Patterns of mussel bed infaunal community structure and function at local, regional and biogeographic scales

A thesis submitted for the degree of Doctor of Philosophy

Andrew James Richardson

(BSc. (Hons) Coastal Marine Biology)

List of contents

Chapter 1 – General Introduction

Chapter 2 – Optimal sampling and assemblage description

Chapter 3 – A Functional Grouping Approach to Infaunal Research

Chapter 4 – How do infaunal assemblage patterns vary at large biogeographical scales and what drives them?

Chapter 5 – Infaunal communities in Falkland Island mussel beds

---

Chapter 6 – General discussion

List of figures

List of tables

List of tables

List of plates

Acknowledgments

In the course of planning, sampling, processing and writing of this thesis work I have had incalculable support from many people and organisations.

Firstly, I must recognise the professionalism, knowledge and guidance of my two academic supervisors, Dr Sue Hull and Dr Cath Waller from the Centre for Environmental and Marine Science at the University of Hull. To them I say thankyou for your patience, advice, time and friendship during my time of study. I also wish to acknowledge the assistance, friendship and support of other CEMS staff and postgraduate students during my time in Scarborough.

The South Atlantic research of this thesis was only possible with the logistical and financial support if the Collaborative Gearing Scheme (87) through the British Antarctic Survey. To the staff of BAS and associated organisations I express my gratitude, as well as to the Shallow Marine Surveys Group in the Falkland Islands for their generosity in allowing access to their facilities during southern fieldwork.

Last of all, but foremost in my mind I say thankyou to my family, without the support of whom this research would not have been possible. Throughout my life they have always encouraged me to broaden my horizons and shown the value of education and the gathering of knowledge. I also wish to acknowledge family members who are no longer with us but still stood beside me with sample collected and every word written.

Chapter 1 – General Introduction

“The punctual tide draws up the bay,

With ripple of wave and hiss of spray.”

Coolidge (1880)

1.1 Ecological diversity

Biodiversity is defined as the ecosystem, genetic and species diversity in an area (Swingland, 2001). However, biodiversity, as an ecological term, is often difficult to determine. This is due to the range of scales at which biodiversity is measured, from ecosystem down to genetic variation (Purvis & Hector, 2000; Hooper *et al.*, 2005). What also must be considered is the context of the variation, whether measuring diversity between genetic populations, functional traits, morphology and others besides (Purvis & Hector, 2000; Hooper *et al.*, 2005; Etienne *et al.*, 2007).

Species range, abundance and diversity are often considered cornerstones of ecological assemblage studies, but the resulting patterns are often extremely complex, and not consistent across spatial scales (Bell, 2001; Blanchette *et al.*, 2008). Diversity is usually classed into three genres; alpha, beta and gamma diversity. Alpha (α) diversity is the mean species diversity within a habitat, whereas beta (β) diversity is the differentiation between habitats (Magurran, 2004; Jost, 2007). Gamma (γ) is the overall mean diversity, produced by the combination of these two independent diversity variables ($\gamma=\alpha*\beta$ or $\gamma=\alpha+\beta$) (Magurran, 2004; Jost, 2007; Rosindell *et al.*, 2011).

Ecosystem processes do not only affect biodiversity, but ecosystem processes may in turn be affected by biodiversity (Purvis & Hector, 2000). It has been theorized for some time that stable ecosystems often coincide with more diverse communities (Darwin & Wallace, 1858; Chapin *et al.*, 2000; Purvis & Hector, 2000; Schwartz *et al.*, 2000). More diverse communities are theorized to be more resistant to invasion/immigration as there is unlikely to be a resource surplus (Knops *et al.*, 1999) and ecological associations between species (plants and pollinators for example) are maintained (Schwartz *et al.*, 2000).

Biodiversity studies often approach the subject of diversity in three key ways; difference, evenness and number (Purvis & Hector, 2000). Difference may be described as simply the degree to which two species differ; this may be genetically, morphotypically, amongst others (Purvis & Hector, 2000). Evenness may be defined as the distribution of species in a community and number measures, the number of species, often called species richness (Purvis & Hector, 2000). However, these three facets are not exclusive, and must be combined to effectively measure biodiversity, for example, Etienne *et al.* (2007) suggest that species richness (numbers) is not sufficient, and that abundance measures (evenness) must also be included. This is supported by studies such as Gestoso *et al*. (2013), which found that intertidal community evenness increased in the presence of an invasive mussel species (*Limnoperna securis*), in addition to an overall descrease in richness.

Two key approaches in biodiversity are the niche concept and neutral theory (Krebs, 2009). The niche concept works on the premise that some species are more able to survive and thrive under specific environmental condition(s) than others, so having an advantage (Leibold, 1995). It implies that some species possess certain advantages over others, allowing them to fulfill certain roles within communities but not others (Rosindell *et al.*, 2011). These advantages also limit the environmental conditions under which a single species may thrive and so prevent the emergence of "super-species" which dominate all communities in a habitat (Leibold, 1995; Rosindell *et al.*, 2011). This advantage may be based on two key variables; how a species uses finite resources, as discussed by Elton (1927), or the direct effect of environmental pressures on a species (Grinnell, 1917). Due to this difference in population fitness, under the niche concept the distribution of species should be determined by environmental conditions, whether biotic or abiotic (Leibold, 1995). However, as argued by Whittaker *et al.* (1973) there is a blurring of the boundaries of these two variables, as the resource use by one species may become an environmental pressure upon another species. Conversely, Leibold (1995) proposed a mechanistic approach, based upon modelling the exploitation of resources from an environment by organisms and the impact of such exploitation on the environement, concluding that they could be considered as distinct components. An additional consideration could be the incidence of facilitation and mutualism (community-derived benefits either one-way or mutual), particularly at a community level as the limits of niches are blurred (Bruno *et al.*, 2003). However, critics of niche theory have indicated that niches are often too loosely defined to permit effective testing in real-world ecosystems (Hubbell, 2005; Alonso *et al.*, 2006; Etienne *et al.*, 2007). Additonally, while niche models are often hailed as remaining stable across large spatial and temporal scales, the study by Dornelas *et al*. (2006) found that it fails to reflect environmental fluctuations within ecosystems. It is also important to consider the possibility of habitat creation through the behaviour by which another organism uses a resource, such as the burrowing action of marine polychaetes which may increase nutrient movement and oxygenation of sediment, thus altering the habitat (Mermillod-Blondin & Rosenberg, 2006; Volkenborn et al., 2007). One alternative to niche theory in ecology that emerged in the 1990's is that of neutral theory.

The first unified neutral theory is attributed to Hubbell (1997, 2001) and while the niche concept involves adaptive advantages, neutral theory operates under the assumption that no one species has a competitive advantage over the others (Hubbell, 1997, 2001), i.e. species within a community are functionally equivalent (McKane *et al.*, 2004; Hubbell, 2005). Species distribution is, therefore, determined by replacement of dead individuals within a community (Yu *et al.*, 1998; Rosindell *et al.*, 2011). This is often summarized as a succession of immigration, extinction and species emergence (Gravel *et al.*, 2006). As neutral theory operates on the assumption that no one species has an advantage with regards these processes, distribution over space and time is random, that is, ecological drift (Hubbell, 2001; Gravel *et al.*, 2006). The theory often hinges on three key assumptions; that all species are functionally equivalent, that speciation occurs by point mutation and the zero-sum assumption (that there is never unoccupied ecological space) (Hubbell, 2001; Etienne *et al.*, 2007). However, the theory has been criticized for ignoring the complexity of trophic relations between species, the implication that rare species must logically be recently evolved (Yu *et al.*, 1998; McKane *et al.*,

2004) and dismissing the effects of density or population size (Ricklefs, 2006). Though perhaps the most unpopular facet of the theory to some ecologists, such as Fuentes (2004), is that under neutral theory, the distribution of species is based entirely on chance and not forms of selection (Alonso *et al.*, 2006), in defiance of popular ecological reasoning since Darwin (1859). However, despite it's alleged flaws, neutral theory can be useful in producing a null model of biodiversity, against which other approaches can be compared (Rosindell *et al.*, 2011).

1.2 Functional Groups

In times where concerns over habitat degradation, extinctions and reductions in biodiversity are high, the study of community structure is seen as increasingly important (Keddy, 1992; Bellwood *et al.*, 2006; Gall & Le Duff, 2014). Biodiversity is often used as a measure to inform policy and direct conservation efforts, despite the definition of biodiversity being somewhat of a grey area as diversity at taxonomic, genetic and functional levels are all applicable (Zak *et al.*, 1994; Petchey & Gaston, 2006). Whichever unit of measure is adopted it should allow for survey information to be both detailed and useful in revealing community structure (Steneck & Dethier, 1994). Despite the options available, the traditional mainstay of community ecology remains a community description using species as the fundamental unit (Keddy, 1992; Steneck & Dethier, 1994; Zacharias & Roff, 2001; Elliott *et al.*, 2007; Gall & Le Duff, 2014).

However, there is value to the argument that functional diversity is more important to maintaining community structure and processes than species diversity (Tilman *et al.*, 1997; Arenas *et al.*, 2006; Villéger *et al.*, 2008; Griffin *et al.*, 2009). Additionally, there is a belief among some ecologists that research in ecology should strive to find general rules of ecological systems (Padilla & Allen, 2000; McGill *et al.*, 2006). A traditional taxonomic approach risks limiting community structure and process information, which might be provided by using an approach independent of taxonomy (Cummins, 1974; Steneck & Watling, 1982; Bustamante & Branch, 1996a). Whilst the species level approach is undoubtedly thorough, there is often a large number of species (Keddy, 1992; Jonsson & Malmqvist, 2003) and the associated relationships between them would thus increase exponentially. This increasingly complex matrix might even begin to occlude the patterns sought in community studies and subsequent detection of community change (Steneck & Watling, 1982).

The use of non-taxonomic classification is not a new concept (Keddy, 1992; Bustamante & Branch, 1996a; Bremner *et al.*, 2006). Indeed, for organisms that are notoriously complicated to identify, such as nematode worms, classification into higher guilds is commonplace (Bongers & Bongers, 1998). This approach may involve discarding traditional phylogenetic associations between organisms and instead group by shared characteristics, into “guilds” or “functions” (Gall & Le Duff, 2014). Guilds have traditionally been used to group organisms by similarities in how resources are obtained, while functions have often related to similarities in ecological roles within communities (Blondel, 2003). Some groupings may be both guilds and functional groups, as they include both resource acquisition (guild) and also the effect on the ecosystem (functional). An example of this could be the organisms that fall into the category of “predator”, as while it describes how resources are obtained, it also provides information on the effect upon the community. For example in a food web interaction as described by Paine (1969; 1974), Dayton (1971) and summarised by Seed (1976) the echinoderm *Pisaster*, (Muller & Troschel, 1840), a predator, both acquires resources by predatory means and as a consequence of its predation on *Mytilus* (Linnaeus, 1758) also performs an ecosystem service by clearing substrate space that other sessile species may colonise. Despite these small differences, the adoption of a non-phylogenetic group approach may be useful in studying ecological communities (Fauchald & Jumars, 1979) and the common basis for both frequently makes them interchangeable (Blondel, 2003). For the purposes of this study, grouping of organisms by shared traits is termed “functional groups” or “functions”.

Grouping species into functional groups reduces the requirement for specialised taxonomic knowledge on the part of the researcher, the key benefit of this being that larger scale surveys may be possible, especially in particularly diverse or complex communities (Fagerstrom, 1991; Zak *et al*., 1994). The grouping approach does also not rely on organisms being taxonomically related (Blondel, 2003), such as intertidal mussels and barnacles, which are both sessile filter feeders despite being in separate phyla (Bustamante & Branch, 1996b). Functional diversity may also be advantageous over traditional taxonomic diversity as the latter is often restricted to descriptive studies (Zak & Visser, 1996), though by their nature, functional and taxonomic diversity will show different information about the system being studied (Hoeinghaus *et al*., 2007). A key benefit of a non-species approach is that comparisons across broad spatial scales are possible, particularly when species are not shared between communities (Cummins, 1974; Littler & Littler, 1984; Steneck & Dethier, 1994). There may be, however, limitations of functional grouping approaches when considering habitat scales (Zak & Visser, 1996). Several authors, inclunding Zak & Visser (1996) and Petchey & Gaston (2006) maintain that the hierarchy of spatial scales that exist within ecosystems may make inferring patterns one one tier to another, such as patterns of functional diversity derived at meiofaunal scales cannot be accurately transferred to mesoscales without experimental analysis. However, the same statement may also be made about patterns observed while using taxonomic diversity (Zak & Visser, 1996).

Identifying key groups of organisms can be an important tool in monitoring and predicting community change, including the effects of anthropogenic disturbances (Damianidis & Chintiroglou, 1998; Bonsdorff & Pearson, 1999; Blondel, 2003; Duffy, 2006). Predicting community change is also simplified by using functional approaches, as there is a reduced need to understand the responses of individual species to disturbance (Steneck & Watling, 1982). Practical examples of functional groupings being used to monitor community change in addition to water and habitat quality in freshwater systems are relatively common (MacNeil *et al*., 1997; Kenney *et al*., 2009; Borja *et al*., 2010; Feio & Dolédec, 2012). An example of this is the "River Continuum Concept" which assesses environmental influences and resulting community change by monitoring macroinvertebrate functional feeding groups (Vannote *et al*., 1980; Statzner & Higler, 1985).

Taken at face value, the use of functional groups is not congruent with some larger ecological theories. Because niche theory operates on the assumption that species in a habitat are ecologically unique (Krebs, 2009), there should be no ecological space for more than one species in each functional group (Steneck & Watling, 1982; Blondel, 2003). However, it is inevitable that communities are collections of, and interactions between, ecologically similar species that exploit resources in similar ways (Steneck & Watling, 1982; Steneck & Dethier, 1994; Blondel, 2003).

While there are many attributes by which organisms may be grouped, it is important that such traits be shared across species boundaries (McGill *et al*., 2006). The earliest examples, as far back as the late 19th Century, were based on broad morphological characteristics (MacNeil *et al*., 1997), although traits such as beak shape, seed size and body mass are still employed in organisms such as birds and plants (Keddy, 1992; McGill *et al*., 2006). It is also common for organisms to be grouped by behavioural traits (Steneck & Dethier, 1994) such as pollinating behaviour in bee species (Hoehn *et al*., 2008). Still another possible grouping might be based on resource acquisition (Bonsdorff & Pearson, 1999; Blondel, 2003), including how the organism feeds. Despite the apparent variety of groupings available, several authors have noted how critical it is that the correct functional grouping is selected (Petchey & Gaston, 2006) and also that the selected grouping approach be rigorously tested to determine suitability (Bengtsson, 1998; Mason *et al*., 2005). One suggested method to test suitability is the correlation between taxonomic and functional diversities (Michel & Halpern, 2005). However, as noted by the same authors (Michel & Halpern, 2005), such correlation is unstudied for most ecosystems and so functional grouping resolution may have to rely on weightings, themselves often unestablished, thus introducing subjectivity on the behalf of the researcher.

Functional grouping by feeding mechanism may aid in the understanding of food webs as well as nutrient and energy cycling within and through a community (MacNeil *et al.*, 1997; Trussell *et al.*, 2003; Petchey & Gaston, 2006; Elliott *et al.*, 2007). Understanding and tracking this energy flow is important beyond the intertidal as benthic invertebrates are often a key link between primary producers and higher trophic feeders such as birds (Ricciardi & Bourget, 1999). However, it has been noted that the complexity of energy flows within ecosystems is not merely a product of the number of ecological functions, but also the number of interactions within and between trophic levels (Zak & Visser, 1996). The use of functional feeding groups (FFG's) is especially common in freshwater invertebrate research (Cummins, 1973; Cummins & Klug, 1979; Vannote *et al.*, 1980; Jonsson & Malmqvist, 2003; Feio & Dolédec, 2012). The basis for the majority of these studies is the feeding mechanism employed by each organism, rather than by gut content analysis (Tomanova *et al.*, 2006) and is often described as the method by which a species exploits a nutrient resource (Christie *et al.*, 2009). Examples are the behaviour exhibited whilst feeding (Rosenberg, 2001), such as "scapers" (Cummins & Klug, 1979), or by the form and shape of the mouthparts, such as rasping mouthparts in freshwater gastropods (Cummins, 1973). However, variations within feeding groups may influence the effect of the group on the community as a whole. For example, while several species may fall into the predator feeding group, there may exist within the same group both specialist and generalist predators (MacNeil *et al.*, 1997). Each of these two predator types may have different effects upon the demographics of the associated community (Schluter, 1982). Specialist predators are more likely to directly influence the size-structure of prey (Yamada & Boulding, 1998), possibly leading to local increases in competition or even total exclusion of some prey (Symondson *et al*., 2002). While generalist predators may also influence, amongst others, the size-distribution of prey the effect tends to be more subtle and harder to quantify (Yamada & Boulding, 1998), the effect often being spread across the prey community, often leading to an overall reduction in competition (Symondson *et al*., 2002).

1.3 Spatial scales in ecology

Ecological systems, or ecosystems, are constructed from a multitude of species, interactions and processes (Brown, 1999), these systems existing at an array of spatial and temporal scales (Krebs, 2009). Perhaps the most simple and well-studied scale is geographical range, being the distance spread of areas inhabited by a species (Golikov *et al*., 1990; Bell, 2001). The study of communities at spatial scales is often termed biogeography, a discipline that encompasses scale from within habitats or species distribution ranges, all the way to global patterns of biodiversity (Heaney, 2000; Lomolino, 2000; Bell, 2001). An alternative term for the study of ecological patterns at larger scales, as coined by Brown & Maurer (1989), is “macroecology” (Briggs, 2007). Macroecology usually considers spatial scales of tens to thousands of miles and has seen an increase in interest from researchers in recent years (Blanchette *et al*., 2008).

Macroecological studies allow researchers to combine community effects, and their driving factors, with biogeographical patterns (Briggs, 2007). The biogeographical pattern of the distribution of a species is often determined by the adaptive or functional limits of the species to various biotic and environmental driving factors (Lüning, 1984; Golikov *et al*., 1990). Understanding the causes and drivers of large-scale patterns may help to predict future changes, especially in response to anthropological influences such as biological invasions and climate change (Bell, 2001; Sagarin & Gaines, 2002; Cadotte *et al*., 2006; Blanchette *et al*., 2008; Sorte *et al*., 2010).

Historically, the majority of biogeographical studies have been conducted in terrestrial ecosystems (Paine, 2010). However, there is disagreement between authors as to whether fundamental differences exist between dynamics and interactions of marine and terrestrial systems. There are undoubtedly fundamental differences in biological interactions between the marine and terrestrial mediums, notably the widespread competition for substrate in marine habitats between sessile invertebrates and the plant kingdom, a conflict almost totally absent in terrestrial systems (Paine, 2010). Webb (2012), however, suggests that despite the physical differences between marine and terrestrial ecosystems, there is no essential difference in how environment influences ecological processes. Despite this statement by Webb (2012), many other studies consider that marine and terrestrial systems differ significantly. Carr *et al*. (2003) and Kearney *et al*. (2013) are examples of such studies, showing that reliance on external recuitment, primary producer turnover and phyletic diversity are higher in marine systems while sensitivity to habitat fragmentation and interpopulation gentic diversity is higher in terrestrial systems. Additionally Carr *et al*. (2003) and Kearney *et al*. (2013) consider marine ecosystems to have a 3-dimensional species distribution with larger scales of propagules and higher per-capita fecundity, compared to terrestrial ecosystems with 2-dimensional distribution and smaller propagule scales and lower fecundity per capita. These differences have possible implications for management and conservation (Kearney *et al*., 2013).

1.4 Temperate intertidal systems

Rocky shores form the interface between the terrestrial and marine environments in many parts of the world (Thompson *et al*., 2002; Little *et al.*, 2009), a vital link in energy and nutrient transfer between the two systems (Ricciardi & Bourget, 1999). Characterised by a hard substrate, rocky shores are often extensive in temperate latitudes (Thompson *et al*., 1996). Their distribution may be altered by anthropogenic influences such as the construction of rock groynes or concrete docks, increasing or decreasing the amount of hard substrate available in intertidal zones (Thompson *et al*., 2002). However, human influences may also be negative in nature, particularly with regards to the distribution of species (Cabral-Oliveira *et al*., 2014). A direct avenue of negative influence is the overexploitation of some intertidal species such as bivalves for food, lowering abundances (Thompson *et al*., 2002). Perhaps one of the major concerns regarding human influence is the artificial introduction of non-native or invasive species to areas outside their natural geographical ranges (Smith *et al.*, 2006). Examples of invasive species in rocky shore habitats, facilitated by human actions, include the mussel *Mytilus* *galloprovincialis* (Lamarck, 1819) in South Africa (Robinson & Griffiths, 2002; Robinson *et al*., 2007) and the barnacle *Balanus glandula* (Darwin, 1854) in Patagonia (Vallarino & Elias, 1997) by larval transport in ship ballast tanks. Another indirect influence may be that of climate change, a current concern in many branches of ecology (Thompson *et al*., 2002). Variations in climate may limit reproductive success in native species, facilitating and expanding the range of other species such as the encroachment of the higher-temperature tolerant limpet *Patella depressa* (Pennant, 1777) into areas previously dominated by *P. vulgata* (Linnaeus, 1758) during a temporary warmer period in the 1950's (Thompson *et al*., 2002). Climate fluctuations were also considered to be a significant contributing factor in the expansion of *Patella rustica* (Linnaeus, 1758) in Portugal during the 1990's, higher temperatures being conducive to higher reproductive success in the species (Lima *et al*., 2006). Quantifying the effect of external influences on a community may, however, be complicated by the differentiation between proximate and ultimate factors (Olive, 1995). Proximate factors may be defined as being at local scales or over shorter time periods, but having a direct effect on the system (Biggs, 1995), such as predation (Stevenson, 1997) or benthic slope (Gherardi & Vannini, 1993). However, ultimate factors operate at the largest of spatial and temporal scales, indirectly affecting community structure (Biggs, 1995), such as mesoscale nutrient flow or seasonal air temperatures (Gherardi & Vannini, 1993).

