella vulgata, Littorina littorea, Littorina obtusata* and *Littorina saxatilis*. The comparison was made using Kruskal-Wallis Test and Pairwise Wilcoxon Rank Sum PostHOC Test (Dytham, 2011). The mean density of grazing species in each habitat for each month sampled was plotted to visualise changes in the density and structure of mobile communities throughout the duration of the study.

To answer the second hypothesis that within each habitat, S, N, and H’ of sessile and mobile communities was significantly different over time, the following procedure was adopted for both sessile and count per unit area data. One-Way Analysis of Variance (ANOVA) was used to identify significant differences in mean S, N and H’ over time for each habitat separately. Data from July 2018 for AP and GB habitats was included in ANOVA analyses. While a normal distribution and homogenous variances are key assumptions of One-Way ANOVA, data which did not meet these assumptions was still tested and the test residuals were examined (Zuur et al., 2007). A normality plot and histogram plot of test residuals, alongside plots of residuals versus fitted and observed values to assess the goodness of ANOVA model fit were examined (Oehlert, 2010). The adjusted R-Squared value provided an indication of the percentage of variation in the data accounted for within the model and was examined as a measure of how well the model fit (Dytham, 2011). An additional precaution where parametric tests were used with data which did meet the assumptions of the test was to set a higher level of acceptance (Zuur et al., 2007). As such, the significance level alpha was set to 0.01 (Kim, 2017). Where One-Way ANOVA found a significant difference, a Tukey PostHOC test was applied to identify which groups were significantly different (Dytham, 2011). Instances where One-Way ANOVA could not be validated through examination of residuals, the non-parametric equivalent Kruskal-Wallis Test and Pairwise Wilcoxon Rank Sum PostHOC Test were applied instead (Dytham, 2011).

Finally, to test the hypothesis that the S, N and H’ of sessile and mobile communities in each habitat was significantly higher at the end of the study than at the start, comparisons of S, N and H’ of sessile and mobile species were made using data collected in the first month of sampling (February 2019) and the final month of sampling (October 2019). All comparisons were made using Mann Whitney U-tests as S, N and H’ data for both sessile and mobile species did not conform to a normal distribution (Kolmogorov-Smirnov test, $P < 0.05$).

Analyses was completed in Minitab 17 Statistical Software (2010), R (R Core Team, 2019), and PRIMER-e V6 Multivariate Analysis for Ecology statistical software (Clarke and Warwick, 2001).

2.3 Results

The composition of species was different between habitat types. At the end of the sampling period, there was a slightly higher number of sessile taxa in AP habitats (21) than in SB habitats (18), with markedly fewer sessile taxa being recorded in GB habitats (12), (Table 2.1). A similar number of mobile taxa (6) were identified in both AP and SB habitats, and again by comparison, fewer mobile taxa were present in GB habitats at the end of the sampling period (Table 2.1).

Table 2.1 – Presence and absence of species after the 14-month sampling period AP, SB ad GB habitats at Runswick Bay (* indicates presence at end of sampling period).

	Habitat Type		
	Artificial Pools (AP)	Sandstone Boulders (SB)	Granite Boulders (GB)
Sessile Species			
Porphyra linearis	*	*	*
Porphyra dioica	*	*	*
Ulva intestinalis	*	*	*
Ulva linza	*	*	*
Ulva lactuca	*	*	
Ulva sp.	*	*	*
Filamentous Greens	*	*	*
Filamentous Browns	*		*
Fucus Sporling	*	*	*
Fucus vesiculosus	*	*	*
Fucus spiralis	*	*	*
Ascophyllum nodosum		*	
Rhodochorton sp.		*	
Ceramium spp.	*	*	
Pylaiella littoralis	*	*	
Mastocarpus stellatus		*	*
Aoudinella sp.		*	*
Ulothrix sp.	*		
Scytosiphon lomentaria	*		
Polysiphonia sp.	*		
Ectocarpus sp.	*		
Cladophora sericea	*		
Pink Crusts		*	
Blidingia maritima	*		
Eudesme virescens	*		
Semibalanus balanoides	*	*	
Mobile Species			
Patella vulgata	*	*	*
Littorina littorea	*	*	*
Littorina obtusata	*	*	*
Littorina saxatalis	*	*	*
Carcinus maenas	*	*	
Lipophrys pholis	*		
Actinia equina		*	

2.3.1 Variation in Sessile Communities in Different Habitat Types Over Time

There was a significant difference in mean S, N and H‘ of sessile species, both between habitat types and over time, and a significant interaction between habitat type and time (Table 2.2). Mean S and mean H’ of sessile species, averaged across all months sampled, was significantly different between habitat types (Table 2.3), with mean S and mean H’ being significantly higher in AP habitats and significantly lower in GB habitats (Tukey $P < 0.05$, in both cases). Mean N of both AP and SB was significantly higher than GB (Tukey $P < 0.05$, in both cases), however AP and SB were not significantly different (Tukey $P > 0.05$).

There was a significant interaction between habitat type and time, indicating an inconsistent pattern of change in mean S, N and H’ of sessile species between habitats over time. Mean S of sessile species was significantly higher in AP habitats in August and September than in other habitats over time (Tukey $P < 0.05$, in both cases), (Table 2.4), however mean S between these two months was not significantly different. Similarly, mean S was significantly lower in GB habitats in September and July, compared to other habitats over time (Tukey $P < 0.05$, in both cases) , but not significantly different from each other. Mean N of sessile species was significantly higher in AP in June, compared to other habitats over time (Tukey $P < 0.05$) (Table 2.5), and significantly lower in GB in September than in other habitats over time (Tukey $P < 0.05$). Mean H’ of sessile species was significantly higher in AP in August and September to other habitats over time (Tukey $P < 0.05$, in both cases) although were not significantly different to each other, (Table 2.6). Mean H’ was significantly lower in GB habitats in July and May compared to other habitats over time (Tukey $P < 0.05$, in both cases) but again these months were not significantly different to each other.

Table 2.2 – GLM analysis for the effect of Time (month sampled) and Habitat type on the mean S, N and H' of sessile species on the ecologically enhanced rock armour at Runswick Bay.

i) Species Richness (S)

Source	**DF**	**Adjusted MS**	**F**	**P**
Time	7	49.88	23.24	< 0.001
Habitat	2	359.47	167.49	< 0.001
Time * Habitat	14	21.52	10.03	< 0.001
Error	310	2.15		

ii) Total Abundance (N)

Source	**DF**	**Adjusted MS**	**F**	**P**
Time	7	8605.00	5.12	< 0.001
Habitat	2	117724.00	69.99	< 0.001
Time * Habitat	14	6697.00	3.98	< 0.001
Error	310	1682.00		

iii) Shannon-Wiener Diversity (H')

Source	**DF**	**Adjusted MS**	**F**	**P**
Time	7	1.60	12.63	< 0.001
Habitat	2	13.64	107.71	< 0.001
Time * Habitat	14	0.58	4.57	< 0.001
Error	310	0.13		

Table 2.3 – Tukey postHOC test of mean S, N and H' (averaged across all months sampled) of sessile species between habitat types on the ecologically enhanced rock armour at Runswick Bay. Means which do not share a letter are significantly different.

i) Species Richness (S)

Habitat type	**Mean**	**SD**	**Grouping**		
AP	6.24	2.73	A		
GB	2.65	0.90		B	
SB	4.48	1.92			C

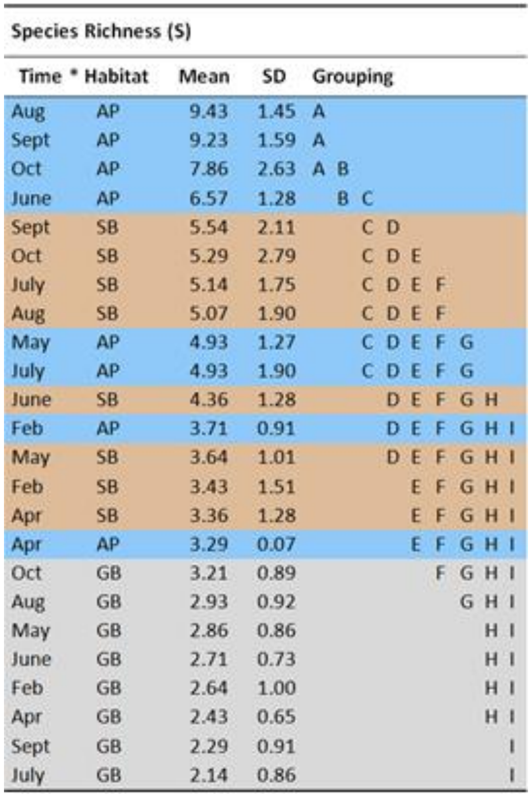
ii) Total Abundance (N)

Habitat type	**Mean**	**SD**	**Grouping**	
AP	122.28	51.69	A	
SB	122.75	39.07	A	
GB	66.43	43.84		B

iii) Shannon-Wiener Diversity (H')

Habitat type	**Mean**	**SD**	**Grouping**		
AP	1.27	0.48	**A**		
GB	0.58	0.33		B	
SB	0.94	0.44			C

Table 2.4 – Tukey postHOC test of mean S for the GLM interaction between Time and Habitat type (where 🟦 = AP, ⬜ = GB and 🟫 = SB), means which do not share a letter are significantly different.



Species Richness (S)

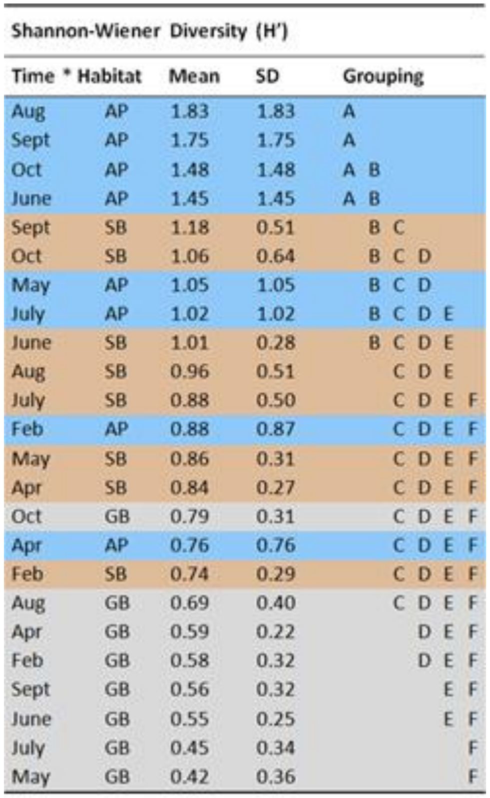
Time * Habitat		Mean	SD	Grouping
Aug	AP	9.43	1.45	A
Sept	AP	9.23	1.59	A
Oct	AP	7.86	2.63	A B
June	AP	6.57	1.28	B C
Sept	SB	5.54	2.11	C D
Oct	SB	5.29	2.79	C D E
July	SB	5.14	1.75	C D E F
Aug	SB	5.07	1.90	C D E F
May	AP	4.93	1.27	C D E F G
July	AP	4.93	1.90	C D E F G
June	SB	4.36	1.28	D E F G H
Feb	AP	3.71	0.91	D E F G H I
May	SB	3.64	1.01	D E F G H I
Feb	SB	3.43	1.51	E F G H I
Apr	SB	3.36	1.28	E F G H I
Apr	AP	3.29	0.07	E F G H I
Oct	GB	3.21	0.89	F G H I
Aug	GB	2.93	0.92	G H I
May	GB	2.86	0.86	H I
June	GB	2.71	0.73	H I
Feb	GB	2.64	1.00	H I
Apr	GB	2.43	0.65	H I
Sept	GB	2.29	0.91	I
July	GB	2.14	0.86	I

Table 2.5 – Tukey postHOC test of mean N for the GLM interaction between Time and Habitat type(where 🟦 = AP, ⬜ = GB and 🟫 = SB), means which do not share a letter are significantly different.

Total Abundance (N)

Time * Habitat		Mean	SD	Grouping
June	AP	174.36	51.0	A
Sept	AP	158.31	27.10	A B
June	SB	142.07	33.08	A B C
May	AP	139.89	35.84	A B C D E
Aug	AP	131.50	33.73	A B C D E F
Oct	SB	127.68	67.1	A B C D E F
Oct	AP	125.79	65.30	A B C D E F
Apr	SB	125.71	32.91	A B C D E F
Sept	SB	123.00	33.50	A B C D E F G
May	SB	121.32	47.30	A B C D E F G
Feb	SB	116.82	36.51	B C D E F G H
July	SB	113.61	20.19	B C D E F G H
Aug	SB	111.79	23.00	B C D E F G H I
July	AP	95.00	38.8	C D E F G H I J
Apr	AP	84.00	35.08	D E F G H I J
June	GB	79.79	46.30	E F G H I J
Feb	GB	77.68	43.80	E F G H I J
May	GB	74.75	35.35	F G H I J
Apr	GB	73.18	38.20	F G H I J
Feb	AP	72.00	12.67	F G H I J
Aug	GB	68.86	49.50	G H I J
Oct	GB	61.58	51.80	H I J
July	GB	56.07	40.80	I J
Sept	GB	39.57	38.3	J

Table 2.6 – Tukey postHOC test of mean H' for the GLM interaction between Time and Habitat type (where 🟦 = AP, ⬜ = GB and 🟫 = SB), means which do not share a letter are significantly different.



Shannon-Wiener Diversity (H')

Time * Habitat		Mean	SD	Grouping
Aug	AP	1.83	1.83	A
Sept	AP	1.75	1.75	A
Oct	AP	1.48	1.48	A B
June	AP	1.45	1.45	A B
Sept	SB	1.18	0.51	B C
Oct	SB	1.06	0.64	B C D
May	AP	1.05	1.05	B C D
July	AP	1.02	1.02	B C D E
June	SB	1.01	0.28	B C D E
Aug	SB	0.96	0.51	C D E
July	SB	0.88	0.50	C D E F
Feb	AP	0.88	0.87	C D E F
May	SB	0.86	0.31	C D E F
Apr	SB	0.84	0.27	C D E F
Oct	GB	0.79	0.31	C D E F
Apr	AP	0.76	0.76	C D E F
Feb	SB	0.74	0.29	C D E F
Aug	GB	0.69	0.40	C D E F
Apr	GB	0.59	0.22	D E F
Feb	GB	0.58	0.32	D E F
Sept	GB	0.56	0.32	E F
June	GB	0.55	0.25	E F
July	GB	0.45	0.34	F
May	GB	0.42	0.36	F

Algal community similarity was found to be significantly different both between habitat types (averaged across all months sampled) (ANOSIM, Global R = 0.698, P = 0.1%) and over time (averaged across all habitat types) (ANOSIM, Global R = 0.516, P = 0.1%), indicating differences in algal community structure both as a result of habitat type and time. Pairwise comparison found that algal community similarity was significantly different between Habitat groups (pooled across months, in all cases, P < 0.1%) and between all Month groups (pooled across habitats, in all cases, P < 0.1%).

An MDS plot of samples categorised by both month and habitat (Figure 2.3) showed clear clustering of samples by habitat type, however the plot has a high stress value (0.24) and therefore is not completely reliable. Overall, samples taken from each habitat type clustered together with a small amount of overlap between clusters. Clustering of samples taken from each habitat type showed no clear monthly pattern, suggesting a high degree of variability in community structure between sampling locations throughout the sample period. However, this may be to be expected as the community develops and establishes.

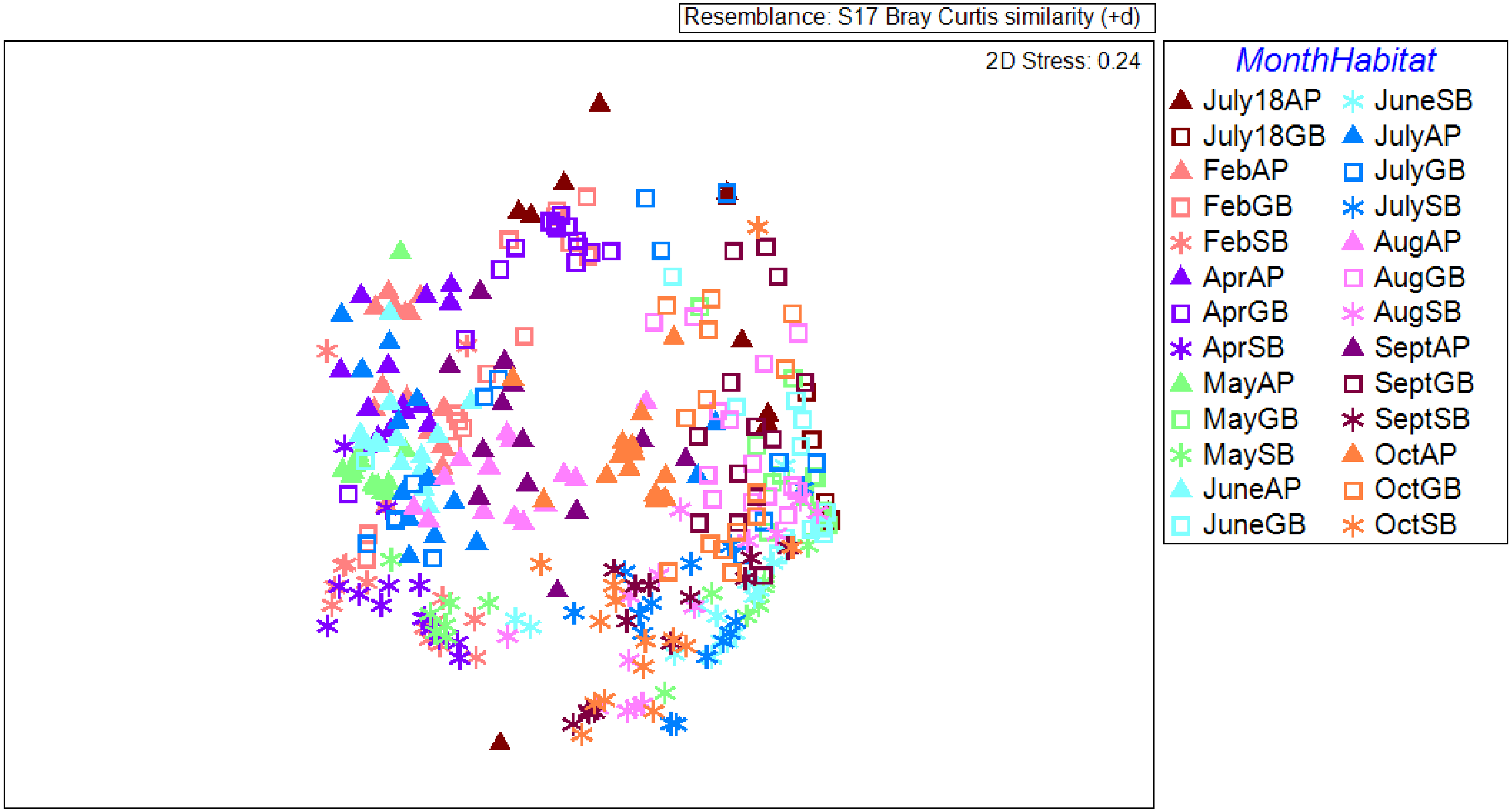


Figure 2.3 – The results of MDS analysis based on a Bray-Curtis similarity matrix for data collected from all habitat types between July 2018 and October 2019. Month in which samples were collected is denoted by colour and habitat type is indicated by symbol where ▲= Artificial Pool (AP), ☐ = Granite Boulders (GB) and ✱ = Sandstone Boulders (SB).

SIMPER analysis was used to identify species responsible for producing the dissimilarity observed between habitat types. Although the barnacle species was identified in a handful of samples in AP and SB habitats, coverage was to too sparse for the species to be highlighted by SIMPER analyses. Examination showed that each habitat type appeared to host a distinct community with only a handful of species in common (Table 2.7). For example, 3 of the 4 taxa in samples from AP were unique to this environment, with GB and SB also hosting 2 unique taxa each. *Ulva linza* and *Ulva sp.* were common across habitat types with *Ulva linza* being identified in samples from AP and SB, and *Ulva sp.* being identified in GB and SB. Interestingly, both AP and GB had more in common with SB (both having 1 taxa in common) than with each other (no taxa in common). There was a clear shift in algal community composition over time for all habitat types (Figure 2.4). Filamentous algae (*Ulva intestinalis, Ulva linza* and *Ulva sp.*) were abundant on all habitat types during the study period, but constituted a larger proportion of the community present on GB compared to AP and SB. *Ulva sp.* and *Ulva linza* were the predominant species in GB habitats however their relative mean abundance varyied over time. SB had a greater proportion of leathery macrophytes than any other habitats (Figure 2.4). SB had a consistently higher relative mean abundance of *Fucus spiralis*, *Fucus* sporlings and *Fucus vesiculosus* than other habitat types and was the only habitat in which *Ascophyllum nodosum* was recorded. *Fucus spiralis* was recorded in the later months of sampling for both AP and GB habitats but in a markedly lower relative mean abundance compared to SB. *Pylaiella littoralis* and *Filamentous Brown* algae were identified in samples taken from AP only.

Table 2.7 – SIMPER Table indicating average abundance of algal species contributing to similarity observed between samples from a) Artificial pools (AP), b) Granite boulders (GB) and c) Sandstone boulders (SB) (Av.Abund = mean abundance (raw % cover data), Av.Sim = Average Similarity, Sim/SD = Similarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) Artificial Pools (AP) **Average Similarity = 55.05 %**

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ulva intestinalis	4.13	15.87	0.92	28.84	28.84
Ulva linza	3.38	9.88	0.90	17.95	46.79
Pylaiella littoralis	2.19	5.54	0.57	10.07	56.86
Filamentous Browns	2.71	5.51	0.62	10.02	66.87

b) Granite Boulders (GB) **Average Similarity = 48.09 %**

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Ulva sp.	3.66	22.34	0.92	46.46	46.46
Filamentous Greens	1.68	8.18	0.46	17.01	63.47
Porphyra linearis	1.57	7.90	0.76	16.42	79.90

c) Sandstone Boulders (SB) **Average Similarity = 46.74 %**

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Fucus spiralis	4.03	13.60	0.87	29.09	29.09
Fucus vesiculosus	3.78	8.68	0.66	18.57	47.67
Ulva linza	2.61	8.19	0.59	17.53	65.20
Ulva sp.	2.96	7.50	0.58	16.05	81.25

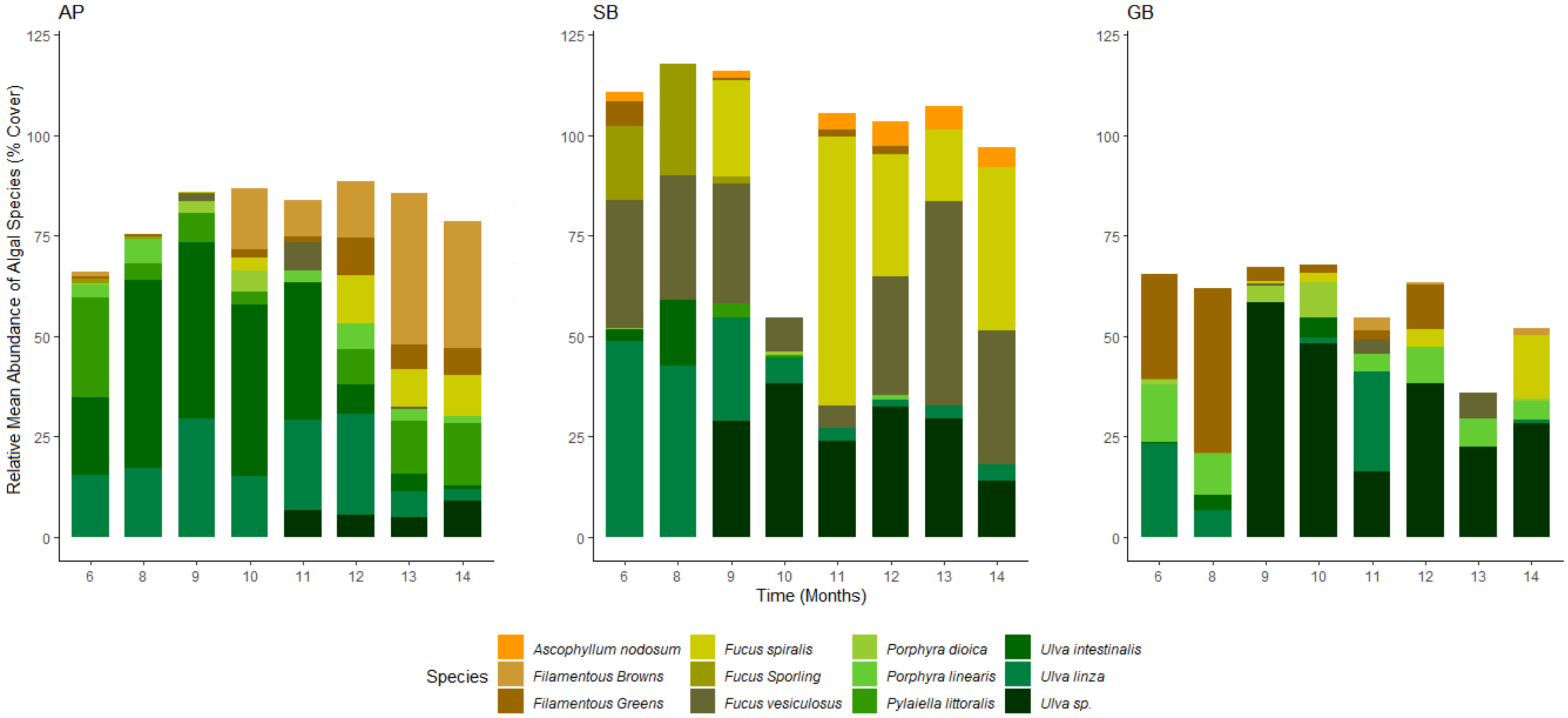


Figure 2.4 – Relative mean abundance (% cover) of algal species identified through SIMPER as being key contributors to the similarity observed between habitat types over time (Artificial pools = AP, Granite boulders = GB and Sandstone boulders = SB).

Further analyses of each habitat type independently, found that the S, N and H’ of sessile species differed significantly over time. Overall, all habitats showed an increase in mean S and H’ of sessile species (Figure 2.5) however there was considerable seasonal variation due to factors which were not examined.

Within AP habitats, there was a significant difference in mean S of sessile species in over time (Table 2.8a). Mean S in AP was significantly higher in August and September than in other months (Tukey $P > 0.05$), although mean S was not significantly different between August and September. Mean S in AP was lowest in July 2018, immediately after construction was completed, and highest in August, (Figure 2.5a). Mean N of sessile species in AP was also significantly different over time (Table 2.8a). Mean N was significantly higher in June and September (Tukey $P < 0.05$), and significantly lower in July 2018 and February compared to other months (Tukey $P < 0.05$), however neither June and September nor July 2018 and February were significantly different to each other (Tukey $P > 0.05$). There was considerable variation and no clear increase in mean N of sessile species in AP over time (Figure 2.5b). There was also significant difference in median H’ of sessile species in AP over time (Table 2.8a). Median H’ of sessile species in October was significantly higher and median H’ in July 2018 was significantly lower than all other months (Tukey $P < 0.05$, in all cases). Although there was considerable variation, median H’ of sessile species in AP showed an increase over time (Figure 2.5c). See Appendix 1 for the descriptive statistics.

Analyses also found there to be a significant difference in the mean S of sessile species in GB habitats over time (Table 2.8b). Mean S of sessile species was significantly higher in October and significantly lower in July 2018 compared to every other month (Tukey $P < 0.05$, in all cases). Generally, there was an overall increase in mean S in GB habitats over time (Figure 2.5a). There was also a significant difference in median N of sessile species in GB over time (Table 2.8b). Median N was found to be significantly lower in July 2018 compared to all other months surveyed (Tukey $P < 0.05$, in all cases), with the exception of September 2019 (Tukey $P > 0.05$). No other significant differences were recorded. Mean H’ of sessile species in GB was a significantly different over time (Table 2.8b), with October having a significantly higher mean H’ than other months (Tukey $P < 0.05$, in all cases). Mean H’ was lowest in July 2018 compared to all other months (see Appendix 1 the descriptive statistics).

Additionally, a significant difference in median S of sessile species for SB over time was found (Table 2.8c). Pairwise differences could not be resolved and thus it could not be determined between which month’s median S were most different, however there was an overall increase in median S of sessile species in SB habitats over time (Figure 2.5c). There was no significant difference in mean N or mean H’ of sessile species over time (see Appendix 1 for the descriptive statistics).