Rocky shore habitats have played an important role in the history of ecological research (Underwood (2000). This may be attributed to the relative ease of access to rocky shore systems, their widespread distribution and the facilitation of experimental manipulation of communities (Paine, 1974; Bosman *et al*., 1987; Bertness *et al*., 1999; Underwood, 2000). Found at both exposed and sheltered locations, rocky shores are connected to the wider marine environment by larval transport, nutrient transfer and physical influence (Thompson *et al*., 2002; Sale *et al*., 2006; Bryson *et al*., 2014). Indeed, virtually all of the species found on temperate rocky shore have an obligate pelagic larval phase (Ayre *et al*., 2009). Unlike other marine environments however, intertidal habitats are regularly exposed to physical stresses akin to those found in terrestrial systems, due to the diurnal tidal cycle (Helmuth & Hofmann, 2001; Saier, 2002).

Due to the periodic emersion caused by the diurnal tidal cycle, rocky shores frequently have a gradient of environmental pressure over a scale of a few tens of metres, revealing patterns that may only exist over mesoscales in terrestrial ecosystems (Underwood, 2000; Webb, 2012), making rocky shores a useful testing ground for ecological models (Menge, 1976; Ricciardi & Bourget, 1999; Chappuis *et al*., 2014). While many of the organisms that reside in intertidal zones are also found in exclusively sub-tidal marine habitats (Little *et al*., 2009), intertidal species must be tolerant to variations in temperature, salinity and dissolved oxygen and be able to withstand desiccation (Thompson *et al*., 2002). As would be expected, the duration of emersion depends greatly upon the position on the shore, with higher shore heights having a longer emersion period (Connell, 1972; Thompson *et al*., 2002; Nicastro *et al*., 2012; Chappuis *et al*., 2014).

In the upper shore, physical factors are often the primary influence on intertidal organisms (Connell, 1972; Menge, 1976; Lubchenco & Menge, 1978; Bertness &

Leonard, 1997). Periodic exposure to terrestrial environmental conditions is, as expected, physiologically and behaviourally challenging to organisms that are effectively adapted to a marine environment (Helmuth *et al*., 2006). Marine organisms exposed to the lower humidity of air risk water loss from their body tissues (desiccation), causing dehydration, salt imbalance and physiological stress (Kensler, 1967; Nicastro *et al*., 2012). Exposure to the atmosphere and limited access to moisture may also result in a large temperature variance during low tide, meaning that intertidal organisms must have considerable physiological thermal tolerance limits (Somero, 2002; Hooper & Davenport, 2006) or adaptive behaviours (Kensler, 1967; Lowell, 1984). Temperature variations resulting from exposure to the terrestrial environment conditions can cause marine and aquatic organisms to experience thermal shock; reducing respiration and denaturing enzymes (Helmuth & Hofman, 2001; Somero, 2002). Studies by authors such as Somero (2002), Waller *et al.* (2006) and Anestis *et al.* (2008) into the thermal tolerances of marine organisms suggest that species that are found in intertidal zones, or at a higher shore height, are more tolerant of thermal stress than those at lower shore heights. When exposed to excess heating or cooling, intertidal species tended to react more effectively with either physiological or behavioural responses (Waller *et al.*, 2006). However, there is evidence for geographic variation in thermal tolerance between populations of the same species (Sorte *et al*., 2011), including latitudinally (Tomanek, 2010). This has obvious implications when considering community change in response to climate change (Sutherland *et al*., 2010). Species in polar, intertidal environments often have a wider temperature tolerance than those at tropical latitudes and so high-latitude communities may be more resistant to climate-linked biodiversity loss (Sunday *et al*., 2011; Madeira *et al*., 2012).

In the lower heights of intertidal habitats, however, the period of emersion at low tide is shorter, with the lowest reaches of the intertidal zone often only being exposed during extreme spring tides (Thompson *et al*., 2002). It is often considered that the influential stresses in lower shore regions are biotic, namely, competition and predation (Dayton, 1971; Connell, 1972; Menge, 1976; Gaylord, 1999; Webb, 2012). As rocky shore organisms effectively inhabit a two-dimensional habitat (during emersion), there is significant competition for substrate space (Dayton, 1971; Paine & Levin, 1981; Underwood, 2000). This is especially important between sessile organisms such as mussels and barnacles where mussels may overgrow and smother barnacles (Menge, 1976; Underwood, 2000). Indirect competition for substrate may also occur by one organism preventing recruitment of another, such as the sweeping action of macroalgal fronds preventing the settlement of barnacle larvae on to substrate (Dayton, 1971; Underwood, 2000). In addition to competition for physical space, species compete for resources such as nutrients, based on shared resource requirements (Hunt & Scheibling, 2001), one example being competition for suspended prey between the filter-feeding bivalves *Modiolus modiolus* (Linnaeus, 1758) and *Argopecten irradians* (Lamarck, 1819) in an intertidal habitat (Gillmor, 1982). Predation may also exert significant pressure on prey populations at lower shore levels, such as the grazing of ephemeral algae by littorinid gastropods (Lubchenco, 1983; Van Tamelen, 1996). Competition and predation stress may drive a vertical organism-size gradient on the shore, with larger, more competitive species being more abundant in the lower shore with size decreasing with an increase in shore height (Underwood, 2000).

Being connected to the larger marine environment, rocky shores are subject to marine physical influences. Wave action is an important influence on the structure of rocky shore communities (Dayton, 1971; McQuaid & Branch, 1985; Van Tamelen, 1996; Gaylord, 1999; Hunt & Scheibling, 2001; Arribas *et al.*, 2014). The higher mechanical stress by increased wave action may dislodge individuals or populations of organisms or cause the clustering of individuals into physical refuges (Connell, 1972; Sousa, 1979; Zacharias & Roff, 2001). Higher water velocities may also re-suspend sediment (altering nutrient availability), which may in turn reduce light levels, lowing photosynthesis in marine algae and ultimately affect primary production (Zacharias & Roff, 2001). Higher wave action may, however, mediate some of the effects of emersion by providing spray moisture to higher shore heights (Connell, 1972; Thompson *et al.*, 2002; Nicastro *et al.*, 2012).

Owing to the vertical environmental gradient, many temperate rocky shore communities show a trend of decreasing species diversity with increased shore height (Connell, 1972; Saier, 2002). The relative tolerances of species to these physical and biotic stresses will exclude species from different shore heights, setting upper and lower height limits, determining their vertical distribution on the rocky shore (Kensler, 1967; Menge, 1976; Helmuth *et al.*, 2006; Nicastro *et al.*, 2012). Examples of this are the desiccation-vulnerable *Porcellana platycheles* (Pennant, 1777) being restricted to lower shores while the tolerant *Littorina saxatilis* (Olivi, 1792) is found at high shore heights (Kensler, 1967). Adaptations to physical stresses in the upper shore may result in a trade-off for competitive ability in the lower shore, setting a lower limit for the distribution of a species (Connell, 1972). The combination of these upper and lower limits creates a pattern of vertical zonation within rocky shore communities (Connell, 1972; Menge, 1976; Bertness & Leonard, 1997; Sale *et al*., 2006; Chappuis *et al*., 2014). A typical pattern in temperate-latitude rocky shores is a mosaic of barnacles, mussels and fucoid algae in the upper, mid and low shore respectively (Thompson *et al*., 1996; Vallarino & Elias, 1997; Coates, 1998; Chiba & Noda, 2000).

Due to the hardness of the rock, there is often little potential for organisms to burrow into the substrate to find refuge (Bertness & Leonard, 1997). Therefore rocky shore species may be reliant on the availability of physical structures, such as rockpools (van Tamelin, 1996; White *et al*., 2014), as refuge from abiotic and biotic stresses. Such refuges are particularly important at higher shore heights where physical stress tends to be highest (Jenkins *et al*., 2008). Tidal rock pools may raise the upper limit of a species distribution by providing a moisture-rich refuge from emersion period stresses (Connell, 1972; White *et al*., 2014). Rock crevices and gaps in the substrate may also provide, albeit to a lesser extent, localised moisture-rich refuges for physical-stress vulnerable species (Kensler & Crisp, 1965).

It is clear that increased habitat complexity is often correlated to greater community complexity and diversity, often attributed to higher resource availability due to the increased surface area (Thompson *et al*., 1996; Gutierrez *et al*., 2003; Kelaher, 2003; Matias *et al*., 2007). It must also be considered that increased complexity might not only increase resource availability, but also create more niches for species to inhabit (Rosindell *et al*., 2011). However, many rocky shores are dominated by a few competitively superior groups of organisms, particularly macroalgae and sessile invertebrates (Seed & O'Connor, 1981; Menge, 1995; Prathep *et al*., 2003; Valdivia & Thiel, 2006; Cole & McQuaid, 2010; Kim *et al*., 2014).

The dominance of such species on substrate might be expected to result in competitive exclusion of most intertidal organisms, but the situation is not so simple (Miyamoto & Noda, 2004). While space is often a limiting factor in ecological communities, some habitat forming species provide secondary space (Paine & Levin, 1981; Witman & Suchanek, 1984; Commito & Rusignuolo, 2000; Cartwright & Williams, 2014), turning species interactions from competitive to facilitative or positive (Jones *et al*., 1994; Bertness & Leonard, 1997; Jenkins *et al*., 2008). These organisms may be considered to be ecosystem engineers, creating secondary space and substrate from either their living or dead tissues or as a result of their ecosystem processes (Jones *et al*., 1994; Jungerstam *et al*., 2014). Ecosystem engineers are common in benthic marine environments (Barrell & Grant, 2015), including rocky shores, and have an important influence on community structure by altering the impact of physical and biotic factors within the habitat (Lohse, 1993; Bertness *et al*., 1999; Commito *et al*., 2005; Tam & Scrosati, 2014).

The creation and provision of refuges from physical and predation stresses by ecosystem engineers may benefit other species living beneath or within the engineer populations (Witman & Suchanek, 1984; Gutierrez *et al*., 2003; Folmer *et al*.; 2014), such as understorey algae communities beneath macroalgal canopies (Underwood, 2000; Jenkins *et al*., 2008). Algal canopies and other ecosystem engineers may provide protection to understorey species from severe fluctuations in temperature, solar radiation and also retain moisture (Lilley & Schiel, 2006; Cartwright & Williams, 2014; Watt & Scrosati, 2014). These biologically engineered habitats may also increase structural complexity by adding shell surfaces or dense frond aggregations to the overall surface area (Thompson *et al*., 1996; Kelaher, 2003; Cartwright & Williams, 2014). However, while increased biological habitat complexity might lead to an increase in community richness (Thompson *et al*., 1996; Hooper & Davenport, 2006; Christie *et al.*, 2009; Watt & Scrosati, 2013), larger organisms might be excluded, an example being the exclusion of large gastropods from the space between tightly packed algae fronds (Kelaher, 2003). Additionally, while ecosystem engineer habitats may provide refuge from predation in lower shore heights (Seed & O'Connor, 1981; O'Connor & Crowe, 2008), richness and diversity of associated fauna may decrease with shore height as the natural mediation of physical stresses reduces the refuge-dependence of organisms (Crain & Bertness, 2006).

Alongside secondary space creation, ecosystem engineers may alter the topography of benthic marine habitats, influencing water flow and thus affecting sediment transport, nutrient availability and larval transport and settlement in the habitat (Seed, 1976; Seed & O'Connor, 1981; Svane & Ompi, 1993; Commito & Rusignuolo, 2000; Prathep *et al*., 2003; Valdivia & Thiel, 2006; Arribas *et al*., 2014; Jungerstam *et al*., 2014).

Despite being buffers from physical stress (O'Connor & Crowe, 2008; Christie *et al.*, 2009), populations of ecosystem engineers may be dislodged by high wave exposures (Witman & Suchanek, 1984; Valdivia & Thiel, 2006; Kim *et al.*, 2014; Tam & Scrosati, 2014). Rocky shores may be subjected to high water velocities of up to 16ms^{-1} (Witman & Suchanek, 1984), meaning that sessile organisms must be effective at attaching themselves to the substrate to avoid being dislodged (Valdivia & Thiel, 2006; Kim *et al.*, 2014). This ultimately affects the presence of individual ecosystem engineer species on rocky shores, with sessile bivalves, such as *Mytilus edulis* (Linnaeus, 1758) (Seed, 1976), being abundant on shores with high wave action and macroalgae, such as *Ascophyllum nodosum* (Le Jolis, 1863) (Scrosati & Heaven, 2007) being dominant in sheltered locations in the northern hemisphere (Menge, 1995; Jenkins *et al.*, 1999; Thompson *et al.*, 2002; Branch *et al.*, 2008). The distribution of these sessile, habitat-forming species is dependent on patterns of disturbance, predation and recovery (Paine, 1974; Chiba & Noda, 2000; Menge *et al.*, 2005). While disturbance events may clear patches in established habitats (Sousa, 1979; Ragnarsson & Rafaelli, 1999), the success of ecosystem engineers depends greatly upon recolonisation success by larval recruitment (Sousa, 1984; Underwood, 2000; Thompson *et al.*, 2002).

Table 1.1 Intertidal, habitat-forming mussel genera and typical geographical distribution

Genus	Distribution	Reference
Aulacomya sp.	South Atlantic	Pollock (1979) Stuart *et al.* (1982)
Brachidontes sp.	West Atlantic, Pacific	Lopez Gappa *et al.* (1990) Peake & Quinn (1993)
Geukensia sp.	North America	Bertness & Grosholz (1985)
Musculista sp.	West Pacific	Crooks & Khim (1999)
Mytilus sp	Worldwide (except Antarctica)	Seed (1976) Lintas & Seed (1994)
Perna sp.	Worldwide	McQuaid & Lindsay (2000)
Trichomya sp.	Australia	Catterall & Poiner (1987)

Ecosystem engineers that frequently form extensive beds of complex habitat on rocky shores are mussels (Mollusca: Bivalvia) (Borthagaray & Carranza, 2007), some examples of which are displayed in Table 1.1. One important habitat-forming genus of mussel in intertidal zones is *Mytilus* (Navarrete & Castilla, 1990; Peake & Quinn, 1993; Commito & Rusignuolo, 2000; Robinson & Griffiths, 2002).

1.5 *Mytilus edulis*

One species of the Mytilidae family is the blue mussel, *Mytilus edulis* Linneaus 1758, which appears in the fossil record around 2 million years ago (Seed, 1976) and is often extremely abundant on rocky shores (Lintas & Seed, 1994). *M. edulis* is often considered to have several subspecies including the Chilean mussel *M. edulis chilensis* and the Californian mussel *M. edulis californianus* (Seed, 1976; Gosling, 1994). Additionally, there is often extensive hybridization in overlapping ranges between *M. edulis* and the Mediterranean mussel, *M. galloprovincialis* (Gosling, 1994; Hilbish *et al.*, 2002). As with many species of *Mytilus*, *M. edulis* is primarily found in and above the shallow sublittoral zone, on both hard and soft substrates (Seed, 1969; Frandsen & Dolmer, 2002).

M. edulis is a commercially important species, with a large aquaculture industry built around the cultivation of mussels either from benthic cultures, or suspended structures (Buck *et al.*, 2005; Murray *et al.*, 2007; Van Cauwenberghe & Janssen, 2014). As a sessile, filter-feeding, energy-efficient organism, *M. edulis* is an attractive option as an aquaculture specimen as cultivation and harvesting costs are much lower than that of mobile or higher trophic species (Mason, 1976). However, the filter feeding nature of *M. edulis* also makes them significant bioaccumulators of suspended contaminates, including heavy metals (such as cadmium) and dinoflagellate toxins, causing health problems if they enter the human food chain (Mason, 1976; *Bricelj et al.*, 1990; Szefer *et al.*, 1999). A growing concern in bivalve aquaculture is the accumulation of microplastics in mussel soft tissue as such plastics may either contain, or absorb, harmful organic compounds which are then concentrated at higher trophic levels (Farrell & Nelson, 2013; Van Cauwenberghe & Janssen, 2014). Another particular issue with inshore mussel aquaculture can be reduction or destruction of stock quality by parasitic infection by such organisms as trematodes and parasitic copepods (Buck *et al.*, 2005). However, the same filtering trait that causes quality issues can also be useful in environmental remediation where *M. edulis* may be used to remove excess nutrients, microorganisms or chemical contaminants from a local environment (Gifford *et al.*, 2007; Petersen *et al*., 2014).

M. edulis has an extremely widespread geographic distribution, particularly in temperate waters (Seed, 1969; 1976; Lintas & Seed, 1994). Much of the distributional success of *M. edulis* maybe owed to the species' wide salinity tolerence (Seed, 1976; Kautsky, 1982). This has facilitated the colonisation and dominance in the shallow sublittoral of the Baltic Sea where tolerances of 5‰ have been recorded, albeit with an associated physiological cost (Kautsky, 1982). It also allows this species to exploit benthic habitat in brackish estuaries (Seed, 1976) and areas of salinity of around 40‰ (Brenko & Calabrese, 1969). *M. edulis* is also pervasive in areas where intertidal habitats may be subjected to air temperatures of -20 to -30°C, with intertidal mussels showing recovery even after several hours of being in a frozen state (Kanwisher, 1955; Aarset & Zachariassen, 1982). However, the upper temperature tolerance of around 27°C prevents *M. edulis* from settling in low latitudes, limiting success to further north and south (Wallace, 1975; Seed, 1976). Despite this restriction, *M. edulis* and its subspecies are found throughout the Atlantic coasts of Europe and both South and North America, and the Pacific coasts of Asia and North and South America (Seed, 1976; Levinton & Suchanek, 1978; Suchanek, 1978; Tsuchiya & Nishihira, 1985; Varvio *et al.*, 1988; Gray *et al.*, 1997).

While *M. edulis* is resistant enough to colonise exposed locations, populations are still susceptible to destruction by periodic or unusually high disturbance events such as storms (Seed, 1976; Nehls & Thiel, 1993). Additionally, despite the tolerance of the species to soft-tissue freezing in low temperatures, shallow water or intertidal aggregations are vulnerable to removal by ice-scour (McCook & Chapman, 1991; Heaven & Scrosati, 2008). While such events can locally decimate populations *M. edulis*, like many bivalves, has an r-selective reproductive strategy, producing large numbers of young (Seed, 1976; Bayne *et al.*, 1983; McMahon, 2002). However, populations are also greatly influenced by the supply of such recruits (Hunt & Scheibling, 2001; van Broekhoven *et al.*, 2015), a process affected by local water movement and topography (Webb *et al.*, 2009).

Reproduction occurs, as in many bivalves, through the release of gametes into the water column (Bayne *et al.*, 1983), with females often releasing upwards of 10,000 eggs in a single spawning event (Bayne *et al.*, 1983). While it is a species that displays different sexes, there is no outward evidence of sexual dimorphism in *M. edulis* (Seed, 1969). Indeed, often the only physical clue to determining sex is a change in gonadal colour during the active stage of the reproductive cycle (Chipperfield, 1953; Seed, 1969). However, it is recognised elsewhere in the literature that this colour change is not always a reliable indicator of sex (Pieters *et al.*, 1980).

The major annual breeding period for *M. edulis* in the UK is April-May (Lebour, 1938; Chipperfield, 1953; Seed, 1969). However, some studies, including Seed (1969) show evidence for limited spawning events in late summer. The period over which spawning occurs tends to be a maximum of 3-4 weeks (Chipperfield, 1953; Seed, 1969) although some variation has been recorded. Many authors, including Young (1942), Chipperfield (1953), Seed (1969), Bayne *et al.* (1978)

Littorin & Gilek (1999), have attributed *Mytilus sp.* spawning duration to variations in lunar cycles, spring tides, both water and air temperature and availability of food. Gametes are fertilised externally, following the discharge of separate eggs and sperm from the genital ducts (Bayne, 1976).

Once gametes are fertilized, the juvenile cycle of *M. edulis* involves a sequence of pelagic and benthic phases (Bayne, 1964; Torp-Christensen *et al*., 2015). The first stage of development occurs within the plankton. Lebour (1938) noted that *M. edulis* larvae constitute a significant fragment of planktonic larvae in May and June within UK waters. Beyond the extremely spacious medium that pelagic development provides, the planktonic stage facilitates gene flow over wide geographical areas as well as aiding dispersal (McQuaid & Phillips, 2000), particularly in benthic molluscs (Jablonski & Lutz, 1983). *Mytilus sp.* larvae develop a shell (dissoconch) quite early in their development, around 100μm in length (Bayne, 1976; Fuller & Lutz, 1989), and are comparatively large compared to many planktonic larvae (Booth, 1977). By this point the juveniles have the same external body form as adults (Bayne, 1976; van Broekhoven *et al*., 2015). Studies estimate that the planktonic stage of blue mussel larvae lasts approximately 3-4 weeks (Chipperfield, 1953; Seed, 1969).

Following the planktonic phase, *M. edulis* plantigrades undergo primary settlement, a process that generally occurs on substrates with complex structures, typically filamentous algae (Bayne, 1964; Seed, 1969; Grizzle *et al*., 1996; Newell *et al*., 2010). The settlement on to the primary site is aided by the presence of a long byssal thread, often twice the length of the plantigrade (Lane *et al*., 1985). This monofilamentous thread is secreted by glands at the base of the foot, increasing viscous drag and extending the suspension time of post-larvae (Lane *et al.*, 1982; 1985). The byssal thread drifting mechanism almost certainly aids the distribution of *M. edulis* plantigrades (Lane *et al.*, 1982). Not only do filamentous algae increase the area of settlement sustrate available, but as shown by Grizzle *et al.* (1996), they also screen a larger area of the water column, intercepting higher abundances of larvae, especially in medium currents (Eyster & Pechenik, 1987). Although in some areas seagrasses (such as *Zostera marina*) act as an important host, the presence of epiphytes is often correlated to numbers of settled plantigrades (Newell *et al.*, 2010), epiphytes including the genera *Polysiphonia* and *Ceramium* (Seed, 1969). A secondary pelagic phase follows the primary settlement period (Bayne, 1964; Seed, 1976; *King et al.*, 1990). This transition from primary settlement into a pre-secondary settlement phase appears to be driven by a change in the habitat requirements for the developing plantigrades, related to size (Seed, 1969; Torp-Christensen *et al.*, 2015).