Table 2.8 – One-Way ANOVA and Kruskal-Wallis for S, N (% cover) and H’ of sessile species over time (month) for a) Artificial pools (AP), b) Granite boulder (GB) and c) Sandstone boulder (SB) habitats. NS denotes Not Significant, * denotes significant to 0.01, ** denotes significant to 0.001, *** denotes significant to <0.001.

a) Artificial Pool (AP)

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	AN		AN		KW	
		F	P	F	P	H	P
Month	7	47.31	***	12.37	***	93.84	*

b) Granite Boulder (GB)

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	AN		KW		AN	
		F	P	H	P	F	P
Month	7	15.01	***	32.15	*	7.77	***

c) Sandstone Boulder (SB)

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	KW		AN		AN	
		H	P	F	P	F	P
Month	7	20.41	*	0.84	NS	1.41	NS

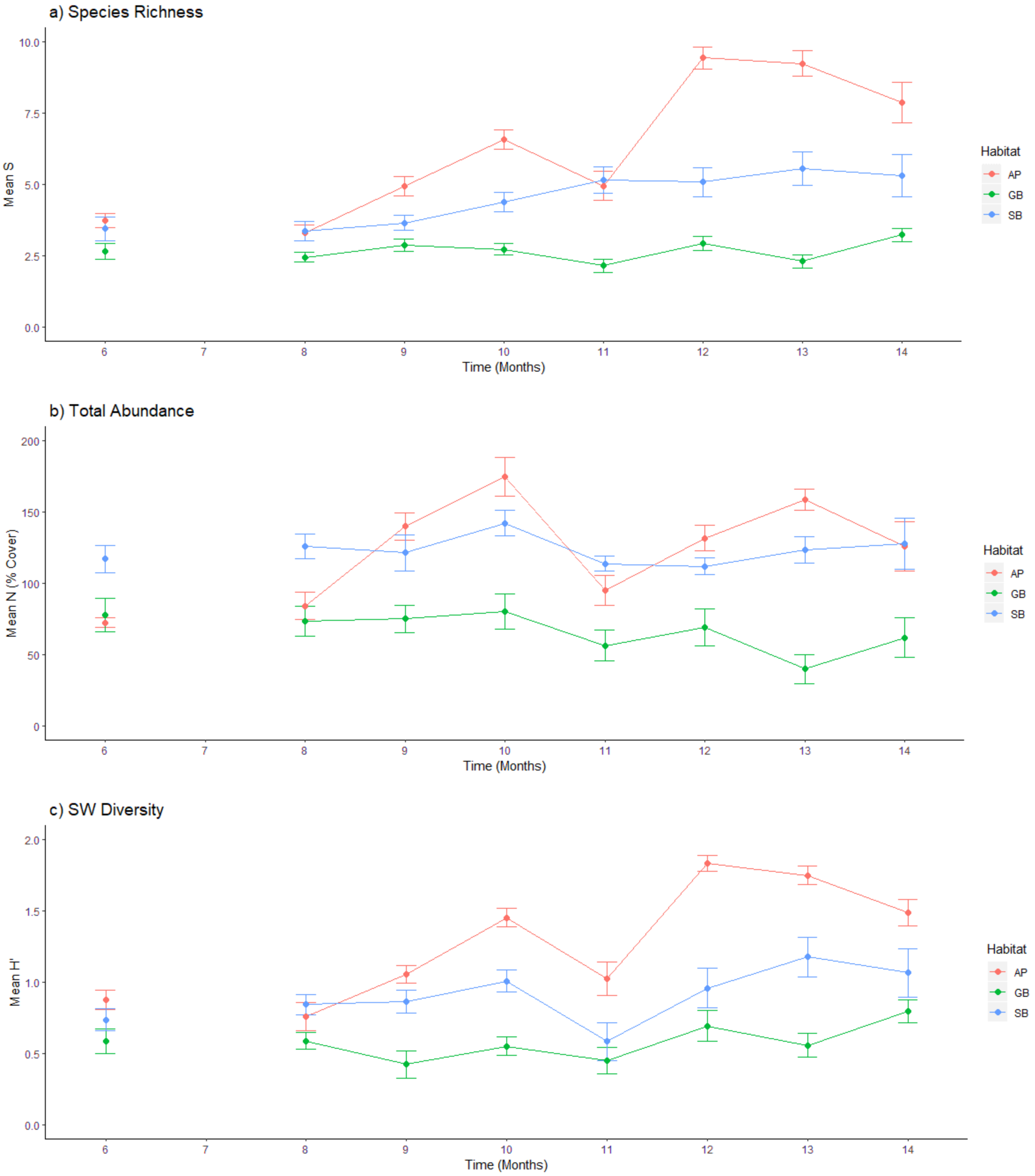


Figure 2.5 – Variation over time in a) mean S, b) mean N and c) mean H’ of sessile species from three habitat types examined; Artificial pools = AP, Granite boulders = GB and Sandstone boulders = SB.

Finally, comparison of S, N and H’ of sessile communities between the start and end of the sampling period found that median S (Mann Whitney U-test, W = 285.0, df = 14, $P < 0.05$), median N (Mann Whitney U-test, W = 249.5, df = 14, $P < 0.05$) and median H’ (Mann Whitney U-test, W = 285.0, df = 14, $P < 0.05$) of AP was significantly different. S, N and H’ was higher at the end of the study compared to the start (Table 2.9). However median S, median N, or median H’ of GB was not significantly higher at the end of the study compared to the start (Mann Whitney U-test, $P > 0.05$, in all cases). The same was true for SB, as median S, median N, or median H’ at the start and end of the study were not found to be significantly different (Mann Whitney U-test, $P > 0.05$, in all cases).

Table 2.9 – Median and range data for S, N and H’ of sessile species at a) the start of the study and b) the end of the study for all habitats examined (Artificial pools = AP, Granite boulders = GB and Sandstone boulders = SB).

a) Start of the sampling period

Habitat	**S**		**N**		**H’**	
	Median	Range	Median	Range	Median	Range
AP	3.00	3.00 – 5.00	74.00	42.00 – 93.00	0.80	0.62 – 1.47
GB	2.50	1.00 – 5.00	72.50	25.00 – 177.00	0.62	0.00 – 1.15
SB	3.00	2.00 – 7.00	114.00	64.00 – 193.00	0.71	0.39 – 1.34

b) End of the sampling period

Habitat	**S**		**N**		**H’**	
	Median	Range	Median	Range	Median	Range
AP	8.00	2.00 – 12.00	150.50	9.00 – 218.00	1.55	0.35 – 1.82
GB	3.00	1.00 – 4.00	59.50	4.00 – 152.00	0.91	0.00 – 1.17
SB	6.00	1.00 – 9.00	121.00	4.00 – 240.00	1.07	0.00 – 1.96

2.3.2 Variation in Mobile Communities in Different Habitat Types Over Time

Examining how species richness (S), total abundance (N) and the Shannon-Wiener Diversity Index (H’) of mobile species differed between habitat type and over time found that mean S, mean N and mean H’ were low in in all habitats throughout the sampling period.

Mean S was marginally higher in AP than both GB and SB irrespective of month sampled (Table 2.10a), whereas GB had the lowest mean S of all habitats consistently throughout the study.

Mean N was also very low in all habitats over time (Table 2.10b). Mean N was slightly higher in AP than other habitats however mobile species were largely absent from GB and SB throughout the sampling period. There was some variability in mean N between sample stations for AP and SB, in some instances with as many as 14 and 21 mobile animals present, respectively. However, in many instances mobile animals were also absent (Table 2.10b). Overall, mean N of mobile species did not appear to increase noticeably in AP and SB habitats over time and there was little change in mean N in GB habitats as mobile species were sparse.

There was no overall increase in mean H’ of mobile species in habitats over time (Table 2.10c). Again, mobile species were largely absent from GB samples, meaning the mean H’ of mobile species on GB was zero, continuously throughout the study (Table 2.10c). The range of H’ for AP and SB habitats showed that there was variability in H’ between samples taken each month.

Table 2.10 – Median and range data for S, N (counts) and H’ of mobile species over time for a) Artificial Pool (AP), b) Granite boulder (GB) and c) Sandstone boulder (SB) habitats. Where Kruskal-Wallis test was used the median and range have been reported.

a) Artificial Pools (AP)

Time in Months	S		N		H’	
	Median	Range	Median	Range	Median	Range
0 July 18	0.00	0.00 – 2.00	0.00	0.00 – 9.00	0.00	0.00 – 0.69
6 February	0.00	0.00 – 2.00	0.00	0.00 – 6.00	0.00	0.00 – 0.45
8 April	0.50	0.00 – 1.00	0.50	0.00 – 7.00	0.00	0.00 – 0.00
9 May	1.00	0.00 – 4.00	1.00	0.00 – 14.00	0.00	0.00 – 1.33
10 June	0.50	0.00 – 4.00	0.50	0.00 – 11.00	0.00	0.00 – 1.04
11 July	1.50	0.00 – 4.00	7.00	0.00 – 11.00	0.29	0.00 – 1.31
12 August	1.00	0.00 – 3.00	1.00	0.00 – 12.00	0.00	0.00 – 1.04
13 September	1.00	0.00 – 4.00	1.00	0.00 – 14.00	0.00	0.00 – 1.32
14 October	1.00	0.00 – 3.00	1.50	0.00 – 11.00	0.00	0.00 – 1.10

b) Granite Boulders (GB)

Time in Months	S		N		H’	
	Median	Range	Median	Range	Median	Range
0 July 18	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
6 February	0.00	0.00 – 2.00	0.00	0.00 – 2.00	0.00	0.00 – 0.69
8 April	0.00	0.00 – 1.00	0.00	0.00 – 1.00	0.00	0.00 – 0.00
9 May	0.00	0.00 – 1.00	0.00	0.00 – 2.00	0.00	0.00 – 0.00
10 June	0.00	0.00 – 1.00	0.00	0.00 – 1.00	0.00	0.00 – 0.00
11 July	0.00	0.00 – 1.00	0.00	0.00 – 1.00	0.00	0.00 – 0.00
12 August	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
13 September	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
14 October	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00

c) Sandstone Boulders (SB)

Time in Months	S		N		H’	
	Median	Range	Median	Range	Median	Range
0 July 18	NA					
6 February	0.00	0.00 – 1.00	0.00	0.00 – 5.00	0.00	0.00 – 0.00
8 April	0.00	0.00 – 1.00	0.00	0.00 – 1.00	0.00	0.00 – 0.00
9 May	0.00	0.00 – 1.00	0.00	0.00 – 21.00	0.00	0.00 – 0.00
10 June	1.00	0.00 – 2.00	1.00	0.00 – 3.00	0.00	0.00 – 0.69
11 July	1.00	0.00 – 3.00	1.00	0.00 – 10.00	0.00	0.00 – 1.10
12 August	0.00	0.00 – 2.00	0.00	0.00 – 2.00	0.00	0.00 – 0.69
13 September	0.00	0.00 – 1.00	0.00	0.00 – 5.00	0.00	0.00 – 0.00
14 October	1.00	0.00 – 2.00	1.00	0.00 – 9.00	0.00	0.00 – 0.69

Within each habitat type, the median S, N and H' of mobile species was variable both spatially and temporally. Overall, there was no clear increase in median S, median N or median H' of mobile species in AP habitats over time.

Comparison of mobile species in AP over time found there was a significant difference in median S over time (Table 2.11a), however only median S in July 2019 was found to be significantly higher than July 2018 and April 2019 (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$ in both cases). Pairwise comparisons found no further differences. Median N of mobile species in AP habitats was also found to be significantly different over time (Table 2.11a). Again, median N of mobile species was significantly higher in July 2019 compared to July 2018, and February and April 2019 (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$ in all cases). Pairwise comparisons found no further differences. There was also a significant difference in median H' of mobile species over time (Table 2.11a), however median H' was only >0 in July which is likely what made this result significant. Pairwise comparisons found no further differences than those given above suggesting that, although the median S, N and H' of mobile species were statistically significant, the community did not change all that much during the sampling period (See Table 2.10a for median and range data).

In GB habitats mobile species were largely absent and so there were no significant differences in the median S, median N or median H' over time (Table 2.11b). Similarly, in SB habitats there were no significant differences in median S, median N or median H' of mobile species over time (Table 2.11c).

Table 2.11 – One-Way ANOVA and Kruskal-Wallis for S, N (counts) and H’ of mobile species over time (month) for a) Artificial pools (AP), b) Granite boulder (GB) and c) Sandstone boulder (SB) habitats. NS denotes Not Significant, * denotes significant to 0.01, ** denotes significant to 0.001, *** denotes significant to <0.001.

a) Artificial Pool (AP)

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	KW		KW		KW	
		F	P	F	P	H	P
Month	7	17.75	*	21.61	*	17.72	*

b) Granite Boulder (GB)

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	KW		KW		KW	
		H	P	H	P	H	P
Month	7	6.35	NS	6.3	NS	8	NS

c) Sandstone Boulder (SB)

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	KW		KW		KW	
		H	P	H	P	H	P
Month	7	11.18	NS	9.18	NS	8.14	NS

Population density of mobile species was low in all habitats throughout the study. Examination of grazing assemblages found differences in the diversity of animal communities between habitat types and over time. There was no significant difference in the median S, median N or median H’ of grazing species (Kruskal Wallis, $P > 0.05$, in all cases) between habitats at the start of the sampling period. Mean density of all grazing taxa was low at the start of the sampling period (Figure 2.6). Of grazing taxa identified, *Patella vulgata* was present in all habitats and *Littorina littorea* was present in GB and AP. *Littorina saxatilis* was absent from all habitats and *Littorina obtusata* occurred in low densities in SB habitats only.

However, at the end of the sampling period, there was a significant difference in the median S (Kruskal Wallis, H (adjusted for ties) = 12.41, df = 2, $P < 0.05$), median N (Kruskal Wallis, H (adjusted for ties) = 12.04, df = 2, $P < 0.05$) and median H’ (Kruskal Wallis, H (adjusted for ties) = 8.61, df = 2, $P < 0.05$) of grazing species between habitats. GB had a significantly lower median S and median N compared to both AP and SB (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in all instances), however median S and median N of grazing species was not significantly different between AP and SB at the end of the sampling period (Pairwise Wilcoxon Rank Sum Test, $P > 0.05$). Pairwise comparison could not resolve the differences in median H’ between habitats likely as a consequence of being data sparse.

The mean density of grazers in each habitat varied over time, with very few grazers recorded in all habitats (Figure 2.6). *Patella vulgata* occurred in all habitat types, being continuously present in SB habitats throughout the study and occurring in increasing densities in AP habitats over time (Figure 2.6). *Littorina littorea* was most common of all Littorinid species recorded. *Littorina littorea* and *Littorina saxatilis* were more abundant in AP habitats than in other habitats. *Littorina saxatilis* became more abundant in AP after the start of the sampling period but remained sparse in SB habitats (Figure 2.6). All species were scarce in GB habitats.

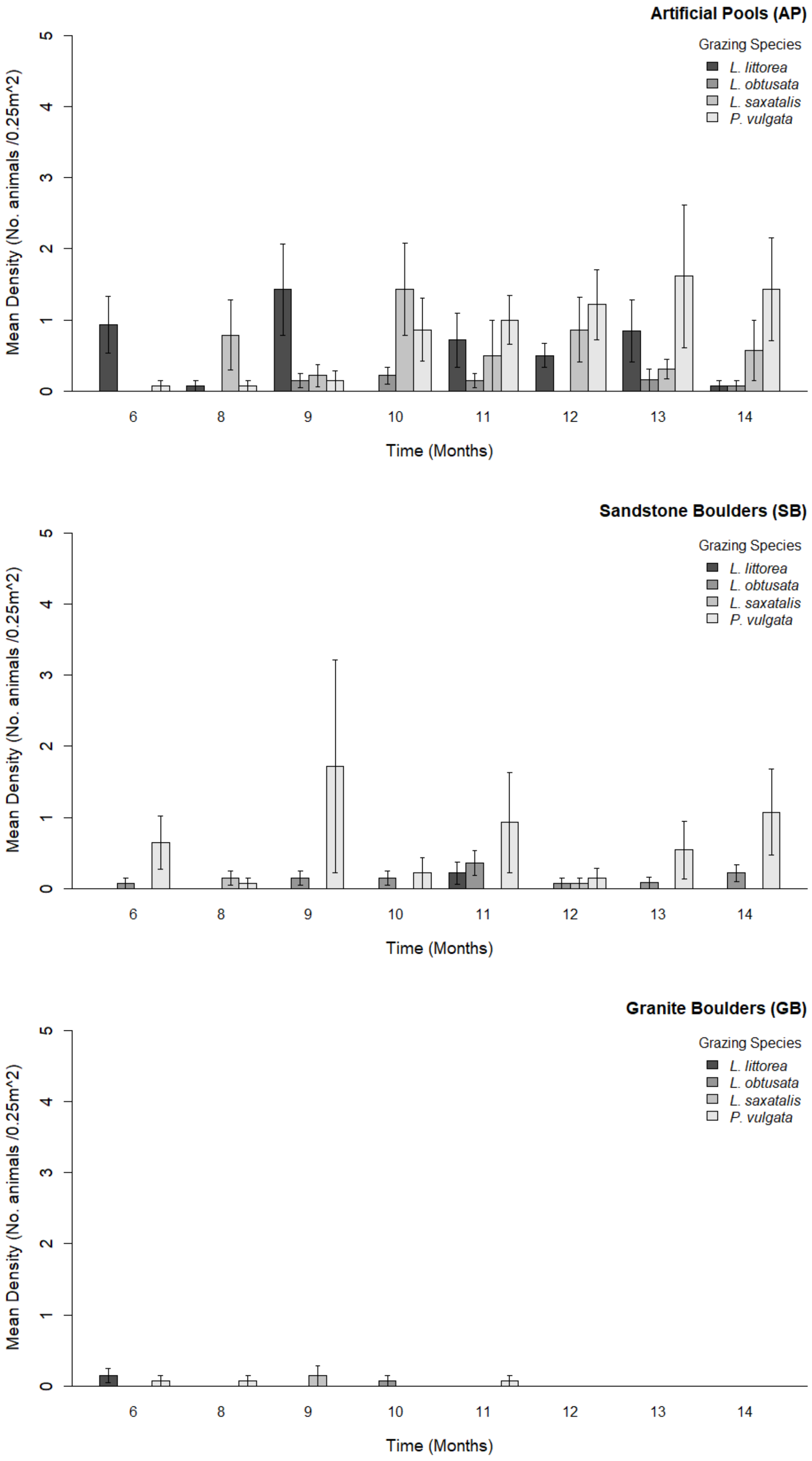


Figure 2.6 – Mean density (number of animals per 0.25m2) of grazing species *Patella vulgata, Littorina littorea, Littorina obtusata and Littorina saxatilis* for each habitat examined (Artificial pools = AP, Sandstone boulders = SB and Granite boulders = GB). Note: Grazer density data was not available for month 7.

In all habitat types median S, N and H’ of mobile species was not significantly higher at the end of the study than at the start (Mann Whitney U-test, P > 0.05, in all cases – for medians see Table 2.12).

Table 2.12 – Median and range data for S, N and H’ of mobile species at a) the start of the sampling period and b) the end of the study for all habitats examined (Artificial pools = AP, Granite boulders = GB and Sandstone boulders = SB).

a) Start of the study

Habitat	**S**		**N**		**H’**	
	Median	Range	Median	Range	Median	Range
AP	0.00	0.00 – 2.00	0.00	0.00 – 6.00	0.00	0.00 – 0.45
GB	0.00	0.00 – 2.00	0.00	0.00 – 2.00	0.00	0.00 – 0.69
SB	0.00	0.00 – 1.00	0.00	0.00 – 5.00	0.00	0.00 – 0.00

b) End of the study

Habitat	**S**		**N**		**H’**	
	Median	Range	Median	Range	Median	Range
AP	1.00	0.00 – 3.00	1.50	0.00 – 11.00	0.00	0.00 – 1.10
GB	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
SB	1.00	0.00 – 2.00	1.00	0.00 – 9.00	0.00	0.00 – 0.69

2.4 Discussion

The findings of this study support previous assertions that increasing habitat heterogeneity and physical complexity on rock armour coastal defences is an effective means of enhancing biodiversity (Hall *et al.,* 2018). The main findings from the first part of this study show that diversity and composition of sessile and mobile communities differed between the three main habitat types on the enhanced coastal defence at Runswick Bay.

The results of this chapter confirm the hypothesis that species richness (S), total abundance (N), diversity (H') and community similarity of sessile communities was significantly different between habitats and over time. Richness, abundance, and diversity of sessile species were significantly higher in artificial pool (AP) and sandstone boulder (SB) habitats compared to granite boulder habitats (GB) (Table 2.3). This was especially evident in AP habitats. As discussed in Chapter 1 Section 1.4, coastal defences are typically low-diversity environments (Chapman and Bulleri, 2003) and although pools represent an uncommon feature on coastal defence structures (Firth *et al.,* 2013a), numerous studies have found their incorporation to greatly increase biodiversity on artificial shores (Firth *et al.,* 2014; Evans *et al.,* 2016). Both naturally-occurring and artificially-created pools offer greater protection from desiccation than emergent rock (Browne and Chapman, 2014), which creates refuges for invertebrates (Bowman and Lewis, 1977) and may enable some mid-shore species to expand their vertical distribution into higher shore environments (Evans *et al.,* 2016). The algal community in AP habitats was a relatively simple assemblage of predominantly filamentous and foliose algae (Figure 2.4). Small abundances of mid-shore species *Ceramium sp.* and *Polysiphonia sp*. were identified in AP habitats, however opportunistic species such as *Ulva linza* and *Ulva sp*. were predominant, which was to be expected as the area was still undergoing succession (Benedetti-Cecchi and Cinelli, 1996). SB habitats also had an abundance of filamentous algae (Table 2.7) but hosted a greater coverage of leathery macrophytes including *Ascophyllum nodosum, Fucus vesiculosus* and *Fucus spiralis* (Figure 2.4). Having hosted an assemblage of filamentous algae when incorporated into the rock armour, SB habitats were likely further along in the successional process than AP and GB habitats (Chapman, 2003b), and that the rate of succession in SB habitats was somewhat faster (Benedetti-Cecchi, and Cinelli, 1996). Macroalgal canopy on SB habitats likely redeveloped after boulder placement due to regrowth of Fucoids from holdfasts on boulders not damaged during construction (Keser, Vadas and Larson, 1981; Jenkins, Hawkins and Norton, 1999) which would account for the sustained cover of *Ascophyllum nodosum, Fucus vesiculosus* and *Fucus spiralis* throughout the study. The presence of *Fucus spiralis* in AP habitats in later months indicated that the sandstone boulders appeared act as “seed” boulders however the amount of connectivity between habitats was not clear (Figure 2.4).

Within each habitat, species richness (S) and diversity (H’) of sessile species had significantly increased over time, but only AP habitats had a significantly higher richness, abundance and diversity of sessile species at the end of the study (Table 2.9). Abundance of sessile species showed considerable variation over time, likely as a result of biotic factors such as seasonal variation and patterns of recruitment (Foster *et al.,* 2003) which were not examined here. GB habitats were the most homogenous of the three habitats, and consistently recorded the lowest richness, abundance and diversity of sessile species of all habitat types examined. As discussed in Chapter 1 Section 1.4, lack of biodiversity in artificial marine environments can be attributed to lack of heterogeneity of available habitats (Bulleri and Chapman, 2004; Aguilera, 2018). Indeed, an absence of microhabitats, such as pits, crevices and channels, leaves invertebrates without refuge from predation or wave action (Fretter and Manly, 1977; Underwood and Chapman, 1998; Chapman, 2003a), and prevents algal colonisation beyond the establishment of a few desiccation-resistant pioneer species (*Ulva sp., Porphyra sp*.) (Moschella *et al.,* 2005). This was true of GB habitats in this instance, given the dominance of ephemeral algae (Figure 2.4) and a paucity of fauna (Figure 2.6) throughout the study. Mobile species were rare in GB habitats and although more fauna were observed in AP and SB habitats, density of mobile species was low in all habitat types throughout the study (Table 2.10). It is well established that faunal abundance differs between naturally-occurring and artificial habitats (Forrest *et al.,* 2013), and coastal defences which lack habitat heterogeneity and physical complexity are known to support lower densities of mobile species (Chapman, 2003a; Chapman & Blockley 2009). In natural habitats, greater densities of predator species may offer some resistance to colonisation by non-native species (Forrest *et al.,* 2013), however an absence of predator species on coastal defences may provide opportunities for non-native species to colonise (Dumont *et al.,* 2011; Firth *et al.,* 2013a). The invasive Australasian barnacle *Austrominius Modestus* has become widespread on coastal defences throughout the UK in part due to an absence of predators (Bracewell *et al.,* 2012), but also as result of preferential feeding habits by predator species. For example, the common dog whelk *Nucella lapillus*, has been documented to selectively feed on the native barnacle *Semibalanus balanoides*, over *Austrominius Modestus* (Barnett, 1979). However, given the short timescale of this study, it was likely that succession and establishment of new species was ongoing.

At the end of the study, richness and abundance of grazing limpets and gastropod snails was higher in AP and SB habitats compared to GB habitats (Table 2.12), likely due to greater protection from thermal and desiccation stress and better foraging (Jenkins and Hartnoll, 2001; Browne and Chapman, 2014). Filamentous algae in natural rock pools has been documented as a nursery for marine invertebrates (Preston and Moore, 1988) however distribution of invertebrates has been linked to the physical characteristics (depth, substratum incline) of the pool itself (Goss-Custard *et al.,* 1979; Kooistra *et al.,* 1989; Bussell and Lucas, 2007).

The richness, abundance and diversity of mobile species in each habitat type (Table 2.12) had not increased significantly at the end of the study. One explanation for the paucity of mobile species across habitats may be that colonisation of the structure is still ongoing. Abundance of invertebrates may be influenced by the mechanism through which species recruit. For example, invertebrates with limited mobility which utilise direct development, such as *Littorina saxatilis*, have limited dispersal capabilities (Reid, 1996; Gefaell, Varela and Rolán-Alvarez, 2020), which will impact upon the time it takes for animals to migrate into a new habitat and for a population to establish. In contrast, species which release planktonic larvae, such as *Patella vulgata*, may be more able to disperse into new habitats but recruitment will also be limited. For example, limited food availability will affect survival rates of newly settled invertebrates during the early phases of colonisation (Lewis and Bowman, 1975). In addition, a number of animals were likely removed from the area during construction (Moschella *et al.,* 2005) and given that the results presented here represent only one recruitment year, it was possible that not enough time was allowed for faunal communities to fully re-establish (Thompson, 1980).

This study finds that species richness (S), total abundance (N), diversity (H’) and community similarity of sessile communities differed significantly different between habitats type and over time, and that within each habitat type, S, N, and H’ of sessile communities was significantly different over time. This indicates that increasing habitat heterogeneity by creating more varied habitat types has considerable potential to increase richness and biodiversity within coastal defence environments. Although the patterns of change in the richness and diversity of communities, both between and within habitat types, varied considerably over time, the findings of this study show that increasing habitat heterogeneity by creating more varied habitat types has considerable potential to increase richness and biodiversity within coastal defence environments. The incorporation of artificial pool habitats and the placement of native sandstone boulders at the foot of the rock armouring proved to be an effective means of improving and maintaining biodiversity over time. This study reiterates the importance of water-retaining features in upper-shore artificial environments.

It was clear in this instance that species richness (S), total abundance (N), diversity (H’) of sessile and mobile communities in each habitat was not significantly higher at the end of the study than at the start, however further monitoring of the site would be necessary to provide a longer-term assessment of how the community at the site changes. The under-abundance of mobile species meant that species richness (S), total abundance (N), diversity (H’) and community similarity of mobile communities did not differ significantly different between habitats type and over time, nor was species richness (S), total abundance (N), diversity (H’) within GB and SB habitats significantly different over time. Previous studies have found that most species will have settled into an engineered habitat within approximately two years of installation (Sempere-Valverde *et al.,* 2018), with colonisation of artificially-created rock pools typically occurring within 18 – 24 months (Evans *et al.*, 2016; Firth *et al.*, 2016a). Although still early in the colonisation process, the community that has developed here indicates that incorporating ecological enhancements into the design of rock armour defences, in particular the inclusion of artificial pool habitats, can positively impact how such a structure is colonised. Thus, creating a biologically valuable, multifunctional structure.

Chapter 3 Colonisation in areas of increased small-scale physical complexity on an ecologically enhanced rock armour defence in Runswick Bay, North Yorkshire.

3.1 Introduction

Microhabitats, such as grooves, channels, pits, holes, and crevices, create physical complexity on natural substrata and provide important refuges and nursey habitats (Bowman and Lewis, 1977). As discussed in Chapter 1 Section 1.5, habitat enhancements to increase biodiversity on coastal defences vary in style, size, and application however, it has been suggested that small- to medium- sized enhancements may be more likely to sustain increased biodiversity (Browne and Chapman, 2014). Cm-scale physical features provide additional space for species to settle into and increase the likelihood of survival for newly settled algal spores and invertebrate larvae by offering protection from grazing and predation (Mineur *et al.*, 2012; Firth *et al.*, 2013b). For example, small pits (12mm in diameter and 10mm depth) and medium pits (24mm in diameter and 10mm in depth) were created in a basalt wall by Martins *et al.,* (2010) to test whether the presence of these pits enhanced stocks of the commercially important limpet, *Patella candei*. This investigation found that the physical complexity created by pits increased the abundance of limpets at tests sites and that a greater number of adults occupied the larger pits, whereas recruitment of juvenile limpets was higher in smaller pits. Other trials utilising cm-scale enhancements have also resulted in increases in greater richness of species and greater abundance of habitat-forming species. In a trial by Evans et al., (2016), eighteen drill-cored pits were installed on a granite breakwater. These pits were designed to mimic small, unshaded rock pools similar to those on a nearby natural shore. Each measured 12 cm in diameter however pit depth was varied with “deep” pits being drilled to a depth of 12 cm and “shallow” pits being drilled to a depth of 5 cm. After allowing the drill-cored pits to colonise for 18 months, Evans et al., (2016) found that the pits supported a greater species richness compared to adjacent, unalter granite surfaces and that the richness of pit was similar to that of nearby natural pools. However, although species richness was equitable to that of nearby natural pools, community composition in drill-cored pits was different to that of natural pools.

Although in this trial, pit depth did not affect species richness, varying the type and dimensions of cm-scale enhancements has the potential to maximise the settlement and survival of species (Firth *et al.*, 2013b). Another trial by Hall *et al.,* (2018), deployed cm-scale grooves of varying widths on granite boulders at Boscombe in Dorset and Runswick Bay in North Yorkshire. Grooves were created in arrays of two thin grooves and one larger coarser groove, measuring approximately 1cm deep and 0.3cm wide, and 1 cm deep and 2 cm wide, respectively. The intention here was to recreate naturally occurring groove and channel microhabitats on granite boulders to encourage the settlement of habitat forming species (such as *Semibalanus balanoides*), and facilitate colonisation and succession (Jenkins *et al.,* 1999; Thomsen *et al.,* 2016). The addition of grooves in this instance had a significant positive affect on the richness abundance of organisms in treated areas. After 12 months, Hall *et al.,* (2018) recorded an additional 5 taxa on grooves at Runswick Bay, and 15 taxa on grooves at Boscombe, and the addition of grooves at Runswick Bay significantly increased richness, abundance, and diversity of both floral and faunal species (Hall *et al.,* 2018). However, in both trials' cm-scale enhancements to increase physical complexity were only applied in a small number of select places. For example, Hall *et al.,* (2018) implemented arrays of grooves on only 7 boulders at Runswick Bay, whereas grooves were implemented on 24 boulders across two rock groynes at Boscombe. In comparison, Evans *et al.,* (2016) implemented 18 drill-cored rock pools.