The main period of secondary settlement tends to be during the winter months (Bayne, 1964; Dare & Davies, 1975; van Broekhoven *et al.*, 2015), often following winter events associated with high disturbance (Seed, 1976). Upon descent from the plankton the juveniles may move short distances to their final attachment point by crawling using their extended foot or, less commonly, swimming back into the water column (Bayne, 1976). There are conflicting opinions within the literature over whether secondary settlement is more common on adult mussel beds or open, unsettled areas (Bayne, 1964; Seed, 1969; McGrorty *et al.*, 1990). The annual recruitment cycle of small, juvenile *M. edulis* can vastly alter the size profile of mussels within established beds (Littorin & Gilek, 1999). There is also evidence that, when settling on intertidal substrates colonised by barnacles, large spatfall events can lead to *M. edulis* outcompeting the resident barnacles, creating a mussel monoculture community (Navarrete & Castilla, 1990). However, is is certain that secondary settlement tends to be higher in areas of higher habitat complexity or rugosity (Chipperfield, 1953, Seed, 1969; Okamura, 1986). The byssal thread mass of adult beds offers a good settlement matrix for juvenile mussels, in addition to forming a habitat for other species (Theisen, 1972; Svane & Setyobudiandi, 1996; Jungerstam *et al*., 2014). In addition to providing settlement surfaces, adult beds retain a higher humidity than bare substrate, providing moisture to settled juveniles, moisture being an otherwise limiting factor in intertidal communities (Seed, 1969).

Studies by Bayne & Worrall (1980) and Wallace (1980) showed that intertidal *M. edulis* might grow to around 50mm over a 5-6 year period. However, while recently settled *Mytilus* have been shown to grow at a rate of up to 11.1 mm/month (Camacho *et al.*, 1995), there is an overall decline in rate of growth with advancing mussel age (Hawkins *et al.*, 1986; Sukhotin *et al.*, 2002). Mussel growth rate has also been shown to decrease with periods of lower temperatures and also high gamete production (Beaumont & Budd, 1982; Craeymeersch *et al.*, 1986). It is perhaps this temperature effect that results in the reduction in growth during the winter period as observed by Pieters *et al.* (1980), Kautsky (1982), Mallet *et al.* (1987) and Nielsen (1988). It has also been observated that in experimental populations of *M. edulis*, reabsorption of soft tissue during periods of low temperature can occur (Kautsky, 1982).

Shell thickness may increase in specimens which are more exposed to predators such as the crab *Carcinus maenas*, gastropod *Nucella lapillus* or echinoderm *Asterias rubens* (Côté, 1995; Calderwood *et al*., 2016). A thicker shell is likely to withstand predator action, such as compressive force in the case of predatory crabs (Elner, 1978). However, overall shape of mussels may also change in response to predator pressures (Reimer & Harms-Ringdahl, 2001). While *M. edulis* are characteristically wedge-shaped (Seed, 1976; Guinez & Castilla, 1999), individual mussel profiles may be influenced by genetic factors and environmental pressures (Seed, 1968; Lauzon-Guay *et al.*, 2005). In denser aggregations, *M. edulis* shape was found to change with a reduction in the width-to-length ratio and, overall, a lower soft tissue-to-shell ratio (Lauzon-Guay *et al.*, 2005). Seed (1968) also reported the same observation in areas of increased wave exposure, with *M. edulis* on sheltered substrates displaying a more typical triangular profile with reduced dorsal flattening.

In addition to the calcareous shell, another key external feature of *M. edulis* is the byssal thread matrix. While most bivalves have some form of byssal production capability in their larval forms, it is not always retained in adult form (Yonge, 1962; Waite, 1983). As with the planktonic stage, the adult byssal threads primarily consist of proteins, especially collagen proteins (Bairati & Zuccarello, 1976; Qin & Waite, 1995; Torp-Christensen *et al*., 2015). The threads are often classed as being in three sections; the root (within the mussel), the thread, and the plaque (on the substrate), also known at the attachment disc (Allen *et al.*, 1976; Price, 1982; Waite, 1983). Byssal threads were shown to have an average breaking load of 1.6kg (Allen *et al.*, 1976), perhaps demonstrating the effectiveness of the structure in maintaining organism position on substrate. Byssal thread production rate is seasonal (Price, 1980) though larger specimens of *M. edulis* are consistently shown to produce thicker threads at a slower rate (Allen *et al.*, 1976). However, production rates in all sizes of mussel were shown to be lower at lower temperatures (Allen *et al.*, 1976; Price, 1980). This difference in byssal thread production suggests that the rate of byssal thread production is a metabolic consideration, rather than reacting to seasonal changes in factors such as wave action which is often higher in winter (Price, 1980; Moeser *et al.*, 2006). This would correspond to the decrease in resource availability and feeding activity and the increase in reproductive effort prior to the spawning event in spring (Allen *et al.*, 1976; Price, 1982; Moeser *et al.*, 2006). Price (1982) and Bell & Gosline (1996) demonstrated that in areas subject to long-term high wave action, an increased rate of byssal secretion is evident. Byssal production in *M. edulis* has also been shown as being influenced by the presence of a decapod predator with the stimulus corresponding to an increase in the thickness of threads (Côté, 1995; Reimer & Tedengren, 1997).

The structure of the byssal threads is that of multiple micro-fibres (Bairati & Zuccarello, 1976), a factor that may increase the suitability of the threads as a settlement surface for young mussels and other species as rugosity is increased at micro-scales (Commito & Rusignuolo, 2000), Also, the gaps between the byssal threads, together with old shells and other large debris trapped by the byssal mass provide far more spatial complexity than bare substrate, increasing the amount of secondary space available (Dayton, 1971; Lohse, 1993; Svane & Setyobudiandi, 1996; Borthagaray & Carranza, 2007; Tam & Scrosati, 2014).

M. edulis often aggregates on substrate to form extensive patches and beds (Tsuchiya & Nishihira, 1985; Seed, 1996; Hunt & Scheibling, 2001; Torp-Christensen *et al.*, 2015). As with many group-living animals, mussels living in denser aggregations tend to experience a decreased likelihood of mortality by environmental pressures, including predation and exposure (Bertness & Grosholz, 1985; Okamura, 1986; Côté & Jelnikar, 1999). Seed (1969) and Arribas *et al.* (2014) also suggest that, living in the intertidal zone, *M. edulis* benefits from protection from dessication as mussel patches may retain a higher level of humidity than bare substrate. Mussels in patches also benefit from the effect of byssal attachment by neighbouring mussels, the resulting network of threads able to withstand more hydraulic drag force than the byssal threads of a single animal (Bayne, 1976; Witman & Suchanek, 1984; Nicastro *et al.*, 2012).

Reimer & Tedengren (1997) reported that predator presence may cause an increase in the size of aggregations perhaps due to, as previously suggested, group living may reduce the frequency of predation both by crushing (Côté & Jelnikar, 1999) and drilling predators (Casey & Chattopadhyay, 2008). This may be due to lower exposed surface area per mussel (Côté & Jelnikar, 1999), although this disputes the findings of Okamura (1986), and also the possibility of trapping predators (especially gastropods) by the secretion of byssal threads by multiple mussels (Day *et al.*, 1991). Younger mussels have shown to experience decreased levels of mortality when attached within byssal masses of adults as the altered cost-benefit of searching for them appears to deter decapod predators (Lin, 1991; Nicastro *et al*., 2012). However, despite the apparent benefits from aggregated living, mussels in the centre of patches are usually observed to have lower reproductive success and reduced growth rate (Okamura, 1986 Svane & Ompi, 1993).

The major limiting factor to individual growth is food availability (Bayne *et al.*, 1978; Widdows, 1978; Guinez, 2005). While in planktonic larval form *M. edulis* uses velum cilia for both swimming and as a feeding mechanism, the beating action of the cilia moving food towards the mouth (Bayne, 1976). The adult *M. edulis* is a suspension feeder, filtering out organic material from water drawn through the valve opening (Jørgensen *et al.*, 1988; Dolmer, 2000; Petersen *et al*., 2014; Riisgard *et al*., 2014). As an active pumping process there is obviously a metabolic cost and studies such as Ward & Targett (1989) demonstrated that there is a physiological response to density of suspended particulates, a reduction in organic material causes a reduction in feeding activity. Several authors, including Asmus & Asmus (1991), Norén *et al.* (1999) and Dolmer (2000), show that the feeding action of *M. edulis* beds can significantly alter the abundance and composition of phytoplankton communities.

Another important component of *M. edulis* feeding is the production of pseudofaeces, which is organic material that has been filtered but not absorbed by the gills or feeding palps (Widdows *et al.*, 1979; Bayne *et al.*, 1993; van Broekhoven *et al*., 2015). The accumulation of pseudofaeces, together with faecal aggregates, is often termed as biodeposition (Haven & Morales-Alamo, 1966) and these biodeposits can alter the environmental properties within the mussel bed (Tsuchiya, 1980; Dahlback & Gunnarsson, 1981; Hatcher *et al.*, 1994; Ragnarsson & Raffaelli, 1999). These pseudofaeces, in combination with shell fragments and trapped sediment particles, generate a nutritionally rich matrix for the infaunal community (Seed, 1996; Folmer *et al.*, 2014). During peak periods of biodeposition, specimens of *M. edulis* havexs been shown to produce biodeposits equal to their own body weight daily (Lucas & Watson, 2002). The rate of biodeposition has been shown as being positively correlated to mussel size, although, relative to body weight, biodeposition is higher in younger, smaller mussels (Tsuchiya, 1980; van Broekhoven *et al.*, 2015). This may be attributed to the higher metabolic requirement for younger mussels, to provide energy and resources for higher rates of growth and reproductive effort (Bayne, 1976). Tsuchiya (1980) and Flemming & Delafontaine (1994) also demonstrated that rates of biodeposition in *M. edulis* beds varied by season, being and highest during the summer months. This can be directly related to an increase in summer feeding activity, stimulated by peak phytoplankton populations during this period (Eilertsen *et al.*, 1989; Carstensen *et al.*, 2004; Riisgard *et al.*, 2014).

Common in mid and low heights of exposed rocky shores (Lubchenco & Menge, 1978; Lintas & Seed, 1994), mussel beds are effective secondary habitats as they are structurally complex due to their multi-layering and byssal thread matrix (Dittmann, 1990; Lintas & Seed, 1994; Iwasaki, 1995; Valdivia & Thiel, 2006; Robinson *et al.*, 2007). The irregular topography of mussel beds alters the flow of water across the bed, changing the rate and profile of sediment deposition locally (Commito & Boncavage, 1989; Svane & Ompi, 1993; Commito *et al.*, 2005;

Jungerstam *et al.*, 2014), particularly when combined with biodeposition processes (Seed, 1996).

Intertidal mussels on rocky shore have, for some time, been associated with high-richness, secondary communities of other organisms (Newcombe, 1935; Shelford, 1935; Witman & Suchanek, 1984; Buschbaum *et al.*, 2009). The secondary space created by mussel beds is frequently habitat for other species of mollusc, as well as polychaetes, amphipods and decapods (Tsuchiya & Nishihira, 1985; Santelices & Martínez, 1988; Peake & Quinn, 1993; Seed, 1996; Svane & Setyobudiandi, 1996; Ragnarsson & Raffaelli, 1999; Valdivia & Thiel, 2006). Mussel beds may also be important habitats for algal species (Witman & Suchanek, 1984; Arribas *et al.*, 2014), including *Fucus serratus*, *Enteromorpha* spp., *Porphyra* spp. and *Ceramium* spp. (Seed, 1976; O'Connor & Crowe, 2008). Communities associated with mussel beds may be divided on how habitat space is exploited; epibiotic organisms grow on the secondary substrate created by the mussel shells (e.g. bryozoans) while infaunal species inhabit the spaces and sediment between the mussels and byssal threads (Seed, 1996; Miyamoto & Noda, 2004). Several studies have investigated the associations between intertidal mussel populations and infaunal species (Murray *et al.*, 2007; Cole & McQuaith, 2010; Arribas *et al.*, 2014), the summary results of some being displayed in Table 1.2. As shown in Table 1.2, infaunal richness varied greatly between studies, a low of 32 taxa in Tsuchiya & Nishihira (1985) to a high of 69 in Tsuchiya & Nishihira (1986). Generally, members of the group Crustacea were the most abundant organisms in infaunal communities, although Mollusca and Polychaeta were often also well represented (Table 1.2).

Table 1.2 Summary of results from studies of infaunal communities within intertidal mussel patches, grouped by most abundant taxa

Study	Mussel species	Richness (infaunal taxa)	Dominant taxa
Reish (1964)	*Mytilus edulis*		Mollusca Crustacea Polychaeta
Tsuchiya & Nishihira (1985)		32	
Tsuchiya & Nishihira (1986)		69	
Asmus (1987)		40	
Seed (1996)		56	
Peake & Quinn (1993)	*Brachidontes rostratus*		
Iwasaki (1995)	*Sepifer virgatus* *Hormoya mutabilis*	38 43	
Thiel & Ullrich (2002)	*Perumytilus purpuratus*	66	
Newcombe (1935)	*Mytilus edulis*		Mollusca Crustacea
Lintas & Seed (1994)		59	
Robinson & Griffiths (2002)	*Mytilus galloprovincialis*	66	
Tsuchiya & Retiere (1992)	*Mytilus edulis*	60	Crustacea Polychaeta
Tsuchiya (2002)			
Valdivia & Thiel (2006)	*Perumytilus purpuratus*	54	Crustacea

Whilst mussel bed habitats have been shown to have significantly higher richness than surrounding bare substrate (Underwood, 2000; Robinson & Griffiths, 2002; Sousa *et al*., 2009), variation in environmental conditions can also influence these infaunal communities.

As previously discussed in Section 1.4 of this chapter, wave exposure may have a significant influence upon rocky shore communities (Dayton, 1971; Dittmann, 1990). While this relationship is supported by Lintas & Seed (1994); Seed (1996) and Tsuchiya (2002), the study by Hammond & Griffiths (2004) concluded that wave exposure was not linked to changes in infaunal abundance. However, the findings of this study did show that richness and diversity was higher in intertidal habitats with sheltered and high wave exposures whilst reducing in those of intermediate wave exposure (Hammond & Griffiths, 2004). Physical factors may also influence infaunal communities in the form of shore height, increased shore height being inversely correlated to infaunal abundance (Iwasaki, 1995), richness (Tsuchiya & Retiere, 1992; Seed, 1996) and diversity (Lintas & Seed, 1994). This may be attributed to the reduced immersion time experienced by higher shore heights (Dittmann, 1990) and the associated physiological stress from dehydration and thermal variation (Kensler, 1967; Helmuth *et al*., 2006). Shore height may be considered an example that while mussel beds are a mediator of physical stress, the influence of physical factors is not entirely eliminated thus the potential for decreased infaunal diversity remains (Lintas & Seed, 1994).

One topic that is an important consideration in community ecology is that of facilitation. As discussed previously, some key ecosystem engineers may facilitate settlement of other fauna by creating suitable habitat (Jones *et al*., 1994; Jungerstam *et al*., 2014). However, there is evidence to suggest that the succession of other species within these habitats may facilitate further settlement (Rosenberg, 2001). Succession may lead to the extension and increased complexity of food chains within a community, increasing the variety of niches available and also increasing the rate of energy flow through the system (Margalef, 1963). As a consequence of this increased complexity, such succession may subsequently facilitate settlement of other species, until the community reaches an equilibrium (Margalef, 1968; Krebs, 2009).

Patch size has been shown to be a key influence upon infaunal community structure in many previous studies. As might be expected, larger patches have been shown to support higher infaunal richness (Tsuchiya & Nishihira, 1985; Tsuchiya & Retiere, 1992; Lintas & Seed, 1994; Seed, 1996; Thiel & Ullrich, 2002; Cole & McQuaid, 2010), higher abundance (Tsuchiya & Nishihira, 1985; Peake & Quinn, 1993) and increased diversity (Lintas & Seed, 1994; Thiel & Ullrich, 2002). However, despite overall increases in abundance, richness and diversity shown by some studies there was often a decrease in richness and diversity per unit area in larger mussel patches (Tsuchiya & Nishihira, 1985; Tsuchiya & Retiere, 1992). Despite these reductions in richness and diversity, research by Tsuchiya & Retiere (1992) suggested that abundance per unit area remained constant between different patch sizes. Infaunal richness and diversity have also been shown as being influenced by edge effects, often being higher in the centre of mussel patches than on the periphery (Tsuchiya & Nishihira, 1986; Svane & Setyobudiandi, 1996).

1.6 Aims of the present work

The broad objective of this study was to investigate the structure of infaunal communities of mussel beds within the intertidal zone. The possibility and suitability of an alternative to taxonomic assemblage description is addressed, using a functional grouping approach based on dominant feeding function. This approach is applied and tested at a range of geographic scales in the UK and elsewhere. Additionally, while taxonomic descriptions of such communities already exist from many areas, none have yet described those of the Falkland Islands. In the context of the limited knowledge in this area this thesis describes and compares these unstudied communities. The main inquiries of this thesis are:

1. Chapter 2 looks at the effects of exposure and temporal variation on the selection of the appropriate quadrat size to describe the infaunal communities of *M. edulis* patches.

2. Chapter 3 attempts to devise a functional grouping approach and tests the hypotheses that the effects of exposure and season on infaunal assemblage patterns using a grouping based on dominant feeding function are comparable to those using a traditional taxonomic approach.

3. The variation in mussel bed infaunal composition at larger scales is examined in Chapter 4 where the hypotheses that assemblage patterns using an approach based on feeding function are representative of those from a taxonomic approach at a national scale in the United Kingdom. Additonally the chapter analyses seek to identify the key environmental variables in determining infaunal assemblage structure at a functional level.

4. Chapter 5 investigates infaunal assemblage structure of mussel beds in the Falkland Islands, an assemblage unstudied until now. In addition to the first assemblage description of such an assemblage in this region, the functional group approach testing in Chapters 3 & 4 is further analysed, this time in a Southern Hemisphere location. As in Chapter 4, the key environmental variables that shape infaunal assemblage structure in Falkland Island mussel beds are identified.

Chapter 2 – Optimal sampling and assemblage description

2.1 Introduction

Since the start of the 20th century, accurate sampling has been a requirement in research (Seng, 1951; Kruskal & Mosteller, 1980). In the world of business, appropriate and accurate sampling can mean the difference between success and failure (Hair *et al.*, 2007). Perhaps one of the earliest and well-known advocates of sampling was Anders Kiaer (1838-1919) who identified that a representative sample was as justifiable as surveying an entire population (Kruskal & Mosteller, 1980). Prior to this, surveying entire volumes or populations or using an unquantifiable and non-standardized sample was the norm in most research (Kruskal & Mosteller, 1980). Possibly, the first reconstruction of *Iguanodon* with the notoriously incorrect nasal horn would have benefitted from a more accurate and methodical sample of the fossil record by Mantell and Owen (Desmond, 1979). Even in the 1990s, several stock models used in fisheries policy were rejected after years of favour when flaws were found as the source data was either lacking in quantity or merely based on assumptions (Schnute & Richards, 2001). A retrospective assessment by Thornley & Adams (1998) concluded that half a century of inadequate sampling in some areas of mental health research had led to ineffective treatment, indicating an ethical cost associated with sampling.

Having established that sampling protocol is essential; the next, obvious consideration must be that of the size of sample (Lenth, 2001). The size of a sample must be relative to the scope and subject of study (Underwood & Chapman, 2005) or else might be considered inappropriate (Lenth, 2001). In ecology, for example, the size of a sample must be appropriate to the organisms to be studied. The distribution of populations of different species is not uniform, some being regularly distributed, some scattered and clustered (Underwood & Chapman, 2005). Thus for all species to represented appropriately, samples must be of the correct size. It is also generally accepted that larger samples provide a higher degree of precision, as a consequence of an inverse relationship between standard test error and sample size (Anderson, 2001; Underwood & Chapman, 2005). However, a balance between maximizing precision and practicality (time and resources) must be found to generate an appropriate sample size (Cao *et al.*, 2002; Hernandez *et al.*, 2006).

Determining an appropriate, or optimal, sample size may be based on two approaches; model sourced or design-based (Edwards, 1998; Nusser *et al.*, 1998). A design-based approach derives results purely from sample population parameters while model sourced combines design-based with auxiliary information and compares resulting matrices with model-sourced patterns (Nusser *et al.*, 1998). As discussed by Tokeshi (1993), the role of models in ecological studies may be best applied either towards indicating underlying trends or interpreting patterns produced from design-based sampling. One major limitation of using generalized ecological models is heterogeneity in the presence or occurrence of different organisms (Burnham & Overton, 1979), thus either a very robust model would be required, or else a design-based system.

A traditional design-based approach towards optimal sample size determination is the species-area relationship (Cain, 1934; Connor & McCoy, 1979; Ulrich & Ollick, 2005; Tjørve *et al.*, 2008). This is based on the understanding that the number of species increases with an expansion of sample size (Watson, 1835; Goldberg & Estabrook, 1998; Gotelli & Colwell, 2001; Ugland *et al.*, 2003). As larger areas are sampled, richness increases sharply as the more common species are counted, but as rare species are added, the rate of increase in richness slows (Ugland *et al.*, 2003). In addition, larger areas often display higher degrees of heterogeneity, increasing the variation of habitats and associated specialized species (Scheiner, 2003). When the rate of richness increase has slowed to a critical point, the corresponding sample size can be established as the optimal sample size. One example shown in Connell & McCoy (1979) is that in log-log models, any slope value of between 0.0-1.0 demonstrates a diminishing return in species number per unit area.

As shown by Table 2.1, when consulting the literature there was no general consensus about optimal sample size for conducting infaunal studies in mussel habitats. There is an indication that square sample quadrats are used in the majority of studies and that a consistent size be used for each sample. The two exceptions are Tsuchiya & Nishihira (1985) and Peake & Quinn (1993) where the entirety of the mussel patch was removed as a sample and thus size was impossible to standardise. The only justification of sample sizes mentioned in the literature reviewed in Table 2.1 is in Sousa (1984), where the dimensions were based on the average area of mussel patch within the study site. Indeed, within the existing literature there are far more experimental studies to determine the quantity of sample replicates than the actual sample area. While the sample sizes in the studies listed in Table 2.1 were undoubtedly useful in the course of the investigations, the absence of an agreed optimal sample size in infaunal studies in *Mytilus* patches prompts the need for a size to be established and then implemented throughout the current study.

Table 2.1 Literature review of sample sizes in mussel associated infaunal studies

Mussel-infauna study	**Area shape**	**Sample area (m^2)**
Tsuchiya & Nishihira (1985)	Patch defined	0.000056-0.0072
Peake & Quinn (1993)	Patch defined	0.0004-0.0300
Lintas & Seed (1994)	Square	0.0025
Creese *et al*. (1997)	Circular	0.0030
Ragnarsson & Rafaelli (1999)	Circular	0.0044
Hammond & Griffiths (2004)	Square	0.0050
Thiel & Ullrich (2002)	Square	0.0050
Murray *et al*. (2007)	Circular	0.0079
Buschbaum *et al*. (2009)	Circular	0.0085
Tokeshi (1993)	Square	0.0100
Asmus (1987)	Square	0.0100
Commito & Boncavage (1989)	Square	0.0200
Lawrie & McQuaid (2001)	Square	0.0625
Sousa (1984)	Square	0.2500
Witman (1985)	Square	0.2500
Seed (1969)	Unspecified	Unspecified
Seed (1996)	Unspecified	Unspecified
Svane & Ompi (1993)	Unspecified	Unspecified

This chapter aims to determine the optimal sample size for studies of the infaunal communities of intertidal *M. edulis* beds on rocky shores, achieved by the investigation of the species-area relationship and assemblage similarity between sites, seasons and different quadrat sizes. The importance of this study is high as it informs the optimal quadrat size for subsequent sampling design to be applied, not only at the local scale, but to be used for sampling the same biogenic habitat on a national and international scale.

2.2 Methods

2.2.1 Site description

To maximize the robustness of a developed sampling regime, study sites with differing physical attributes were chosen. The major distinction between the sites was the degree of wave exposure at each site as both would be subjected to the same tidal and meteorological conditions (Ballantine, 1961; Denny, 1995). Both sites had extensive mussel beds, accessible enough to permit replicated sampling over a 12-month period. Both shores are situated on the Yorkshire coast of the North Sea (Fig 2.1) and have a barnacle fucoid mussel mosaic, with *Mytilus edulis* communities in large contiguous beds and isolated, smaller patches. Both sample sites had a tidal range of 1.0-5.6m (mean spring range) and were subject to almost identical meteorological conditions.

The exposure level at each site was quantified using the Baardseth Index, as used in studies by Ruuskanen *et al.* (1999) and Westerbom & Jattu (2006), by determining the total number of 9^{o} arcs facing the open sea within 7.5km generated the index for each site. The site as defined in this study as “Exposed” was at Ravenscar (R), North Yorkshire (54^{0} 24’ 34.9” N; 29’ 31.9” W) and had a Baardseth Index of 19. The mussel beds were situated on the apex of a rocky promontory at the furthest point East of the site. The underlying bedrock consists mainly of Jurassic sandstone (Ensom, 2009). The contrasting site was at Filey Brigg

(F), North Yorkshire (54^0 13’ 2” N; 16’ 24.1” W); a site consisting of a Jurassic sandstone and oolitic limestone mixture (Ensom, 2009) with a southern aspect. The site is protected from the prevailing wave direction by a large rocky headland and was thus described as “Sheltered” with a Baardseth Index of just 6.

Figure 2.1 Position of Ravenscar and Filey Brigg on the Yorkshire coast

2.2.2 Sampling regime

As described by Seed (1969; 1996), *Mytilus edulis* beds vary seasonally, partly due to recruitment of juvenile mussels and associated infaunal species. In order to determine if this variation showed similar patterns at Ravenscar and Filey, both sites were sampled 4 times over a 12-month period from winter 2010 to autumn 2011, inclusively. Each of these four sampling events was defined as the factor SEASON.

To discern whether there was a species-area relationship, an increasing size of quadrat was used at each site (Underwood & Chapman, 2005). The quadrat sizes used in this sampling regime were the areas 0.0025, 0.005, 0.01, 0.015, 0.0225, 0.04 and 0.0625m^2. This range of sample areas fits within the ranges used by other studies, as outlined in Table 2.1. As explained by Underwood & Chapman (2005), a range of sample sizes this helps to ensure that species of different distribution patterns are appropriately represented within the data.

All sampling took place at low spring tides during daylight hours. Three replicate samples of each quadrat size were collected from within patches of *M. edulis.* All sampled patches were of approximately the same size, covering an area of between 0.36m^2 and 0.64m^2, samples being taken from the middle of the patch. Mussels were removed using a scraper and stored in polythene bags to prevent loss of material. All organisms, byssal masses, sediment and shell fragments within the boundaries of each quadrat was collected down to the rocky substrate of the shores (Tsuchiya & Nishihira, 1985). A total of 21 samples per season per site was collected. Prior to being processed, all samples were stored at -20°C until required (Hunt & Scheibling, 2001).

Under laboratory conditions the samples were defrosted and sieved through a 0.5mm mesh (Reish, 1964; Eleftheriou & Moore, 2005) to remove fine sediment and retain macrofauna. The sediment and infauna were then preserved in 70% ethanol for future analysis and identification. *M. edulis* were manually removed from the samples using forceps, with any byssal threads being removed from the shell and returned to the infaunal sample. Epibiotic organisms including bryozoans, hydroids and sponges were not included in species analysis due to complexities in identifying these to a comparable taxonomic level. Additionally, as these are often colonial organisms it can be difficult to precisely quantify individual abundances.

Macrofaunal organisms in the samples for each season were hand sorted and identified using dissection microscopes (Lintas & Seed, 1994), and all organisms were identified to species level with the exception of Oligochaeta, Ostracoda, Nematoda, Halacaridae and unidentifiable (often through damage to diagnostic features) Polychaeta, where the epithet “sp.” and “spp.” were used in place of the specific name. Mobile organisms situated upon the surface of the mussel beds, such as mature *Littorina littorea*, were included due to the complexity of predator-prey relationships with species such as *Carcinus maenas*. The abundance of all taxa was recorded. The resources used for identification were Hayward and Ryland (1995) and various keys from the Synopses of the British Fauna (Appendix 1). Being the key habitat-forming species (Seed, 1976), specimens of *M. edulis* were excluded from calculations of diversity, abundance and richness in subsequent analysis. A list of identified taxa is included in Appendix 2 and a sample list included in Appendix 3.

2.2.3 Data analysis

Two approaches were taken to indicate the appropriate and optimal sample size for subsequent investigations, a species-area approach and an assemblage similarity method.

2.2.3.1 Comparison of species-area curves between SITE and SEASON

In order to standardize the sampling regime and generate an optimal sample area for assemblage analysis, reducing the incidence and influence of sampling error by reducing the range of sample area, a measure of species diversity for each sample size was required (Zar, 1999).

The diversity measure selected was Richness (number of species) per sample as this quantity allowed the generation of species-area curves. The results were then Log10 transformed as the variances of the samples was higher than the mean and so the transformation normalised the data. Log richness and log area conformed to a normal distribution (Kolmogorov Smirnov test, $P>0.05$) but were still transformed to fit to a $\log y = m \log x + c$ linear regression model as species-area relationships are normally curvilinear (Fowler *et al.*, 1998).

A Pearson's Product Moment correlation coefficient was used to determine if there was a significant linear relationship between Log10 area and Log10 richness for each site and season, (Zar, 1999). Where correlations were significant the relationship between the variables was described using the Method of Least Squares Regression analysis in order to determine the slope and intercept of the line of best fit through the data (Fowler *et al.*, 1998; Clarke & Gorley, 2006).

An Analysis of Covariance (ANCOVA) model was applied as outlined in Field *et al.*, (2012). Initially, the hypothesis that the independent variable (SITE/SEASON) was independent of the covariate (Log 10Size) was tested using a one-way ANOVA. As the average level of Log 10 Size was not significantly different between SITE/SEASON (ANOVA, P>0.05) a full ANCOVA model was used to determine if the covariate (Log 10 Size) and independent variable (SITE/SEASON) had a significant effect on the independent variable (Log 10 Richness), and then the hypotheses that there was homogeneity in the slopes between the different SITE/SEASON (Field et al., 2012). Type I Sum of Squares was used to test the homogeneity of the slopes of the scatterplot of Log10 area and Log10 Richness as sample sizes were equal and independent of each other and provided meaningful demonstrations of interactions (Field et al., 2012). Where the homogeneity of slopes could not be assumed, an *a posteriori* pairwise Tukey HSD test was used to indicate where the differences occurred between the different levels of Site/season (Field *et al.*, 2012).

A 10% increase in sample size should be associated with a 5% increase in richness per sample (Williams, 1987), a ratio also discussed in Cain (1938). The percentage increases in number of species and area of quadrat were calculated and displayed in tabular form, providing an indication of the appropriate sample sizes to use in the analysis of assemblage structure (Chapter 3). The appropriate ratio for richness-area increases was based on interpretations of the slope parameter as covered by Cain (1938) and Williams (1987) and elaborated on in Connor & McCoy (1979).

2.2.3.2 Comparison of assemblage similarity between quadrat sizes

Whilst species area relationships are often used to determine the size of quadrat required, an assemblage level approach was also undertaken. The species abundance data was imported into PRIMER and used to generate a similarity matrix based on the Bray Curtis similarity coefficient (Clarke & Warwick, 2001). Bray Curtis was chosen as addition of samples does not influence the relationship between existing samples, unlike some other coefficients such as Wisconson (Gauch, 1973), it is easy to interpret and effectively accounts for differences between total and relative abundances (Clarke & Warwick, 2001).

The similarity matrix was then used to perform a non-parametric ordination using non-metric Multi Dimensional Scaling (MDS), which produced a plot representing the similarity between the different samples with quadrat Size used as a factor (Clarke & Gorley, 2006). The minimum stress value generated indicated the representativeness of the MDS plot (Clarke & Gorley, 2006). To determine if there was a significant difference in assemblage similarity between the different sized quadrats across all sites/seasons, Analysis of Similarity (ANOSIM) was then performed on the similarity matrix (Clarke & Gorley, 2006). Pairwise comparisons were used to determine the source of any significance between the different sized quadrats.

2.3 Results

2.3.1 Comparison of species area curves between SITE and SEASON

Across all sites and seasons, there was a positive relationship between log10 area and log10 richness. As shown in Figure 2.2, at all SITE/SEASON there was an increase in Richness with increased sample area. The Filey samples all have a lower intercept (Log10 Richness = 1.376 + 0.372 Log10 Area) than the Ravenscar ones (Log10 Richness = 1.787 + 0.361 Log10 Area) indicating that there was higher initial richness at Ravenscar than Filey. The covariate (Log 10 Area) had a significant positive effect on Log 10 Richness (ANCOVA, $F_{1,38}$=242.48, P<0.01etc) and there was a significant effect of SITE/SEASON after controlling for Log10 Area (ANCOVA $F_{7,38}$=6.47, P<0.01).

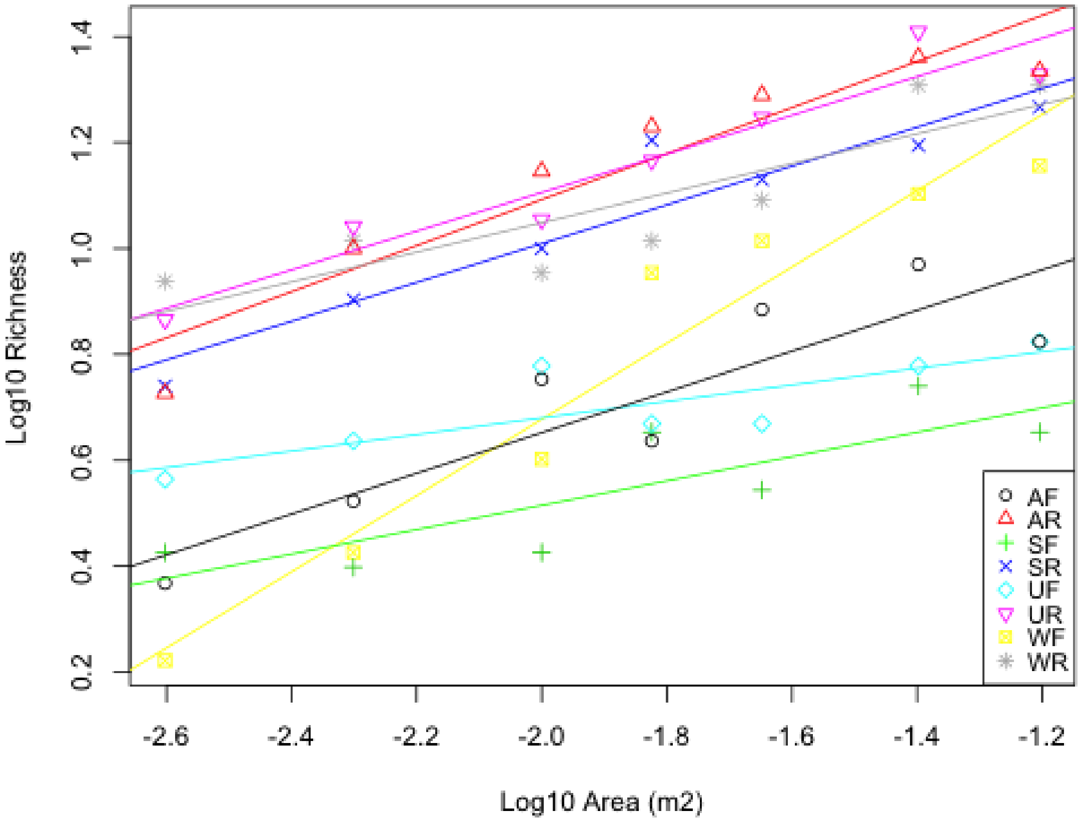

Figure 2.2 Scatterplot for Log10 Richness (y) and Log10 sample area (x), across each season (Winter, Spring, Summer, Autumn) at both sites (Filey, Ravenscar)

However, the slopes of the regression lines could not be considered homogenous between SITE/SEASON (ANOVA, $F_{7,48}$=63.667,P<0.001). Table 2.2 presents the results of the Tukey pairwise comparisons of slopes for each SITE/SEASON. All the slopes of the Ravenscar samples were significantly different to those of the Filey samples (Tukey, P<0.05), and apart from WF being significantly different to SF, there was no significant difference in slopes within SITE (Table 2.2).

Table 2.2 Tukey *post hoc* comparisons of slopes for each SITE/SEASON following ANCOVA (A=Autumn, S=Spring, U=Summer, W=Winter, F=Filey, R=Ravenscar)

Code	AF	SF	UF	WF	AR	SR	UR	WR
AF		ns	ns	ns	<0.01	<0.01	<0.01	<0.01
SF			ns	<0.01	<0.01	<0.01	<0.01	<0.01
UF				ns	<0.01	<0.01	<0.01	<0.01
WF					<0.01	<0.01	<0.01	<0.01
AR						ns	ns	ns
SR							ns	ns
UR								ns
WR								

Whilst there was a difference in the relationship between Log 10 richness and Log 10 area between sites/seasons (fig. 2.3) there was an overall shared trend across all SITE and SEASON (Figure 2.2). The clustering of points around the 95% confidence interval in the samples with larger areas suggests that there was a convergence in Richness between the samples in larger areas. This suggests that the adoption of larger sample sizes would be representative of the *M. edulis* infaunal communities across both sites and in all seasons.

Table 2.3 Mean percentage (+/-) change in number of species per sample for all seasons at both sites

Quadrat size (m^2)	% increase in sample area	Mean % change in number of species per sample	STDev
0.0025-0.005	100.00	39.473	17.27
0.006-0.01	100.00	24.150	25.62
0.011-0.015	50.00	15.457	43.76
0.016-0.0225	50.00	10.766	9.49
0.0226-0.04	77.70	32.523	17.32
0.041-0.0625	56.25	3.526	7.70

According to Williams (1987), an increase in sample area of 10% should be matched by a 5% increase in richness (ratio of 2:1). Apparent from the results in Table 2.3, the closest ratio of change to that stated by Williams (1987) was between 0.015-0.0225m^2. This further supports the Pairwise Comparison results as seen in Table 2.4, which separates 0.04m^2 and 0.0625m^2 from the remaining samples.

2.3.2 Comparison of assemblage structure between quadrat sizes

Figure 2.3 illustrates the MDS results on a Bray Curtis Similarity matrix for all samples (irrespective of SITE and SEASON) with quadrat size as the factor. While there is a certain degree of overlapping of sample sizes in the centre of the plot, the quadrats of 0.04-0.0625m^2 show almost complete overlap to the right side of the plot but are near separate from the from the smaller sample sizes. The maximum stress value of the plot was 0.05, which would indicate that Figure 2.3 is a very good representation of the similarity between sample sizes (Clark & Warwick, 2001).

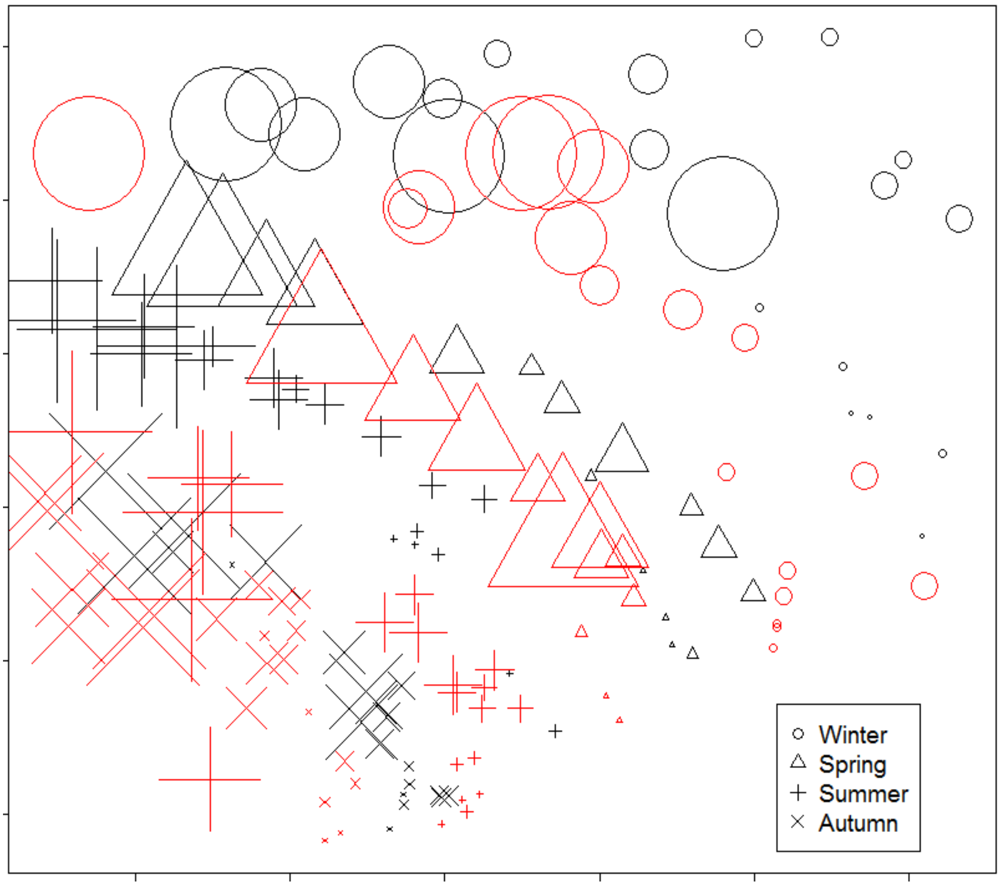

Figure 2.3 Results of nMDS analysis on Bray Curtis Similarity matrix quadrats of all areas (irrespective of SITE and SEASON). Point character is determined by season (see legend) while point size is determined by sample area. Site is the determinant of colour, Filey (black) and Ravenscar (red).

There was a significant difference in overall assemblage similarity between the different quadrat sizes (ANOSIM, Global R=0.283, p<0.05). However, pairwise comparisons between quadrat sizes indicated that whilst the two largest sizes (0.04 and 0.0625 m2) were not significantly different to each other, they were significantly different in terms of assemblage similarity to all other sized quadrats (P<0.05; Table 2.4). The smallest quadrats (0.0025 – 0.01) were also not significantly different from each other in terms of assemblage similarity, but were significantly different from the rest (P<0.05; Table 2.4). All other pairwise comparisons showed there was a significant difference in assemblage similarity with quadrat size (P<0.05; Table 2.4).

Table 2.4 Results of Pairwise Comparisons after ANOSIM between quadrat sizes

	0.0025	0.005	0.01	0.015	0.0225	0.04	0.0625
0.0025		ns	ns	P<0.05	P<0.05	P<0.05	P<0.05
0.005			ns	P<0.05	P<0.05	P<0.05	P<0.05
0.01				ns	P<0.05	P<0.05	P<0.05
0.015					ns	P<0.05	P<0.05
0.0225						P<0.05	P<0.05
0.04							ns
0.0625							

2.4 Discussion

The current results of have profound implications for the key research questions posed by this body of work. An appropriate and efficient sample size of 0.04-0.0625m^2 will optimise further study of *M. edulis* patch infaunal communities and can be applied both at local and larger scales. The results of this study (Section 2.3) will facilitate the forthcoming investigations of heterogeneity in assemblage structure, both at small scales and wider geographic areas.