Thus far, trials deploying cm-scale enhancements to increase physical complexity on artificial defences have been somewhat limited in scope as a result of having to retrofit enhancements to existing defences (Firth *et al.,* 2020). This has created some uncertainty among coastal planners, developers and stakeholders who perceive that existing examples of mostly small-scale applications will not perform as intended when deployed over a larger area (Evans *et al.*, 2019). Grooves inspired by those deployed by Hall *et al.,* (2018) were incorporated into the design of the Runswick Bay Coastal Protection Scheme rock armour (See Chapter 1 Section 1.6). The scheme represents a rare example of cm-scale enhancements being deployed copiously along the length of a rock armour defence (Latham *et al.*, 2020), and nearly every accessible boulder of the defence bears grooves (Pers. Obs.). As such the Runswick Bay Coastal Protection Scheme provides an ideal opportunity to monitor colonisation of the grooves designed to increase the small-scale physical complexity of the rock armour and unaltered granite rock, to determine if a more diverse floral and faunal community established over time, and to determine how community composition varied between habitat types over time. The hypotheses to be tested under this aim were;

1. Within treated and untreated substrates, S, N, H' and community similarity of sessile and mobile communities was significantly different over time.
2. S, N and H' of sessile and mobile communities from each treatment type was significantly higher at the end of the study than at the start.

3.2 Method

3.2.1 Site Description

This investigation took place on the new ecologically enhanced rock armour defence at Runswick Bay, described previously in Chapter 1 Section 1.6 and Chapter 2 Section 2.2.1. Again, sample stations where an area of substrate treated with grooves (GS) and an area of untreated substrate without grooves (US) (N = 14) were selected (See Figure 2.1 in Chapter 2 Section 2.2.1).

Only stations located in the intertidal where both treatment types were present were selected for sampling (as illustrated in Figure 3.1). All stations were moderately exposed. Care was taken to ensure that treatments at each station were located at the same tidal height and that boulder orientation was consistent (Kim and DeWreede, 1996). All samples were taken from the upper shore, which was determined using the same biological indicators as described in Chapter 2 Section 2.2.1.

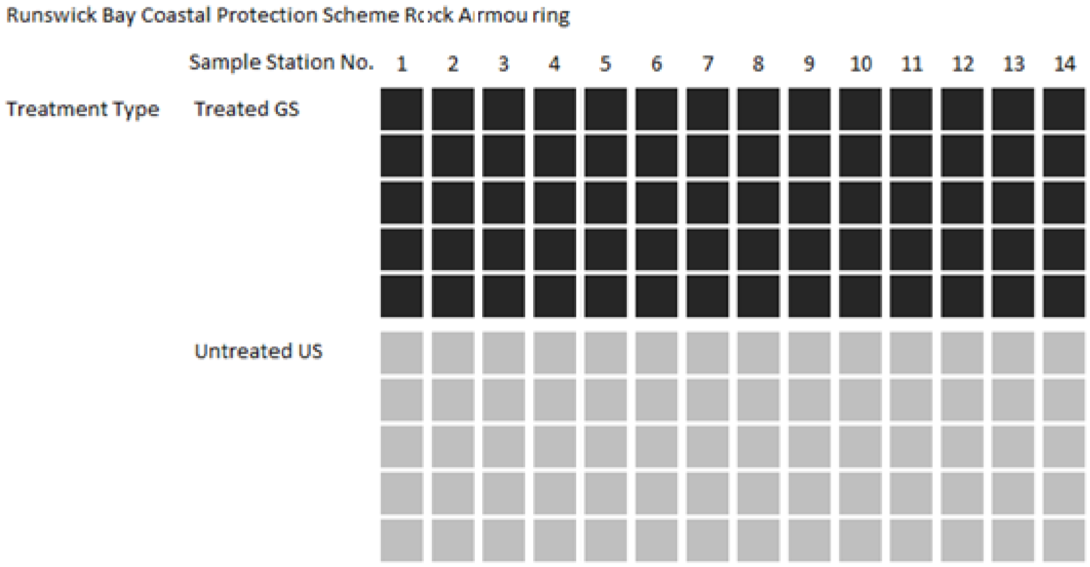


Figure 3.1 – The experimental design. 5 photo-quadrats were taken from both treatment types: treated substrates with grooves (GS) and untreated substrates without grooves (US) at each of the 14 sample stations.

3.2.1 Method

To monitor floral and faunal communities present on substrates treated with grooves (GS) and untreated substrates (US) a 5 x 5 cm quadrat was held flat against the rock. GS samples had two horizontal grooves within the bounds of the quadrat and US samples encompassed unmodified rock which was directly adjacent the GS quadrat. The use of a 5 x 5 cm quadrat was a suitable scale at which to monitor the colonisation and population dynamics of small invertebrates such as barnacles (Jenkins *et al.*, 2001; Jenkins *et al.*, 2008b). Photographs of five replicate GS and US quadrats were taken at each station using a digital camera (FUJIFILM Finepix Z80). From each photograph, the percentage cover of sessile species and counts of mobile species were recorded (Bulleri and Chapman, 2004; Chapman, 2006), as defined in Chapter 2 (Section 2.2.2). As in Chapter 2 Section 2.2.2, identification of species was facilitated using Bunker *et al.,* 2017 for algae and Cremona, Simms and Ward, 2001 for fauna.

3.2.2 Statistical Analyses

To address the second aim of this chapter, the variation in sessile and mobile communities on substrates treated with grooves (GS) and untreated substrates (US) was analysed as detailed below to answer each hypothesis individually. As in Chapter 2 Section 2.2.2, percentage cover of sessile flora and faunal species and count per unit area (number of individuals per 50cm^2) of mobile species was split and analysed separately. The DIVERSE routine in PRIMER was used to calculate S, N and H'. The Shannon-Wiener Diversity Index was used as it is representative of both the richness and the evenness of species in a sample (Spellerberg and Fedor, 2003).

The hypotheses that within treated and untreated substrates, S, N, H' and community similarity of sessile and mobile communities was significantly different over time, was tested using Kruskal-Wallis Test and subsequent Pairwise Wilcoxon Rank Sum PostHOC Test as S, N and H' sessile and mobile species data for both treatment types did not conform to a normal distribution (Kolmogorov-Smirnov test, $P < 0.05$) or have equal variances (Levene's test, $P < 0.05$). A descriptive comparison of S, N and H' of sessile and mobile species between treatments over time was also made.

To examine community similarity between treated and untreated substrates over time, a square root transformation was applied to raw sessile species data and a Bray-Curtis Similarity Matrix was generated. There were a high number of zero-samples recorded for both treatment types. This was mitigated by adding a dummy variable (value of 1) prior to generating the zero-adjusted Bray-Curtis similarity matrix (Clarke *et al.,* 2006a). A Two-Way Crossed ANOSIM with replicates was applied to the similarity matrix to test for significant differences in community similarity between both time (month sampled) and treatment type (GS and US) factors. An nMDS plot was generated from the similarity matrix to show the similarity between samples (Legendre and Gallagher, 2001). SIMPER analysis was used to identify species responsible for the dissimilarity in algal communities for each treatment type throughout the study. Relative abundance of these species was then plotted (Menge and Farrell, 1989). Diversity in animal communities between treatment types and over time was analysed by examining the S, N and H’ of grazing fauna between treatments at the start and end of the sampling period using Kruskal-Wallis Test and Pairwise Wilcoxon Rank Sum PostHOC Test. Differences in the density and structure of grazing communities throughout the duration of the study was descriptively analysed by plotting mean density of grazing species on each treatment type for each month sampled.

The hypothesis that the S, N and H’ of sessile and mobile communities from each treatment type was significantly higher at the end of the study than at the start, was completed using Mann Whitney U-test to directly compare the S, N and H’ of sessile and mobile species between the first month of sampling (February 2019) and the final month of sampling (October 2019).

Analyses was completed in Minitab 17 Statistical Software (2010), R (R Core Team, 2019), and PRIMER-e V6 Multivariate Analysis for Ecology statistical software (Clarke and Warwick, 2001).

3.3 Results

The composition of sessile species was not different between substrates types and at the end of the sampling period, both GS and US shared a similar number of taxa of sessile taxa. Six algal taxa were identified in samples from both GS and US whereas a very small number of individual *Semibalanus balanoides* was present in samples from GS only (Table 3.1). Conversely, composition of mobile taxa differed between substrate types. Three species of gastropod snail and one species of predatory whelk were identified on GS whereas mobile taxa were absent from samples taken from US (Table 3.1).

Table 3.1 – Presence and absence of species after the 14-month sampling period on Substrate Treated with Grooves (GS) and Untreated Substrate without Grooves (US) at Runswick Bay (* indicates presence at end of sampling period).

	Substrate Type	
	Substrate Treated with Grooves (GS)	Untreated Substrate without Grooves (US)
Sessile Species		
Filamentous Greens	*	*
Ulva sp.	*	*
Ulva linza	*	*
Porphyra linearis	*	*
Porphyra dioica	*	*
Fucus spiralis	*	*
Semibalanus balanoides	*	
Mobile Species		
Littorina littorea	*	
Littorina obtusata	*	
Littorina saxatalis	*	
Nucella lapillus	*	

3.3.1 Variation in Sessile Communities on Substrates Treated with Grooves and Untreated Substrates Over Time

Analyses found that within substrates treated with grooves (GS) and untreated substrates (US), mean S, N and H’ of sessile species was significantly different over time, however overall, there was no clear increase in median S, median N or median H’ of sessile species on either GS or US over time (See Appendix 2 for median and range data).

Analyses of sessile species on GS found that there was a significant difference in the median S of sessile species over time (Table 3.2a). Median S was significantly higher in May and June, and significantly lower in February compared to other months sampled (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in all cases). In addition, the median S of GS in May was significantly higher than that of September 2019 (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in all instances), (See Appendix 2 for median and range data). There was a significant difference in median N of sessile species on GS over time (Table 3.2a). Median N was significantly lower in February than in May, June, July, August and October (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in all instances). Similarly, median N was significantly lower in April relative to June (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$). There was also a significant difference in median H’ of sessile species on GS over time (Table 3.2a). Unsurprisingly, median H’ was significantly lower in February relative to May and June (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in both cases) in addition to median H’ in October being significantly lower than in May (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$).

There was a significant difference in median S of sessile species on US over time (Table 3.2b). Median S of US was significantly higher in May compared to February, September and October (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in all cases) although no other significant differences were observed (Pairwise Wilcoxon Rank Sum Test, $P > 0.05$, in all cases). Likewise, there was a significant difference in median N of sessile species (Table 3.2b) on US over time. Median N of sessile species on US was significantly lower in February compared to May, July and August (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in all cases), but was not significantly different to other months sampled (Pairwise Wilcoxon Rank Sum Test, $P > 0.05$, in all cases). There was also a significant difference in median H’ of sessile species on US over time (Table 3.2b), however, there was no clear overall increase in in median S, median N or median H’ of sessile species on US over time (See Appendix 2 for median and range data). Median H’ was significantly higher in May compared to February, October and September (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in all cases). Median H’ of sessile species was also significantly lower in September than in June and July (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in both cases).

Table 3.2 – Kruskal-Wallis for S, N (% cover) and H’ of sessile species over time (month) for a) Substrates treated with grooves (GS), b) Untreated substrates without grooves (US). NS denotes Not Significant, * denotes significant to 0.01, ** denotes significant to 0.001, *** denotes significant to <0.001.

a) Substrates Treated with Grooves (GS)

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	KW		KW		KW	
		H	P	H	P	H	P
Month	7	29.67	***	30.76	***	22.89	*

b) Untreated Substrates without Grooves (US)

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	KW		KW		KW	
		H	P	H	P	H	P
Month	7	29.22	***	27.15	***	37.28	***

At the end of the study, median N of sessile species on GS was significantly higher than at the start (Mann Whitney U-test, W = 2438.0, df = 55, P < 0.05). However median S and median H’ of sessile species on GS were not significantly higher than at the start (Mann Whitney U-test, P > 0.05, in both instances) (See Table 3.3 for median and range data).

On US, median S, median N and median H’ of sessile species were not significantly higher the end of the study than at the start (Mann Whitney U-test, P > 0.05, in both instances) (See Table 3.3 for median and range data).

Table 3.3 – Median and range data for S, N and H’ of sessile species at a) the start of the sampling and period b) the end of the sampling period for all treatment types examined (Substrates treated with grooves = GS and Untreated Substrates = US).

a) Start of the sampling period

Treatment	**Species Richness**		**Total Abundance**		**Diversity**	
	Median	Range	Median	Range	Median	Range
US	1.00	0.00 – 3.00	1.00	0.00 – 72.00	0.00	0.00 – 1.01
GS	0.00	0.00 – 4.00	0.00	0.00 – 96.00	0.00	0.00 – 1.19

b) End of the sampling period

Treatment	**Species Richness**		**Total Abundance**		**Diversity**	
	Median	Range	Median	Range	Median	Range
US	1.00	0.00 – 3.00	6.00	0.00 – 137.00	0.00	0.00 – 0.71
GS	1.00	0.00 – 3.00	15.00	0.00 – 136.00	0.00	0.00 – 0.90

Algal community similarity was found to be significantly different over time (averaged across both treatment types) (ANOSIM, Global R = 0.075, P = 0.1%) but not between treatment types (averaged across all months sampled) (ANOSIM, Global R = 0.006, P > 5 %), indicating time was a more important determinant of community composition and structure than treatment type. Algal community composition was significantly different in the first month of sampling, February, compared to every other month with the exception April (Pairwise Comparison P < 0.1 %, in all cases). Community composition in both April and May was also significantly different to every other month sampled (in all cases, P < 0.1 %). Additionally, sample months June, July, August, September and October were found to be significantly different to each other (in all cases, P < 5 %), this was due to the relative abundances of species present as identified in SIMPER analyses below. However, no significant differences were found between July and June, August and September (in all cases, P > 5%).

When plotted, there was considerable overlapping of groups and no clear clustering of samples grouped by month (Figure 3.2). The stress value given (0.07) indicated that the plot was reliable. Plotting of samples did not show clustering by treatment type as ANOSIM did not identify a significant difference, (See Appendix 3 for the MDS plot).

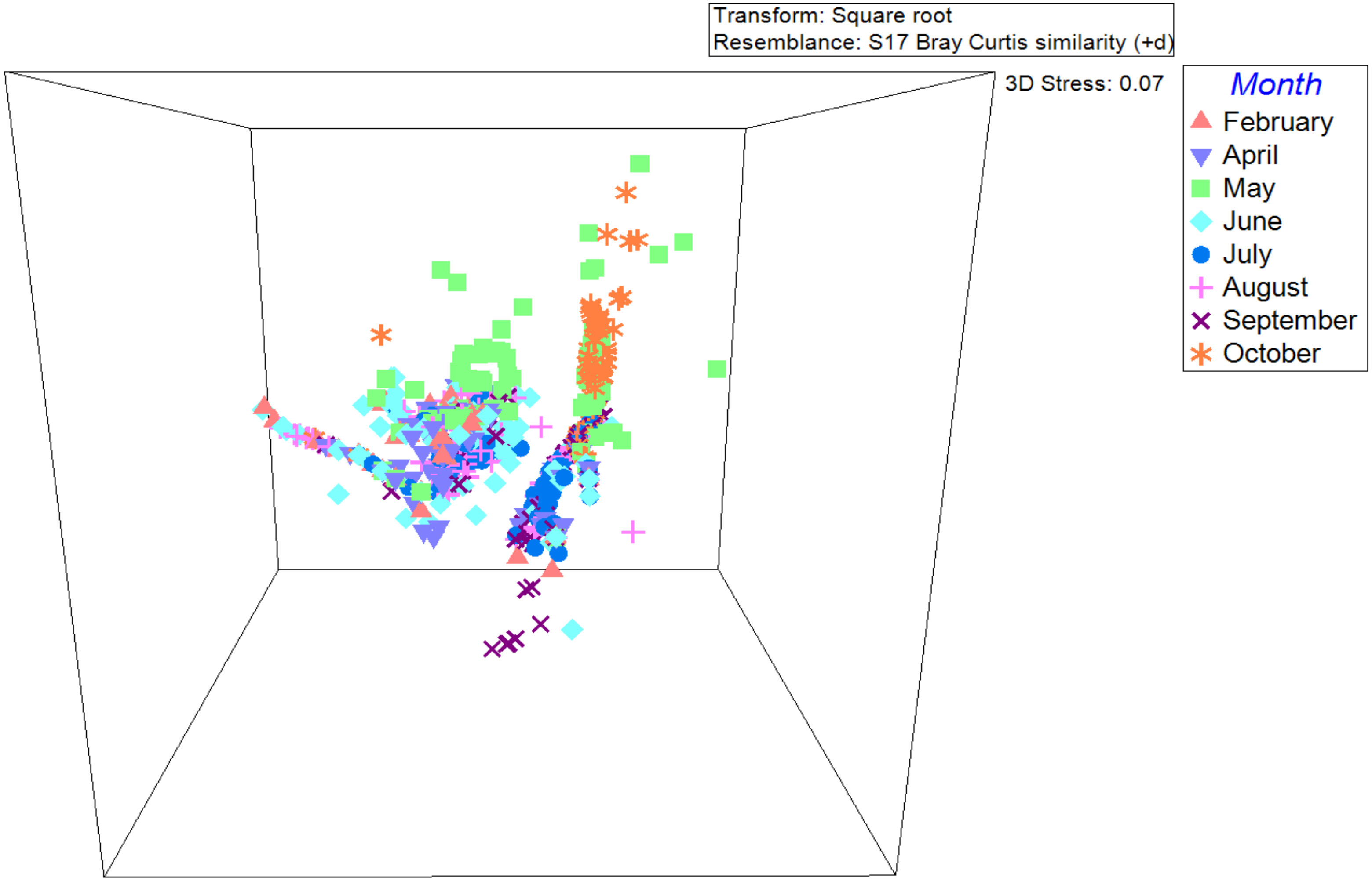


Figure 3.2 – The results of MDS analysis based on a Bray-Curtis similarity matrix of data grouped by month sampled (averaged across both treatment types) at Runswick Bay.

Similar algal communities developed on both treatment types (Table 3.4), and overall relative mean abundance of algal species increased over time on both GS and US (Figure 3.3).

SIMPER analyses identified algal species which contributed to similarity observed between treatment types over the duration of the study. *Ulva sp.*, filamentous greens and *Porphyra linearis* were identified as contributing most to the similarity observed between samples from each treatment type; together accounting for 93.25% of the overall 55.05% similarity observed between samples taken from GS and 98.96% of the overall 48.09% similarity observed between samples taken from US respectively (Table 3.4). SIMPER analyses also found *Porphyra dioica* and *Ulva linza* to contribute to the similarity observed between treatment types in different months.

Table 3.4 – SIMPER Table indicating average abundance of sessile species contributing to similarity observed between samples from a) Substrates treated with grooves (GS), b) Untreated substrates (US) (Av.Abund = mean abundance (raw % cover data), Av.Sim = Average Similarity, Sim/SD = Similarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) Grooved Substrates (GS)		**Average Similarity = 55.05 %**			
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Ulva sp.	3.11	16.45	0.72	61.62	61.62
Filamentous Greens	0.92	4.68	0.38	17.52	79.13
Porphyra linearis	1.11	3.77	0.38	14.12	93.25

b) Untreated Substrates (US)		**Average Similarity = 48.09 %**			
Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Ulva sp.	2.83	13.17	0.56	63.08	63.08
Filamentous Greens	0.90	5.08	0.34	24.33	87.41
Porphyra linearis	0.70	1.58	0.25	7.56	98.96

Ulva sp. was the predominant alga on both GS and US throughout the study and occurred in similar relative abundances on both treatments. Filamentous green algae and *Porphyra linearis* were the next most abundant species recorded. Relative mean abundance of Filamentous green algae was similar for both treatment types in each month whereas the relative mean abundance of *Porphyra linearis* was higher on GS compared to US throughout the study (Figure 3.3). Both *Ulva linza* and *Porphyra dioica* were present in low relative abundances in samples from GS and US.

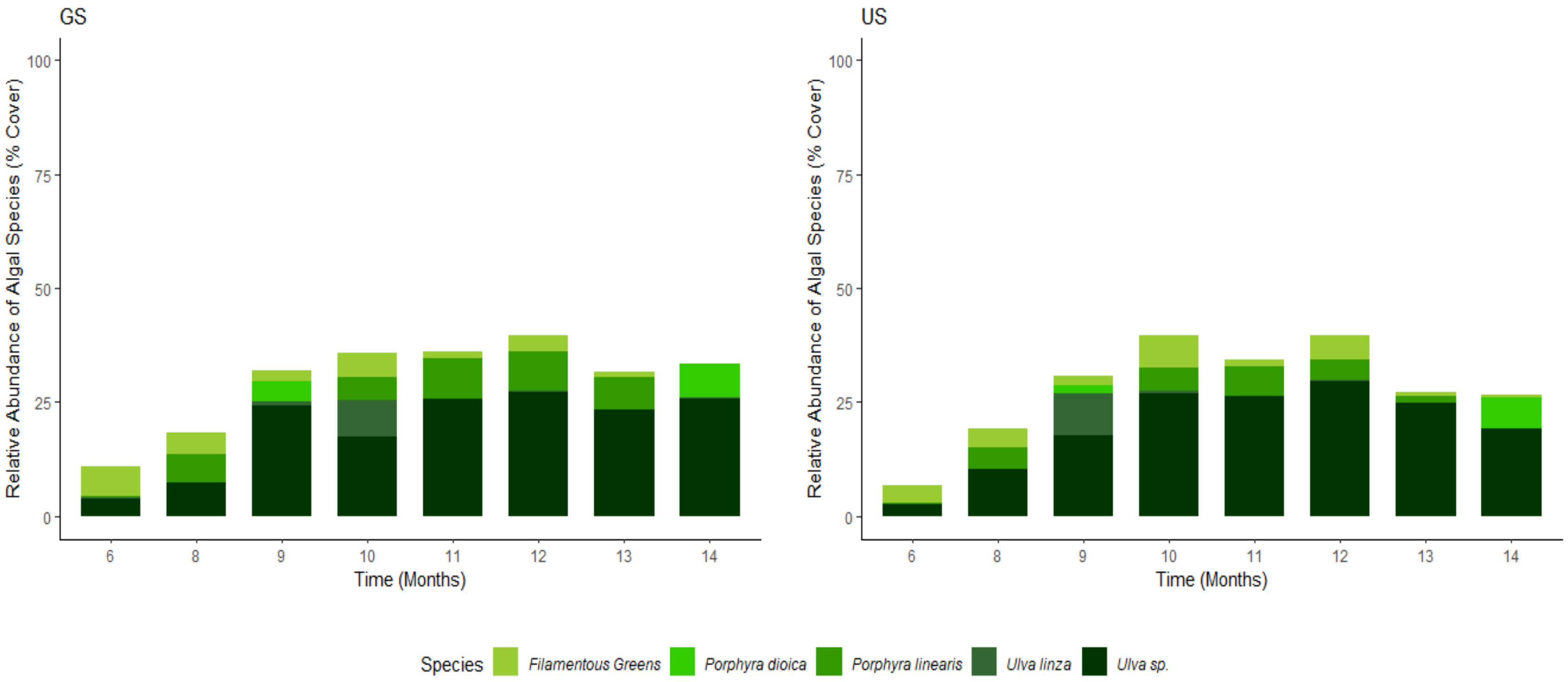


Figure 3.3 – Relative abundance (% cover) of algal species identified through SIMPER as being key contributors to the similarity observed between treatment types over time (Substrates treated with grooves = GS and Untreated Substrates = US).

3.3.2 Variation in Mobile Communities on Substrates Treated with Grooves and Untreated Substrates Over Time

As shown in Table 3.1, no mobile species were identified in samples from untreated substrates (US) at any point during the sampling period. Analyses found that within substrates treated with grooves (GS), median S, median N and median H’ of mobile species was significantly different over time, however the distribution of mobile species on this treatment type was also sparse.

Analyses of mobile assemblages on GS found significant differences in the median S (Table 3.5) and median N (Table 3.5) of mobile species over time. Pairwise differences could not be resolved to identifiy which months were significantly different due to paucity of mobile species on GS treatments (See Appendix 4 for median and range data). There was no clear overall increase in median S, median N of mobile species on GS over time. Median H’ of mobile species on GS was not found to be significantly different over time (Kruskal Wallis, $P > 0.05$).

Table 3.5 – Kruskal-Wallis for S, N (count) and H’ of mobile species over time (month) for Substrates treated with grooves (GS). Comparison of Untreated substrates without grooves (US) could not be completed due to absence of mobile species. NS denotes Not Significant, * denotes significant to 0.01, ** denotes significant to 0.001, *** denotes significant to <0.001. Comparison of

Substrates Treated with Grooves (GS)							
		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	KW		KW		KW	
		H	P	H	P	H	P
Month	7	21.49	*	21.52	*	11.48	NS

Mobile species were incredibly sparse on both treatment types at the start and at the end of the sampling period (Table 3.6). At the end of the study, median S and median N of mobile species were not significantly higher on GS than at the start (Mann Whitney U-test, $P > 0.05$, in both instances). Median H’ of mobile species on GS could not be compared as a result of data being sparse (See Table 3.6 for median and range).

As mobile species were absent from US. Analyses of median S, median N and median H’ of mobile species over time and comparisons between the start and end of the study were not undertaken, nor could any comparison be made with GS (see Appendix 4 for median and range values).

Table 3.6 – Median and range data for S, N and H' of mobile species at a) the start and b) the end of the study for both treatment types (Substrates treated with grooves = GS and Untreated Substrates = US).

a) Start of the sampling period

Treatment	**S**		**N**		**H'**	
	Median	Range	Median	Range	Median	Range
US	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
GS	0.00	0.00 – 2.00	0.00	0.00 – 3.00	0.00	0.00 – 0.64

b) End of the sampling period

Treatment	**S**		**N**		**H'**	
	Mean	SD	Median	Range	Median	Range
US	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
GS	0.00	0.00 – 1.00	0.00	0.00 – 1.00	0.00	0.00 – 0.00

Statistical comparison of the density of grazing animals between substrate types could not be made as no grazers were identified in samples from US, and densities of grazing species identified on GS were very low. *Littorina littorea* was recorded on GS however mean density of this species decreased over time. *Littorina saxatilis* was present on GS in very low densities at the beginning of the study and *Littorina obtusata* occurred on GS in the first month of sampling only.

3.4 Discussion

Using engineered grooves as a means to increase small-scale (cm) physical complexity of the rock armour at Runswick Bay did not improve biodiversity as anticipated and the number of mobile species found throughout the study was very low. Although richness (S), abundance (N) and diversity (H') of sessile and mobile species was found to vary significantly within both substrates treated with grooves (GS) and on untreated substrates (US) over time, no clear increase over time was observed on either treatment type. Additionally, species richness (S), total abundance (N), diversity (H') of sessile and mobile communities in each habitat was not significantly higher at the end of the study than at the start.

A sparseness of mobile species on US treatments was anticipated for the same reasons regarding GB habitats, discussed in Chapter 2, Section 2.4. The under-abundance of fauna on GS treatments was attributed to engineered grooves not being wide enough to allow access to hard-shelled animals. As described in Chapter 1 Section1.6, the grooves examined here were modelled on those trialled by Hall *et al.,* (2018) the openings of which measured between 0.3 – 2 cm wide and were designed to encourage settlement of the barnacle *Semibalanus balanoides* and limpet *Patella vulgata*. Where Hall *et al.,* (2018) had created an array of two thin grooves and one wide groove, grooves deployed in this study were not widened and measured only 0.3cm wide. The trial by Hall *et al.,* (2018) lasted for 12 months and is therefore comparable to the present study. Although the grooves deployed in this instance follow the design of the thinner grooves in Hall's trial, the use of thin grooves exclusively precluded the use of this microhabitat by marine invertebrates bigger than 3 mm in this instance. For example, common upper-shore intertidal grazers *Patella vulgata* and *Littorina littorea* are understood to have shell lengths of approximately 0.2 mm (Smith, 1935; Lewis and Bowman, 1975) and 0.3 mm (Thorson, 1946), respectively at metamorphosis. However, both species are capable of quickly growing their adult shells in the months following metamorphosis, increasing to 4 – 5 mm in size (Moore, 1937; Blackmore, 1969). *Littorina littorea* have been documented to grow to 5 mm after only 2 months and to 10 mm after 1 year (Moore, 1937; Williams, 1964), which may explain why this species became absent in GS treatments over time. In addition, it was possible that the use of thin grooves installed higher on the defence did not provide sufficient protection from harsh conditions in the upper shore artificial habitat. Grooves implemented by Hall *et al.,* (2018) had a significantly higher count of *Semibalanus balanoides* after 12 months, whereas *Semibalanus balanoides* was rare on both GS and US treatment types despite recruitment having taken place in other locations at the study site (Pers. Obs.).

In the present study, both GS and US treatments had a sustained coverage of filamentous and ephemeral algae throughout the study period (Figure 3.3). Algal community composition was not significantly different between treatments but did differ significantly over time as treatments underwent colonisation and succession (Benedetti-Cecchi and Cinelli, 1996). Similar assemblages of hardy ephemeral species such as *Ulva sp.* and *Porphyra sp*. were present on both treatment types in similar relative abundances throughout the study (Figure 3.3). Sustained coverage coupled with an absence of grazers on both treatments, likely slowed the succession of species within the habitat. For example, grazers would feed on ephemeral algae thus clearing space for barnacle spat to settle, around which more complex algal communities would develop (Benedetti-Cecchi, 2000b). Without grazers filamentous and ephemeral algae acted as a barrier to barnacle settlement (Hargenrader, 2018), therefore it was no surprise that barnacle settlement rates were low on both treatment types while cover by ephemeral algae was so high. Barnacle settlement rates are known to vary according to environment and are driven by availability of free space (Noda *et al.,* 1998; Hargenrader, 2018). Grazing species clear space for barnacles to settle by removing algae from substrates while foraging (Ansell, Gibson and Barnes, 2002) and while grazing animals were absent from GS treatments the algae continued to inhibit barnacle settlement. While Hall *et al.,* (2018) did not directly compare the effectiveness of thin and wide grooves in their 2018 study they did show that using grooves of varying size can vastly improve invertebrate diversity.