There appeared to be a positive relationship between quadrat area of *M. edulis* and infaunal richness. This corresponds with findings in sample size methodology investigations based in terrestrial habitats such as lichens (Innes, 1984) and soil microbes (Youssef & Elshahed, 2008). However, beyond such studies, the findings agree with a key aspect of island biogeography theory (MacArthur & Wilson, 1967) in that an increase in island size and by extension, quadrat size, will result in an increase the richness of the island (or quadrat) (Simberloff, 1974; Kohn & Walsh, 1994). This may be attributed to an increase in habitat and assemblage heterogeneity within quadrats (Kohn & Walsh, 1994), supporting a higher diversity of species. As sampled patches were of approximately the same area, and taken from the middle of the patch to avoid edge effects (Bowden *et al*., 2001), differences in communities represented within quadrats was likely to be due to the effect of sample area, rather than patch size. However, it should be noted that in infuanal studies conducted in seagrass habitats, the effect of proximity to habitat edge varied (Tanner, 2005; Murphy *et al*., 2010). While some influences may increase with proximity to edges, others may decrease, such as predation as the centre of the aptch may offer more suitable hbait tfor some predators, thus increasing overall predation in areas towards the centre of patches (Tanner, 2005). Clearly there is an indaication that faunal responses to edges of habitats cannot be geenralised, due to the range of spatial scales that difference species operate across and also the small scale variabilites that may be found throughout patches of habitat (Bostrom *et al*., 2006; Murphy *et al*., 2010). As some species have differing distributions, such as clustered instead of scattered (Underwood & Chapman, 2005; 2006), larger sample areas may also show a higher richness as a variety of these distribution patterns are included. Additionally, as variation in assemblage diversity and richness may occur at a variety of spatial scales (Chapman *et al*., 2010), larger sample areas may include a higher variety of such scales. However, while this research has shown that generally, richness increases with sample area, an optimal sample size must still be established for the target study assemblage to make the methodology efficient and suitable for the scope and aims of the research (Length, 2001; Underwood & Chapman, 2005).

A key aspect of the increase in richness with increased area is that of species accumulation. It would appear that as sample area increased, more species were added to the sample assemblage, to the point where different sample sizes became dissimilar to each other. This is supported by the significant dissimilarity between samples of 0.0025-0.0225m^2 and 0.04-0.0625m^2, suggesting that sample areas of 0.04-0.0625m^2 may accumulate species at a higher rate than smaller samples (0.0025-0.0225m^2) and also due to differences in the relative abundances of such species the communities in the larger samples are distinct from those of the smaller samples. This is further supported by the significant similarity between the communities in smaller sample sizes (Figure 2.4) and, separately, the significant similarity between the two largest sample areas. This would suggest that a combination of a peak in the species-area curve and relative abundances of species leads to differences between infaunal communities in *M. edulis* in sample areas of somewhere around 0.04m^2. It would thus be prudent to assume that samples of

0.04-0.0625m^2 were more representative of the communities sampled than those from smaller areas. However, the analysis also shows that while SITE was a significant factor in the traditional species richness approach, it was not so in the assemblage approach. This suggests that it may be prudent to reject the traditional species richness approach and instead use an assemblage level approach in infaunal studies. However, it is important to acknowledge that while an assemblage level approach might be more appropriate, it does provide different information than a species richness approach.

In addition to the similarity/dissimilarity approach to identifying optimal sample size, the reasoning as suggested by Williams (1987) was also useful in determining an optimal sample size threshold from the results of this study. While Cochran (1963) and other researchers developed complex equations for determining optimal sample size, as suggested by Southwood (1966), fluctuations in populations and distribution in natural communities often make such models unsuitable. A simpler method proposed by Williams (1987) is that a 10% increase in sample size should result in a 5% increase in richness. Thus, for further assemblage analysis only data from samples of 0.04m^2 and 0.0625m^2 were used, as the increase in area to richness increase was closest to that suggested by Williams (1987).

As suggested by Moreno & Halffter (2000) and Willott (2001), a difference in sampling effort between samples or within a study would have an effect upon species-area curves. It might be considered that a difference in the taxonomic level to which organisms are identified could be considered a different sampling effort.

This variation in taxonomic level is sometimes unavoidable, with cryptic species and sample organisms lacking key diagnostic features (Bengtsson, 1998). A solution to a species level approach might be to classify organisms according to broader traits (Ghiselin, 1974; Petchey & Gaston, 2002). Using the optimal sample size from this study, the use of a functional based approach to describing and comparing communities will be investigated and evaluated in Chapter 3.

The results of Chapter 2 suggest using quadrats of 0.04-0.0625m^2 to optimally sample *M. edulis* infaunal communities and also, indirectly, indicate that perhaps an assemblage approach is a representative method comparing infaunal communities across spatial scales than a traditional species richness approach.

Chapter 3 – A Functional Grouping Approach to Infaunal Research

3.1 Introduction

Although, as previously stated, the use of traits to group organisms is not new in ecological study, its expansion into the marine ecological field has been limited (Fagerstrom, 1991), being mainly applied to sub-tidal, soft-sediment, benthic habitats (Roth & Wilson, 1998; Bonsdorff & Pearson, 1999). However, the field of functional groupings is constantly expanding in marine research, particularly based on traits that may affect the distribution of species. While not as widespread as in freshwater, some studies have used feeding function to group subtidal organisms such as coral reef fish (Bellwood *et al*., 2006), polychaetes (Damianidis & Chintiroglou, 1998), bioturbators (Michaud *et al*., 2005), estuarine fish (Elliott & Dewailly, 1995; Mathieson *et al*., 2000; Elliott *et al*., 2007) and overall soft-sediment communities (Pinn & Robertson, 2003; Thrush *et al*., 2006; MacDonald *et al*., 2010; Paganelli *et al*., 2012). The use of functional groupings in sediment communities is particularly important for groups of organisms such as nematode worms (Bongers & Bongers, 1998). The results of soft-sediment functional group studies have been incorporated into ecological monitoring systems such as the Infaunal Trophic Index (Word, 1979) and the Ecological Evaluation Index (Orfanidis *et al*., 2003), which are used to show broad scale changes in assemblage composition.

If functional studies in the marine environment are infrequent, then functional studies in intertidal habitats can be considered even more rare. Littler & Littler (1984), Steneck & Dethier (1994) and Phillips *et al*. (1997) used a simple yet effective traits approach by grouping intertidal macroalgae by growth form (such as sheet, jointed-calcareous, crustose) and Bosman *et al*. (1987) grouped benthic invertebrates by their mobility. Other authors adopted and tested a functional approach such as feeding groups in rocky shore molluscs (Raffaelli, 1985). In temperate intertidal communities, increased numbers of grazers such as amphipods and gastropods may alter the presence and diversity of algae and epiphytic growth (Hay *et al*., 1988; Duffy, 1990). This may demonstrate the effectiveness of a hybrid approach in studying communities using both grazer feeding method and algal growth form as used by Steneck & Watling (1982) to relate abundance of different grazing method to algal functional form on a shore. Many of these previous studies were successful but grouped only selected closely related organisms within taxonomic groups such as gastropods or polychaetes. However, some rocky shore studies have used feeding functional groups across taxa in assemblage studies such as McQuaid & Branch (1985), Bustamante & Branch (1996) and Arenas *et al*. (2006). In these studies, species were assigned into feeding groups according to their trophic level, such as autotrophs, filter feeders, predators and scavengers.

Other aquatic studies have used traits not directly based on resource acquisition, but instead on traits that may influence assemblage structure such as grouping by life cycle (McGill *et al*., 2006; Feio & Dolédec, 2012). Due to the fluid medium, the dispersal of marine larvae may be considered similar to seed dispersal in terrestrial plants (Cowen & Sponaugle, 2009), a field studied in considerable literature including Baker (1972), Howe & Smallwood (1982) and Nathan & Muller-Landau (2000). Because many benthic marine organisms have an obligate planktonic phase (Underwood & Fairweather, 1989), not only may reproduction and dispersal strategy affect assemblage structure, but may also indicate how open or closed the system is (Gaines & Bertness, 1992; Grantham *et al*., 2003; Christie *et al*., 2009).

However, some authors have identified some potential limitations to a non-taxonomic approach. Phillips *et al*. (1997), Bongers & Bongers (1998), Bonsdorff & Pearson (1999), Villéger *et al*. (2008) and Gall & Le Duff (2014) suggest that using a broader scale approach may risk losing information and detail on communities. This does, however, dispute earlier works by authors including Somerfield & Clarke (1995). It might be assumed that the feeding functional groups common in freshwater systems, such as shredders (MacNeil *et al*., 1997), may not be applicable or suitable in a marine habitat (Gerino *et al*., 2003). Indeed, Damianidis & Chintiroglou (1998) indicated that the results of their own feeding function study on sub-tidal *Mytilus galloprovencialis* infauna may be species specific, not applicable to other bioengineers or habitats. Complex ecosystems, and associated complex interactions, may require a more complex traits regime (Keddy, 1992). Several authors, including Fauchald & Jumars (1979), Bonsdorff & Pearson (1999), Tomanova *et al*. (2006) and Villeger *et al*., (2008) suggested a a hybrid approach may be effective in assemblage studies. Combined functional group approaches have been used successfully, often combining broad-scale trophic groupings with those such as mobility; longevity and body form both in subtidal benthic communities (Bremner *et al*., 2003; 2006), littoral algal understorey habitats (Bustamante *et al*., 2014) and across entire intertidal environments (Scrosati *et al*., 2011).

This chapter investigates the suitability of a non-taxonomic grouping approach, referred to hereafter as "functional" in examining the structure of infaunal communities in mussel patches at two rocky intertidal locations. In addition to describing communities at a species level, it develops and tests a functional classification scheme based on both dominant feeding mode (feeding function approach) and reproductive mode method (reproductive mode function). It also determines whether a combined approach of the two functional classifications is effective in assemblage analysis.

3.2 Methods

3.2.1 Sampling regime

All assemblage data for this study was sourced from the assemblage data presented and analysed in Section 2.2.2. The assemblage data was at a species taxonomic level from two sites, Filey and Ravenscar across four contiguous seasons of collection. Site descriptions are presented in Section 2.2.1, along with a summary of collection and identification procedures. The chosen sample size of $0.04m^2$ and $0.0625m^2$ was based on the results presented in Chapter 2.

3.2.1.1 Feeding function approach

Using the species list produced in Chapter 2, across both sites and four seasons, each species or lowest taxonomic group was assigned into a feeding functional group according to the dominant feeding mode. Feeding morphology was used rather than gut content analysis, as suggested by Palmer *et al*. (1993) and Tomanova *et al*. (2006). Six distinct feeding functional groups were identified, with an amalgamation of groups (such as grazer-detritivores) where more than one mode of feeding was recognized (Table 3.1).

Table 3.1 Final assigned feeding functions for lowest taxonomic group

No.	Feeding function	Description	Example organism
1	Grazer	Rasps benthic algae or sessile organisms (e.g. bryozoans)	*Skeneopsis planorbis* (Fretter, 1948)
2	Detritivore	Feeds on fragmented organic matter (detritus)	*Onoba semicostata* (Killeen & Light, 1998)
3	Predator	Feeds by preying on other organisms, killing them for food	*Eulalia viridis* (Emson, 1977)
4	Surface deposit feeder	Obtains particulate matter from the substrate	*Tharyx marioni* (Gibbs *et al*., 1983)
5	Passive suspension feeder	Food caught on filter from flowing water	*Nephasoma minutum* (Adrianov & Maiorova, 2010)
6	Active suspension feeder	Food caught from water by active pumping or sweeping	*Lasaea rubra* (Ballantine & Morton, 1956)
7	Predator-Parasite	Feeds both parasitically and as 3.	Halacaridae (Pugh & King, 1985)
8	Predator-Detritivore	Combination feeding of 2 & 3	*Carcinus maenas* (Rangeley & Thomas, 1987)
9	Surface deposit feeder-Grazer	Combination feeding of 1 & 4	*Hydrobia ulvae* (Newell, 1965)

The primary source of the feeding mode information was existing literature, including Hayward and Ryland (1995), Fauchald & Jumars (1979) and various publications from the Synopses of the British Fauna (Appendix 1).

3.2.1.2 Reproductive mode function approach

As with the dominant feeding function, a functional approach using reproductive mode was assigned to the species list produced in Chapter 2. Reproductive mode was selected as an alternative to feeding function as it represents a simpler approach (three groups) but relies on similar driving environmental influences, such as water transport and rugosity (Elliott & Dewailly, 1995; Franco *et al*., 2008). While several studies, including Christie *et al*. (2009) have used the Biological Traits Information Catalogue (www.marlin.ac.uk/biotic/) this particular reproductive mode grouping was rejected as some dispersal information is missing for some taxa, including species found in mussel bed infaunal communities. Additionally, most intertidal species have some form of planktonic juvenile phase, even in brooding species. During this time the mechanisms, which affect the adult assemblage such as sedimentation, may not be influential. However, identifying the purely planktonic dispersal species (such as *Modiolus modiolus*) from brooders and other methods allows for within-patch processes to be represented. Using this approach, distinct functional groups were identified, as displayed in Table 3.2. While it was recognised that there are different types of planktonic reproduction (planktotrophic, leukotrophic etc.), the functional grouping was more concerned with colonisation and transport processes than fertilisation and gametes so the planktonic group was not subdivided.

Table 3.2 Final assigned reproductive mode function for lowest taxonomic group

No.	Reproductive mode	Description	Example organism
1	Brooding	Larvae or eggs incubated/retained in a brood pouch or similar organ	*Hyale nilssoni* (McBane & Croker, 1984)
2	Benthic	Eggs deposited and attached/glued to substrate or similar structure	*Nucella lapillus* (Feare, 1970)
3	Planktonic	Fertilized or unfertilized gametes are dispersed into plankton	*Polititapes rhomboides* (da Costa *et al*,, 2012)

The grouping was identified as the primary method of reproductive mode, that is, how the egg/larvae is dispersed in the first stage, as well described in Highsmith (1985). As with the dominant feeding function approach, information on reproductive mode was sourced from Hayward and Ryland (1995) and the Synopses of the British Fauna (Appendix 1).

3.2.2 Data analysis

3.2.2.1 Species level approach

Using the data collected in the previous chapter the diversity between sites and seasons was compared using Shannon-Weiner (H') indices (Fowler *et al.*, 1998; Zar, 1999).

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

where p_i is the abundance of each species (i) and R is the total number of species i.e. richness. Shannon-Weiner was selected as samples were of equal size from comparable populations and, additionally, it considers measures of abundance and richness (Fowler *et al.*, 1998; Zar, 1999). Diversity indices generated richness (S), Shannon-Weiner index (H') and total abundance (N) in the statistical package PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke & Warwick, 2001).

Richness (S), abundance (N) and diversity (H) data conformed to a normal distribution (Kolmogorov Smirnov test, P>0.05 in all cases). A Levene's test was used to confirm that there was no significant departure from homogeneity of variances for all variables (Fowler *et al.*, 1998; Ryan *et al.*, 2005) (Levene's test, P>0.05 in all cases).

A two-way ANOVA was performed for each variable using a General Linear Model with both site and season as fixed factors with two levels (Clarke & Gorley, 2006). This approach tested the following hypotheses that there was no significant difference in average S, N or H between the two sites between the seasons and no significant interaction between site and season.

A similarity matrix was generated from the raw data using the Bray Curtis similarity index (Clarke & Gorley, 2006) and this was then used to generate an MDS plot using non-parametric ordination (Clarke & Gorley, 2006). The similarity matrix was then used to run a two-way ANOSIM, which tested the hypotheses that there was no significant difference in assemblage similarity between sites (averaged across all seasons) or between seasons (averaged across both sites) (Clarke & Gorley, 2006).

To determine which species defined the communities and contributed the most to either the similarity within site and season or the dissimilarity between sites and seasons, the Similarity Percentages Routine (SIMPER) available as part of the PRIMER package was used (Clarke & Gorley, 2006). Only species that contributed equal to or more than 10% to the overall similarity or dissimilarity were reported (Clarke & Gorley, 2006) and findings displayed in tables. Due to the lower resolution to which Oligochaetes were identified, they were included in multivariate analysis but their contributions are displayed in grey shades within tables.

3.2.2.2 Feeding function approach

The organisms identified in the species level analysis were then classified into the feeding function groups outlined in Table 3.1. A full list of taxa and assigned feeding functions is included in Appendix 2, To compare the diversity of feeding functional groups by sites and seasons the Shannon-Weiner (H') diversity index was used as above (Fowler *et al.*, 1998; Zar, 1999). Logarithmic (Log/Log10) and square root transformation of H' had no effect on the normalisation of the data, however the variance of the data could be considered equal (Levene's test, $P<0.05$). Despite non-normal distribution of the diversity data, the equal variances allowed a two-way ANOVA using a General Linear Model to be performed to test the null hypothesis that there was no significant difference in the diversity of feeding function between seasons and site (Clarke & Gorley, 2006). The two-way ANOVA also tested for a significant interaction between the variables site and season (Clarke & Gorley, 2006). Tukey Pairwise comparisons were used as an a posteriori test to identify the source of the significance between means (Clarke & Gorley, 2006).

Using the Bray-Curtis similarity matrix, the similarity of the communities by site and season at a feeding function level was compared, and the results displayed using Multidimensional Scaling (MDS) plot using non-parametric ordination (Clarke & Gorley, 2006). A two-way ANOSIM was then run to test the null hypothesis that there was no significant difference in assemblage similarity between sites (averaged across all seasons) or between seasons (averaged across sites) (Clarke & Gorley, 2006). The contribution of each feeding function to the similarity or dissimilarity of the communities was defined using the Similarity Percentages Routine (SIMPER) with species contributing >10% to the overall similarity or dissimilarity being reported (Clarke & Gorley, 2006).

3.2.2.3 Reproductive mode function approach

As with the feeding function approach, organisms identified in the species level analysis were then classified into the feeding function groups based on reproductive mode as displayed in Table 3.2. The same data analysis methods were applied to the reproductive mode function data as described in Section 3.2.2.2.

3.2.2.4 Comparison of approaches

As a basic test of how effectively the diversity of the assemblage using the feeding function and dispersal function approaches reflects the diversity at the species level, the relationship between them was investigated. As the diversity data did not conform to a normal distribution (Kolmogorov Smirnov test, $P<0.05$) a non-parametric Spearman Rank correlation test and Method of Least Squares Regression were used to describe and explore the relationships (Fowler *et al.*, 1998).

As an additional test of the suitability of the approaches, 2nd-stage MDS was used to compare the three separate Bray Curtis similarity matrices (i.e. matrices generated using the species, feeding function and dispersal function data) (Clarke & Warwick, 2001). The 2nd-stage MDS methods might be considered as analysis of the pairwise similarities between MDS plots (Clarke *et al*., 2006). The test statistic (R) generated indicates the strength of the correlations between the Bray Curtis similarity matrices with a stronger correlation being represented by values further away from zero. As well as individually comparing the functional approaches to the species level matrices, the feeding and reproductive mode functions were also compared to indicate whether a multiple functional group approach might be most representative, as suggested by Fauchald & Jumars (1979), Bonsdorff & Pearson (1999) and Tomanova *et al*. (2006).

3.4 Results

3.3.1 Variation in assemblage structure using the species level approach

The average diversity for both sites for each season is shown in Figure 3.1, visually demonstrating the higher diversity at Ravenscar and differences between the seasons.

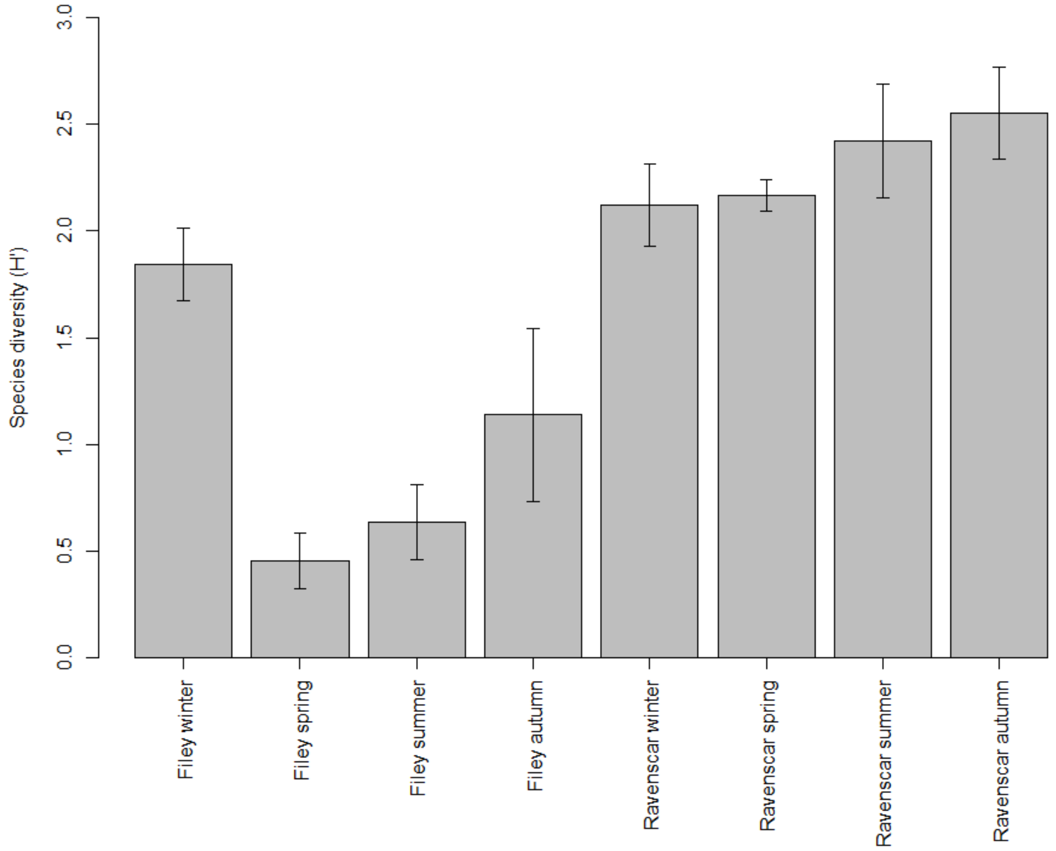

Figure 3.1 Mean (+/-s.d.) Shannon Weiner diversity (H') by site and season.

As shown in Figure 3.1, overall diversity was higher at Ravenscar than at Filey and there was also a difference in diversity across both sites between the seasons. There was a significant difference in mean diversity between sites (Filey mean=1.07 +/-0.60, Ravenscar mean=2.31 +/-0.26), and seasons (Table 3.3, p<0.05). There was also a significant difference between seasons (Table 3.3), however Tukey post-hoc testing (P=0.05) showed that, overall, only winter (mean=1.096 +/-0.118) was significantly different from the other three seasons. Summer (mean=0.869 +/-0.317), spring (mean=0.808 +/-0.328) and autumn (mean=0.838 +/-0.329) were not significantly different from one another in Shannon Weiner diversity (Tukey, P=0.05).

Table 3.3 Results of two-way analysis of variance using GLM to determine the effects of site and season on the diversity (Shannon Weiner H').

Source	d.f	Adjusted M.S.	F	P
Site	1	17.59	238.58	<0.001
Season	3	1.12	15.18	<0.001
Site*Season	3	1.29	17.49	<0.001
Error	38	0.07		

Tukey post-hoc testing (P=0.05) found that there was no significant difference in diversity between seasons at the Ravenscar site. Table 3.3 also shows that there was a significant interaction between site and season, indicating that variation in mean diversity with season was not consistent over the sites. All samples at Filey had a significantly lower diversity than Ravenscar with the exception of those taken during the winter season at Filey (mean=1.844 +/-0.17). Diversity during winter at Filey was found to be significantly lower than at Ravenscar during autumn and also significantly higher than the remaining seasons at Filey. Whilst Filey winter samples were significantly higher in diversity than Filey autumn (mean=0.648 +/-0.296), Filey spring (mean=0.477 +/-0.092) and summer (mean=0.617 +/-0.217) samples were significantly lower in diversity than Filey autumn.

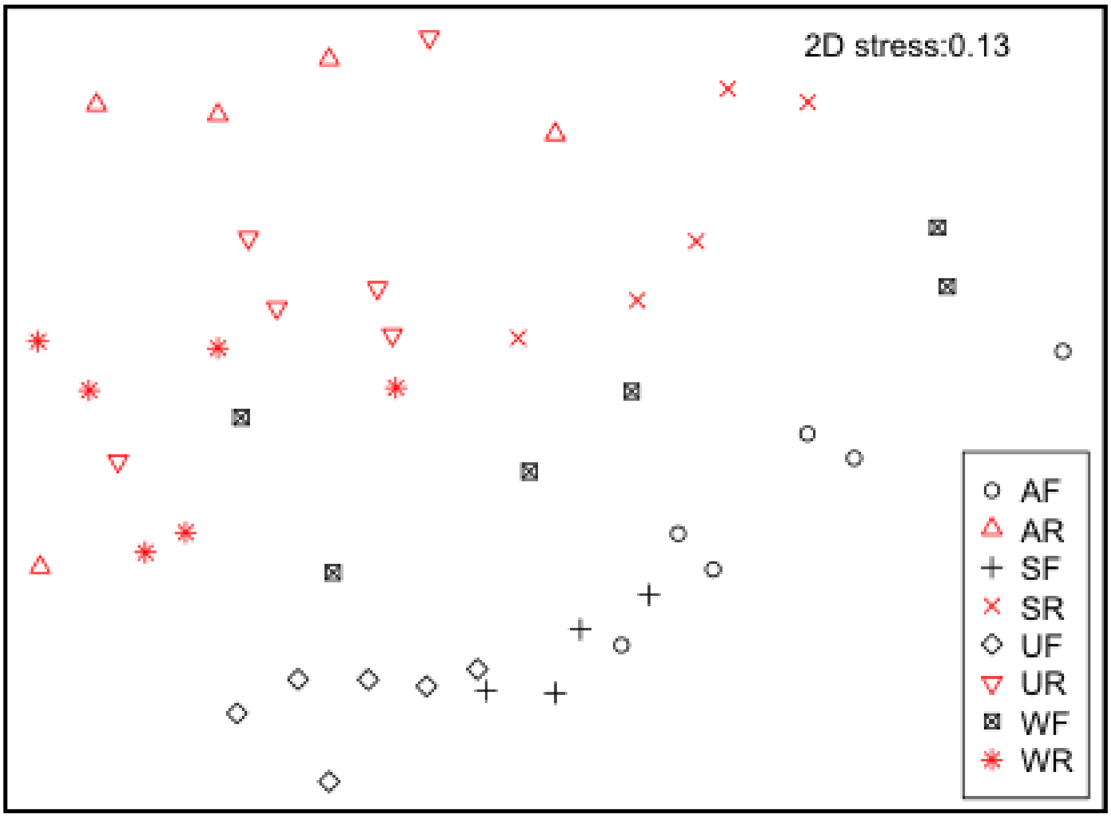

Figure 3.2 MDS analysis on the Bray Curtis Similarity matrix for Filey (F) and Ravenscar (R) in seasons; winter (W), spring (S), summer (U) and autumn (A). Samples from the FIley site are shown in black and those from the Ravenscar site in red.

Figure 3.2 shows a stress value of 0.13, suggesting an adequate representation of the communities (Clarke & Warwick, 2001) and, as illustrated, there are two distinct clusters of points, corresponding to the two different sample sites and this was reflected in the significant difference in assemblage similarity between the two sites, across all seasons (ANOSIM, Global R=0.38, p=0.001). There was also a significant difference in overall assemblage similarity between seasons (ANOSIM, Global R=0.172, p<0.05) with the exception of spring and autumn. These two seasons were not significantly different (ANOSIM, R statistic=-0.008, p=0.43) due to the influence of the Filey site on those seasons (ANOSIM, R statistic=0.155, p=0.129). In contrast, Ravenscar spring and autumn communities were significantly different (ANOSIM, R statistic=0.388, p=0.024). Thus it can be determined that there was an overall significant difference in assemblage similarity between sites and season but this was not always true in single-site samples such as Filey.

Across all seasons, two taxa accounted for the 50.75% similarity between the Filey samples; Oligochaete sp. had an average abundance of 133.14 and contributed 77.29% to the overall similarity followed by *Littorina littorea* with average abundance of 12.59, contributing 9.41%.

The same two taxa accounted for 46.22% of similarity between Ravenscar samples across all seasons, with Oligochaete sp. contributing 32.56% of the overall similarity (average abundance= 60.77) and *L. littorea* with 13.66% (average abundance, 26.86). An additional species contributing to assemblage similarity at Ravenscar was *Modiolus modiolus* with an average abundance of 21.68 and contributing 11.24% towards similarity. Oligochaete sp. provided 37.85% of the dissimilarity between the Filey (average abundance, 133.14) and Ravenscar (average abundance, 60.77) samples across all seasons.

Table 3.4 Average percentage similarity of communities within seasons, with major contributing taxa abundance and percentage contribution towards overall similarity. Where contribution of taxa was less than 10%, only <10% is displayed

Season	Spring	Summer	Autumn	Winter
Overall similarity	46.52%	49.11%	38.51%	49.78%
Oligochaete sp.	90.00 (72.28%)	155.33 (63.06%)	60.64 (47.34%)	77.08 (41.52%)
L. littorea	< 10%	22.08 (12.37%)	14.00 (19.56%)	32.67 (12.75%)
M. modiolus	<10%	31.42 (11.24%)	<10%	29.50 (15.63%)

Table 3.4 shows that samples from individual seasons had a comparable overall similarity within season, with Oligochaete sp. having the highest abundance and being the highest contributors to overall similarity in each season. The next highest contributor was *L. littorea* in summer and autumn, unlike in winter where *M. modiolus* was the second highest contributor.

Table 3.5 SIMPER results for contributory taxa to the dissimilarity between seasons and the percentage contribution of each taxa. Only taxa with >10% contributions were included. Ave. diss denotes the average percentage dissimilarity between seasons.

	Spring	Summer	Autumn
Winter	Ave. Diss. – **60.02** Oligochaete sp. (31.72) *M. modiolus* (11.42) *L. littorea* (11.23)	Ave. diss. – **57.06** Oligochaete sp. (39.20) *M. modiolus* (10.19)	Ave. diss. – **61.46** Oligochaete sp. (26.35) *M. modiolus* (11.30) *L. littorea* (10.22)
Spring		Ave. diss. – **58.05** Oligochaete sp. (46.96) *M. modiolus* (11.87)	Ave. diss. – **58.50** Oligochaete sp. (42.80)
Summer			Ave. diss. – **61.63** Oligochaete sp. (45.95) *M. modiolus* (10.95)

Table 3.5 displays the percentage contribution towards dissimilarity between seasons across both sites. The relative abundance of Oligochaete sp. was the highest contributor to dissimilarity between samples, with *M. modiolus* being the second highest contributor, where the contribution to dissimilarity was less than 10%. The third highest contributor was always *L. littorea*, in all season comparisons (Table 3.5).

In the Filey samples across all seasons, a higher proportion of the assemblage was accounted for by a few dominant species, notably Oligochaete sp. (Table 3.5). At Ravenscar, however dominance was spread across more species, the percentage contribution by most dominant species being comparatively lower than the same species at Filey. This was supported by the SIMPER outcomes, which showed that *M. modiolus* was a higher contributor to similarity at Ravenscar (11.24%) than at Filey (<10%).

3.3.2 Assemblage variation with a feeding function approach

Illustrated by Figure 3.3, there was a higher average diversity of feeding functional groups at Ravenscar than at Filey.

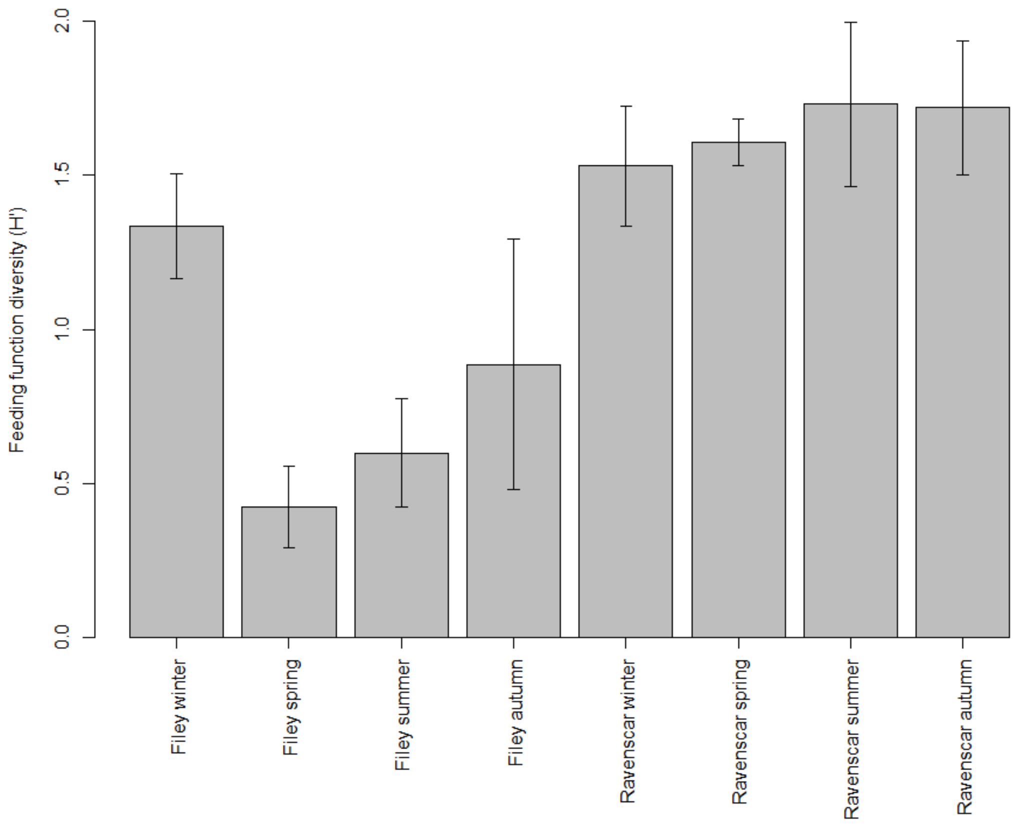

Figure 3.3. Mean (+/-SD) feeding functional group diversity (Shannon Weiner H') by site and season

Feeding function diversity was significantly higher at Ravenscar (mean=1.646 s.d.+/-0.132) than Filey (mean=0.846 s.d.+/-0.393) (ANOVA, $F_{3,47}$=281.51, P<0.0001). However, there was no significant difference in mean feeding function diversity by season (Table 3.6) (ANOVA, $F_{3,47}$=0.7168, P=0.54).

Table 3.6 Results of a two-way ANOVA using GLM to determine the effects of SITE and SEASON on feeding function diversity (Shannon Weiner H').

Source	Df	Adjusted MS	F	P
Site	1	7.6529	281.5110	<0.001
Season	3	0.1597	0.7168	0.5469
Site*Season	3	0.5498	20.2258	<0.001
Error	43	0.0272		

There was, however, a significant interaction between SITE and SEASON (Table 3.6), indicating that the effect of season on feeding functional diversity varied between sites, as also illustrated in Figure 3.4. Feeding function diversity was significantly higher at Ravenscar during spring (mean=1.608 +/-0.068), summer (mean=1.731 +/-0.090) and autumn (mean=1.719 +/-0.130) than at Filey during the same periods (spring mean=0.423 +/-0.113; summer mean=0.598 +/-0.173; autumn mean=0.886 +/-0.299). Feeding function diversity at Filey alone was higher during winter (mean=1.334 +/-0.133) than in other seasons at the same site (in all cases, P<0.05). Conversely, there was no significant difference in diversity by season at the Ravenscar site (in all cases, P>0.05).

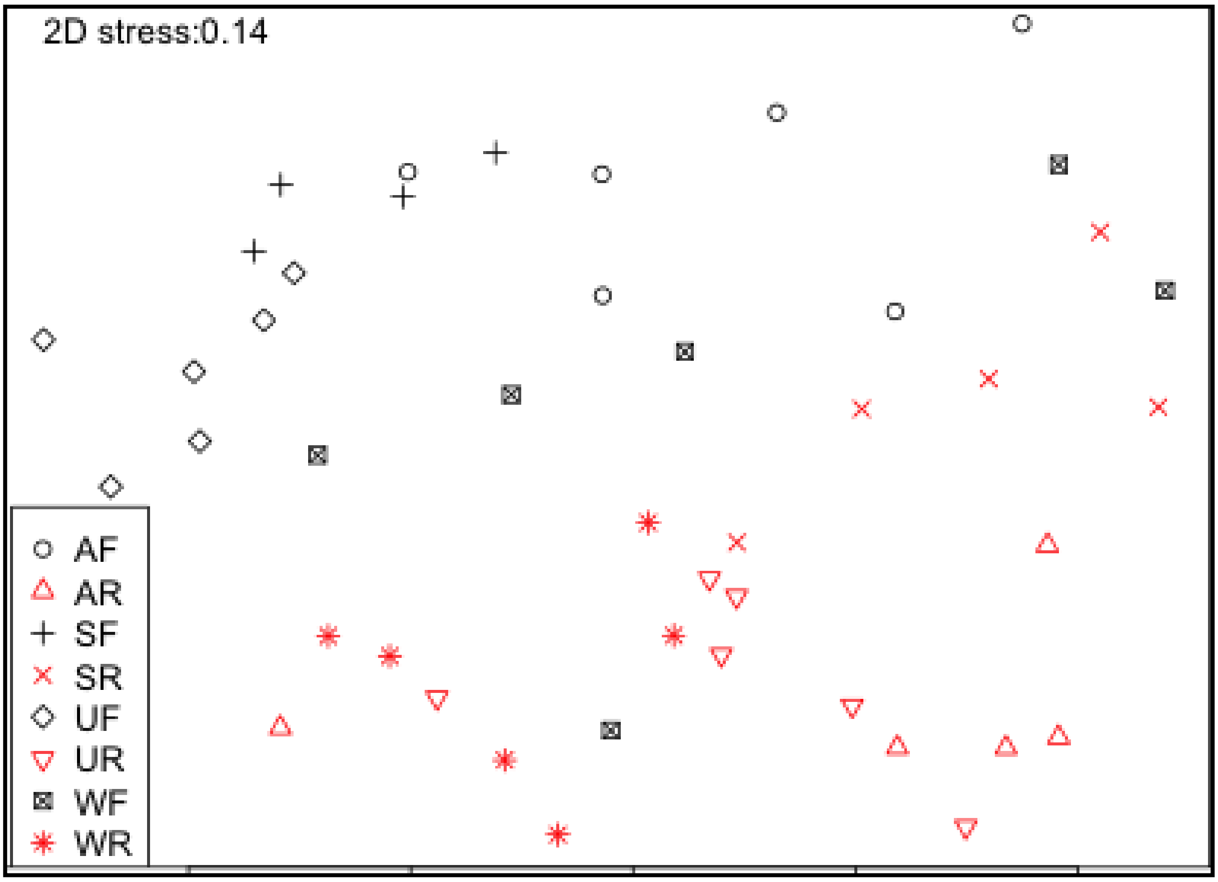

Figure 3.4 nMDS analysis on Bray-Curtis similarity matrix for feeding function by site and season. Legend abbreviations are explained in Figure 3.2

Figure 3.4 shows results of MDS analysis for each season at each site, showing noticeable clustering by site but there was no clear separation between seasons across the sites, suggesting that, overall, communities were not apparently distinct between seasons. However, within each site there was some degree of clustering by season suggesting site-specific variation. The stress value of 0.14 suggests that this was an adequate representation of the similarity between the samples (Clarke & Warwick, 2001).

There was a significant difference in feeding function assemblage similarity between the different sample sites, Filey and Ravenscar (ANOSIM, Global R=0.521, P=0.029). There was also a significant difference in feeding function assemblage similarity between the different sample seasons; winter, spring, summer and autumn (ANOSIM, Global R=0.402, P=0.001). Pairwise comparison of the seasons confirmed the functional communities were significantly different between all seasons (P<0.05).

Two feeding functions accounted for 85.94% of the 66.71% overall similarity between the Filey samples. Detritivores had the highest abundance with 138.55 and contributed to 73.57% of similarity between the samples. Grazer-detritivores had the next highest abundance with 17.91, contributing to 12.37% of the similarity between samples at the Filey site. At Ravenscar, four feeding functions accounted for 90.68% of the 59.80% overall similarity between samples. Detritivores had the highest abundance (53.55) and contributed to 30.07% of the sample similarity. Grazer-detritivores (abundance=40.48) and grazers (abundance=28.97) contributed 23.54% and 20.09% to the sample similarity, respectively. Active suspension feeders had an average abundance of 26.79 and contributed to 16.99% of the similarity between samples.

Table 3.7 Feeding functions contributing towards the 61.18% dissimilarity between the Filey and Ravenscar samples

Feeding function	Average abundance at Filey	Average abundance at Ravenscar	% contribution to dissimilarity between sites
Detritivore	138.55	53.55	56.15
Grazer-Detritivore	17.91	40.48	12.52
Grazer	1.91	28.97	12.39

Table 3.7 displays the feeding functions providing the highest contribution to the average dissimilarity (61.18%) between the Filey and Ravenscar samples. Detritivores were far more abundant at Filey than Ravenscar, although the abundances of Grazer-Detritivores and Grazers were much higher at Ravenscar than at Filey.

Table 3.8 Average percentage similarity of communities within seasons, with major contributing feeding function abundance and percentage contribution towards overall similarity. Where contribution was less than 10%, only <10% is displayed

Season	Spring	Summer	Autumn	Winter
Overall similarity	57.06%	74.20%	60.45%	63.17%
Detritivore	55.88 (39.68%)	159.33 (58.51%)	64.45 (47.90%)	90.50 (39.30%)
Grazer	9.38 (20.54%)	<10%	<10%	30.75 (11.26%)
Grazer-detritivore	12.56 (18.66%)	32.50 (15.73%)	39.09 (26.40%)	45.58 (20.95%)
Active suspension feeder	8.31 (16.13%)	<10%	<10%	45.58 (19.79%)

Table 3.8 shows that samples from individual seasons had a comparable overall similarity within season. Detritivores were consistently the highest contributors to overall similarity in each season. Grazer-detritivores were the next highest contributors in all seasons with the exception of spring, when grazers replaced the group.

Table 3.9 SIMPER results for contributory feeding functional groups to the dissimilarity between seasons and the percentage contribution of each feeding function. Only feeding functions with >10% contributions were included. Ave. diss denotes the average percentage dissimilarity between seasons.

	Spring	Summer	Autumn
Winter	Ave. Diss. – **62.25** Detritivore (38.37) Grazer-Detritivore (21.27) Active suspension feeder (17.86) Grazer (14.79)	Ave. diss. – **43.59** Detritivore (55.96) Grazer-detritivore (14.92)	Ave. diss. – **45.80** Detritivore (43.57) Active suspension feeder (64.37) Grazer-detritivore (78.90)
Spring		Ave. diss. – **52.59** Detritivore (32.62) Grazer-detritivore (19.30) Active suspension feeder (15.19) Grazer (13.61)	Ave. diss. – **53.05** Detritivore (33.15) Grazer-detritivore (56.34) Grazer (68.08) Active suspension feeder (79.27) Predator-detritivore (89.58)
Summer			Ave. diss. – **46.87** Detritivore (63.79) Active suspension feeder (12.85)

Table 3.9 displays the percentage contribution towards dissimilarity between seasons across both sites. The relative abundance of detritivores was the highest contributor to dissimilarity between seasons, with grazer-detritivores and active suspension feeders often being the second highest contributors. Grazers and predator-detritivores were also significant contributors to overall dissimilarity between some seasons (Table 3.9).

3.3.3 Assemblage variation with a reproductive mode function approach

There was a higher mean diversity of reproductive mode at Ravenscar than at Filey, as shown by Figure 3.5. Reproductive mode diversity was significantly higher at Ravenscar (mean=1.069 +/-0.139) than Filey (mean=0.752 +/-0.329) (ANOVA, $F_{3,47}$=327.108, P<0.0001) and there was also a significant difference in mean reproductive mode diversity by season (Table 3.13) (ANOVA, $F_{3,47}$=13.464, P<0.0001).