Despite the results presented here showing that species richness (S), total abundance (N), diversity (H’) and community similarity of sessile and mobile communities differed significantly over time within treated and untreated substrates, there was no significant increase in species richness (S), total abundance (N), diversity (H’) of sessile and mobile communities on each treatment type at the end of the study than at the start. This study highlights the need for enhancements to be deployed correctly in order to deliver maximum ecological benefits. The small-scale (cm) physical complexity of the rock armour was increased by adding grooves; however, in this instance, these features provided only limited refuge for marine invertebrates. Further monitoring of the treatments over a longer time frame may find that the community changes as succession progresses. It is also possible that with time and prolonged environmental weathering, the edges of engineered grooves in this study may fracture and the rock may chip away (Coombes, 2014) causing the entrances to widen, and creating a more useful habitat for mobile organisms. However, the physical complexity aspect of this investigation raises questions about fine-scale physical complexity of granite substrates, which is examined in Chapter 4.

Chapter 4 Does substrate rugosity affect diversity and community structure at one site in Scarborough North Bay, and at multiple locations over a regional scale?

4.1 Introduction

Material choice is an important aspect in ensuring the stability and longevity of coastal defences, in addition to being an important determinant of diversity in artifical intertidal environments (Mcglashan and Williams, 2003; Reeve *et al.*, 2012). The fine-scale physical complexity (mm) of a substrate, including surface texture and roughness, is known to impact structure and diversity of invertebrate and algal communities (Minchinton and Scheibling, 1993; Hutchinson *et al.,* 2006). The rugosity of a surface, defined as the degree of fine-scale (mm) unevenness or topographic complexity (Luckhurst and Luckhurst, 1978; Collins et al., 2013), can greatly influence patterns of distribution by impacting the settlement and survivorship of invertebrate larvae (such as newly settled barnacles) and algal spores (Wahl and Hoppe, 2002; Sueiro *et al.*, 2011). Minute depressions, indentations and peaks on rugose substrates may provide small refuges for recently settled algal spores (Fletcher and Callow, 1992) and offer some protection from predation by grazers (Lubchenco, 1982). Substrate lithology and mineral composition is also thought to have some influence in structuring benthic and epilithic communities (Holmes, Sturgess, and Davies, 1997; Canessa et *al.,* 2019). For example, lithological differences between rock types, including mineral composition, thermal capacity, porosity, colour (Yule and Walker, 1984; Raimondi, 1988; Herbert and Hawkins, 2006), can produce differences in the level of cover by barnacles, particularly in the genera *Chthamalus* and *Balanus* (Holmes, Sturgess, and Davies, 1997; Canessa *et al.,* 2019). Shallow-water algal assemblages have also indicated a sensitivity towards substrate lithology (Bavestrello et al., 2018). However, the structuring effects of substrate mineralogy in intertidal benthic communities has been somewhat neglected in the literature and accounts of the importance of mineralogy on structuring communities conflict (Canessa *et al.,* 2019).

Trials which have previously investigated fine-scale complexity as a means to ecologically enhance coastal defences have largely used concrete tiles (MacArthur *et al.,* 2018), (Chapter 1, Section 1.5). However, granites are also widely used in coastal defence building (Burden *et al.,* 2020; MacArthur *et al.,* 2020). Granite was one of five materials examined in a study by Sempere-Valverde *et al.,* in 2018, which examined colonisation of different substrates by algae. The surface rugosity of sandstone, limestone, granite, concrete, and slate was quantified by creating latex profiles of each surface, and colonisation of tiles by intertidal and subtidal biota was monitored. Sempere-Valverde *et al.,* (2018) found that granite and sandstone tiles, which had a greater surface roughness than other substrates examined, supported a greater abundance and richness of filamentous algae suggesting that greater rugosity enhanced algal colonisation of the tiles. Similarly, a laboratory trial by Hutchinson *et al.,* in 2006, examined marine biofilm accumulation on granite tiles with different grades of surface rugosity, and found that biofilm cover was higher on more rugose granite substrates as filamentous microalgae had naturally accumulated in and around depressions in the substrate surface. Hutchinson *et al.,* (2006) also examined the effect of surface rugosity on grazing activity and found that rugosity strongly impacted grazing by limiting how effectively the radula of a grazing animal could remove algae. The structural differences in the radula of different species determined how successfully they could graze a particular substrate. For example, patellid limpets possess docoglossoan radula with few teeth per row (Padilla, 1985). Teeth are fixed to the radular ribbon and cannot be articulated (Fretter and Graham, 1962). In the trial by Hutchinson *et al.,* (2006), the limpet *Cellana toreuma* which had a docoglossoan radula significantly reduced biofilm cover on smooth substrates but was less able to remove biofilm from rougher, more pitted substrates. In contrast, chitons possess a polyplacophoran radula, which is composed of a bilaterally symmetrical row of teeth with differing shapes (Brooker and Shaw, 2012). The arrangement of teeth is the same in each row of teeth along the length of the radula (Brooker and Shaw, 2012). In the Hutchinson *et al.,* (2006) trial, the chiton *Acanthopleura japonica* removed more biofilm from pitted surfaces than *Cellana toreuma* due to its polyplacophoran radula being more able to access small pits and crevices where biofilm was trapped.

The surface texture of granite used in coastal defence works is often determined by the way the material was quarried (MacArthur *et al.,* 2020). Quarried boulders which have been cut to size mechanically typically have cleaner edges and smoother surfaces (Mancini *et al.,* 2001), whereas boulders extracted using explosives often have rougher surfaces where the rock has naturally fractured or possess features such as blast holes or lines (Yarahmadi *et al.,* 2019; MacArthur *et al.,* 2020). Both smooth machine-cut granite boulders and rough fractured granite boulders were present in rock armouring at North Bay in Scarborough, North Yorkshire. The present study examined the rugosity of substrate types (smooth granite, rough granite and sandstone) at North Bay in Scarborough, to determine whether diversity and structure of sessile and mobile communities differed between substrate types.

The first aim of this chapter was to determine whether there was a difference in the rugosity, species richness (S), total abundance (N), Shannon-Wiener diversity (H’) and community similarity of sessile and mobile communities between the substrate types at North Bay (Rough granite, Smooth granite and Sandstone). The specific hypotheses to be tested under this aim were;

1. Rugosity was significantly different between substrata at North Bay.
2. There was a significant correlation between overall rugosity and S, N and H' of sessile and grazing communities at each tidal height.
3. S, N, H' and community similarity of sessile and grazing communities was significantly different between substrate types at each tidal height.

The study also examined the rugosity of five granite boulder defences at locations in North and East Yorkshire in order to determine whether rugosity and community similarity differed between locations. Therefore, the second aim of this chapter was to determine whether there was a difference in the rugosity of granite substrates between five rock armour defences from locations across North and East Yorkshire, and whether rugosity affected community similarity between locations. The specific hypotheses to be tested under this aim were;

1. Rugosity was significantly different between five granite boulder defences in North and East Yorkshire.
2. Similarity of sessile and grazing communities was significantly different between the five granite boulder defences in North and East Yorkshire.

4.2 Method

4.2.1 Site Description

To address the first aim of this study, the rugosity of three substrate types at North Bay in Scarborough, North Yorkshire were examined. North Bay was the only location examined in this part of the investigation due to there being three distinct substrate types present.

North Bay, Scarborough

North Bay is a bay to the north of the town of Scarborough with a 2 km long beach (TA 04530 89235). The granite rock armour site surveyed at this location was constructed at the southern end of North Bay in 2002 as part of a wider coastal defence scheme (Scarborough Borough Council, 2010). North Bay was chosen to examine rugosity on a local scale as the rock armouring at this location had granite boulders with visually distinct surface textures (Figure 4.1). An equal number of samples were taken from smooth granite boulders which had smooth machine-cut surfaces with very little surface texture (Figure 4.1a), and rough granite boulders with textured surfaces which had been cut using explosives (Scarborough Borough Council, 2010) (Figure 4.1b), in addition to natural sandstone boulders located adjacent on the mid shore. To control for the effect of shore height on community composition, mid and upper shore heights were compared independently (as illustrated in Figure 4.2. This location had clear mid and upper shore regions, which were determined using biological indicators (as described in Chapter 2, Section 2.2.2). The rock armouring is approximately 700 m in length and extends from the southern end of North Bay beach around Scarborough Castle Headland (Figure 4.5a), where the granite boulders are gradually replaced with larger concrete acropodes (Scarborough Borough Council, 2010).

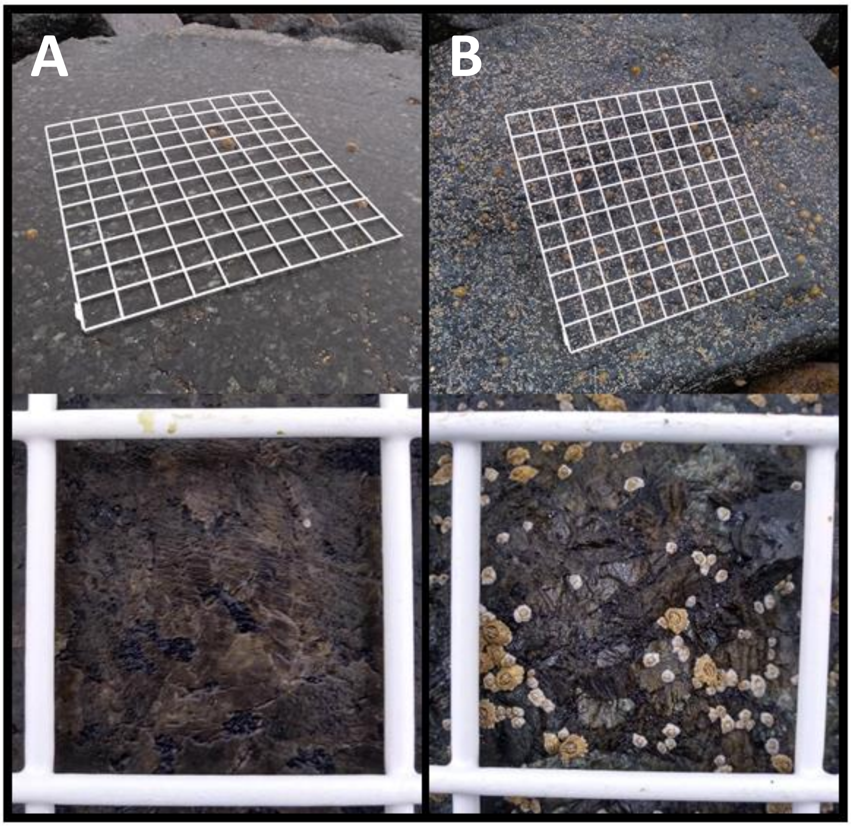
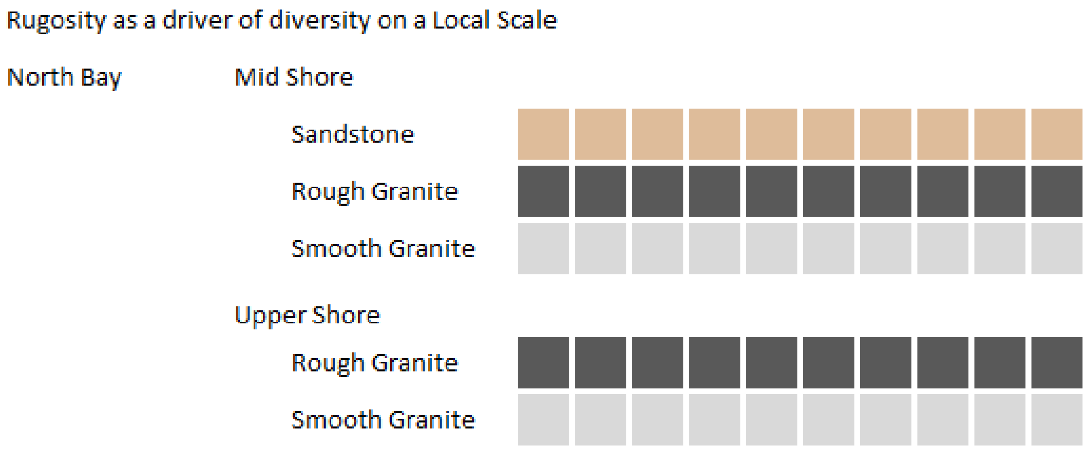


Figure 4.1 – Granite boulders at North Bay; a) Smooth granite substrates with very little texture and b) Rough granite substrates with visibly more surface texture.



Rugosity as a driver of diversity on a Local Scale

North Bay
Mid Shore
Sandstone
Rough Granite
Smooth Granite
Upper Shore
Rough Granite
Smooth Granite

Figure 4.2 – The experimental design where 10 boulders of each substrate type were selected at Mid shore height; Sandstone, Rough Granite and Smooth Granite and at Upper shore height; Rough Granite and Smooth Granite.

To determine whether rugosity differed between granite substrates from rock armour defences across North and East Yorkshire, and whether rugosity affected community similarity between sites, the second part of this study examined five granite rock armour defences from four locations in North and East Yorkshire; Scarborough North Bay, Scarborough South Bay (Holbeck), Withernsea and Runswick Bay. Locations were selected to be representative of granites used in coastal protection strategies in the region (Figure 4.3). In this investigation only granite boulders at each rock armour site were sampled and shore height was controlled for by only sampling from the upper shore area of each defence, as illustrated in Figure 4.4. For this investigation, boulders at all sites were randomly selected for sampling. All sites were surveyed between July and August 2019.

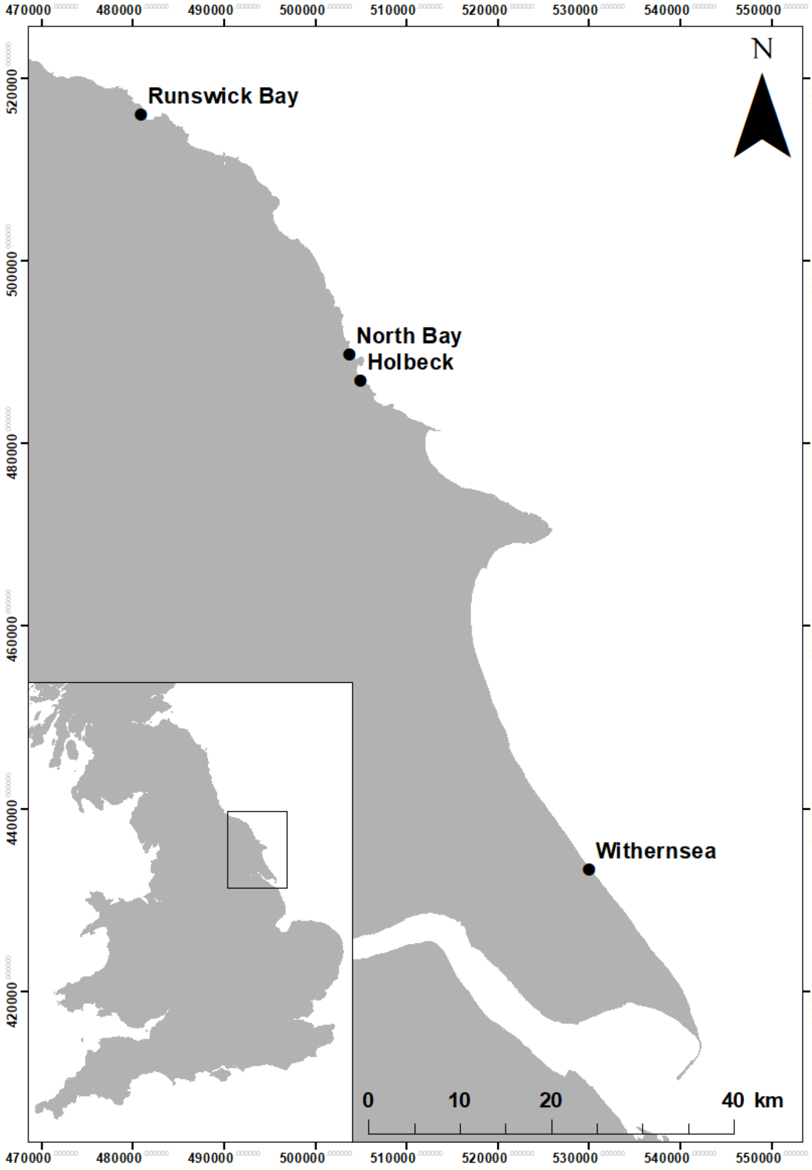


Figure 4.3 – A further four granite rock armour defences from three locations (additional to North Bay) along the East Riding of Yorkshire and North Yorkshire coastline were examined.

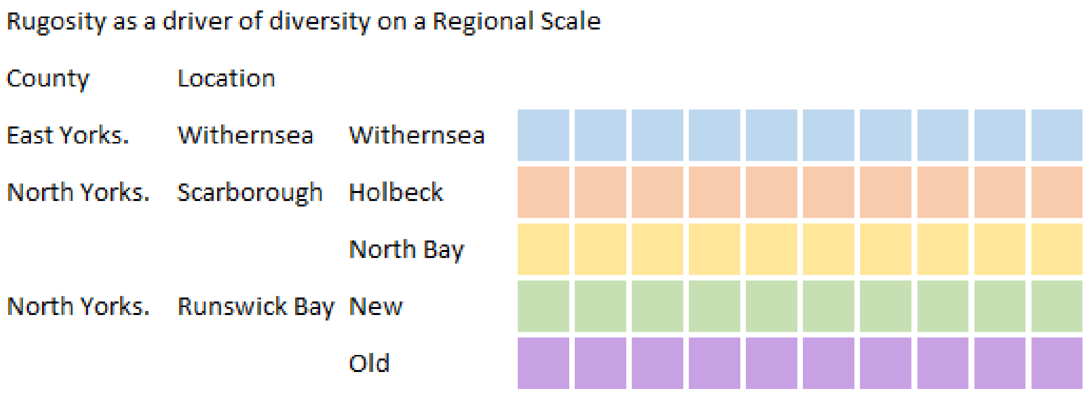


Figure 4.4 – The experimental design where 10 boulders from the upper shore of the rock armour defences at each location; Withernsea, Holbeck, North Bay and from 2 defences (Old and New) at Runswick Bay.

Withernsea

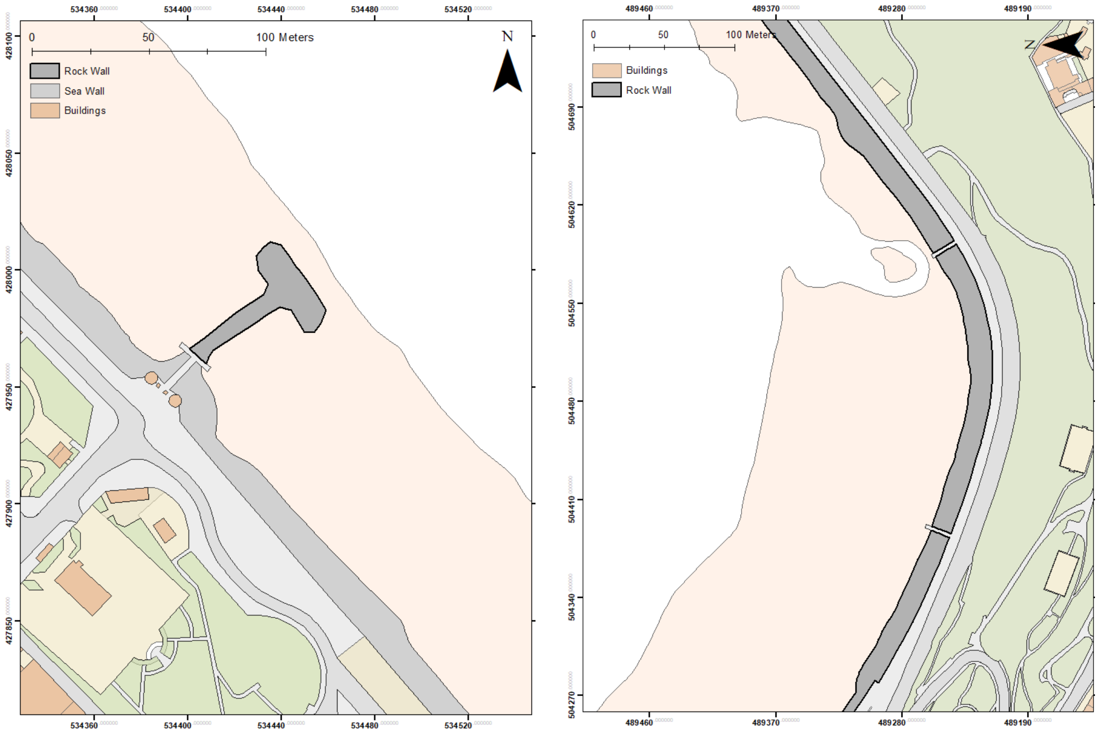
The popular tourist town of Withernsea is located on the Holderness coast in the East Riding of Yorkshire (TA 34436 27989), approximately 15 km north of the Spurn Peninsula and mouth of the Humber estuary. The area is widely renowned for its high rates of erosion and coastal retreat and defences have been in place at this site since 1875 (East Riding of Yorkshire Council, 2006; Pye and Blott, 2015). The rock armour site sampled at this location was located in front of the central promenade gates on the seafront (Figure 4.5a), and underwent extensive general repairs in 2017 (East Riding of Yorkshire Council, 2017). Samples were taken from the upper shore of this defence only.

Holbeck, Scarborough

The rock armour site at Holbeck in Scarborough (South Bay), North Yorkshire (TA 05003 87094) was constructed from Norwegian granite boulders following a large landslip in 1994 to stabilise the debris flow from the hillside (Scarborough Borough Council, 2010). The rock wall was located at the southern end of Scarborough South Bay beach and adjoins a rocky intertidal platform that extends around the base of the wall (Figure 4.5c). Samples were taken from the upper shore only, which was determined using biological indicators (as in Chapter 2, Section 2.2.2).

Runswick Bay

Two rock amour sites were sampled at this location (Figure 4.5d). See Chapter 2, Section 2.2.1 for a description of the Runswick Bay location. The first defence site examined at this location (Runswick Old) was located on the beach to the south of Runswick Bay village. It was constructed from Durham Granite in 2000 to reduce wave over topping and provide protection to the boat and car parking areas (Scarborough Borough Council, 2019). The second defence site (Runswick New) examined at this location was located on the rocky shore to the north of the village. This structure was constructed in 2018 from Norwegian granite (JBA Consulting, 2017a), see Chapter 1, Section 1.6 for full description of the new rock armouring. Samples from the Runswick New site were taken from boulders which had not been enhanced or modified. Samples were taken from the upper shore only of both defences.


a) Withernsea

b) North Bay


c) Holbeck

d) Runswick Bay

Figure 4.5 – Five Rock armour structures at four locations across North and East Yorkshire were sampled to examine rugosity over a regional scale for the second part of this study.

4.2.2 Method

To investigate rugosity as a driver of diversity on a local scale at North Bay only, samples were taken from each substrate type (Rough granite, Smooth granite and Sandstone) at each shore height (N=10). GPS coordinates of each station were logged using a Garmin eTrex10 Handheld GPS. Rough granite and smooth granite substrates at mid and upper shore height were sampled, however sandstone substrates were present on the mid shore only.

To investigate rugosity across a regional scale, samples were taken from the upper shores (N=10) of granite boulder defences at Holbeck, Runswick Old, Runswick New and Withernsea. A subset was created from 10 samples pooled from upper shore boulders at North Bay (5 rough and 5 smooth), (Evans *et al.*, 2016).

The following protocol was the same for both investigations. Shore height was determined using biological indicators (as in Chapter 2, Section 2.2.2), where *Fucus spiralis* was a marker of upper shore environments (White, 2008a) and *Fucus vesiculosus* indicated mid shore environments (White, 2008b). 50 x 50 cm gridded quadrats were used to take samples from the seaward-facing surfaces of randomly selected boulders, to ensure consistency between samples (Kim and DeWreede, 1996). An estimate of the percentage cover of algal and sessile animal species, and a count of mobile species was collected from each quadrat (Bulleri and Chapman, 2004; Chapman, 2006). Identification of species was facilitated using Bunker *et al.,* 2017 for algae and Cremona, Simms and Ward, 2001 for fauna.

The fine-scale physical complexity of each substrate was quantified by generating a rugosity index value for each sample. The rugosity index provided a numerical measurement of the topographic complexity of each substrate (Kovalenko *et al.,* 2012; Aguilera *et al.,* 2014). In order to quantify the rugosity of the substrate for each sample taken, a chain-and-tape method was used (Beck, 1998) as this approach has proved an effective way of measuring complexity in intertidal environments previously (Beck, 2000; Aguilera *et al.*, 2016). A 1 m length of stainless steel 1.5 mm fine-link chain was draped across a known linear distance (50 cm as marked out by the quadrat). The chain was draped in a straight line across the contours of the substrate surface. The chain was pressed into any peaks or depressions and not deployed over encrusted biota. The length of chain was measured, and the rugosity index value of the substrate for each sample was calculated using the following equation (Friedman *et al.*, 2012):

$$\text{Rugosity} = \text{Chain Length (cm)} / \text{Linear Distance (cm)} \qquad (1)$$

4.2.3 Statistical Analyses

To analyse substrate types (Rough granite, Smooth granite and Sandstone) at North Bay, percentage cover data of sessile species and count per unit area (number of individuals per 50cm^2) of grazing species was split and analysed separately. Only grazing species were examined as only grazing invertebrates *Patella vulgata*, *Littorina littorea*, *Littorina obtusata* and *Littorina saxatilis* were present across samples. To control for the effect of shore height, comparisons between substrate types will be made for mid and upper shores separately. The DIVERSE routine in PRIMER was used to calculate S, N and H'. The Shannon-Wiener Diversity Index was used as it is representative of both the richness and the evenness of species in a sample (Spellerberg and Fedor, 2003).

To answer the first hypothesis that rugosity was significantly different between substratum types at North Bay, rugosity data collected from substrate types was tested for conformation to a normal distribution and homogeneity of variances using Kolmogorov-Smirnov test and Levene's test, respectively (Dytham, 2011). Rugosity data was found to be normally distributed ($P > 0.05$) and have equal variances ($P > 0.05$) meaning that One-Way Analysis of Variance (ANOVA) and Tukey PostHOC tests were appropriate to compare rugosity between substrate types (Dytham, 2011). To test whether there was a significant correlation between overall rugosity and S, N and H' of sessile and grazing communities at each tidal height, the following procedure was adopted: Sessile and grazing S, N and H' data from mid and upper shores was analysed separately to account for natural zonation and distribution of species between shores (Sadchatheeswaran *et al.,* 2018). Data did not conform to a normal distribution ($P < 0.05$) and was therefore ranked. The relationship between overall rugosity and S, N and H' of sessile and grazing species for each tidal height was analysed using a Spearman's Rank-Order Correlation (Dytham, 2011).

The third hypothesis that S, N and H' of sessile and grazing communities was significantly different between substrate types at each tidal height, was tested using One-Way ANOVA to compare mid shore substrates (Rough granite, Smooth granite and Sandstone) and Mann-Whitney U-test to compare upper shore substrates (Rough granite and Smooth granite). N and H' sessile species data was found to be non-normal ($P < 0.05$) but have equal variances ($P < 0.05$). S, N and H' grazing species data were all found to be non-normal ($P < 0.05$), with S data having equal variances ($P > 0.05$) whereas N and H' data did not ($P < 0.05$). One-Way ANOVA was applied to S, N and H' sessile and grazing species data to identify significant differences between substrate types at mid shore height (Rough granite, Smooth granite and Sandstone), ANOVA models were validated using the procedure described in Chapter 2, Section 2.2.3. The significance level alpha was set to 0.01 (Kim, 2017). Where One-Way ANOVAs were significant, a Tukey PostHOC test was applied. Where One-Way ANOVAs could not be validated, Kruskal-Wallis and Pairwise Wilcoxon Rank Sum PostHOC Tests, the non-parametric equivalent, were applied instead (Dytham, 2011). Mann Whitney-U tests were used to compare differences in S, N and H' sessile and grazing species data between substrate types at upper shore height (Rough granite and Smooth granite), (Dytham, 2011).

To examine community similarity between substrate types overall a Bray-Curtis Similarity Matrix was generated from raw percentage cover sessile species data which had been square-root transformed to down-weight the influence of very abundant species (Clarke *et al.,* 2006b). An MDS plot was produced from the similarity matrix to visualise similarity between samples (Legendre and Gallagher, 2001). A One-Way ANOSIM was used to identify significant differences in community similarity overall between substrate types, followed by SIMPER analyses to identify differences in community similarity between substrate types and across tidal heights. Differences in diversity of animal communities were identified by plotting and comparing density of grazing species between substrate types.

For the second part of this investigation, determining whether rugosity of granite substrates differed between the five sites; Holbeck, North Bay, Runswick Old, Runswick New and Withernsea, and whether rugosity affected community similarity between sites, the following analyses was completed. To answer the hypothesis that rugosity was significantly different between the five sites across North and East Yorkshire, One-Way ANOVA and Tukey PostHOC tests were used as rugosity data was both normally distributed ($P > 0.05$) with equal variances ($P > 0.05$). To test whether community similarity was significantly different between the five sites, raw percentage cover sessile species data was square-root transformed to down-weight very abundant species (Clarke *et al.,* 2006b). Transformed data was used to generate a Bray-Curtis Similarity Matrix and MDS plot. A One-Way ANOSIM was applied to the similarity matrix to identify significant differences in community similarity between sites. SIMPER analysis was then used to identify which sessile species were responsible for the differences observed. Diversity in animal communities was analysed by examining the S, N and H' of grazing fauna between sites. S, N and H' grazing species data were all found to be non-normal ($P > 0.05$). S data was found to have equal variances ($P > 0.05$) and was tested using One-Way ANOVA and Tukey PostHOC tests subject to model validation. N and H' data did not possess equal variances ($P < 0.05$) and so were tested using Kruskal-Wallis and Pairwise Wilcoxon Rank Sum PostHOC tests (Dytham, 2011). Density of grazing species between was plotted and compared.