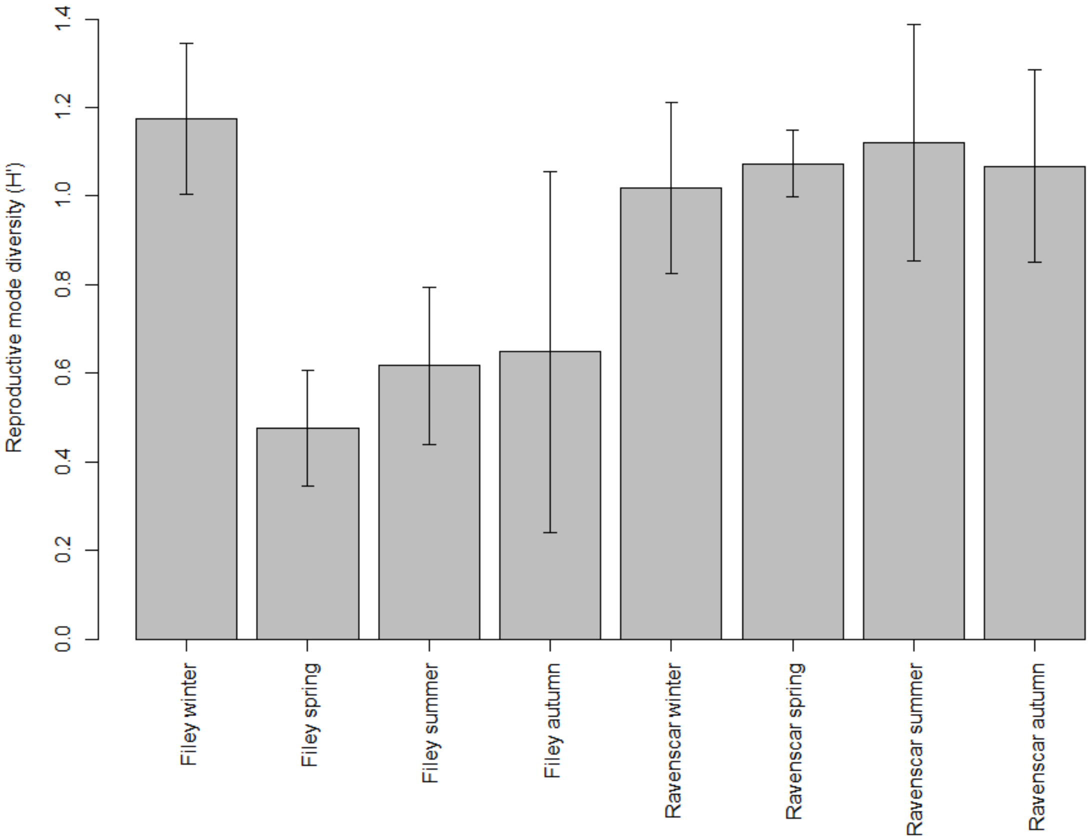

Figure 3.5 Mean (+/-SD) reproductive mode diversity (Shannon Weiner H') by site and season

There was also a significant interaction between site and season (Table 3.10), indicating that the effect of season on reproductive mode diversity varied by site. Reproductive mode diversity was significantly higher at Ravenscar during spring (mean=2.167, s.d.=0.075), summer (mean=2.422, s.d.=0.266) and autumn (mean=2.554, s.d.=0.217) than at Filey during the same period (spring mean=0.450, s.d.=0.131; summer mean=0.633, s.d.=0.177; autumn mean=1.136, s.d.=0.408).

Table 3.10 Results of a two-way ANOVA using GLM to determine the effects of Site and Season on reproductive mode diversity (Shannon Weiner H').

Source	Df	Adjusted MS	F	P
Site	1	17.6085	327.108	<0.001
Season	3	0.7248	13.464	<0.001
Site*Season	3	1.4209	26.395	<0.001
Error	36	0.0538		

Reproductive mode diversity at Filey alone was higher during winter (mean=1.844, s.d.=0.171) than in other seasons at the same site (in all cases, P<0.001). Additionally, at Filey, diversity was significantly higher in spring and summer than in autumn (in both cases, P<0.05). However, there was no significant difference in reproductive mode diversity by season at the Ravenscar site (in all cases, P>0.05).

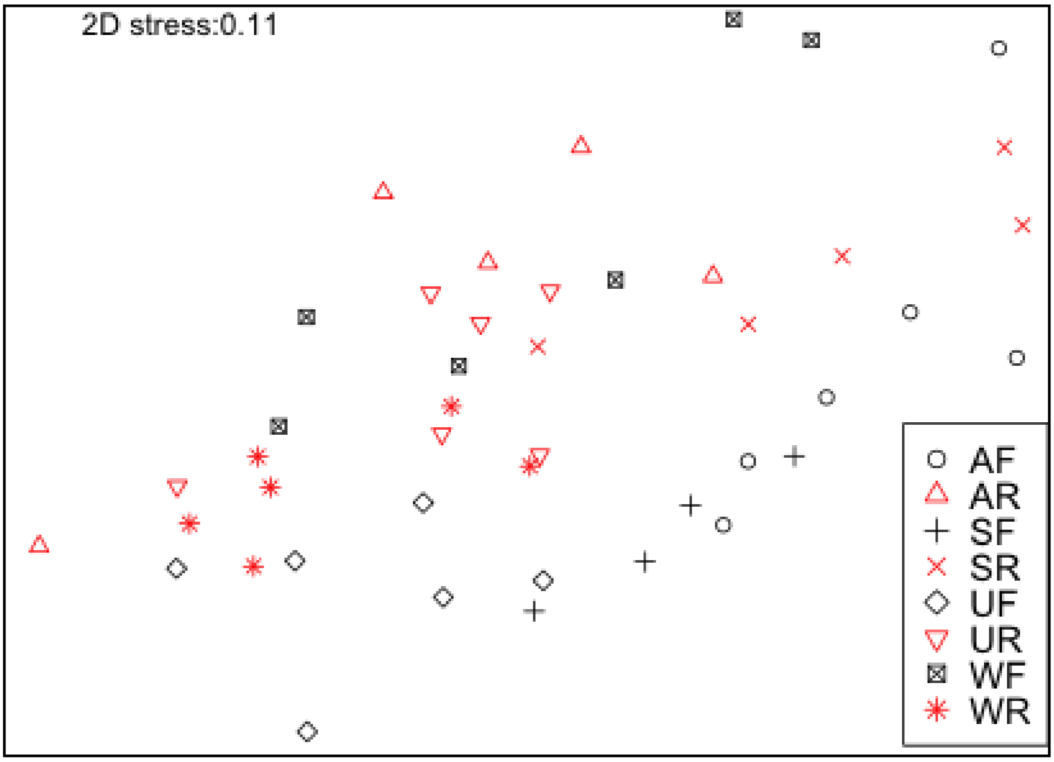

Figure 3.6 MultiDimensional Scaling analysis on a Bray-Curtis similarity matrix for reproductive mode by site and season. Legend abbreviations are explained in Figure 3.2

Figure 3.6 displays the results of MDS analysis on a Bray-Curtis similarity matrix for reproductive mode at the Filey and Ravenscar sites, with two relatively distinct clusters; matching the sites of sample collection. Distinct clustering was also somewhat evident between the seasons, suggesting a degree of dissimilarity between seasons. This indicates that the communities were partly distinct between Filey and Ravenscar. A stress value of 0.11 suggests that this was an adequate representation of the similarity between the samples (Clarke & Warwick, 2001).

There was a significant difference in reproductive mode similarity between the two sites (ANOSIM, Global R=0.065, P<0.05). Two reproductive mode mechanisms accounted for 94.45% of the 68.80% overall similarity within the Filey samples. Benthic dispersal had an average abundance of 153.95 and contributed to 81.94% of the overall sample similarity. Planktonic dispersal had an average abundance of 27.95 and contributed 12.51% to the overall similarity. The same two dispersal mechanisms accounted for 90.42% of the 73.44% overall similarity between Ravenscar samples. At Ravenscar, benthic dispersal had an average abundance of 146.50, contributing 68.46% and planktonic had an average abundance of 47.91 and contributed to 21.96% of the overall similarity between samples.

Table 3.11 Reproductive mode mechanisms contributing towards the 40.40% dissimilarity between the Filey and Ravenscar samples

Reproductive mode	Average abundance at Filey	Average abundance at Ravenscar	% contribution to dissimilarity between sites
Benthic	153.95	146.50	67.44
Planktonic	27.95	47.91	21.63
Brooding	8.71	23.14	10.89

Table 3.11 illustrates the reproductive mode mechanisms, which provide the highest contribution to the 40.40% average dissimilarity between Filey, and Ravenscar *M. edulis* patch samples. Benthic dispersal was slightly higher in the

Filey samples but planktonic and brooding mechanisms were far more abundant at Ravenscar than Filey.

There was also a significant difference in reproductive mode similarity between the different seasons (ANOSIM, Global R=0.279, P<0.01). Pairwise comparison of the seasons confirmed that all seasons were significantly different (P<0.05).

Table 3.12 Average percentage similarity of communities within seasons, with major contributing reproductive mode function abundance and percentage contribution towards overall similarity. Where contribution was less than 10%, only <10% is displayed

Season	Spring	Summer	Autumn	Winter
Overall similarity	64.29%	70.54%	60.46%	64.11%
Benthic	113.00 (87.28%)	207.08 (80.55%)	112.18 (78.02%)	153.17 (64.19%)
Planktonic	11.56 (7.84%)	44.83 (14.55%)	<10%	62.50 (28.96%)
Brooding	<10%	<10%	21.55 (12.19%)	<10%

Table 3.12 shows that samples from individual seasons had relatively similar overall similarity of reproductive mode function within season. The benthic functional group always the highest contributors to overall similarity in each season. Planktonic dispersers were the second highest contributors in all seasons,

except for in autumn samples when the brooding functional group was highest after the benthic functional group.

Table 3.13 SIMPER results for contributory reproductive mode functional groups to the dissimilarity between seasons and the percentage contribution of each reproductive mode function. Only functional groups with >10% contributions were included. Ave. diss denotes the average percentage dissimilarity between seasons.

	Spring	Summer	Autumn
Winter	Ave. Diss. – **41.87** Benthic (59.80) Planktonic (32.51)	Ave. diss. – **33.42** Benthic (68.28) Planktonic (1.50)	Ave. diss. – **43.22** Benthic (61.23) Planktonic (29.07)
Spring		Ave. diss. – **40.48** Benthic (67.44) Planktonic (22.88)	Ave. diss. – **37.15** Benthic (65.51) Planktonic (18.37) Brooding (16.12)
Summer			Ave. diss. – **43.51** Benthic (70.14) Planktonic (19.89)

Table 3.13 displays the percentage contribution towards dissimilarity of reproductive mode function between seasons across both sites. The average dissimilarity was relatively similar across all seasonal comparisons. Benthic dispersal was the highest contributing functional group to dissimilarity between seasons, with the planktonic functional group being the second highest contributor in all comparisons. The brooding functional group was only a significant

contributor to dissimilarity between spring and autumn communities, as shown in Table 3.13.

3.3.4 Comparison of approaches

Figure 3.7 displays a scatter plot of species diversity (x-axis) against feeding function diversity (y-axis), the points separated according to site. As shown in the figure, there was an overall increased feeding function diversity as species diversity increased, at both sites.

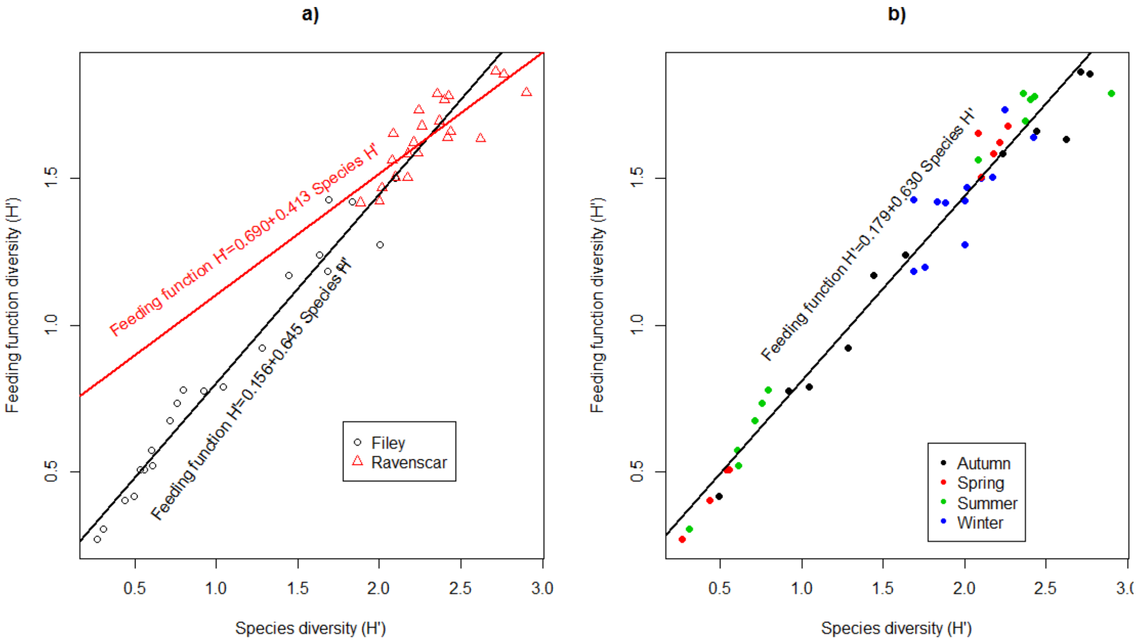

Figure 3.7 Scatterplots for species diversity (H') (x-axis) and feeding function diversity (H') (y-axis) at a) two sample sites (across all seasons) and b) four seasons (across both sites)

The positive relationship was significant at both Filey (Spearman Rank, r=0.984, df=20, P<0.001) and Ravenscar (Spearman Rank, r=0.0.843, df=20, P<0.001). There was a significant relationship determined by Method of Least Squares Regression at Filey (Regression ANOVA, $F_{1,20}$=476.5, P<0.001) and Ravenscar (Regression ANOVA, $F_{1,20}$=40.9, P<0.001). The equation for the line of fit at Ravenscar was feeding function diversity (H') = 0.690 + 0.413 species diversity (H') which accounted for 65.52% (R^2) of the variation in the y variable. The equation for the line of fit through the Filey points, accounting for 95.77% of the y variable variation, was feeding function diversity (H')= 0.157 + 0.645 species diversity (H').

Table 3.14: Significant results of Regression ANOVA for feeding function diversity (FF) and species diversity (Sp) at each season

Season	Regression ANOVA			
	F	P	R^2 (%)	Equation of line
Winter	16.83	0.002	59.01	FF 1.115 + 0.386 Sp
Spring	1310	<0.001	99.39	FF 1.440 – 0.153 Sp
Summer	408.4	<0.001	97.37	FF 1.564 – 0.293 Sp
Autumn	448.7	<0.001	97.82	FF 1.627 - 0.277 Sp

Table 3.14 shows there were significant positive relationships between feeding function diversity and species diversity in samples from all seasons. As shown in Figure 3.8, there was an overall increased feeding function diversity as species diversity increased, at both sites, although when divided into seasons, all seasons except winter follow a positive trend.

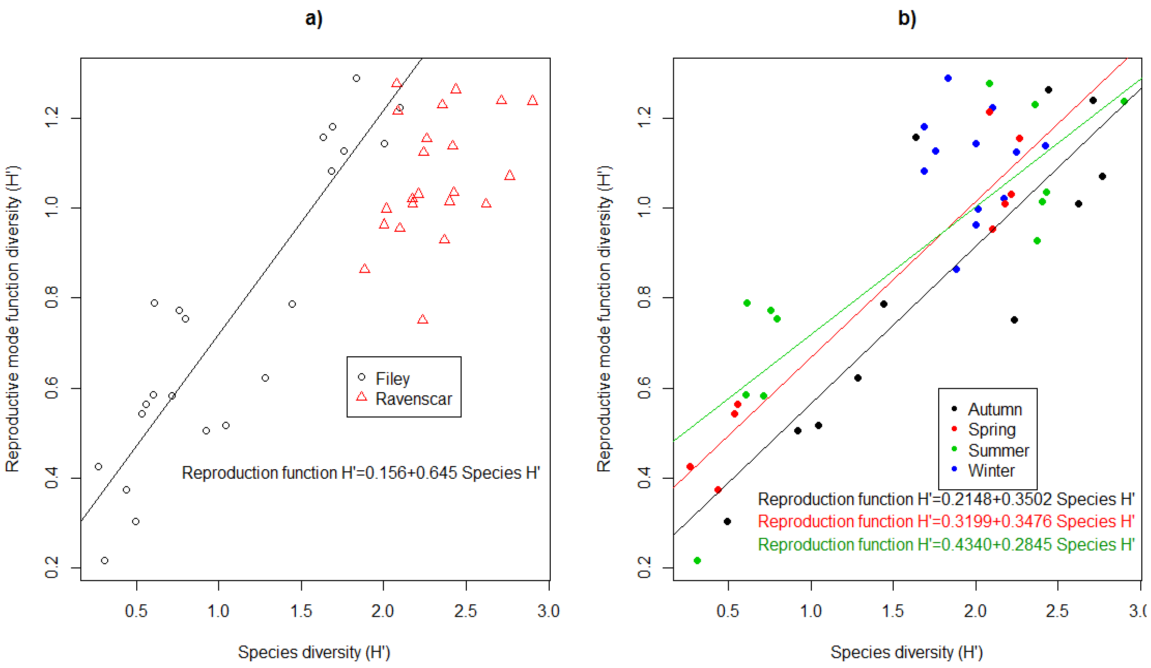

Figure 3.8 Scatterplots for species diversity (H’) (x-axis) and reproductive mode diversity (H’) (y-axis) at a) two sample sites (across all seasons) and b) four seasons (across both sites). Only sites/seasons with significant regression results are shown as lines.

Only samples from Filey showed a significant positive relationship (Spearman Rank, r=0.870, df=20, P<0.001) whereas the relationship between reproductive mode diversity and species diversity was not significant at Ravenscar (Spearman Rank, r=0.411, df=20, P>0.05). At Filey, determined by Method of Least Squares Regression (Regression ANOVA, $F_{1,20}$=108, P<0.001), the equation of the line was feeding function diversity (H’)= 0.033 + 0.461 species diversity (H’) accounting for 83.59% (R^2) of the variation in the y variable.

Table 3.15 Significant results of Regression ANOVA for reproductive mode diversity (FF) and species diversity (Sp) at each season

Season	Regression ANOVA			
	F	P	R^2 (%)	Equation of line
Spring	53.55	<0.001	86.79	FF 0.085 + 0.311 Sp
Summer	25.64	<0.001	69.14	FF 0.211 + 0.269 Sp
Autumn	29.80	<0.001	74.22	FF 0.103 + 0.334 Sp

Table 3.15 shows there were significant positive relationships between reproductive mode diversity and species diversity in samples from all seasons (across both sites) except winter. There was no significant relationship between reproductive mode diversity and species diversity in winter (Pearson's Product Moment, r=-0.04, df=10, P=0.893).

The result of the 2nd-Stage MDS indicated a stronger correlation between the species level and the feeding function approach (test statistic=0.906) than between species and reproductive mode approach (test-statistic=0.683). A comparison of the similarity matrices at the two functional approaches generated a test statistic of 0.743.

3.4 Discussion

The results of species level analysis showed a higher diversity (H') at Ravenscar than Filey, linking with a difference in exposure between the two sites. The

Intermediate Disturbance Hypothesis (IDH) may explain this significant difference, where diversity is maximised where biological and physical disturbances are close to equilibrium (Connell, 1978; Roxburgh *et al*., 2004). This equilibrium may be closer at Ravenscar at a higher exposure than at Filey, supporting a higher diversity of species. This exposure may also influence the profile of mussel sizes within a habitat, with larger mussels often having a higher probability of being dislodged by wave action than smaller specimens (Seed, 1976; Tam & Scrosati, 2014). As larger mussels have the effect of increasing the amount of secondary substrate in patches (Dayton, 1971; Borthagaray & Carranza, 2007), the absence or reduction in abundance of these larger mussels may influence the habitat space available for infaunal species. A related effect of the removal of these larger mussels is the potential reduction in pseudofaeces deposition (Tsuchiya, 1980; Dahlback & Gunnarsson, 1981; Hatcher *et al.*, 1994; Ragnarsson & Raffaelli, 1999), reducing food resource availability for some infaunal species. As well as the reduction in larger mussel abundances, exposure may also lead to the removal or reduced deposition of sediment with increased water movement (Levinton, 1972; Prathep *et al*., 2003).

The combination of deposited sediment and mussel-generated pseudofaeces creates a nutritionally rich matrix for the infaunal assemblage (Seed, 1996; Borthagaray & Carranza, 2007) and so assemblage structure may be affected by variations in this resource availability resulting from different levels of physical disturbance and exposure. This may also be a key underlying factor behind the significant dissimilarity between the communities. It might be expected that where secondary space and biodeposition were more profuse, populations of organisms reliant on these factors might be higher (Commito *et al.*, 2005). Although Ravenscar had a significantly higher diversity, many of the species at Filey were present in much higher abundances than at Ravenscar. An example of this is the high abundance of Oligochaete sp., a group of organisms that are often extremely abundant in sediment-rich mussel beds (Commito, 1987; Borthagaray & Carranza, 2007), in Filey communities, but in considerably lower abundance at Ravenscar where sedimentation may be reduced due to exposure. This would appear to fit to the IDH trend that competitively superior species are often in extremely high abundances in low-disturbance areas while in highly disturbed areas only taxa tolerant to environmental and physical influences will succeed (Cornell, 1978; Lenz *et al.*, 2004). In the intermediate disturbance areas a balance between biotic (such as competition) and abiotic disturbances (such as wave exposure) maximizes diversity (Cornell, 1978; Dial & Roughgarden, 1998).

Although species diversity was not significantly different between seasons, this was shown not to be constant at both sites. The may be due to a more homogenous disturbance regime at Filey, thus creating a bias in the data and eclipsing the differences at Ravenscar. An alternative explanation, however, might be that at Filey the composition of the assemblage did change by season, but overall abundances of some species remained constant with only some species being replaced by others, thus not significantly affecting diversity as suggested by Connell & Slatyer (1977). What seasonal differences did exist may be due to a multitude of factors, including recruitment events, infrequent sediment deposition or an increase in organic matter following seasonal algal growth or similar episodes (Everett, 1991). Seasonal shift in assemblage composition was also found in other intertidal studies, including Holland & Polger (1976).