4.3 Results

For the first investigation in this chapter, which focussed soley on substrates with different rugosities at North Bay, a higher number of sessile taxa were identified on sandstone substrates than on all granite substrates (Table 4.1). Algal species were present on only one of the granite substrates examined (rough granite at upper shore height). *Semibalanus balanoides* was identified in samples from smooth granite from both mid and upper shore, on rough granite from the mid shore and on sandstone substrates but was absent from rough upper shore granite substrates. *Patella vulgata* were present on all substrate types (Table 4.1). Sandstone substrates had the highest count of mobile taxa (4), followed by rough upper shore granite substrates (3). Both rough and smooth mid shore granite substrates shared 2 taxa and only *Patella vulgata* was identified on smooth upper shore granites.

Table 4.1 – Presence and absence table of species identified in samples (N= 10) from each substrate type across mid and upper shore height at North Bay only (* indicates presence).

	Substrate Type				
	Sandstone (Mid only)	Rough Granite		Smooth Granite	
		Mid	Upper	Mid	Upper
Sessile Species					
Ulva linza	*		*		
Ulva lactuca	*				
Filamentous Greens			*		
Porphyra sp.	*		*		
Fucus vesiculosus	*				
Ceramium sp.	*				
Osmundea pinnatifida	*				
Pink Crusts	*				
Rhodochorton purpureum	*				
Verrucaria maura	*				
Rhodothamniella floridula	*				
Lomentaria articulata	*				
Semibalanus balanoides	*	*		*	*
Mobile Species					
Patella vulgata	*	*	*	*	*
Littorina littorea	*				
Littorina obtusata	*				
Littorina saxatalis			*		

For the second investigation in this chapter, comparing granite boulder rugosity and community composition between five rock armour defences across North and East Yorkshire, the highest number of sessile taxa were identified at the Runswick Old and Withernsea defences (6 taxa each), (Table 4.2). The North Bay defence, as examined in this investigation, had the same number of sessile taxa as the Holbeck defence (4 taxa each). The North Bay defence had the highest number of mobile species of all defences examined (4 taxa). Runswick New had the lowest number of both sessile and mobile taxa (Table 4.2).

Table 4.2 – Presence and absence table of species identified in samples (N= 10) from five rock armour defences across North and East Yorkshire. (* indicates presence).

	Site				
Sessile Species	Holbeck	North Bay	Runswick New	Runswick Old	Withernsea
Ulva sp.	*		*		*
Ulva linza		*		*	
Filamentous Greens	*	*	*		
Porphyra sp.		*	*		*
Fucus spiralis	*				*
Fucus vesiculosus				*	
Aoudinella sp.				*	
Mastocarpus stellatus				*	
Rhodochorton purpureum				*	
Semibalanus balanoides	*	*		*	*
Austrominius modestus					*
Mytilus edulis					*
Mobile Species					
Patella vulgata	*	*		*	*
Littorina littorea			*		*
Littorina obtusata	*				
Littorina saxatalis		*		*	

4.3.1 Variation in Sessile Communities Between Substrate Types at North Bay, North Yorkshire.

There was a significant difference in mean rugosity between substrate types at North Bay (ANOVA, $F_{2, 47} = 43.05$, $P < 0.01$). Mean rugosity was significantly greater on sandstone substrates compared to both rough and smooth granite substrates (Tukey $P < 0.05$, in both cases). Mean rugosity of rough granite substrates was significantly greater than that of smooth granite substrates (Tukey $P < 0.05$) (Table 4.3). There was no significant difference in mean rugosity within substrate types between shore heights (Tukey $P > 0.05$) (Table 4.3).

At mid shore height, overall rugosity showed a significant positive correlation with S (Spearman rank Correlation Coefficient, r = 0.656, df = 28, $P < 0.001$), N (Spearman rank Correlation Coefficient, r = 0.7.13, df = 28, $P < 0.001$) and H' (Spearman rank Correlation Coefficient, r = 0.627, df = 28, $P < 0.001$) of sessile species. However, at upper shore height, overall rugosity showed a non-significant correlation with S, N or H' of sessile species (Spearman rank Correlation Coefficient, $P > 0.05$, in all cases).

Table 4.3 – Mean rugosity values for substrate types examined at North Bay.

Mean Rugosity	Mid Shore		Upper Shore	
Substrate	Mean	SD	Mean	SD
Sandstone	1.12	0.04		
Rough Granite	1.08	0.02	1.07	0.02
Smooth Granite	1.04	0.02	1.03	0.02

At mid shore height, there were significant differences in median S (Table 4.4), median N (Table 4.4) and mean H' (Table 4.4) of sessile species between substrate types. Median S was significantly higher on sandstone substrates than on rough and smooth granite substrates (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$), as was mean H' (Tukey > 0.05). Median N was also significantly higher on both sandstone and rough granite substrates than smooth granite substrates (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$), but sandstone and rough granite substrates were not significantly different to each other (Pairwise Wilcoxon Rank Sum Test, $P > 0.05$). See Table 4.5 for descriptive data.

At upper shore height, no significant difference in median S or median N of sessile species between substrate types was found (Mann Whitney U-test, $P > 0.05$, in both cases). Median H' could not be compared between substrate types due to a high number of zero-samples and single species assemblages recorded on smooth granite substrates (Table 4.5).

Table 4.4 – One-Way ANOVA and Kruskal-Wallis for S, N (% cover) and H' of sessile species for Mid shore Substrates examined at North Bay. NS denotes Not Significant, * denotes significant to 0.01, ** denotes significant to 0.001, *** denotes significant to <0.001.

Mid Shore							
		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	KW		KW		AN	
		H	P	H	P	F	P
Substrate	2	26.08	*	15.38	*	68.5	*

Table 4.5 – Descriptive statistics of S, N (% cover) and H' of sessile species for substrate types examined at North Bay. Where One-Way ANOVA was applied, mean and standard deviation (SD) have been reported, where Kruskal-Wallis or Mann Whitney U-tests were used median and range have been reported.

a) Species Richness (S)

Substrate Type	**Mid Shore**		**Upper Shore**	
	Median	Range	Median	Range
Sandstone	7.50	3.00 – 10.00		
Rough Granite	1.00	1.00 – 1.00	2.00	0.00 – 3.00
Smooth Granite	1.00	0.00 – 1.00	1.00	0.00 – 1.00

b) Total Abundance (N)

Substrate Type	**Mid Shore**		**Upper Shore**	
	Median	Range	Median	Range
Sandstone	71.50	58.00 – 118.00		
Rough Granite	55.00	15.00 – 91.00	1.75	0.00 – 100.00
Smooth Granite	7.50	0.00 – 87.00	2.00	0.00 – 30.00

c) Shannon-Wiener Diversity (H')

Substrate Type	**Mid Shore**		**Upper Shore**	
	Mean	SD	Median	Range
Sandstone	0.92	0.35		
Rough Granite	0.00	0.00	0.57	0.00 – 0.79
Smooth Granite	0.00	0.00	0.00	0.00 – 0.00

Sessile community similarity was found to be significantly different between substrate types overall (ANOSIM, Global R = 0.699, P = 0.1%). Pairwise comparison found algal community similarity to be significantly different between all substrate types (in all cases, P < 0.3%), with the exception of smooth mid and smooth upper shore granite substrates (P = 24.7 %). When plotted, samples from sandstone and rough upper shore granite substrates formed distinct clusters which did not overlap with those of other substrate types or each other (Figure 4). Remaining samples formed no distinct clusters. The stress value given (0.02) indicated that the plot was very reliable.

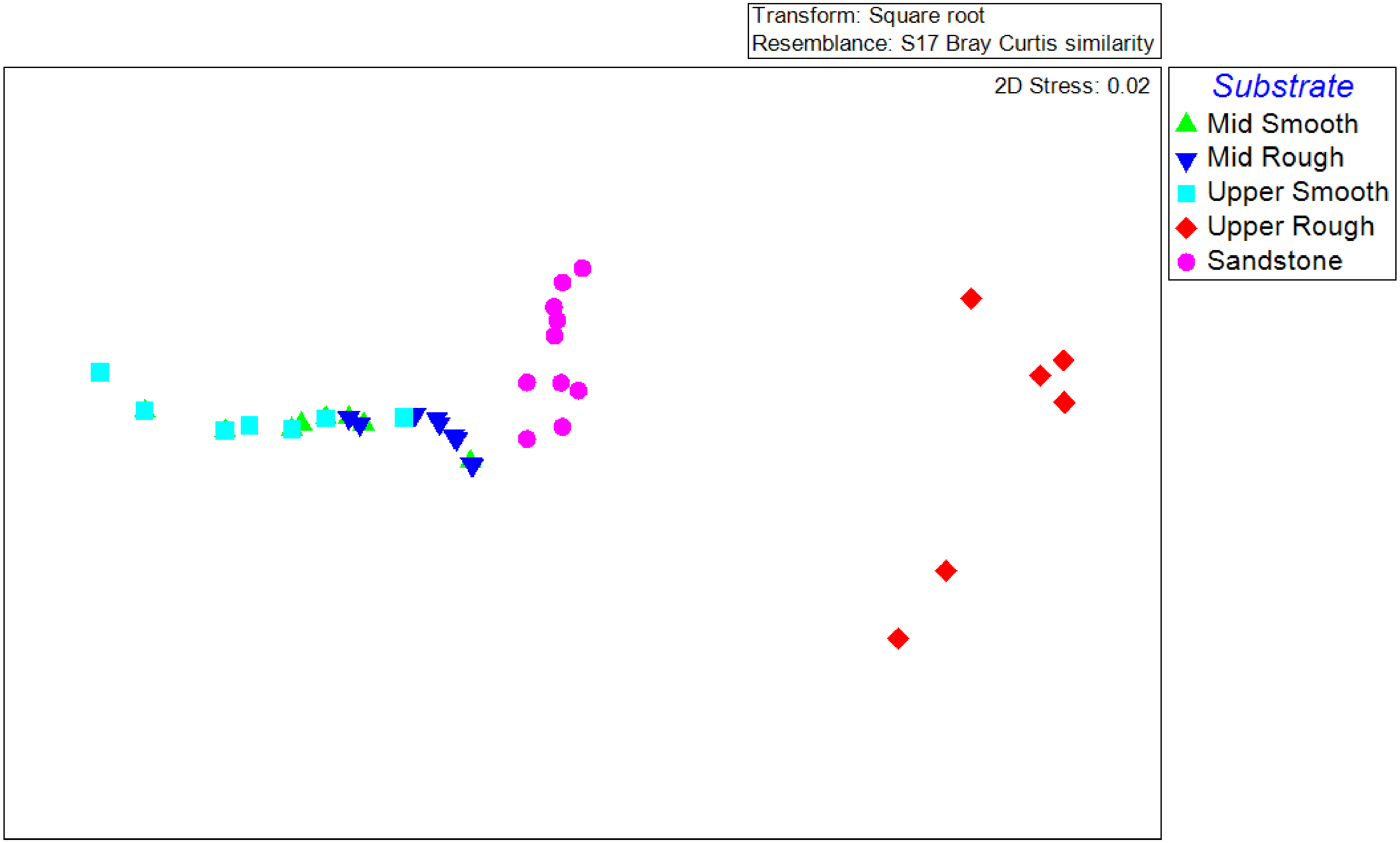


Figure 4.6 – The results of MDS analysis based on a Bray-Curtis similarity matrix for sessile species data collected from all substrate types (Rough Granite and Smooth Granite from the mid and upper shore and Sandstone) examined at North Bay.

SIMPER analysis was used to identify differences in sessile community similarity between substrate types and tidal heights. Firstly sandstone, rough and smooth granite substrate types present at mid shore height were compared (Table 4.6). The dissimilarity observed between sandstone substrates and smooth mid shore granite substrates was relatively low with *Semibalanus balanoides, Fucus vesiculosus, Verrucaria maura* and *Osmundea pinnatifida* accounting for 68.75 % of the overall 69.91 % dissimilarity observed (Table 4.6a).

The same four species also accounted for 61.11 % of the overall 47.57 % dissimilarity observed between sandstone substrates and rough mid shore granite substrates (Table 4.6b). Average abundances of all species recorded were higher on sandstone substrates, with the exception of *Semibalanus balanoides* which had a similar average abundance on rough granite and sandstone substrates.

Table 4.6 – SIMPER Table indicating the average abundance of species contributing to the dissimilarity observed between a) Sandstone substrates and smooth mid shore granite substrates and b) Sandstone substrates and rough mid shore granite substrates sampled at North Bay(Av.Abund = mean abundance (raw % cover data), Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) Sandstone & Smooth Mid		**Average Dissimilarity = 69.91 %**				
Species	**Sandstone Av.Abund**	**Smooth Mid Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Semibalanus balanoides	7.12	3.41	21.99	2.10	31.46	31.46
Fucus vesiculosus	2.63	0.00	11.70	1.19	16.73	48.19
Verrucaria maura	1.45	0.00	7.32	1.58	10.47	58.66
Osmundea pinnatifida	1.46	0.00	7.05	1.87	10.09	68.75

b) Sandstone & Rough Mid		**Average Dissimilarity = 47.57 %**				
Species	**Sandstone Av.Abund**	**Rough Mid Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Fucus vesiculosus	2.63	0.00	10.02	1.17	21.06	21.06
Semibalanus balanoides	7.12	7.05	6.95	1.21	14.62	35.68
Verrucaria maura	1.45	0.00	9.13	1.65	12.89	48.57
Osmundea pinnatifida	1.46	0.00	5.97	1.89	12.54	61.11
Ulva linza	1.31	0.00	5.58	3.30	11.74	72.85

Secondly, rough and smooth granite substrate types from the mid shore were compared (Table 4.7a), as were rough and smooth granite substrate types from the upper shore (Table 4.7b). SIMPER comparisons of rough and smooth granite substrates from the mid shore found that of the overall 41.54 % dissimilarity observed between rough and smooth granite substrates, 100.00 % was accounted for by *Semibalanus balanoides* only. Average abundance of *Semibalanus balanoides* was markedly higher on rough granites compared to the smooth granites at mid shore height (Table 4.7a).

Semibalanus balanoides also accounted for 35.14 % of the overall 92.20 % dissimilarity observed between rough and smooth granite substrates at upper shore height. *Semibalanus balanoides* was recorded on smooth upper shore substrates only (Table 4.7b). A further 64.86 % of the dissimilarity observed was accounted for by higher average abundances of filamentous green algae, *Porphyra sp.* and *Ulva linza* on rough upper shore substrates (Table 4.7b).

Table 4.7 – SIMPER Table indicating the average abundance of species contributing to the dissimilarity observed between a) Rough and smooth mid shore granite substrates and b) Rough and smooth upper granite substrates sampled at North Bay (Av.Abund = mean abundance (raw % cover data), Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) Mid Shore: Smooth & Rough		**Average Dissimilarity = 41.54 %**				
Species	**Smooth Av.Abund**	**Rough Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Semibalanus balanoides	3.41	7.05	41.54	1.92	100.00	100.00

b) Upper Shore: Smooth & Rough		**Average Dissimilarity = 92.20 %**				
Species	**Smooth Av.Abund**	**Rough Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Semibalanus balanoides	2.07	0.00	35.14	1.69	35.14	35.14
Filamentous Greens	0.00	1.85	28.77	2.55	28.77	63.91
Porphyra sp.	0.00	2.59	25.82	1.55	25.82	89.73
Ulva linza	0.00	1.08	10.27	0.82	10.27	100.00

An additional comparison of rough and smooth granite substrates across tidal heights found that *Semibalanus balanoides* accounted for much of the dissimilarity observed. *Semibalanus balanoides* was a key species in the comparison of rough granite substrates from the mid and upper shore, contributing 63.42 % of the overall 100.00 % dissimilarity observed (Table 4.8a). An additional 30.30 % of the dissimilarity recorded was accounted for by higher average abundances of *Porphyra sp.* and filamentous green algae on rough upper shore granite substrates than rough mid shore granite substrates (Table 4.8a). Community similarity between smooth granite substrates from the mid and upper shore was not found to be significantly different by ANOSIM (Table 4.8b).

Table 4.8 – SIMPER Table indicating the average abundance of species contributing to the dissimilarity observed between a) Rough mid shore and smooth upper shore boulders and b) smooth mid shore and rough upper shore boulders sampled at North Bay, Scarborough (Av.Abund = mean abundance (raw % cover data), Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) Rough Granite: Mid & Upper		**Average Dissimilarity = 100.00 %**				
Species	**Rough Mid Av.Abund**	**Rough Upper Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum. %**
Semibalanus balanoides	7.05	0.00	63.42	3.06	63.42	63.42
Porphyra sp.	0.00	2.59	15.62	1.16	15.62	79.04
Filamentous Greens	0.00	1.85	14.68	2.29	14.68	93.73

b) Smooth Granite: Mid & Upper		**Average Dissimilarity = 37.46 %**				
Species	**Smooth Mid Av.Abund**	**Smooth Upper Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum. %**
Semibalanus balanoides	3.41	2.07	37.46	1.60	100.00	100.00

4.3.2 Variation in Grazing Communities Between Different Substrate Types at North Bay, North Yorkshire.

At mid shore height, overall rugosity showed a significant positive correlation with S (Spearman rank Correlation Coefficient, r = 0.67, df = 28, P < 0.001), N (Spearman rank Correlation Coefficient, r = 0.806, df = 28, P < 0.001) and H' (Spearman rank Correlation Coefficient, r = 0.477, df = 28, P < 0.001) of grazing species. In addition, at upper shore height there was a significant positive correlation between overall rugosity and S (Spearman rank Correlation Coefficient, r = 0.632, df = 18, P < 0.05) and N (Spearman rank Correlation Coefficient, r = 0.650, df = 18, P < 0.05) of grazing species. However, there was no significant correlation between overall rugosity and H' of grazing species (Spearman rank Correlation Coefficient, P > 0.05).

Examination of grazing assemblages at mid shore height found significant differences in mean S (Table 4.9), mean N (Table 4.9), and median H' (Table 4.9) between substrate types (Table 4.10). Both mean S and median H' of grazing species was significantly higher on sandstone substrates than on either rough or smooth granite substrate types (Tukey < 0.05, Pairwise Wilcoxon Rank Sum Test, P < 0.05). Mean N was significantly different between all substrates. Sandstone substrate had a significantly higher mean N than both rough and smooth granite substrate types, and smooth granite substrates had a significantly lower mean N than both rough granite and sandstone substrate types (Tukey < 0.05, in all instances), (See Table 4.10 for descriptive data).

At upper shore height, there was a significant difference in median S (Mann Whitney U-test, W = 74.0, df = 10, P < 0.05) and median N (Mann Whitney U-test, W = 74.5, df = 10, P < 0.05) between substrate types. Both median S and median N were significantly higher on rough granite substrates. Median H' could not be compared due to smooth granite substrates having a high number of zero-samples and single species assemblages (see Table 4.10 for median and range values).

Table 4.9 – One-Way ANOVA and Kruskal-Wallis for S, N (counts) and H' of mobile species for Mid shore Substrates examined at North Bay. NS denotes Not Significant, * denotes significant to 0.01, ** denotes significant to 0.001, *** denotes significant to <0.001.

Mid Shore							
		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	AN		AN		KW	
		F	P	F	P	H	P
Substrate	2	19.93	*	57.65	*	20.44	*

Table 4.10 – Descriptive statistics of S, N (count) and H’ of grazing species for substrate types examined at North Bay. Where One-Way ANOVA was applied, mean and standard deviation (SD) have been reported. Where Kruskal-Wallis or Mann Whitney U-tests were used median and range have been reported.

a) Species Richness (S)

Substrate Type	**Mid Shore**		**Upper Shore**	
	Mean	SD	Median	Range
Sandstone	2.00	0.67		
Rough	1.00	0.00	1.00	0.00 – 2.00
Smooth	0.80	0.42	0.00	0.00 – 1.00

b) Total Abundance (N)

Substrate Type	**Mid Shore**		**Upper Shore**	
	Mean	SD	Median	Range
Sandstone	64.10	13.58		
Rough	31.10	6.94	6.50	0.00 – 16.00
Smooth	12.10	11.30	0.00	0.00 – 8.00

c) Shannon-Wiener Diversity (H’)

Substrate Type	**Mid Shore**		**Upper Shore**	
	Median	Range	Median	Range
Sandstone	0.13	0.08 – 0.35		
Rough	0.00	0.00 – 0.00	0.34	0.00 – 0.64
Smooth	0.00	0.00 – 0.00	0.00	0.00 – 0.00

Mean density of grazing species also differed between substrates. *Patella vulgata* was the only species present on all substrate types across both tidal heights. On the mid shore, *Patella vulgata* occurred in higher densities on sandstone substrates than rough or smooth granite substrates (Figure 4.7). Mean density of *Patella vulgata* was also higher on rough granites than on smooth granites. This was also true on the upper shore, however densities of *Patella vulgata* in the upper shore region were much lower than in the mid shore (Figure 4.7). Mean density of *Littorina littorea* and *Littorina obtusata* was low across all substrate types and tidal heights. Both *Littorina littorea* and *Littorina obtusata* were present on mid shore sandstone substrates only. *Littorina saxatilis* was identified on rough granite substrates on the upper shore only (Figure 4.7).

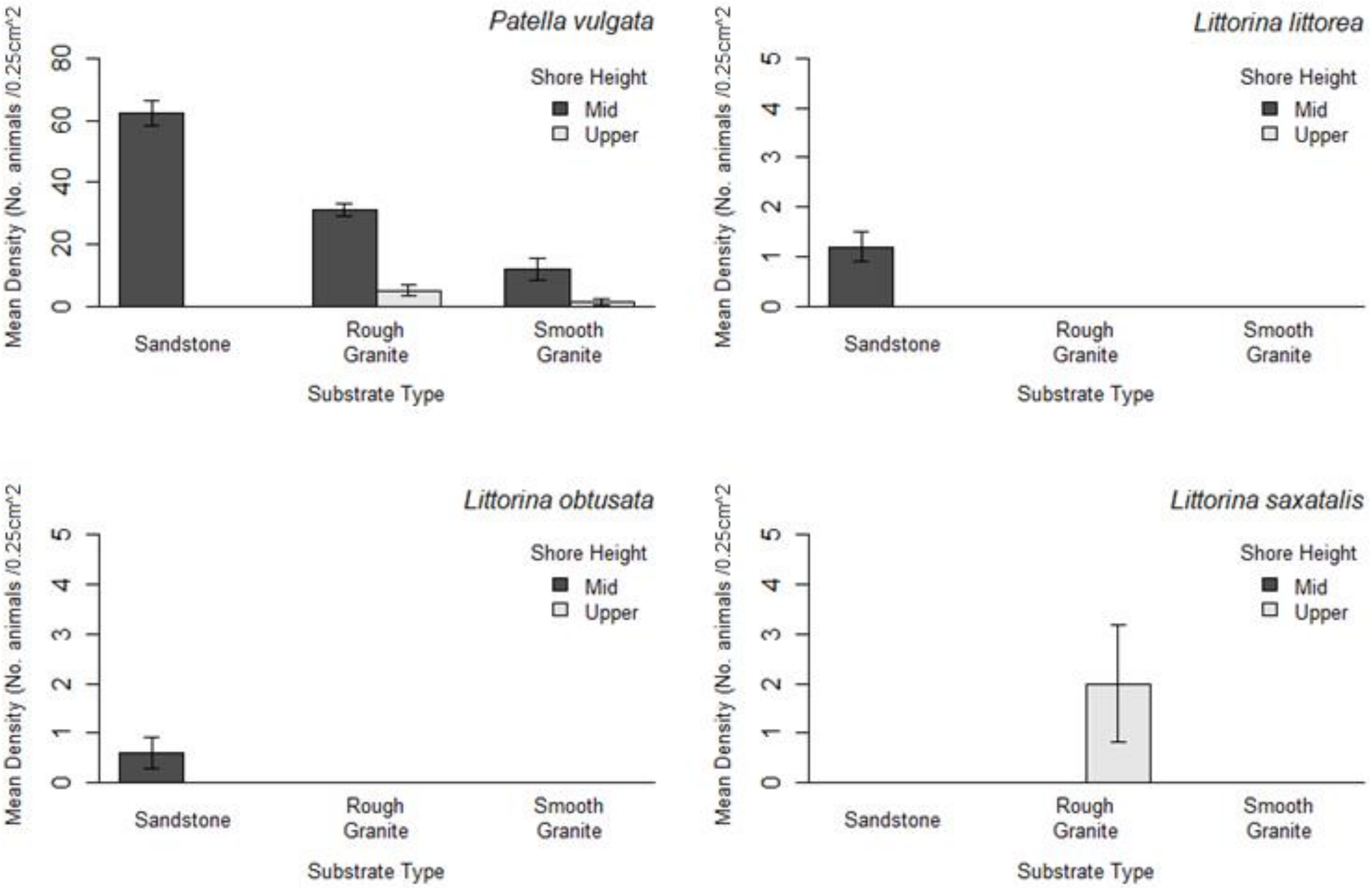


Figure 4.7 – Mean density (number of animals per 0.25m^2) of grazing species *Patella vulgata*, *Littorina littorea*, *Littorina obtusata* and *Littorina saxatilis* for each substrate type examined at North Bay.

4.3.3 Variation in Sessile Communities on Granite Substrates from Five Rock Armour Defences Across North and East Yorkshire

The rugosity of granite substrates from sites across North and East Yorkshire was compared. There was a significant difference in mean rugosity between the five sites (ANOVA, $F_{4, 45} = 9.01$, $P < 0.01$). Granite from the Runswick Old site had a significantly higher mean rugosity than all other sites examined (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$ in all cases). No other significant differences were found (Table 4.11).

Table 4.11 – Mean rugosity of granite substrates from rock armour defences at five sites across North and East Yorkshire.

Site	**Rugosity**	
	Mean	SD
Runswick Old	1.14	0.08
Holbeck	1.07	0.04
Runswick New	1.06	0.02
North Bay	1.05	0.02
Withernsea	1.04	0.02

Sessile community similarity was found to be significantly different between sites (ANOSIM, Global R = 0.304, P = 0.1 %). Pairwise comparison found the sessile community at Withernsea and Runswick New were significantly different to all other sites (in all cases, P = 0.1 %). However, there were no significant difference in community similarity between Holbeck, North Bay and Runswick Old (P > 5 % in all cases). MDS showed clustering of samples by site however there was considerable overlap and the plot had a high stress value (0.17). Samples from Withernsea were clustered away from other sites with no overlap (Figure 4.8). Samples from Runswick New clustered near samples from Runswick Old, but away from the central cluster which contained overlapping samples from Runswick Old, North Bay and Holbeck (Figure 4.8).

SIMPER analyses concluded that Withernsea and Runswick New showed considerable dissimilarity to other sites, which was attributed to 3 taxa at Withernsea and 2 taxa at Runswick New, respectively (Table 4.12 and Table 4.13). *Austrominius modestus* and *Semibalanus balanoides* accounted for 67.98 %, of the overall 76.90% dissimilarity between samples from Withernsea and Runswick Old (Table 4.12a), for 74.48 % of the overall 77.20 % dissimilarity between Withernsea and Holbeck (Table 4.12b) and for 64.58 % of the overall 78.37 % dissimilarity between Withernsea and North Bay (Table 4.12c). Comparison between Withernsea and Runswick New showed 78.77 % of the overall 98.35 % dissimilarity was attributed to higher average abundances of *Semibalanus balanoides* and filamentous green algae at Runswick New, and of *Austrominius modestus* at Withernsea (Table 4.12d). *Austrominius modestus* was only present at Withernsea and so contributed considerably to the dissimilarity observed in all comparisons. Average abundance of *Semibalanus balanoides* was lower at Withernsea than at all other sites, with the exception of Runswick New where this species was absent (Table 4.12).

In samples from Runswick New, filamentous green algae and *Semibalanus balanoides* contributed most notably to the dissimilarity between when compared to other sites (Table 4.13). Filamentous green algae and *Semibalanus balanoides* were found to contribute 73.06 % of the overall 100.00 % dissimilarity between samples from Runswick New and Runswick Old (Table 4.13a). These species contributed 82.18 % of the overall 92.32 % dissimilarity between Runswick New and North Bay (Table 4.13b), and to 70.14 % of the overall 93.73 % dissimilarity observed between Runswick New and Holbeck (Table 4.13c). *Semibalanus balanoides* occurred in higher average abundances at Runswick Old, North Bay and Holbeck whereas higher average abundances of filamentous green algae were present at Runswick New.

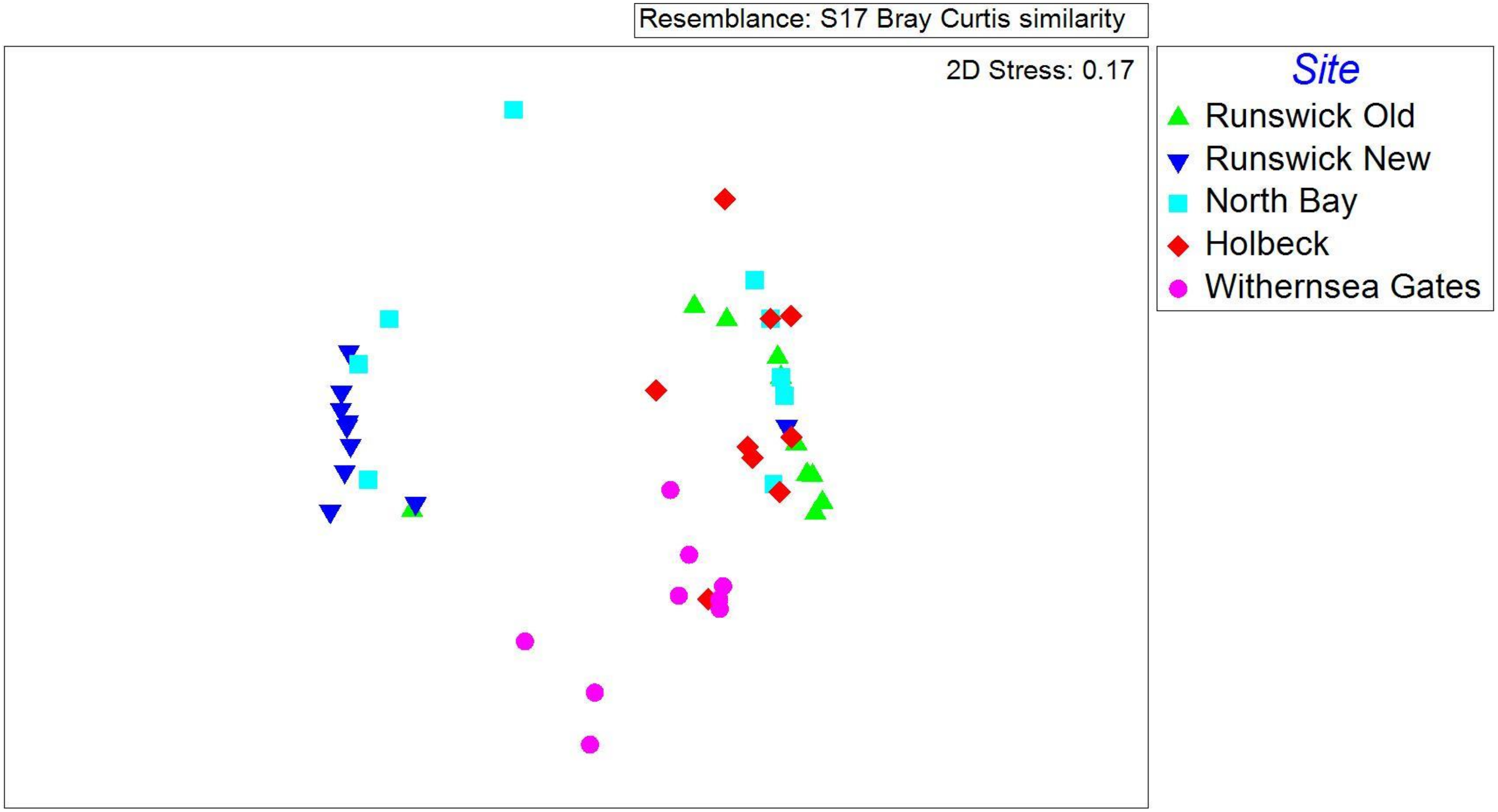


Figure 4.8 – The results of MDS analysis based on a Bray-Curtis similarity matrix for sessile species data collected from granite rock armour defences at five sites in North and East Yorkshire.

Table 4.12 – SIMPER Table indicating average abundance of sessile species contributing to the dissimilarity observed between a) Withernsea and Runswick Old, b) Withernsea and Holbeck, c) Withernsea and North Bay and d) Withernsea and Runswick New (Av.Abund = mean abundance (raw % cover data), Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) Withernsea & Runswick Old		**Average Dissimilarity = 76.90 %**				
Species	**Withernsea Av.Abund**	**Runswick Old Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum. %**
Austrominius modestus	5.85	0.00	36.01	2.80	46.83	46.83
Semibalanus balanoides	2.47	3.46	16.27	1.14	21.15	67.98

c) Withernsea & Holbeck		**Average Dissimilarity = 77.20 %**				
Species	**Withernsea Av.Abund**	**Holbeck Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum. %**
Austrominius modestus	5.85	0.00	31.06	2.41	40.24	40.24
Semibalanus balanoides	2.47	4.57	18.79	1.24	24.34	64.58
Fucus spiralis	1.41	0.89	8.59	0.77	11.12	75.70

c) Withernsea & North Bay		**Average Dissimilarity = 78.37 %**				
Species	**Withernsea Av.Abund**	**North Bay Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum. %**
Austrominius modestus	5.85	0.00	38.50	2.97	49.12	49.12
Semibalanus balanoides	2.47	3.52	19.87	1.21	25.36	74.48

d) Withernsea & Runswick New		**Average Dissimilarity = 98.35 %**				
Species	**Withernsea Av.Abund**	**Runswick New Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum. %**
Austrominius modestus	5.85	0.00	36.23	3.05	36.83	36.83
Filamentous Greens	0.00	3.71	25.18	1.75	25.60	62.44
Semibalanus balanoides	2.47	0.00	16.07	1.63	16.34	78.77

Table 4.13 – SIMPER Table indicating average abundance of sessile species contributing to the dissimilarity observed between a) Runswick New and Runswick Old, b) Runswick New and North Bay and c) Runswick New and Holbeck (Av.Abund = mean abundance (raw % cover data), Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) Runswick New & Runswick Old **Average Dissimilarity = 100.00 %**

Species	**Runswick New Av.Abund**	**Runswick Old Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
Filamentous Greens	3.71	0.00	37.91	2.14	37.91	37.91
Semibalanus balanoides	0.00	3.46	35.15	1.70	35.15	73.06

b) Runswick New & North Bay **Average Dissimilarity = 92.32 %**

Species	**Runswick New Av.Abund**	**North Bay Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
Filamentous Greens	3.71	0.33	39.27	2.00	42.53	42.53
Semibalanus balanoides	0.00	3.52	36.60	1.43	39.64	82.18

c) Runswick New & Holbeck **Average Dissimilarity = 93.73 %**

Species	**Runswick New Av.Abund**	**Holbeck Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib %**	**Cum.%**
Semibalanus balanoides	0.00	4.57	36.54	1.67	38.98	38.98
Filamentous Greens	3.71	0.43	29.20	1.53	31.15	70.14

4.3.4 Variation in Grazing Communities on Granite Substrates from Five Rock Armour Defences Across North and East Yorkshire

Examination of grazing assemblages found that the mean S (Table 4.14) and median N (Table 4.14) of grazing species was significantly different between sites. Mean S of grazing fauna was significantly lower at Runswick New compared to Holbeck and North Bay (Tukey $P < 0.05$). In addition, mean S of grazing species at Withernsea was significantly lower than at Holbeck (Tukey $P < 0.05$) (See Table 4.15 for descriptive data). Mean S of grazing species at Runswick Old was not significantly different to any other site (Tukey $P > 0.05$). Median N of grazing species was significantly higher at Holbeck and North Bay compared to Withernsea and Runswick New (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$, in all cases). Median N of grazing species was not significantly different between Holbeck and North Bay and median N of Runswick Old was not significantly different to other sites (Pairwise Wilcoxon Rank Sum Test, $P > 0.05$ in all cases). There was no significant difference in H' of grazing species between sites (Table 4.14), (See Table 4.15 for descriptive data).

Table 4.14 – One-Way ANOVA and Kruskal-Wallis for S, N (counts) and H' of grazing species from granite substrates from rock armour defences at sites across North and East Yorkshire. NS denotes Not Significant, * denotes significant to 0.01, ** denotes significant to 0.001, *** denotes significant to <0.001.

Grazing species							
		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	AN		KW		KW	
		F	P	H	P	H	P
Site	4	6.83	*	27.21	*	9.86	NS

Table 4.15 – Descriptive statistics of S, N (counts) and H' of grazing species from granite substrates from rock armour defences at sites across North and East Yorkshire. Where One-Way ANOVA was applied, mean and standard deviation (SD) have been reported. Where Kruskal-Wallis test was used the median and range have been reported.

Site	**S**		**N**		**H'**	
	Mean	SD	Median	Range	Median	Range
Holbeck	1.08	± 0.72	6.00	0.00 – 80.23	0.00	0.00 – 0.69
North Bay	0.83	± 0.60	9.00	0.00 – 44.00	0.00	0.00 – 0.64
Runswick New	0.10	± 0.32	0.00	0.00 – 1.00	0.00	0.00 – 0.00
Runswick Old	0.60	± 0.52	1.00	0.00 – 23.00	0.00	0.00 – 0.00
Withernsea	0.76	± 0.76	0.00	0.00 – 40.12	0.00	0.00 – 0.50

Mean density of *Patella vulgata* was greatest at North Bay and Holbeck but much lower at Runswick Old and Withernsea (Figure 4.9). *Littorina littorea* occurred in very low densities at all three of the sites in which it was identified. *Littorina saxatilis* also occurred in similarly low mean densities at sites where the species was identified. *Littorina obtusata* was only present at Holbeck. Mean density of all species was low at Runswick New (Figure 4.9).

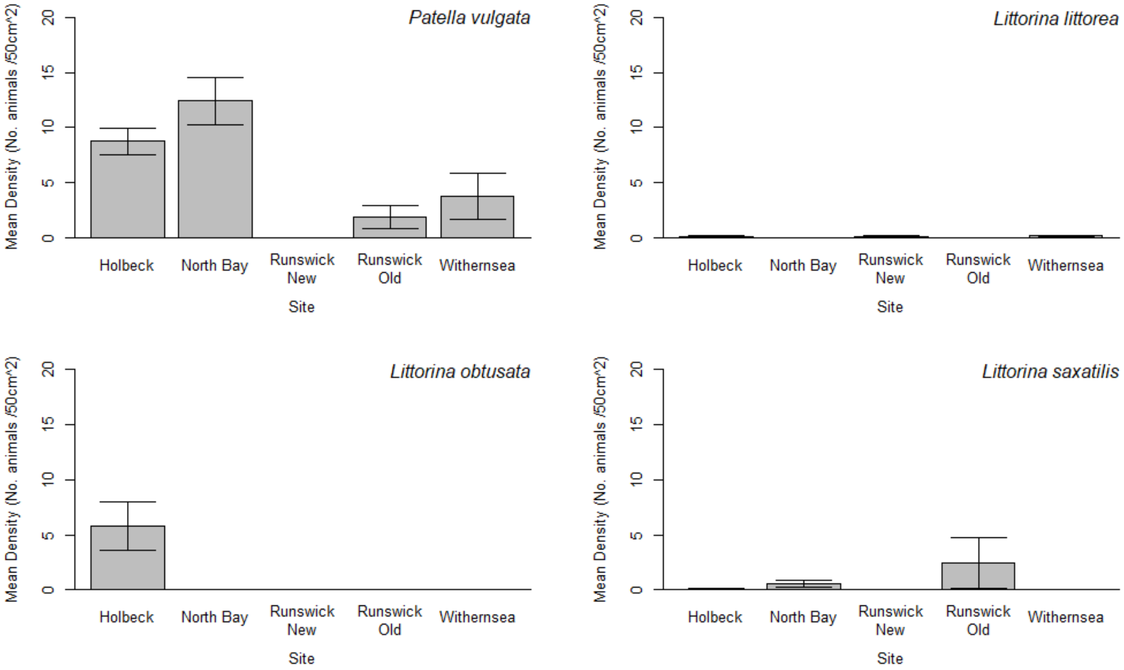


Figure 4.9 – Mean density (number of animals per $0.25m^2$) of grazing species *Patella vulgata, Littorina littorea, Littorina obtusata* and *Littorina saxatilis* on granite substrates from rock armour defences at sites across North and East Yorkshire.

4.4 Discussion

The results presented here show that rugosity differed significantly between smooth granite, rough granite, and naturally occurring sandstone substrates (Table 4.3). In addition, the importance of substrate rugosity to sessile and grazing species differed across tidal heights. Fine-scale physical complexity is known to determine community structure by influencing colonisation (Sweat and Johnson, 2013; Lund-Hansen *et al.,* 2017) and by impacting grazing efficacy (Wahl and Hoppe, 2002). The physical characteristics of a substrate, including its microtopography (Köhler, Hansen and Wahl, 1999; Sempere-Valverde *et al.,* 2018), material composition (Davis, 2009; Liversage and Benkendorff, 2013) and aspect or orientation (Firth *et al.,* 2016c; Hanlon *et al.,* 2018), can influence the physical stress experienced by intertidal organisms, which will impact the abundance and distribution of species. At mid shore height richness, abundance, and diversity of sessile species was positively correlated with rugosity, however at upper shore height no significant relationship was found. This was likely due to there being a much lower coverage of sessile species in the upper shore region (Table 4.5).

At mid shore height, richness, abundance, and diversity of sessile species was higher on sandstone substrates (Table 4.5). This agrees with previous work by Sempere-Valverde *et al.,* (2018), who found sandstone tiles had greater vegetative cover in both subtidal and intertidal environments than other materials investigated. Sandstone substrates are more porous than igneous rocks, such as granite (Ingham, 2013), allowing them to retain water between tidal cycles. Sandstones are also more prone to biological and environmental weathering which will increase surface rugosity and microhabitat availability (Coombes, 2015). As a result, sandstones substrates likely provided greater protection from desiccation stress than either rough or smooth granites in this instance.

In comparison, richness, abundance, and diversity of grazing species was positively correlated with rugosity at both mid and upper shore height. At mid shore height, richness, abundance, and diversity of grazing species also was higher on sandstone substrates than either rough or smooth granite substrates (Table 4.9), possibly because sandstone offered greater protection from thermal stress, for the reasons discussed above. At both tidal heights, richness and diversity of grazing species was higher on rough granite substrates than on smooth granite substrates (Table 4.9). This might suggest that where the surface texture of granite substrates is variable, rougher substrates may be preferred by some species.

This assertion may be supported by considering the distribution of the limpet *Patella vulgata*. This species was present on both rough and smooth granite substrates but occurred in greater densities on rough granite than on smooth granite at both mid and upper shore height (Figure 4.7). Grazing fauna are known to migrate into areas where conditions are more suitable, and away from unfavourable environments (Saier, 2000; Branch, 1975). *Patella vulgata*, for example, has well known migratory tendencies which are often driven by environmental factors including the topography and wetness of a surface, as well as biological factors, such as food availability and intra-specific competition (Lewis and Bowman, 1975). Increasing substratum roughness has previously been identified as one of the most effective ways to improve diversity of invertebrate species on artificial structures (Strain *et al.,* 2018). This may be because surfaces with greater fine-scale (mm) complexity are more able to retain water and accumulate biofilm in small surface pits and depressions, thus providing invertebrates with a means of thermal regulation and better foraging opportunities (Köhler, Hansen and Wahl, 1999).

Texture of granite substrates examined here was created when the granite boulders were quarried, smooth granite substrates would likely had been machine-cut, whereas rough granite substrates would have been quarried using explosives (Mancini *et al.,* 2001; Yarahmadi *et al.,* 2019). Rugose surfaces can facilitate accumulation of biofilm (Hutchinson *et al.,* 2006; Lund-Hansen *et al.,* 2017) and enhance settlement of zoospores (Granhag *et al.,* 2004; Long *et al.,* 2010) by influencing the movement of water over the surface, creating drag and reducing flow speed (Whitman and Reidenbach, 2012; Loke, Bouma and Todd, 2017). This may positively influence algal recruitment by increasing the contact time between the substrate and planktonic propagules and spores (McNair, Newbold and Hart, 1997) and facilitate the likelihood of adhesion to the surface (Crimaldi *et al.*, 2002). Enhanced algal settlement would provide better foraging opportunities for grazing invertebrates. In addition, water retained in the minute depressions of rugose surfaces would provide invertebrates with a means to maintain their body temperatures and reduce desiccation stress between tides (Jones and Boulding, 1999; Firth *et al.,* 2016c).

However, the influence of the fine-scale physical complexity on colonisation and recruitment has been shown to be time-dependant (Hanlon *et al.,* 2018). Rougher surfaces may facilitate and even enhance colonisation of early-successive species (Sempere-Valverde *et al.,* 2018), but subsequent settlement of ecosystem engineering species which create biogenic habitats will reduce the relative importance of fine-scale physical complexity in structuring communities. Indeed, fine-scale physical complexity has been shown to encourage settlement of *Semibalanus balanoides* (Coombes *et al.,* 2015; MacArthur *et al.,* 2019) however once encrusted across a surface, this species will provide a new layer of biogenic complexity and limit access to the surface by other sessile species (Thompson *et al.,* 1996; Holmes, Sturgess and Davies, 1997). Thus, limiting the importance of fine-scale complexity in the recruitment and colonisation of late-successional species.

The temporal limitations of this study meant that succession of species through the habitat and seasonal variation within the community was not captured in detail. For example, the recruitment cycle of the barnacle *Semibalanus balanoides* typically occurs in springtime (Jenkins *et al.,* 2000). Although the substrates in this investigation hosted established barnacle cover, the pattern of recruitment of *Semibalanus balanoides* spat between the substrata could not be observed in this instance. Similarly, seasonal variation in algal cover was not captured. Algal growth on rocky shores is strongest during summer months when environmental conditions are most conducive, whereas during winter, growth is greatly reduced in many species (Emerson and Zedler, 1978; Murray and Horn, 1989). Monitoring seasonal patterns in growth and recruitment of algal and invertebrate assemblages on each substrate over a longer period of time and observing interactions between intertidal species with different substrata would provide a fuller picture of how substrate type and surface rugosity influences community development.

Rugosity was less important over a regional scale as rugosity was significantly different for only one of the five sites examined (Table 4.11). Instead, differences in sessile and grazing communities between sites suggested that the age of the rock armouring was a more important determinant of community structure. At Runswick New, the youngest of the sites examined, sessile communities were characterised by greater cover of ephemeral filamentous green algae and an absence of sessile invertebrates, such as *Semibalanus balanoides* (Table 4.13). In contrast, at Holbeck, North Bay and Runswick Old, sites which were markedly older, sessile communities had greater cover of perennial algae such as *Fucus spiralis*. This was to be somewhat expected given that sessile communities on artificial structures which have been in place fewer than 2 years are often dominated by ephemeral algae, whereas older structures are typically dominated by perennial species (Chapman and Underwood, 1998; Pinn *et al.,* 2005). The richness of grazing species was found to be highest at Holbeck, the oldest structure examined, and lowest at Runswick New, the youngest structure examined (Table 4.15). This was unsurprising though as invertebrate richness is thought to increase with structure age as the availability of food increases (Dong *et al.,* 2018).

Structure age has previously been noted to affect sessile and mobile species on coastal defences (Sedano *et al.,* 2020), and a number of authors have noted that age may be a primary driver of differences in community structure in artificial habitats (Connell and Glasby, 1999; Dong *et al.,* 2018). Artificial structures are thought to host most species within approximately 2 years of installation and, following recruitment and establishment of populations, reach climax communities in 5-20 years (Pinn *et al.,* 2005; Gacia *et al.,* 2007; Sempere-Valverde *et al.,* 2018) although these communities do not remain stable and will change over time (Perkol-Finkel *et al.,* 2005; Pinn *et al.,* 2005). However, the effect of structure age on community development and composition is not well understood (Sedano *et al.,* 2020). Artificial coastal defence structures can have an intended life expectancy of between 50 – 100 years (Cooper, Wilson and Hanson, 2014; JBA Consulting, 2017a). Therefore, it is important to understand how diversity in intertidal communities is influenced by structure age, to ensure that long-term coastal defence and conservation priorities can be managed effectively (Sedano *et al.,* 2020).

The results of this study highlight the importance of fine-scale physical complexity in determining richness and diversity of sessile and grazing species on granite rock armour coastal defences within a localised area. The study found that at mid shore height natural sandstone substrates had significantly more diverse sessile and grazing communities than either type of granite substrate. This supports the conclusions of Chapter 2 that incorporating natural sandstone substrates into coastal defence infrastructure is an effective way to improve biodiversity. This study also found that across tidal heights, diversity of sessile and grazing species was greater on more rugose granite substrates than on smoother granite substrates. This indicated that increased rugosity was beneficial for both sessile and grazing species, however the importance of rugosity is likely limited to the early-stages of colonisation, given that the fine-scale complexity of the substrate will become unimportant as biogenic habitat is formed on top of it. Over a regional scale, fine-scale physical complexity had little impact on the diversity and structure of sessile and grazing communities. Here, structure age appeared to be a more important factor in determining community diversity, however further work is required to isolate and better understand the how the age of a structure influences biodiversity.

Chapter 5 Does the orientation of granite substrates in a rock armour defence affect the diversity and structure of sessile and mobile communities?

5.1 Introduction

Substratum orientation has been identified as a key driver of community structure on both intertidal and subtidal natural and artificial shores (Connell, 1999; Knott *et al.,* 2004). The orientation of a substrate can determine localised environmental conditions including wave exposure, light intensity, and surface temperature (Hanlon *et al.,* 2018). For example, in the northern hemisphere south-facing surfaces will typically experience more hours of sunlight than north-facing surfaces (Firth *et al.,* 2016c), which could potentially produce a 10 – 15 °C difference in surface temperature (Gaines and Denny, 2007). Usually surfaces with greater exposure to light will support greater algal growth (Knott *et al.,* 2004) however exposure to high light intensities for a prolonged period of time can inhibit photosynthesis and cause irreversible damage to the plant (Hanelt *et al.,*1997; Hanelt, Wiencke and Bischof, 2003). The importance of orientation in structuring communities also varies with tidal height and wave exposure (Firth *et al.,* 2016c). By determining abiotic conditions in intertidal environments, substrate orientation can also influence vertical zonation of macroalgal and faunal species across tidal heights (Somero, 2002; Davenport and Davenport, 2005). Similarly, differences in wave exposure between have been shown to influence functional richness in macroalgal assemblages on natural rocky shores (Nishihara, and Terada, 2010; Quintano *et al.,* 2015).

However, the term *orientation* has been used broadly and its definition has varied between studies. Most often, orientation has described comparisons of vertically and horizontally inclined substrates (Connell, 1999; Glasby, 2000; Knott *et al.,* 2004; Miller and Etter, 2008). Similarly, the term has described the upward- and downward-surfaces of horizontal substrates (Hanlon *et al.,* 2018) and the aspect or compass-orientation (North, South, etc.) of vertical surfaces (Firth *et al.,* 2016c; Cefalì *et al.,* 2016; Ramos *et al.,* 2016; Sedano *et al.,* 2019). Here, orientation referred to the compass-orientation of vertical surfaces. Past studies into the influence of compass-orientation (hereafter “orientation”) have found subtle differences in richness and distribution of sessile and mobile communities attributed to environmental conditions consequential of the substrates orientation (Firth *et al.,* 2016c; Nishihara, and Terada, 2010).

In a study of 13 sites along the coast of Cantabria, Ramos *et al.,* (2016) found certain species occurred in higher abundances on coasts with a particular orientation, whereas others did not. For example, *Ceramium spp*., *Falkenbergia rufolanosa* and *Gelidium spinosum* from low shore samples and *Condracanthus acicularis* from mid shore samples occurred in high abundances at North-oriented sites. However, *Corallina officinalis* and *Ellisolandia elongata* occurred in high abundances on all coasts regardless of orientation. Comparisons of artificial coastal defences and adjacent natural rocky shores in North Wales by Firth *et al.,* (2016c), and on the north and south coasts of Crete by Sedano *et al.,* (2019) found substrate type to be a greater driver of community structure than orientation. However, substratum orientation was found to have a strong effect on taxon richness in both high and mid shore environments and a clear impact on distribution of mobile organisms (Firth *et al.,* 2016c). In addition, Nishihara, and Terada (2010) highlighted that taxon and functional richness of macroalgae varied with wave exposure, which is determined by substrate orientation. Although taxon and functional richness appeared to largely decrease as wave exposure increased, richness of thick leathery Phaeophyta was higher on shores where wave exposure was greater.

However, these studies were conducted over large geographic scales where natural variability in substrate composition and species distributions could not be controlled for and examining the effect of substrate orientation in isolation has proven difficult (Sedano *et al.,* 2019). In this investigation, diversity and structure of sessile and mobile communities was examined between different orientations of an artificial rock armour coastal defence at Holbeck in Scarborough South Bay, North Yorkshire. This site presented a unique opportunity to examine orientation in more controlled conditions than available elsewhere in Yorkshire and the crescent shape of the embankment at Holbeck provided three clear orientations for examination. Substrate composition was controlled for as the defence was composed solely of Norwegian granite (Scarborough Borough Council, 2010) and, although the effect of wave exposure could not be completely controlled, differences in the level exposure between orientations would be less pronounced on a localised scale than over a larger geographic area.

As such, this chapter aimed to determine whether diversity and structure of sessile and mobile communities differed between orientations on a rock armour defence at Holbeck in Scarborough South Bay, North Yorkshire.

The specific hypotheses to be tested under this aim were;

1. S, N, H’ and community similarity of sessile and mobile communities was significantly different between orientations at mid and upper shore height.
2. Richness of macroalgal functional groups was significantly different between orientations at mid and upper shore height.

5.2 Methods

5.2.1 Site Description

This investigation was confined to a single site in Scarborough, North Yorkshire. The granite rock armour embankment at Holbeck, described in Chapter 2, was chosen because the unique crescent-shape of the defence provided clear North, North-East and East facing orientations accessible for surveying (Figure 5.1).

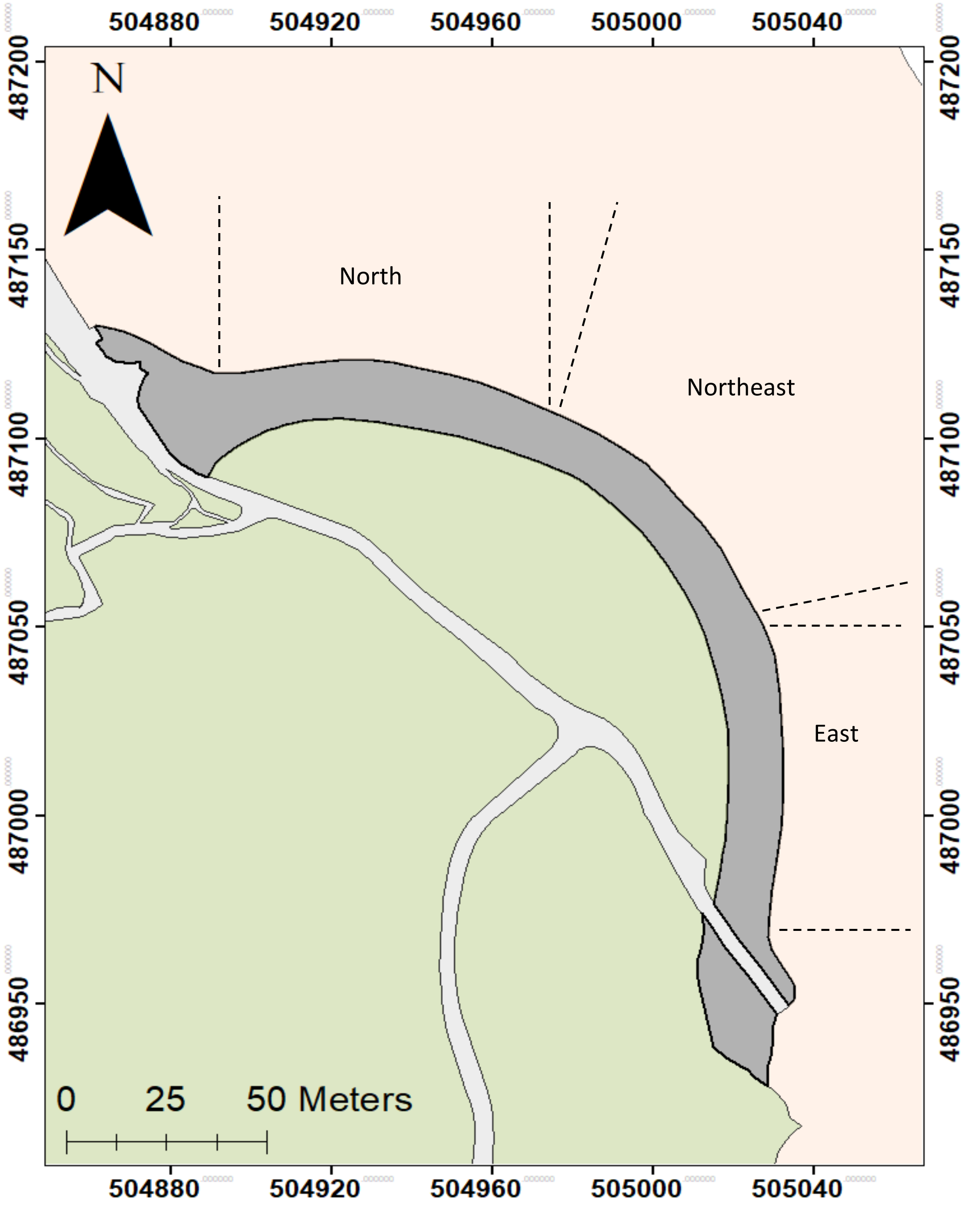


Figure 5.1 – Study site at Holbeck, Scarborough with boundaries of orientations indicated.

5.2.2 Method

Granite boulders were broadly grouped into North, North-east and East facing orientations. Shore height was determined using biological indicators, using *Fucus vesiculosus* to indicate mid shore environments (White, 2008b) and *Fucus spiralis* as a marker of upper shore environments (White, 2008a). There were no low shore boulders available for sampling. Care was taken to ensure samples from each orientation were collected from the same tidal height from both mid and upper shores and that boulder orientation was consistent between stations (Kim and DeWreede, 1996).

Samples were taken from the seaward-facing, vertical surfaces of 10 boulders from each orientation at mid and upper shore height. As described in Chapter 2 (Section 2.2.2), percentage cover of sessile algal and faunal species was estimated from a 50 x 50 cm gridded quadrat and a count per unit area (number of individuals per 50cm^2) of mobile species was made (Bulleri and Chapman, 2004; Chapman, 2006). Identification of species was facilitated using Bunker *et al.,* 2017 for algae and Cremona, Simms and Ward, 2001 for fauna.

Macroalgal functional groups were determined according to Steneck and Dethier's (1994) functional form approach using morphological features. Species with a single layer sheet-like form such as those from the genera *Ulva* and *Porphyra* were categorized as having a “foliose” functional form (Steneck and Dethier, 1994). In the same way, species with uniseriate filaments, such as *Ulothrix sp*., were categorized as having a “filamentous” functional form and thick leathery species, such as *Fucus vesiculosus*, were classified into the “leathery macrophyte” functional form group (Steneck and Dethier, 1994).

5.2.3 Statistical Analyses

Percentage cover data of sessile species and count per unit area (number of individuals per 50cm^2) of mobile species was split and analysed separately. Sessile and mobile S, N and H’ data from the mid and upper shore was also analysed separately to control for natural zonation and distribution of species between shores (Sadchatheeswaran *et al.,* 2018). The DIVERSE routine in PRIMER was used to calculate S, N and H’ (Clarke and Warwick, 2001). The Shannon-Wiener Diversity Index was used as it is representative of both the richness and the evenness of species in a sample (Spellerberg and Fedor, 2003).

To test the hypothesis that S, N, H’ and community similarity of sessile and mobile communities was significantly different between orientations at mid and upper shore height, the following procedure was adopted for both sessile and count per unit area data. Kolmogorov-Smirnov test and Levene’s test were used to test for conformation to a normal distribution and homogeneity of variances, respectively (Dytham, 2011). S and H' data for both sessile and mobile species was found to be normally distributed ($P > 0.05$) and to have equal variances ($P > 0.05$). Sessile and mobile species N data did not have a normal distribution or equal variances and was transformed using a $\log_{10}(x+1)$ transformation, as variances of the data were larger than the mean (Fowler *et al.,* 2013). Following this transformation, N data displayed a normal distribution ($P > 0.05$) and equal variances ($P > 0.05$). One-Way ANOVA was used to test for significant differences in S, N and H between orientations at each shore height separately. The process described in Chapter 2 (Section 2.2.3) was used to validate ANOVA models. Where significant, a Tukey PostHOC test was applied to identify which groups were significantly different (Dytham, 2011).

Community similarity between orientations at mid and upper shore height was examined using the same procedure as described in Chapter 4, Section 4.2.3, for sessile species data, for each shore height separately. Diversity in animal communities was analysed by examining the S, N and H' of grazing fauna between orientations at mid and upper shore height. S and H' data for grazing species was found to be normally distributed ($P > 0.05$) and to have equal variances ($P > 0.05$), however N data for grazing species did not and was transformed using a $\log_{10}(x+1)$ transformation (Fowler *et al.,* 2013). One-Way ANOVA and Tukey PostHOC tests were used subject to model validation as described in Chapter 2 (Section 2.2.3). Where One-Way ANOVA could not be validated, Kruskal-Wallis Test and Pairwise Wilcoxon Rank Sum PostHOC Test were applied (Dytham, 2011). Density of grazing species between was also plotted and compared.

To test whether richness of macroalgal functional groups was significantly different between orientations at mid and upper shore height, the functional richness of each sample was calculated as the number of different functional groups identified (Zuur *et al.,* 2007). Functional groups are defined in Chapter 5 Section 5.2.2 according to Steneck and Dethiers, (1994) approach of using morphological features to categorize algae into the functional form groups: Leathery Macrohptyes, filamentous algae and foliose algae. Functional richness data from both the mid and upper shores was found to be both normally distributed ($P > 0.05$) and had equal variances ($P > 0.05$). Therefore, One-Way ANOVA was used to test for significant differences in functional richness between orientations at mid and upper shore height.

5.3 Results

The composition of species was different between orientations, and there were a higher number of taxa present on the mid shore than on the upper shore or each orientation respectively (Table 5.1). The number of sessile taxa was similar on each orientation irrespective of shore height and *Semibalanus balanoides* was present on all mid shore orientations. *Patella vulgata* was present at both shore heights of all orientations.

Table 5.1 – Presence and absence table of sessile and mobile species identified in samples (N= 10) from the mid and upper shores of each orientation at Holbeck (* indicates presence).

	Orientation					
	North		North-east		East	
	Mid	Upper	Mid	Upper	Mid	Upper
Sessile Species						
Filamentous Greens		*				
Ulothrix sp.		*				
Ulva sp.				*	*	
Ulva linza			*			
Ulva lactuca			*			
Ulva intestinalis	*					
Porphyra sp.	*	*				
Fucus spiralis		*		*	*	
Fucus vesiculosus			*			
Semibalanus balanoides	*		*		*	
Mobile Species						
Patella vulgata	*	*	*	*	*	*
Littorina littorea	*	*	*	*		*
Littorina obtusata	*					
Littorina saxatalis			*			
Nucella lapillus	*					*
Melarhaphe neritoides		*	*			
Actinia equina	*					

5.3.1 Variation in Sessile Communities on Substrates with Differing Orientations at Holbeck, Scarborough.

There was a significant difference in mean S (ANOVA, $F_{2, 27} = 25.77$, $P < 0.01$) and mean H’ (ANOVA, $F_{2, 27} = 24.69$, $P < 0.01$) of sessile species between orientations at mid shore height. However, there was no significant difference in mean N of sessile species (ANOVA, $P > 0.01$) between orientations. Mean S was significantly higher on both the North- and North-east-facing orientations compared to the East-facing orientation (Tukey $P < 0.05$). However, mean S was not significantly different between the North and North-east orientations (Tukey $P > 0.05$) (Table 5.2). Mean H’ was significantly higher on the North-east orientation compared to both the North and East orientations (Tukey $P < 0.05$), (Table 5.2). Mean H’ between the North and East orientations was not significantly different (Tukey $P > 0.05$). Although not significantly different, mean N of sessile species was higher on the North orientation than both the North-east and East orientations (See

Table 5.3 for descriptive statistics).

At upper shore height, analyses found that mean S (ANOVA, $F_{2, 27} = 140.32$, $P < 0.01$), mean N (ANOVA, $F_{2, 27} = 20.16$, $P < 0.01$) and mean H’ (ANOVA, $F_{2, 27} = 74.22$, $P < 0.01$) were significantly different between orientations. Mean S of sessile species was significantly different between all orientations sampled (Tukey $P < 0.05$ in all instances). Mean S was significantly higher on the North orientation compared to both the North-east and East orientations. Mean S was also significantly higher on the North-east orientation compared to East orientation (Table 5.2). Mean N was significantly higher on the North orientation than both the North-east and East orientations (Tukey $P < 0.05$) (Table 5.2), which were not significantly different from each other (Tukey $P > 0.05$). Mean H’ was significantly higher on the North orientation compared to both the North-east and East orientations (Table 5.2). There was no significant difference in H’ between the North-east and East orientations (Tukey $P > 0.05$), (See

Table 5.3 for descriptive statistics).

Table 5.2 – One-Way ANOVA for S, N (% cover) and H’ of sessile species for a) Mid shore and b) Upper shore orientations at Holbeck. NS denotes Not Significant, * denotes significant to 0.01, ** denotes significant to 0.001, *** denotes significant to <0.001.

a) Mid Shore

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	AN		AN		AN	
		F	P	F	P	F	P
Orientation	2	25.77	*	5.2	NS	24.69	*

b) Upper Shore

		Richness (S)		Total Abundance (N)		SW Diversity (H')	
Source	DF	AN		AN		AN	
		F	P	F	P	F	P
Orientation	2	140.32	*	20.16	*	74.22	*

Table 5.3 – Descriptive statistics for S, N (% cover) and H’ of sessile species between orientations at Holbeck, Scarborough.

a) Mid Shore

Orientation	**S**		**N**		**H’**	
	Mean	SD	Mean	SD	Mean	SD
North	2.70	± 0.48	1.73	± 0.16	0.26	± 0.19
North-east	3.00	± 0.47	1.92	± 0.15	0.61	± 0.22
East	1.50	± 0.53	1.76	± 0.11	0.06	± 0.09

b) Upper Shore

Orientation	**S**		**N**		**H’**	
	Mean	SD	Mean	SD	Mean	SD
North	4.50	± 0.53	1.72	± 0.23	1.07	± 0.20
North-east	1.70	± 0.68	0.83	± 0.49	0.23	± 0.30
East	1.00	± 0.00	0.81	± 0.33	0.00	± 0.00

Community analysis found that there was a significant difference in community similarity between mid shore orientations (ANOSIM, Global R = 0.661, P = 0.1%) where all orientations were significantly different to each other (in all cases, P < 0.1%). When plotted, samples showed separation from each other with no overlap (Figure 5.2). The stress value given (0.1) indicated that the plot was reliable. SIMPER analyses found *Fucus vesiculosus* and *Semibalanus balanoides* to be key contributors to the differences observed between communities on the mid shore. Of the overall 44.53 % dissimilarity observed between North and North-east mid shore orientations, 65.52 % was attributed to *Fucus vesiculosus* and *Semibalanus balanoides*, with both having higher average abundances on the North-east orientation (Table 5.4a). The same was true of the comparison between the East and North-East mid shore orientations, where *Fucus vesiculosus* and *Semibalanus balanoides* accounted for 79.57 % of the overall 36.84 % dissimilarity observed. In this instance, *Semibalanus balanoides* had a marginally higher average abundance on the East oriented shore whereas *Fucus vesiculosus* was identified in samples from North-east orientation only (Table 5.4b). Comparison of North and East mid shore orientations found a higher average abundance of *Semibalanus balanoides* on the East oriented shore accounted for 32.85 % of the overall 25.85 % dissimilarity observed. A further 54.10 % of the dissimilarity observed was accounted for by the presence of *Ulva intestinalis* and *Porphyra sp.* in samples from the North orientation only (Table 5.4c).

There was also a significant difference between in community similarity between upper shore orientations (ANOSIM, Global R = 0.708, P = 0.1%). Pairwise Comparisons found both North-east and East upper shore orientations to be significantly different to the North orientation (in both instances, P < 0.1%), but not significantly different from each other (P = 7.2 %). When plotted, samples from the North orientation clustered away from other orientations, whereas samples from North-east and East orientations overlapped (Figure 5.3). The stress value given (0.08) shores indicated that the plot was reasonably reliable. SIMPER analyses found dissimilarity between orientations on the upper shore to be much greater. For instance, of the overall 88.95 % dissimilarity observed between North and North-east upper shore orientations, 88.59 % was attributed to four species: *Porphyra sp.*, *Ulothrix sp.*, filamentous green algae and *Semibalanus balanoides* (Table 5.5a). The same four species accounted for 91.33 % of the overall 89.08 % dissimilarity observed between North and East oriented upper shores (Table 5.5b). In both instances, all algal species either occurred in higher average abundances or were recorded on the North oriented shore only whereas the opposite was true of *Semibalanus balanoides*, which had higher average abundances on both the North-east and East oriented upper shores.

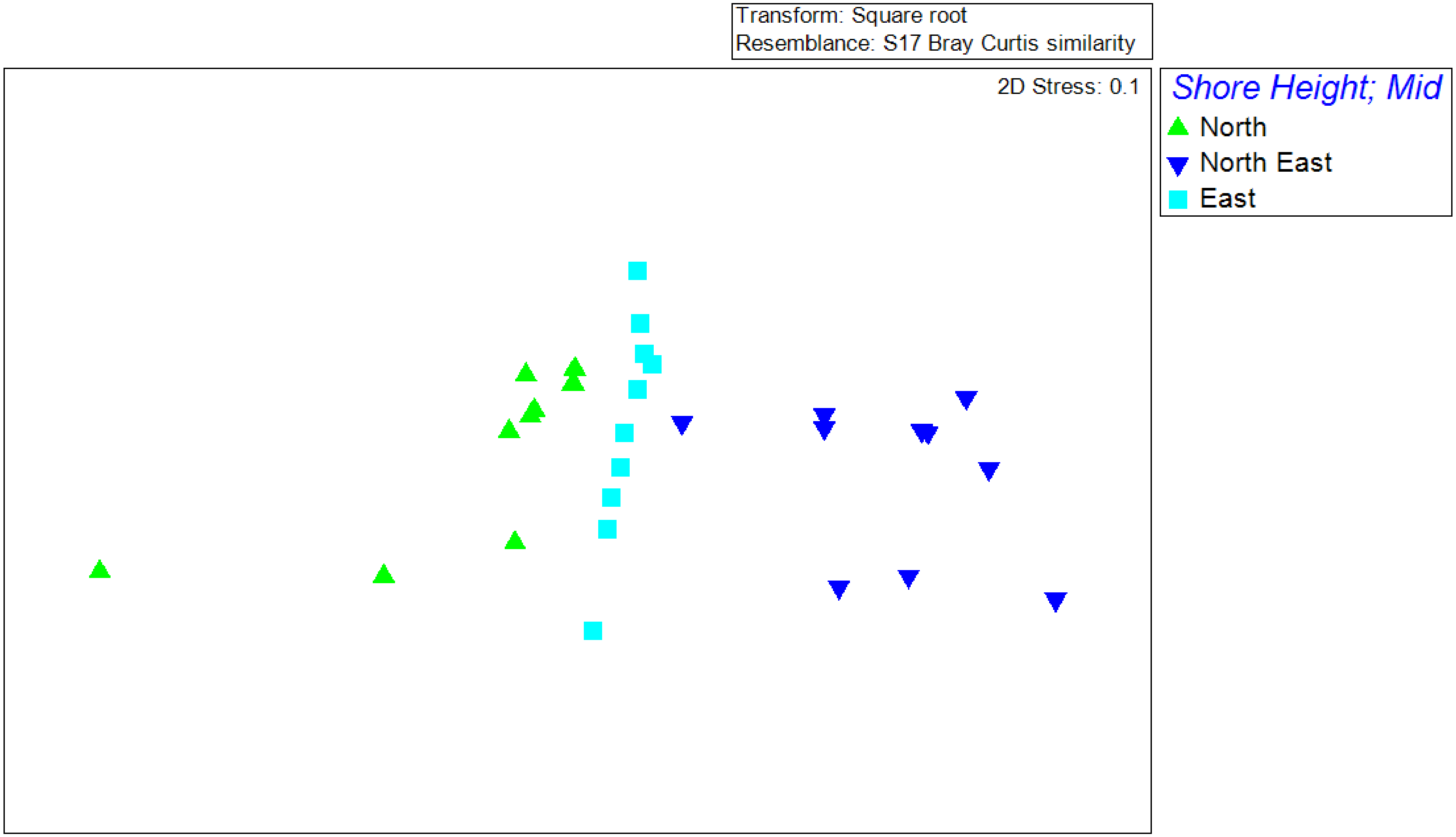


Figure 5.2 – The results of MDS analysis based on a Bray-Curtis similarity matrix for data collected from mid shore orientations examined at Holbeck.

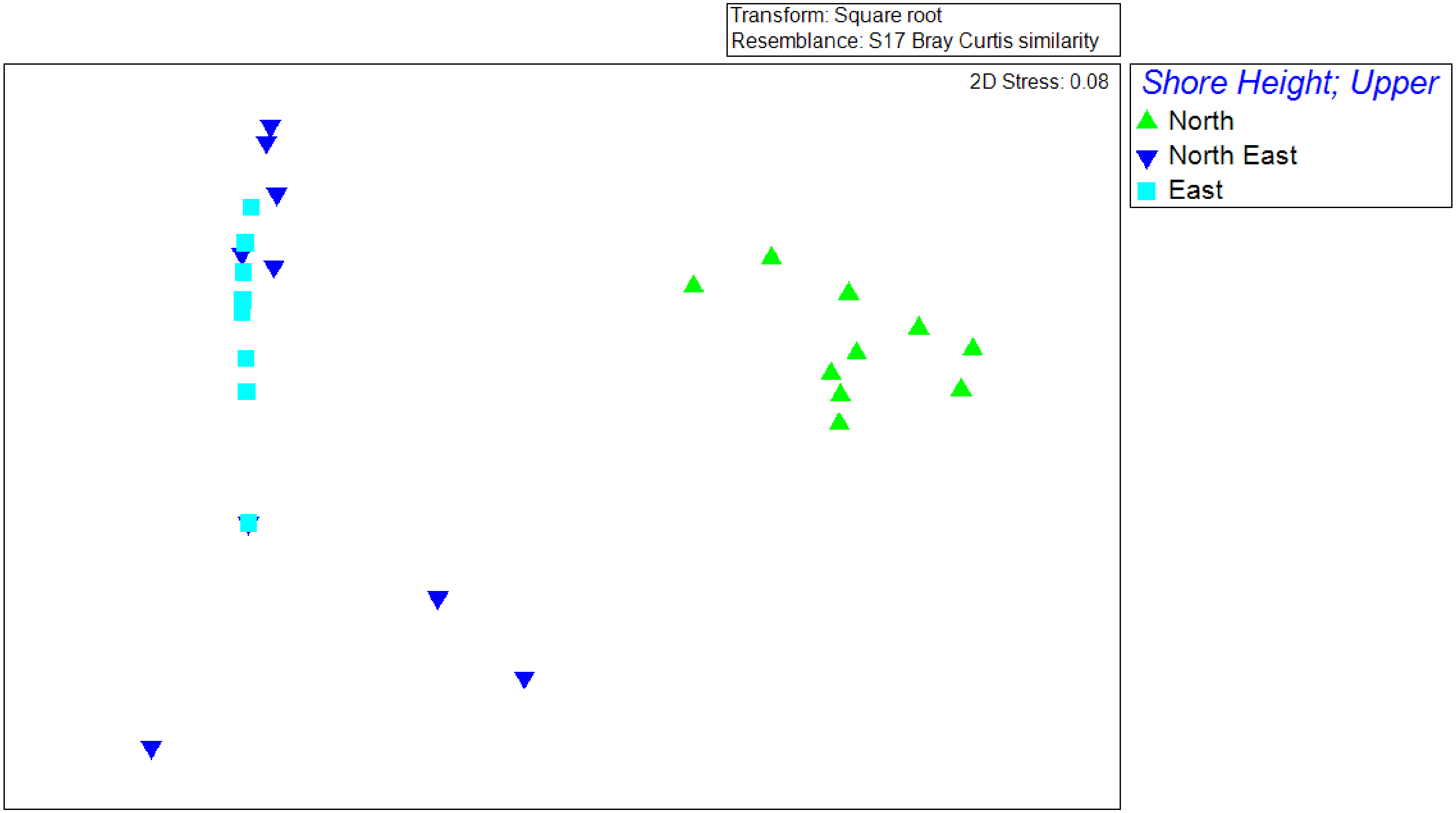


Figure 5.3 – The results of MDS analysis based on a Bray-Curtis similarity matrix for data collected from upper shore orientations examined at Holbeck.

Table 5.4 – SIMPER Table indicating the average abundance of species contributing to the dissimilarity observed between a) North and North-east orientations, b) North-east and east orientations and c) North and East orientations taken from the Mid shore at Holbeck, Scarborough (Av.Abund = mean abundance (raw % cover data), Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) North & North-east — **Average Dissimilarity = 44.53 %**

Species	**North Av.Abund**	**North-east Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Fucus vesiculosus	0.00	5.33	22.31	2.55	50.11	50.11
Semibalanus balanoides	6.92	7.20	6.86	1.09	15.41	65.52
Ulva intestinalis	1.29	0.00	5.73	4.63	12.88	78.39
Porphyra sp.	1.19	0.00	5.12	0.74	11.50	89.89

b) North-east & East — **Average Dissimilarity = 36.48 %**

Species	**North-east Av.Abund**	**East Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Fucus vesiculosus	5.33	0.00	23.51	2.58	63.83	63.83
Semibalanus balanoides	7.20	7.57	5.80	1.21	15.74	79.57
Ulva linza	0.94	0.00	4.29	2.61	11.65	91.21

c) North & East — **Average Dissimilarity = 25.85 %**

Species	**North Av.Abund**	**East Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Semibalanus balanoides	6.92	7.57	8.49	1.12	32.85	32.85
Ulva intestinalis	1.29	0.00	7.42	5.22	28.71	61.56
Porphyra sp.	1.19	0.00	6.57	0.75	25.39	86.95

Table 5.5 – SIMPER Table indicating the average abundance of species contributing to the dissimilarity observed between a) North and North-east orientations and b) North and East orientations taken from the Upper shore at Holbeck, Scarborough (Av.Abund = mean abundance (raw % cover data), Av.Diss = Average dissimilarity, Diss/SD = Dissimilarity SD, Contrib% = Contribution percentage, Cum.% = Cumulative percentage).

a) North & North-east — **Average Dissimilarity = 88.59 %**

Species	**North Av.Abund**	**North-east Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Porphyra sp.	5.19	0.00	30.31	3.48	34.21	34.21
Ulothrix sp.	3.78	0.00	22.31	3.54	25.18	59.39
Filamentous Greens	2.57	0.00	15.63	1.98	17.64	77.03
Semibalanus balanoides	0.88	2.36	10.09	1.17	11.39	88.42

b) North & East — **Average Dissimilarity = 89.08 %**

Species	**North Av.Abund**	**East Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
Porphyra sp.	5.19	0.00	31.45	3.75	35.31	35.31
Ulothrix sp.	3.78	0.00	23.15	3.83	25.99	61.30
Filamentous Greens	2.57	0.00	16.24	2.02	18.23	79.53
Semibalanus balanoides	0.88	2.49	10.51	1.60	11.80	91.33

Richness of macroalgal functional groups was significantly different between orientations at mid shore height (ANOVA, $F_{2, 27} = 39.97$, $P < 0.01$). On the mid shore, functional richness was significantly higher on the North-east orientation compared to the North orientation (Tukey $P < 0.05$), and functional richness was significantly higher on both than on the East orientation (Tukey $P < 0.05$), (Table 5.6a). A total of six species from two functional groups were identified in samples from the mid shore (Table 5.7). Three algal species from two functional groups were recorded on the North-east orientation and two species of foliose algae were recorded on the North orientation. Only one species, *Ulva sp.*, was present on the East orientation (Table 5.7).

Macroalgal functional richness was also significantly different between orientations at upper shore height (ANOVA, $F_{2, 27} = 85.50$, $P < 0.01$). On the upper shore, the North orientation had a significantly higher algal functional richness than both the North-east and East orientations (Tukey $P < 0.05$), (Table 5.6b). The North-east orientation had a significantly higher algal functional richness compared to the East facing shore (Tukey $P < 0.05$). On the upper shore, a total of six species from three functional groups were identified on the North and North-east orientations (Table 5.7). Of these, four species representing three functional groups were present on the North orientation, whereas two species from two functional groups were identified on the North-east orientation. Algal species were absent from the east orientation (Table 5.7).

Table 5.6 – Descriptive statistics for richness of algal functional groups between orientations at Holbeck, Scarborough.

a) Mid Shore

Orientation	**Functional Richness**	
	Mean	SD
North	1.00	± 0.00
North-east	1.90	± 0.32
East	0.50	± 0.53

b) Upper Shore

Orientation	**Functional Richness**	
	Mean	SD
North	2.70	± 0.48
North-east	0.70	± 0.67
East	0.00	± 0.00

Table 5.7 – Presence and absence of species from different functional groups identified on orientations at mid and upper shore height at Holbeck, Scarborough.

Functional Group	**Species**	**Mid Shore**			**Upper Shore**		
		North	North-east	East	North	North-east	East
Filamentous	Filamentous Greens				*		
	Ulothrix sp.				*		
Foliose	*Ulva sp.*			*		*	
	Ulva linza		*				
	Ulva lactuca		*				
	Ulva intestinalis	*					
	Porphyra sp.	*			*		
Leathery	*Fucus spiralis*				*	*	
	Fucus vesiculosus		*				

5.3.2 Variation in Mobile Communities on Substrates with Differing Orientations at Holbeck, Scarborough.

There was a significant difference in mean S (ANOVA, $F_{2, 27} = 14.49$, $P < 0.01$) and mean H' (ANOVA, $F_{2, 27} = 13.08$, $P < 0.01$) of mobile species between orientations at mid shore height. Mean S was significantly higher on both the North and North-east facing sides compared to the East facing side, although the North and North-east facing sides were not significantly different from each other (Tukey > 0.05). Mean H' was significantly lower on the East oriented side compared to both the North-east and North orientations, which were not significantly different o each other (Tukey > 0.05). There was no significant difference in mean N of mobile species between orientations (ANOVA, $P > 0.01$), (see Table 5.8 for mean and SD values).

On the upper shore, there were no significant differences in mean S, mean N or mean H' (ANOVA, $P > 0.01$ in all cases) (see Table 5.8 for mean and SD values).

Table 5.8 – Descriptive statistics for S, N (count) and H' of mobile species between orientations at Holbeck, Scarborough.

a) Mid Shore

Orientation	S		N		H'	
	Mean	SD	Mean	SD	Mean	SD
North	2.50	± 1.18	16.80	± 12.96	0.44	± 0.36
North-east	2.50	± 0.53	47.60	± 28.44	0.61	± 0.32
East	0.90	± 0.32	18.90	± 10.35	0.00	± 0.00

b) Upper Shore

Orientation	S		N		H'	
	Mean	SD	Mean	SD	Mean	SD
North	0.70	± 0.68	1.30	± 2.41	0.06	± 0.18
North-east	0.80	± 0.42	5.80	± 7.63	0.00	± 0.00
East	0.60	± 0.70	3.10	± 4.48	0.05	± 0.15

Comparison of grazer density on the mid shore found that median S (Kruskal Wallis, H (adjusted for ties) = 18.25, df = 2, $P < 0.05$) and mean H' (ANOVA, $F_{2, 27} = 15.29$, $P < 0.01$) of grazing species was significantly different between orientations, whereas mean N of grazing species was not (ANOVA, $P > 0.01$). Median S of grazers was significantly lower on the East orientation compared to both North and North-east orientations (Pairwise Wilcoxon Rank Sum Test, $P < 0.05$ in both cases), (Table 5.9). However, mean H' of grazers was significantly different between all orientations (Tukey > 0.05, in all instances), with mean H' being highest on the North-east orientation and the lowest on the East orientation (Table 5.9).

On the upper shore, there was no significant difference in mean S (ANOVA, P > 0.01), or median N (Kruskal Wallis, P > 0.05) of grazers between orientations. Diversity values could not be calculated or tested as *Patella vulgata* was the only grazing species identified in samples from each orientation (Figure 5.4).

Mean density of grazers varied greatly between orientation and shore height as shown in Figure 5.4. Density of *Patella vulgata* was higher on the mid shore than the upper shore. *Patella vulgata* was present on all orientations at mid shore height, occurring in highest mean density on the East orientation. On the upper shore *Patella vulgata* occurred in similar densities on the North-east and North orientations and was absent from the East orientation (Figure 5.4). High densities of *Littorina saxatilis* were recorded on the North-east mid shore orientation only. *Littorina littorea* and *Littorina obtusata* were sparse and present on the North mid shore orientation only. All species of Littorinid were absent from the upper shore.

Table 5.9 – Descriptive statistics for S, N (count) and H' of grazing species between mid shore orientations only at Holbeck, Scarborough. Where One-Way ANOVA was applied the mean and standard deviation (SD) have been reported, where Kruskal-Wallis test was used the median and range have been reported.

Mid Shore Grazer Density (/0.25m^2)

	Richness			Diversity			
Orientation	n	Median	Range	n	Mean		SD
East	10	1.00	0.00 – 1.00	10	0.00	±	0.00
North	10	2.00	1.00 – 3.00	10	0.51	±	0.24
North-east	10	2.00	2.00 – 2.00	10	0.24	±	0.26

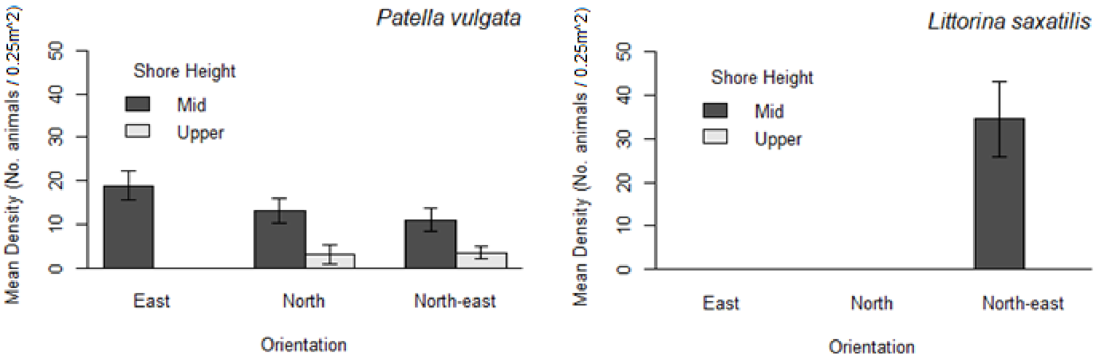


Figure 5.4 – Mean density (number of animals per 0.25m^2) of grazing species *Patella vulgata* and *Littorina saxatilis* from mid shore and upper shore orientations at Holbeck, Scarborough.

5.4 Discussion

The key findings of this study suggest that the diversity and structure of sessile and mobile communities varies with substrate orientation. In this instance, richness and diversity of sessile and mobile communities differed significantly between orientations in both mid and upper shore environments. However, while richness and diversity were found to differ between orientations in this study, this was likely not solely the result of substrate orientation (Sedano *et al.,* 2019).

Substrate orientation can determine a range of environmental factors including level of wave exposure and light intensity (Baynes, 1999; Cefalì *et al.,* 2016). In mid shore environments, wave exposure is a key determinant of macroalgal distribution by mediating desiccation and facilitating growth and reproduction (Underwood and Jernakoff, 1984; Chappuis *et al.,* 2014). In this study, richness and diversity of sessile species was significantly higher on the North-east orientation at mid shore height (

Table 5.3a). However, at upper shore height, richness, abundance, and diversity of sessile species was significantly higher on the North orientation (

Table 5.3b). Community similarity also differed significantly between orientations at both shore heights (Figure 5.2 and Figure 5.3). However, dissimilarity between samples from each orientation was markedly higher on the upper shore than on the mid shore (Table 5.4 and Table 5.5). On the upper shore, dissimilarity was the result of greater average abundances of algal species on the North orientation compared to an absence of algal species on the North-east and East orientations.

All orientations at Holbeck were exposed to wave action however the crescent shape of the defence meant there were likely subtle differences in wave exposure regimes between orientations and tidal heights. For example, on-coming waves would strike the North-east orientation first potentially making it a higher-energy environment than the North and East orientations (personal observation). In addition, the prevailing wind direction incoming from the North Sea would strike this particular defence on its North-east and East orientations (personal observation). This may produce a cooling effect which would act to lower temperatures on the surface of these substrates faster, whereas again, the North orientation would be a more sheltered and protected environment.

Differences in the richness of macroalgal functional groups are sometimes indicative of different levels of wave exposure (Quintano *et al.,* 2015). Here, macroalgal functional richness was significantly different between orientations at both shore heights (Table 5.6). Algal species with different functional forms are known to respond differently to greater wave exposure as a result of substrate orientation (Quintano *et al.,* 2015). For example, density of leathery macrophyte species, such as fucoids, has been shown to increase with increasing wave exposure (Nishihara, and Terada, 2010). Whereas, other functional forms including foliose, filamentous, and coarsely branched forms, show more a negative association with wave exposure (Nishihara, and Terada, 2010). Wave exposure and tidal height are both important factors in determining community structure on rocky shores, however the influence of wave exposure may be less pronounced in higher shore environments (McQuaid and Lindsay, 2005). At Holbeck, substrates with an East orientation experienced more hours of direct sunlight than substrates with a North or North-east orientation, which were more shaded by nearby coastal cliffs and by the defence itself. *Porphyra sp.* was present in high abundances on both shores on the North orientation only (Table 5.4 and Table 5.5). This species is known to grow well in conditions where availability and intensity of light is limited (Green and Neefus, 2016). Although permanently shaded substrates host poor algal communities (Clark, Edwards and Foster, 2004; Blockley, and Chapman, 2006) in this instance, the North orientation would have experienced a shortened period of sun-exposure rather than receive no light at all.

Periods of shade are also important for mobile and invertebrate species (Firth *et al.,* 2016c). On the mid shore, richness and diversity was significantly lower on the East orientation than on either the North or North-east orientations of the defence (Table 5.8). This may have been due to East orientation being exposed to longer periods of sun without shading. Environmental factors such as surface temperature and light intensity can affect the body temperature, distribution, and even the morphology of invertebrates between tides (Gaines and Denny, 2007; Harley *et al.,* 2009). No such differences were observed on the upper shore as it was less populated by invertebrates (Table 5.8). Mid shore environments are often submerged for longer and time between tides is often shorter than in upper shore environments, meaning that mid shore-dwelling invertebrates can maintain their body temperature more easily (Somero, 2002; Fraser *et al.,* 2016). Here, density of grazing species was greater across orientations at mid shore height (Figure 5.4), due to reduced thermal and desiccation stress (Benedetti-Cecchi, 2001). Unsurprisingly, density of grazers was low on the upper shore and grazing invertebrates were absent from the east orientation entirely (Figure 5.4). As discussed above, the East orientation at Holbeck would likely have experienced more prolonged periods of intense sun exposure than other orientations. Exposure to such thermal stress can impact grazing fauna by increasing their body temperature and heart rate above a critical threshold, and result in mortality (Hui *et al.,* 2020). As a result, lower abundances of mobile species and grazing invertebrates in the upper shore region of artificial environments is not unusual (Chapman, 2003a).

The results presented here show that diversity and structure of sessile and mobile communities differed between orientations at both mid and upper shore height, possibly because of subtly different environmental conditions on each orientation. As previous authors have noted, examining the effect of substrate orientation in isolation has proven difficult (Sedano *et al.,* 2019) and further work is needed to understand how substrate orientation influences intertidal communities. Understanding the impacts environmental factors, including wave exposure, light intensity and substrate temperature, on community diversity is also important. There may be potential to examine substrate orientation to identify how environmental conditions differ across the structure and which areas of a coastal defence may be least hospitable to marine organisms. Understanding how community diversity varies with orientation, and what factors drive these differences could have implications for future ecological enhancement work, potentially allowing ecological enhancements to be deployed in a targeted way in areas where they may be more necessary. However, as previous work has shown, substrate orientation and its influence on structure and diversity in sessile and mobile communities on coastal defences, is not clear and more work is needed to address this gap in existing knowledge.

Chapter 6 General Discussion

6.1 Summary and Key Findings

The prevalence of artificial coastal defences in the marine environment has increased in recent years in response to sea-levels rise (IPCC, 2013). Coastal defences are known to support diminished diversity in comparison to natural rocky shore communities (Moschella *et al.,* 2005; Bulleri and Chapman, 2010). However, continued research has highlighted how modifications can create more diverse habitats within artificial environments (Coombes *et al.*, 2015; Evans *et al.*, 2016; Firth *et al.*, 2013b; Hall *et al.*, 2018; Waltham and Sheaves, 2018; MacArthur *et al.,* 2019). The research presented in this thesis adds to our understanding of how creating habitat heterogeneity and physical complexity can improve the diversity of sessile and mobile communities on coastal defences.

This study aimed firstly, to determine whether there were differences in the diversity and composition of sessile and mobile communities between the three main habitat types (artificial pools, granite boulders and sandstone boulders) on the new rock armour at Runswick Bay, and how this varied over time. This was examined in Chapter 2, which found that both artificial pool and sandstone boulder habitats supported a higher richness, abundance, and diversity of sessile and mobile species than granite boulder habitats, throughout the study period (Table 2.3), and that the composition of sessile and mobile communities was also significantly different between habitat types (Figure 2.3). Secondly, this study aimed to monitor colonisation of areas with and without added small-scale (cm) physical complexity (substrates treated with grooves, and untreated substrates without grooves) to determine if diversity and composition of sessile and mobile communities differed between treatment types over time. Chapter 2 found that while the richness, abundance and diversity of sessile and mobile species varied significantly within both treatment types over time (Figure 2.4 and Figure 2.6), the composition of sessile and mobile communities was not significantly different between treatment types (Table 2.8 and Table 2.11).

Alongside this, the study aimed to determine whether diversity and structure of sessile and grazing communities differed between granite and sandstone substrates with different levels of fine-scale (mm) physical complexity at one site in Scarborough North Bay, North Yorkshire. Chapter 3 found that rugosity was significantly different between substrate types present at North Bay (Table 4.3) and that richness, abundance, and diversity of sessile and grazing species was significantly different between substrate types at both mid and upper shore height (Table 4.5 and Table 4.10). This chapter also aimed to determine whether fine-scale physical complexity impacted diversity and community structure over a regional scale. The research in

Chapter 3 showed that, although substrate rugosity was significantly different between the five sites examined across North and East Yorkshire, the composition of sessile and grazing communities (Figure 4.8 and Table 4.15) indicated that structure age was a more important driver of diversity over a regional scale.

And finally, this study aimed to determine whether diversity and structure of sessile and mobile communities was different between granite substrates with different compass orientations at one site in Scarborough South Bay, North Yorkshire. This was addressed in Chapter 4, which showed that the richness, and diversity of sessile and mobile species differed significantly between orientations at both mid and upper shore height (

Table 5.3 and Table 5.8), as did the composition of sessile and mobile communities (Figure 5.2, Figure 5.3, and Figure 5.4).

6.2 Increasing Habitat Heterogeneity on Coastal Defences

This study has shown that increasing habitat heterogeneity by increasing the range of habitat types available can significantly increase diversity on coastal defences (Chapter 2, Section 2.3). On natural rocky shores, rock pools support a greater richness and diversity of species than emergent rock (Schaefer *et al.*, 2019), by providing better foraging opportunities and protection from environmental stress (Martins *et al.,* 2007; Mendonça *et al.*, 2019). Artificial rock pools appear to function in a similar way and have been found to host a higher number and have a different composition of taxa than adjacent artificial substrata as a result (Firth *et al.*, 2016a).

On the new rock armour defence at Runswick Bay, richness, and diversity of both sessile and mobile species was higher in artificial pool habitats than in other habitat types throughout the study (Table 2.2). Increasing habitat heterogeneity by adding water retaining features has become a widely-used method of improving diversity on coastal defences (Loke, Heery and Todd, 2019), and proved a particularly effective way of encouraging recolonisation by mobile invertebrates (Evans *et al.*, 2016; Hall *et al.*, 2018). However, abundance of mobile species was low across all habitat types during this study (Table 2.12), although mobile and grazing species are often slow to colonise artificial environments (Chapman, 2003a).

Many studies examining colonisation of artificially-created rock pools occur over relatively short timescales, mostly between 18 – 24 months (Evans *et al.*, 2016; Firth *et al.*, 2016a; Waltham and Sheaves, 2018), which is also true of the present study. Most species may have settled into an engineered habitat within approximately two years of installation (Sempere-Valverde *et al.,* 2018), however a recent study by Hall *et al.,* (2019) found community composition in artificial concrete rock pools changed considerably three years after installation, when grazing species moved into the habitat. Further time is needed for populations to fully establish on rocky shores, and it may take between 5 – 20 years before a stable climax community is reached (Pinn *et al.,* 2005; Gacia *et al.,* 2007). Therefore, it is likely that the communities which colonised the habitats created at Runswick Bay will continue to develop over time.

Heterogeneity of habitats in artificial environments can also be increased by incorporating a wider variety of materials (Sempere-Valverde *et al.,* 2018), given that substrate type has been identified as a major driver of community structure in sessile benthic communities (Sedano *et al.*, 2019). The defence works at Runswick Bay have shown that sandstone boulders can be incorporated into granite rock armouring without impacting the stability or performance of the defence (JBA Consulting, 2017a). Here, sandstone boulders were intended to act as "seed" boulders to promote colonisation of the granite. This study found that sandstone boulder habitats had a significantly higher richness and diversity of sessile species than granite boulder habitats (Table 2.3), and a greater proportion of leathery macroalgae than either artificial pool or granite boulder habitats (Figure 2.4). It should be noted that succession of the habitat was incomplete at the end of the sampling period, however, within the time allowed sandstone boulder habitats showed signs of function as intended and highlighted that incorporating mixed substrata into coastal defences can enhance biodiversity in several ways.

Firstly, placing natural sandstone boulders or native substrata in close proximity to artificial structures may facilitate connectivity between shores (Hall *et al.,* 2019), particularly for species which disperse planktonically (Liversage and Chapman, 2018), such as *Semibalanus balanoides*, *Actinia equina* and *Patella vulgata* which were identified on samples from sandstone boulders (Table 2.1). There is limited evidence in this study to suggest that there was some connectivity between sandstone boulder and granite boulder habitats. As discussed in Chapter 2, Section 2.4, *Fucus spiralis* was present on sandstone boulder habitats throughout the study and emerged in artificial pool habitats in later months (Figure 2.4), which may indicate some transfer of species between habitat types. However, extent to which this occurred is unclear given that *Fucus spiralis* is a hermaphroditic alga, able to self-fertilise and recruit easily in artificial upper shore environments (Chapman, 1989).

Secondly, the material properties of sandstone substrates may provide better conditions for algal growth than artificial granite substrates. While the presence of leathery macroalgae on sandstone boulder habitats was primarily the result of regrowth from holdfasts not removed during construction (Keser, Vadas and Larson, 1981), the characteristics of sandstone may have enhanced light and moisture availability which facilitated regrowth (Finlay *et al.,* 2008). For example, sandstone was lighter in colour than granite in this instance and would therefore have possessed a higher albedo and better ability to reflect light (Sempere-Valverde *et al.,* 2018). Similarly, the porosity of sedimentary rocks enables water to be retained within the substrate between tides (McGuinness and Underwood, 1986).

Finally, sandstone is susceptible to environmental and biological weathering over time (Coombes, 2014), which is beneficial in ecological engineering as it creates natural physical complexity. As shown in Chapter 4, Section 4.3.1, the fine scale surface rugosity of sandstone substrates was significantly higher than that of either rough fractured or smooth machine cut granite substrates. Regular weathering and disturbance of rocks in the intertidal environment will naturally create greater physical complexity (Coombes *et al.,* 2013), which in turn will influence the richness and diversity of organisms within a habitat (Evans *et al.*, 2016; Firth *et al.*, 2016b; Hall *et al.*, 2018).

6.3 Improving Physical Complexity on Coastal Defences

Introducing mixed substrata is also an effective way to vary the fine-scale (mm) physical complexity on coastal defences. The surface texture or rugosity of a substrate is known to influence composition of rocky shore communities (Sweat and Johnson, 2013; Lund-Hansen *et al.,* 2017), and the results of Chapter 3 highlight the importance of substrate rugosity in structuring sessile and grazing communities across tidal heights on a local scale.

The importance of rugosity was found to vary between sessile and grazing species. Here, substrate rugosity positively correlated with richness and abundance of grazing species at both mid and upper shore height. Richness and abundance of grazing species was highest on the most rugose substrates at each shore height, respectively (Table 4.10). Rugose surfaces accumulate biofilm (Lund-Hansen *et al.,* 2017) and retain water in surface depressions (Köhler, Hansen and Wahl, 1999). This would provide grazers with both better foraging opportunities and a means of thermal regulation (Firth *et al.,* 2016c). In contrast, sessile richness, abundance, and diversity positively correlated with rugosity at mid shore height, but no relationship was found at upper shore height. On the one hand, greater rugosity is thought to facilitate the adhesion of algal propagules to the substrate (Crimaldi *et al.*, 2002), however, the importance of rugosity to sessile species is known to be time-dependant (Hanlon *et al.,* 2018). As discussed in Chapter 4, Section 4.4, the settlement of species, such as *Semibalanus balanoides*, will create a layer of biogenic habitat complexity over the substrate, thus reducing the importance of rugosity through limiting access to the substrate by species which colonise subsequently (Thompson *et al.,* 1996).

Rugosity was also of limited importance over a regional scale. Of the five sites across North and East Yorkshire, rugosity was significantly different at only one site and differences in sessile and grazing community composition indicated that structure age was more important in this instance (Chapter 4, Section 4.4). This was consistent with previous findings that newly installed structures (< 2 years) are invertebrate-poor and largely dominated by ephemeral algae, whereas older structures host established communities of perennial algae and have a greater richness of grazing invertebrates (Chapman and Underwood, 1998; Pinn *et al.,* 2005; Dong *et al.,* 2018). However, deploying enhancements such as holes or grooves (Evans *et al.*, 2016; Hall *et al.,* 2018) which create small-scale (cm) complexity on coastal defence structures may be more effective way of improving biodiversity over a wider geographical area, by creating microhabitats and providing refuges for sessile and mobile species.

The lack of physical complexity in artificial costal defence habitats is known to directly impact biodiversity by limiting communities to only those which can survive without additional protection (Evans *et al.*, 2016). In this study, small-scale complexity was increased by engineering grooves to granite boulders (see Chapter 1, Section 1.6 for description), however, their effectiveness here was limited (Chapter 3, Section 3.4). In this instance, richness, and diversity of sessile species was not significantly higher at the end of the study for either substrates treated with grooves, or untreated substrates. Similarly, sessile community similarity did not differ significantly between treatment types (Figure 6.1). In addition, mobile species were notably sparse on substrates treated with grooves and were absent entirely from untreated substrates throughout the study. This may have been a result of the relatively short timescale allowed for this study and that colonisation of treatment types by mobile species was still ongoing (Thompson, 1980). However, previous work has found cm-scale holes and cm-wide grooves to successfully increase invertebrate diversity over similar timescales (Evans *et al.*, 2016; Hall *et al.,* 2018), although these trials were conducted on structures which had been in place for some time and may have already hosted an established invertebrate community.

In this study, the use of only narrow grooves likely contributed to the under-abundance of fauna by limiting the accessibility of the microhabitat by hard-shelled animals to smaller individuals only, as discussed in Chapter 3, Section 3.4. The grooves implemented as part of the Runswick Bay Coastal Protection Scheme were not widened to follow the original concept of Hall *et al.,* (2018), and so did not perform in the same way within the time allowed. Reporting trials where habitat enhancements have not performed as expected is important to ensure that the application, and limitations of different habitat enhancement methods are understood (Firth *et al.,* 2020). Without this understanding, there is a chance that habitat enhancements could be implemented ineffectively (Firth *et al.*, 2016a; O'Shaughnessy *et al.,* 2020).

6.4 Understanding Substrate Orientation on Coastal Defences

Naylor *et al.*, (2012) showed that habitat enhancements could be easily considered and implemented as part of the planning and development framework used in coastal defence building. However, as Cooper *et al.*, (2016) noted, coastal defence structures are often built on a case-by-case basis, and as a result, vary considerably depending on their location, purpose, and size (Cooper and McKenna, 2008). The orientation and alignment of a defence will determine the environmental conditions that organisms which colonise it are subjected to, such as the level of wave exposure and hours spent in the sun and shaded (Firth *et al.*, 2016c).

When examining the effect of compass-orientation in communities on the rock armouring at Holbeck in Scarborough, this study found sessile and mobile communities differed significantly between orientations, at both mid and upper tidal heights (Chapter 5, Section 5.3). The study also found community similarity differed significantly between orientations at both tidal heights (Figure 5.2 and Figure 5.3), and that the distribution of species was dependent upon the level of wave exposure the substrate experienced, and the time spent shaded from sunlight (Nishihara and Terada, 2010). The results presented in Chapter 4 highlight that complex interactions between coastal defences and their environments can shape the intertidal communities which colonise them. This study also raises how important collaboration between ecologists, engineers and developers is in applying habitat enhancements effectively (Firth *et al.,* 2020).

By examining the physical and environmental attributes of a defence, including structure orientation and the level of sun and wave exposure, ecologists may be able to identify areas where the environment may be especially harsh for marine organisms. Having this understanding could allow ecologists and developers to deploy habitat enhancements in a targeted way with clear ecological goals in mind. However, further research is required to fully understand the effect of deploying habitat enhancements in this way.

6.5 Final Summary

The Runswick Bay Coastal Protection Scheme is an important site in the field of ecological engineering in the UK as it is both the largest application of habitat enhancements on a coastal defence structure in the UK, at present (Latham *et al.,* 2020), and is a rare example of a coastal defence with planned habitat enhancements throughout (JBA Consulting, 2017a). Overall, this study provides a valuable assessment of how creating habitat heterogeneity and physical complexity on a large scale impacted on species richness and diversity in sessile and mobile communities. The study also provided a useful comparison of the fine-scale physical complexity of different materials used in coastal defence building and examined how sessile and mobile communities differ with the orientation of a defence.

Research has shown there are opportunities to consider habitat enhancements throughout the planning and development process (Naylor *et al.*, 2012), and that stakeholders and members of the public prioritise the ecological benefits of coastal defences over economic benefits (Evans *et al.*, 2017). However, barriers to creating ecologically sensitive, multifunctional coastal defences remain (Evans *et al.*, 2019). Perceived barriers include a lack of confidence in existing examples of mostly small-scale applications of habitat enhancements, and questions over the cost-benefit of using habitat enhancements (Evans *et al.*, 2019). The Runswick Bay Coastal Protection Scheme is an excellent case study which provides evidence that habitat enhancements can be planned and incorporated into large coastal development projects to successfully deliver ecological goals. The scheme also highlights the potential of using mixed substrata to enhance both colonisation and biodiversity of coastal defences and provides an example of how mixed substrata could be incorporated into future defence works.

There has been a clear drive in European and UK policy in recent years that supports the application of habitat enhancements in marine infrastructure projects (Firth *et al.,* 2020), and a catalogue of existing habitat enhancement methods and their use with different coastal infrastructure has also been published (O'Shaughnessy *et al.,* 2020). However, it is vital that engineers and developers collaborate with ecologists so that habitat enhancements can be applied in a meaningful and effective way (Evans *et al.*, 2019), rather than as a means to influence consenting on harmful developments (Firth *et al.,* 2020; O'Shaughnessy *et al.,* 2020). Continued monitoring of enhanced structures is also essential to understanding how habitat enhancements perform over longer time periods, and how their use by marine organisms changes (Firth *et al.,* 2020).

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Appendix 1

Descriptive statistics for S, N (% cover) and H’ of sessile species over time for a) Artificial pools (AP), b) Granite boulder (GB) and c) Sandstone boulder (SB) habitats. Where One-Way ANOVA was applied to data the mean and standard deviation (SD) have been reported, where Kruskal-Wallis test was used the median and range have been reported.

a) Artificial Pools (AP)

Time in Months	S		N		H’	
	Mean	SD	Mean	SD	Median	Range
0 July 18	1.07	± 0.83	65.00	± 47.6	0.00	0.00 – 0.69
6 February	3.71	± 0.91	72.00	± 12.67	0.80	0.62 – 1.47
8 April	3.29	± 1.07	84.00	± 35.08	0.79	0.10 – 1.35
9 May	4.93	± 1.27	139.89	± 35.84	1.03	0.71 – 1.38
10 June	6.57	± 1.28	174.40	± 51.00	1.48	1.05 – 1.93
11 July	4.93	± 1.90	95.00	± 38.80	1.03	0.20 – 1.62
12 August	9.45	± 1.45	131.50	± 33.73	1.47	1.47 – 2.16
13 September	9.23	± 1.56	158.31	± 27.10	1.64	1.42 – 2.17
14 October	7.86	± 2.63	125.80	± 65.30	1.55	0.35 – 1.82

b) Granite Boulders (GB)

Time in Months	S		N		H’	
	Mean	SD	Median	Range	Mean	SD
0 July 18	0.29	± 0.47	0.00	0.00 – 95.00	0.00	± 0.00
6 February	2.64	± 1.01	72.50	25.00 – 177.00	0.58	± 0.32
8 April	2.43	± 0.65	78.00	16.20 – 121.00	0.59	± 0.22
9 May	2.86	± 0.86	81.50	9.50 – 125.00	0.42	± 0.36
10 June	2.71	± 0.73	98.50	14.00 – 139.00	0.55	± 0.25
11 July	2.14	± 0.86	57.50	0.00 – 120.00	0.45	± 0.34
12 August	2.93	± 0.92	80.00	5.00 – 136.00	0.69	± 0.40
13 September	2.29	± 0.91	27.00	1.00 – 101.00	0.56	± 0.32
14 October	3.21	± 0.89	59.50	4.00 – 152.00	0.79	± 0.31

c) Sandstone Boulders (SB)

Time in Months	S		N		H’	
	Median	Range	Mean	SD	Mean	SD
0 July 18	NA		NA		NA	
6 February	3.00	2.00 – 7.00	116.82	± 36.51	0.74	± 0.29
8 April	3.00	2.00 – 6.00	125.71	± 32.91	0.84	± 0.27
9 May	3.50	2.00 – 6.00	121.30	± 47.30	0.86	± 0.31
10 June	4.00	2.00 – 7.00	142.07	± 33.08	1.00	± 0.28
11 July	5.50	1.00 – 7.00	113.61	± 20.19	0.88	± 0.50
12 August	5.50	3.00 – 8.00	111.79	± 23.00	0.96	± 0.51
13 September	5.00	2.00 – 9.00	123.00	± 35.50	1.17	± 0.51
14 October	6.00	1.00 – 9.00	127.70	± 67.10	1.06	± 0.64

Appendix 2

Median and range data for species richness (S), total abundance (N) (% cover) and SW diversity (H’) of sessile species over time for a) Substrates treated with Grooves (GS) and b) Untreated Substrates (US).

a) Grooved Substrates (GS)

Time in Months		**S**		**N**		**H’**	
		Median	Range	Median	Range	Median	Range
6	February	0.00	0.00 – 4.00	0.00	0.00 – 96.00	0.00	0.00 – 1.19
8	April	1.00	0.00 – 3.00	2.00	0.00 – 113.00	0.00	0.00 – 1.09
9	May	2.00	0.00 – 4.00	21.00	0.00 – 124.00	0.52	0.00 – 1.09
10	June	2.00	0.00 – 4.00	25.00	0.00 – 139.00	0.42	0.00 – 1.04
11	July	2.00	0.00 – 4.00	35.00	0.00 – 125.00	0.34	0.00 – 1.09
12	August	2.00	0.00 – 4.00	38.00	0.00 – 156.00	0.36	0.00 – 1.24
13	September	2.00	0.00 – 3.00	16.00	0.00 – 120.00	0.13	0.00 – 1.07
14	October	1.00	0.00 – 3.00	15.00	0.00 – 136.00	0.00	0.00 – 0.90

b) Untreated Substrates (US)

Time in Months		**S**		**N**		**H’**	
		Median	Range	Median	Range	Median	Range
6	February	1.00	0.00 – 3.00	1.00	0.00 – 72.00	0.00	0.00 – 1.01
8	April	1.00	0.00 – 3.00	1.00	0.00 – 133.00	0.00	0.00 – 1.09
9	May	2.00	0.00 – 4.00	19.00	0.00 – 123.00	0.31	0.00 – 1.11
10	June	1.00	0.00 – 4.00	6.00	0.00 – 130.00	0.00	0.00 – 1.28
11	July	1.00	0.00 – 3.00	12.00	0.00 – 147.00	0.00	0.00 – 1.02
12	August	1.00	0.00 – 4.00	29.00	0.00 – 141.00	0.00	0.00 – 1.00
13	September	1.00	0.00 – 3.00	2.00	0.00 – 119.00	0.00	0.00 – 0.70
14	October	1.00	0.00 – 3.00	6.00	0.00 – 137.00	0.00	0.00 – 0.71

Appendix 3

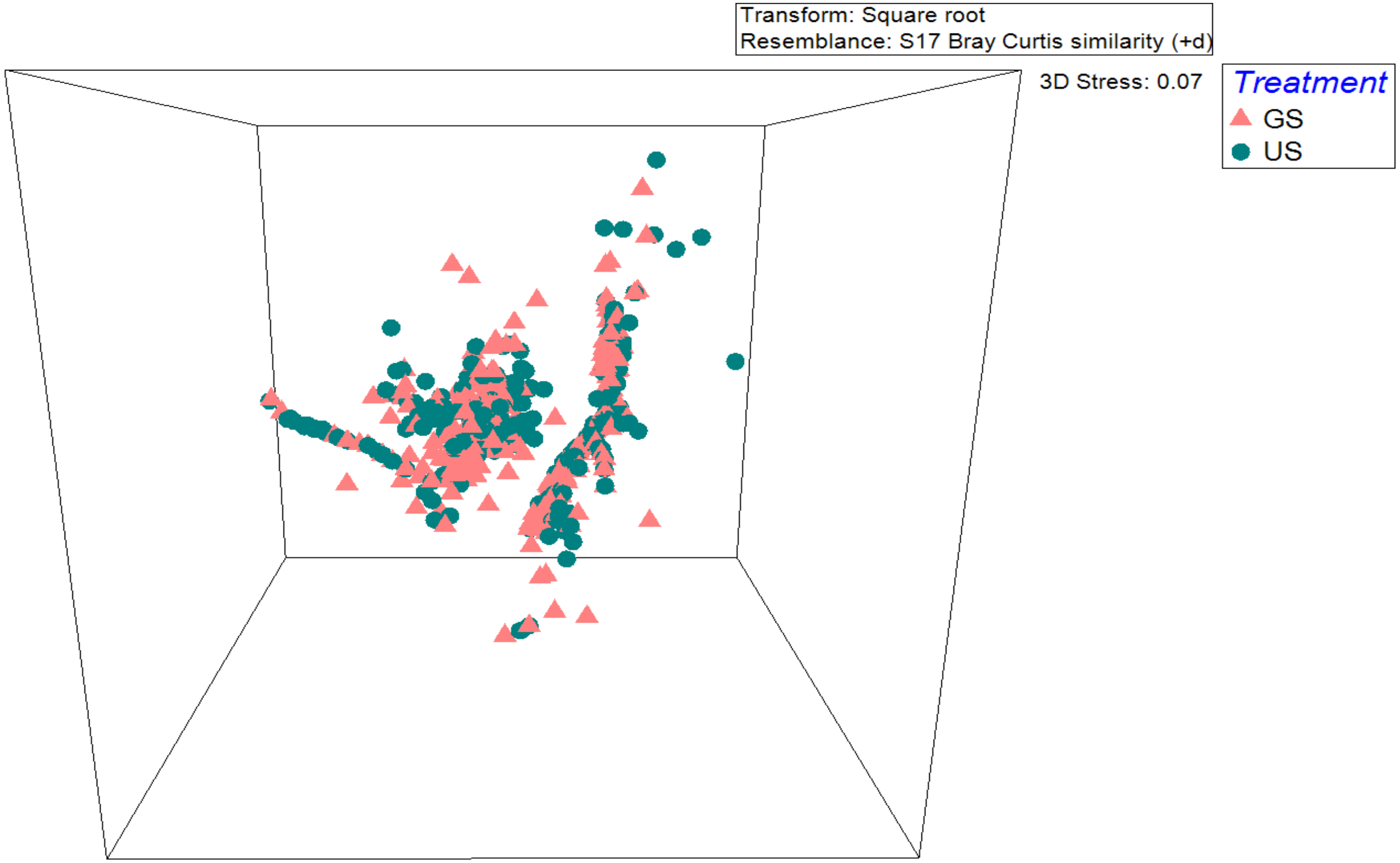

Figure 6.1 – The results of MDS analysis based on a Bray-Curtis similarity matrix of data for substrates treated with grooves = GS and untreated Substrates = US (averaged across all months sampled) at Runswick Bay.

Appendix 4

Median and range data for species richness (S), total abundance (N) (counts) and SW diversity (H’) of mobile species over time for a) Substrates treated with Grooves (GS) and b) Untreated Substrates (US).

a) Grooved Substrates (GS)

Time in Months		S		N		H’	
		Median	Range	Median	Range	Median	Range
6	February	0.00	0.00 – 2.00	0.00	0.00 – 3.00	0.00	0.00 – 0.64
8	April	0.00	0.00 – 2.00	0.00	0.00 – 0.00	0.00	0.00 – 0.64
9	May	0.00	0.00 – 1.00	0.00	0.00 – 1.00	0.00	0.00 – 0.00
10	June	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
11	July	0.00	0.00 – 1.00	0.00	0.00 – 1.00	0.00	0.00 – 0.00
12	August	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
13	September	0.00	0.00 – 1.00	0.00	0.00 – 5.00	0.00	0.00 – 0.00
14	October	0.00	0.00 – 1.00	0.00	0.00 – 1.00	0.00	0.00 – 0.00

b) Untreated Substrates (US)

Time in Months		S		N		H’	
		Median	Range	Median	Range	Median	Range
6	February	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
8	April	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
9	May	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
10	June	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
11	July	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
12	August	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
13	September	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00
14	October	0.00	0.00 – 0.00	0.00	0.00 – 0.00	0.00	0.00 – 0.00