Results of analysis based on feeding function show that detritus feeders, grazers and a combination of the two dominate the mussel infaunal communities at both sites, and all seasons. This supports some of the findings of McQuaid & Branch (1985) and Bustamante & Branch (1996) who also found that grazers and detritivores were an important component of mussel infaunal communities. The patterns in feeding function diversity match those of species diversity, possibly due to similar effect of exposure and seasonal events. Exposure may affect the deposition of organic matter or influence epiphytic algal growth on mussels and so may directly influence the feeding structure of the assemblage (Santelices & Martínez, 1988; Tomanova *et al*., 2006). For example, a water movement-related reduction in biodeposition might reduce the availability of a food resource for detritivores (Commito, 1987; Bonsdorff & Pearson, 1999; Sundblad *et al*., 2014) and a variation in substrate available for epiphytic algal growth may alter the abundance of grazers (Bustamante & Branch, 1996a). Whilst Jenkins & Hartnoll (2001) found higher intertidal microalgal abundance in winter, possibly explaining the higher number of grazers shown in Table 3.8, they also found higher microalgal abundance on sheltered shores, a grazer pattern not replicated in Table 3.7. It is, however, unclear whether this pattern in algal abundance change is reproduced in mussel bed epiphytic microalgae.

As with feeding function, reproductive mode diversity matched the pattern established at a species level with a significant difference between sites. This may be related to the exposure factor driving the species diversity difference. Current eddying, water transport and rugosity (at a range of scales) are important influences on larvae retention (Gaines & Bertness, 1992; Cowen & Sponaugle, 2009), and are often closely tied in to site exposure. These processes may result in clustering at local scales, an important determinant of assemblage structure (Webb *et al*., 2009). Exposure may also have indirect effects on larval recruitment by affecting biological structures such as sublittoral kelp beds, which may act as "filters" on planktonic larval flows (Fairweather, 1991). Localised disturbance can also create ecological space at a variety of intervals, both periodic and random, often leaving areas at different successional stages depending on the temporal and spatial occurrence of the disturbance event (Lubchenco & Menge, 1978; Sousa, 1984; Farrell, 1991).

The lack of significant correlation between species and reproductive mode was unexpected, considering the increased likelihood of correlation with fewer groups (Fowler *et al*., 1998). However, the lack of a significant relationship between species and reproductive mode across all seasons and in the isolated Ravenscar samples, and weaker correlation result in 2nd Stage MDS may have several explanations. The duration, method and timing of reproduction events is an important factor in dispersal (Günther, 1992). The field of supply-side ecology has demonstrated that while larval supply is undoubtedly important in maintaining marine populations, the mechanisms by which adult assemblage structure is influenced by this supply are complex and not fully understood (Underwood & Fairweather, 1989; Fairweather, 1991). For example, it is widely accepted that not all species in marine habitats reproduce at the same time, and also that the duration of the planktonic phase is not equal across taxa (Fairweather, 1991; Pulfrich, 1996; Grantham *et al*., 2003; Cowen & Sponaugle, 2009). It is also possible that reproductive mode alone is not the key biological determinant of distribution and structure in an assemblage as other factors such as adult mobility, lifespan and migration events may also be important (Underwood & Fairweather, 1989; Clarke *et al*., 2006a; Christie *et al*., 2009; Buckley & Freckleton, 2010). These adult behaviours and traits complicate patterns based on juvenile dispersal, as experienced by many assemblage ecologists (Menge, 1991). Such multispecies larval recruitment studies are often hindered by complexities in the fluid medium and adult stages (Sale *et al*., 2006; Webb *et al*., 2009).

The results of correlation tests suggest that the feeding function approach is more representative of the structure of infaunal communities within *M. edulis* patches than one based on reproductive mode (the latter showing no significant correlation at Ravenscar). Analysis also suggested that a combined feeding-offspring approach was less effective than the dominant feeding function approach alone, based on a weaker correlation between the variables than the feeding function approach alone. The evaluation of a combined functional approach based on this testing match the suggestion of Villéger *et al*. (2008) that success of a functional grouping approach in ecological study depends greatly upon the trait selected. The success and widespread use of a feeding function grouping approach in freshwater habitats (Cummins, 1973; Cummins & Klug, 1979; Vannote *et al*., 1980; Jonsson & Malmqvist, 2003) and also in the rocky intertidal (McQuaid & Branch, 1985; Bustamante & Branch, 1996b), together with the results of this analysis suggests that feeding function is suitable non-taxonomic grouping method for studying assemblage structure.

The significant dissimilarity in feeding function between seasons may be attributed to changes in relative abundances of each group (Table 3.9), with certain groups (e.g. detritivores) remaining dominant regardless of season. Thus the results of the SIMPER analysis may be representing seasonal abundance change rather than a shift in feeding function dominance in the assemblage. However, the lack of distinction in feeding function between seasons in Figure 3.7, suggests other factors besides temporal variation may be important influences on assemblage structure. As suggested by Phillips *et al*. (1997), Roth & Wilson (1998) and Padilla & Allen (2000), while functional groupings may not explain the effects of environmental variables, such approaches may facilitate the identification of these key influences. This method is well established in linking macroalgal form to physical and biological disturbance (Dethier, 1994; Tomanova *et al*., 2006). This process often involves studying assemblage changes along environmental gradients such as emersion time and grazing pressures either under natural conditions or artificially replicated (Dethier, 1994). Having established the effects of such factors, Littler & Littler (1984) demonstrated that it is possible to predict assemblage change, an important ecological tool (Dayton, 1971). As one goal of functional analysis may be to detect heterogeneity at biogeographical scales (Steneck & Dethier, 1994; Bonsdorff & Pearson, 1999; Zacharias & Roff, 2001), it is essential that the feeding function approach be tested at broader spatial scales. Additionally, determining the environmental variables that are significant in determining community structure were useful to quantify, in order to understand spatial patterns of heterogeneity in intertidal mussel bed infaunal assemblages.

Chapter 4 – How do infaunal assemblage patterns vary at large biogeographical scales and what drives them?

4.1. Introduction

Connectivity between habitats within the marine environment is often considered to be higher than that in terrestrial systems (Paine, 2010; Witman, 2013). This is often attributed to weaker physical barriers to larval and species dispersal (Engle & Summers, 1999), as well as large-scale mechanisms of movement such as oceanic currents (Riginos & Nachman, 2001; Heads, 2005). This connectivity may be the key factor behind the rarity of marine endemism in the northern hemisphere where the movement of species may be facilitated by a network of oceanic shelves (Golikov *et al*., 1990). Perhaps curiously, despite being part of the larger oceanic environment, intertidal habitats often show more restricted connectivity than neighbouring pelagic environments (Johnson, 2006). This may be attributed to the reality that intertidal habitats often exist only in a narrow coastal strip along landmasses, increasing the potential for fragmentation and heterogeneity (Engle & Summers, 1999; Sagarin & Gaines, 2002).

With the considerable habitat fragmentation and heterogeneity found in coastal habitats, it is important to differentiate between influences at regional and local scales. Broadly speaking, regional effects are those that exist at mesoscales such as oceanic topography and major oceanic currents and upwellings (Blanchette *et al*., 2008). Variables at these regional scales have significant influence on the geographic range of species by determining nutrient and larval flows as well as the availability of suitable physical space (Cornell & Lawton, 1992; Blanchette *et al.*, 2008). Local effects on diversity and richness tend to be a mixture of abiotic and biotic factors. At local scales, often within the same habitat, biotic processes such as predation and competition for resources become increasingly important in determining assemblage patterns (Golikov *et al.*, 1990; Cornell & Lawton, 1992; Briggs, 2007; Hoeinghaus *et al.*, 2007). However, the effects of these biotic factors may still be mitigated or even increased by localized environmental variations (Hoeinghaus *et al.*, 2007). So it may be considered that a regional species pool controls assemblage richness (Cornell & Lawton, 1992; Witman, 2013), the distribution and structure being affected at smaller scales by local variables (Ricklefs, 1987; Loreau, 2000; Wieters, 2001; Heads, 2005).

One consequence of the widespread regional species pool in the marine environment is that two areas may share similar species, but be so geographically distant that their communities are significantly dissimilar (Nekola & White, 1999; Lomolino, 2000). Decreasing similarity of environmental and biotic factors between habitats often drives this "distance decay" (Nekola & White, 1999). However, due to the significant effect on distance decay of the large dispersal ranges of many marine species (Nekola & White, 1999), the influence of environmental factors may play a more important role in assemblage dissimilarity. Local environmental influences may not only affect the abundance and richness of ecosystem engineers, but also the associated infaunal assemblage (Cole & McQuaid, 2010).

The bivalve *Mytilus edulis* is common on both hard and soft marine substrates and is extremely widespread in its geographical range (Seed, 1969; Jones *et al.*, 2009). It is a significant ecosystem engineer in northeastern Atlantic intertidal habitats, demonstrated by the inclusion of several mussel habitat categories under the Joint Nature Conservation Committee (Joint Nature Conservation Committee, 2011). As sessile invertebrates, they are subject to local and regional influences as are other species within the same habitat. However, as ecosystem engineers and a dominant organism in rocky intertidal zones, they contribute significantly to assemblage processes (Golikov *et al*., 1990), particularly with their infaunal assemblage. An important consideration in the UK intertidal zone is the reduction of fragmentation in some habitats such as rocky intertidal substrates as artificial groynes and sea defences are installed in coastal areas (Thompson *et al*., 2002). One opinion raised by Ricciardi & Bourget (1999) was that, at the time of publication, many intertidal studies had only used comparisons between shore pairs, where variations in environmental effects are often very large, with little transition ground. Thompson *et al*. (2002) also advocate the use of sites with different physical variables to predict future assemblage shifts in response to environmental change.

A number of studies, such as Bustamante & Branch (1996) and Ieno (2006) support the use of a functional or trait based approach to biogeographical studies. Using biological traits is advantageous as it can reveal patterns beyond species composition and offer insight into assemblage interactions and dynamics (Bustamante & Branch, 1996a, Tyler *et al*., 2012). However, some degree of caution must be adopted when choosing functional attributes or traits as a species' niche may change across its range, particularly with highly dispersed species (Paine, 2010). For example a species of mussel may dominate and fill one niche in one habitat despite having different feeding or morphological traits in another (Paine, 2010). It is therefore important to test the representativeness of a trait approach when applying it to a study of environmental variable effects.

While some biogeographic studies have been conducted in the marine environment, such as Pacific rocky shores (Sagarin & Gaines, 2002; Blanchette *et al*., 2008) and intertidal sediments (Kraan *et al*., 2009), many have been restricted to using literature metadata or have been limited to assemblage patterns rather than the important underlying variables (Blackburn & Gaston, 1998; 2001; Brown, 1999). It is important to consider both the distribution of species and the underlying variables driving them when investigation assemblage and habitat heterogeneity (Haila, 2002).

This study aims to investigate the effectiveness of a functional group approach to ecological study at a national (United Kingdom) scale biogeographical study of *M. edulis* infauna. The results of this approach will be compared against those of traditional species-level assemblage analysis. This study also aims to identify the key underlying environmental variables that cause heterogeneity between the sites and their effect upon the communities at a functional level. Determining the effect of such environmental variables is expected to facilitate the development of predictive models for functional assemblage structure in subsequent investigations.

4.2 Methods

4.2.1 Site descriptions

The intertidal sites selected for sampling were all situated on the mainland United Kingdom, as shown in Figure 4.1. Maps were generated using the 'maps' (http://cran.r-project.org/web/packages/maps) and 'mapproj' (http://cran.r-project.org/web/packages/mapproj/index.html) packages in R.

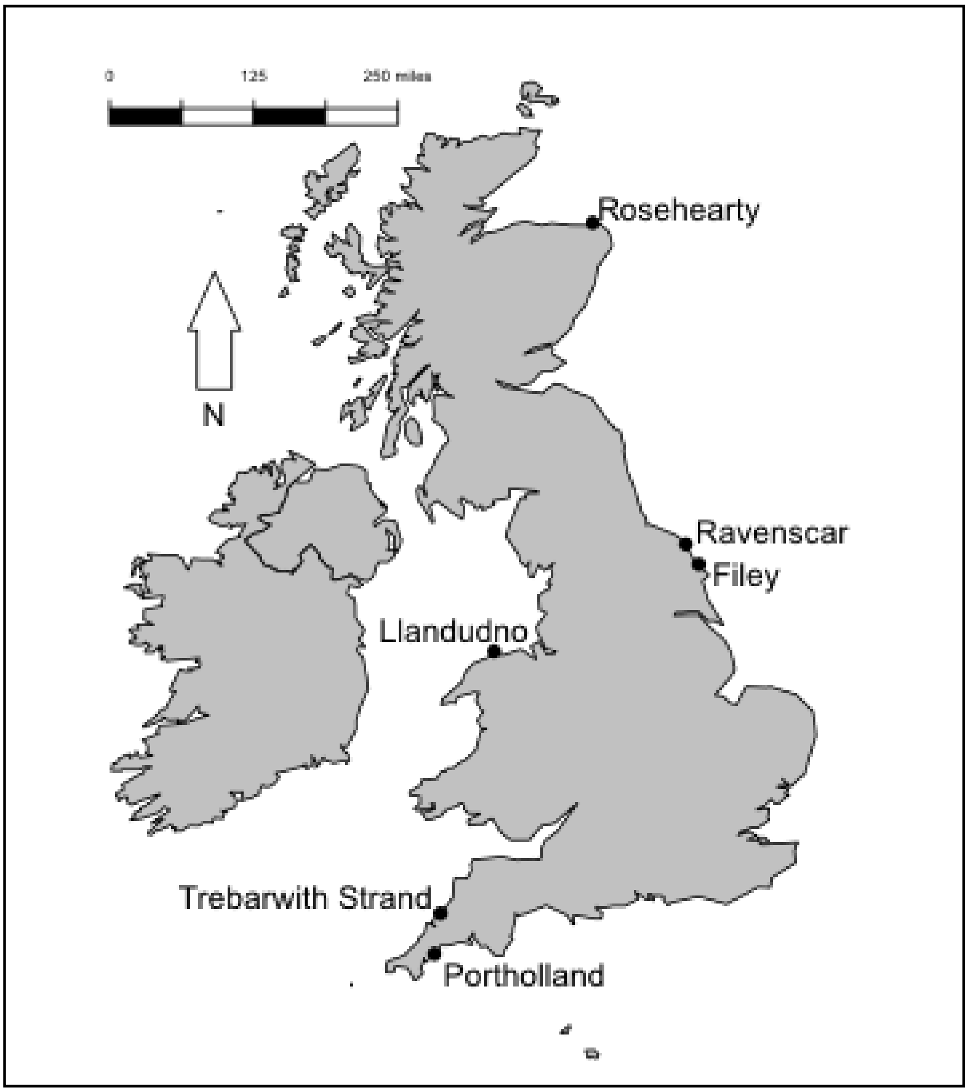

Figure 4.1: United Kingdom map with six intertidal *M. edulis* sampling sites

In order to investigate, as comprehensively as possible, the similarity or dissimilarity between mussel infaunal communities across the UK, sites were sampled on the north, south, east and west coasts. As described in Chapter 2, a key difference between the sites was the degree of wave exposure they were subject to, under standard conditions of tides and weather (Ballantine, 1961; Denny, 1995). This was categorized using the Baardseth Index (Dring, 1991; Ruuskanen *et al.,* 1999; Westerbom & Jattu, 2006), the sites ranging between 6 and 25 on the scale (scale maximum=40). The effectiveness of the Baardseth Index in intertidal studies was tested by Ruuskanen *et al.* (1999) and shown to be a consistent method of categorising exposure of sites. The approach places the site at the centre of a disc of 40 equal segments, the index score being the number of segments that are uninterrupted by islands, skerries etc. to a distance of 7.5km from the site (Ruuskanen *et al.,* 1999). All shores were selected as having a barnacle-mussel or fucoid-mussel mosaic, with *M. edulis* present in contiguous beds or in patch form. Sites were selected based on presence of intertidal *M. edulis* populations, sourced from anecdotal accounts and JNCC biotope maps (Joint Nature Conservation Committee, 2013).

Rosehearty, Aberdeenshire (Plate 2) (57° 41' 55" N; 2° 7' 28" E) was the most northerly and also the most exposed site, having a Baardseth Index of 25. It was a northeasterly facing site, mussel beds being present on the granite bedrock. The second "exposed" site was Ravenscar, North Yorkshire (54° 24' 34.9" N; 29' 31.9" W) that had a Baardseth Index of 20. The site was a rocky promontory with mussel beds at the furthest easterly point.

Both sites identified as "intermediate" were in the southwest of the UK. Trebarwith Strand, Cornwall (50° 38' 39" N; 4° 45' 45" E) had a Baardseth Index of 13, exposed to the northwest and Portholland, Cornwall (Plate 2) (50° 14' 10" N; 4° 51' 49" E) had a Baardseth Index of 11 and was exposed to the south.

Llandudno, Conwy (Plate 3) (53° 19' 48" N; 3° 49' 45" E) had a Baardseth Index of 8 and was an easterly-facing, intertidal site, sheltered to the west by a large limestone headland. The site with the lowest exposure was Filey, North Yorkshire (54° 13' 2" N; 16' 24.1" W); a site protected from the prevailing wave direction by a large rocky headland (Filey Brigg), with a Baardseth Index of 6. All sites had a median high water spring tide of between 4.5-5.9m above chart datum.

4.2.2 Sampling regime

All sampling took place at low tide during daylight hours in June 2013. Five replicate samples of 0.0625cm^2 quadrats were collected from within patches of *M. edulis*, at each site. This sample size was based on the results of optimal sample size study in Chapter 2. The collection and identification process was identical to that described in Chapter 2. The abundance of all infaunal taxa was recorded. The resources used for identification were Hayward and Ryland (1995) and various keys from the Synopses of the British Fauna (Appendix 1). A list of identified taxa is included in Appendix 2 and a list of sample codes in Appendix 3.

4.2.3 Environmental variables

The environmental variable of exposure (EXP) was calculated using the Baardseth Index (Dring,1991), The retained *M. edulis* from the samples were placed into size classes according to the length from the umbo to the posterior margin, the classes being; small (<14.99mm), medium (15-29.99mm) and large (>30mm). The numbers of each class present in each sample was then calculated as percentage of small (PSMALL), medium (PMEDIUM) and large (PLARGE) mussels of total mussels per sample.

In addition to exposure and *M. edulis* size classes other environmental variables were collected. During the extraction of the infaunal assemblage from samples, all sediment larger than 38 microns was retained; allowing sediment characteristics for each sample to be identified. The sediment was oven dried at a temperature of 100^{o}C (Bale & Kenny, 2005) for a period of 8 hours. The dried sediment was then passed through a series of sieves and graded according to the retaining mesh; medium sand (250 microns), fine sand (125 microns), very fine sand (63 microns) and coarse silt (38 microns), based on the Udden/Wentworth grain scale (Wentworth, 1922). The dry weight of each of these divisions per sample was measured using an electronic balance to an accuracy of 0.01g and divided by a factor of 1000 to provide the weight in kilograms. This dry weight was used to calculate the percentage of medium sand (PMED), fine sand (PFINE), very fine sand (PVFINE) and silt (PSILT) for the total dry sediment weight per sample.

Once the sediment profile was established the total organic sediment content per sample was determined by loss on ignition (LOI). The dried sediment was heated to 400°C for a period of 6 hours (Bale & Kenny, 2005) and, once cooled, the sediment from each sample was reweighed to 0.01g and again converted to kilograms. The organic content was calculated by subtracting the LOI weight (kg) from the original total dry weight (kg). The percentage of organic sediment content (PORG) was calculated as a proportion of the total sediment weight per sample.

4.2.4 Data analysis

4.2.4.1 Species approach

Shannon,-Weiner (H') indices were used to compare diversity between the six sites (Fowler *et al.*, 1998; Zar, 1999).

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

R is the total number of species (richness) while p_i is the abundance of each species (*i*). Shannon-Weiner was chosen as sampling area was equal in size from comparable populations and because the method considers measures of abundance and richness (Fowler *et al.*, 1998; Zar, 1999). Diversity indices generated Shannon-Weiner index (H') in the statistical package PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke & Warwick, 2001).

Diversity from samples conformed to a normal distribution (Kolmogorov Smirnov test, P>0.05). Variances could be considered equal for species diversity data (Levene's test, test statistic= 0.573, P>0.05) and species richness (Levene's test, test statistic= 3.376, P>0.05); therefore to test for significant differences between sites a parametric test was suitable (Fowler *et al.*, 1998). Analysis of Variance (ANOVA) was performed, accompanied by Tukey post-hoc testing to determine where a significant difference was present between individual sites (Clarke & Gorley, 2006).

The Bray-Curtis coefficient (in PRIMER) was used to calculate a similarity matrix (Clarke & Warwick, 2001), and the matrix used to visualise the similarity between sites using Multidimensional Scaling (MDS) (Clarke & Gorley, 2006). An Analysis of Similarity (ANOSIM) was used to statistically test the null hypothesis that there was no significant difference in similarity between different sites, (Clarke & Gorley, 2006). To identify which species were the main contributors towards assemblage similarity/dissimilarity between sites, a Similarity Percentages Routine (SIMPER) was used, with only species contributing <10% towards dissmiliarity being reported (Clarke & Gorley, 2006). Due to the lower resolution to which Oligochaetes were identified, they were included in multivariate analysis but their contributions are displayed in grey shades within tables.

4.2.4.2 Feeding function approach

Using the species list generated from all the sites, each species (or the lowest taxonomic group) was assigned a dominant feeding function, as described in Chapter 3 (Table 3.1). The key source of the feeding mode information was existing literature, including Hayward and Ryland (1995) and various publications from the Synopses of the British Fauna (Appendix 1). Feeding function was either sourced from dietry information in the publications or estimated using the form and mechanism of the organism mouthparts, limited by known dietary information from similar species in the same genera.

As with species level data, Shannon-Weiner diversity indices were applied to provide a measure of feeding function diversity (H') (Fowler *et al.*, 1998; Zar, 1999). Feeding function diversity both conformed to a normal distribution (Kolmogorov Smirnov test, P>0.05) and had equal variances (Levene's test, test statistic= 0.398, P>0.05). The data being normally distributed and having equal variances, a parametric test (ANOVA) to determine significant difference in feeding function diversity between sites was used, followed by Tukey post-hoc testing (Clarke & Gorley, 2006).

Following the data analysis methodology of the species data (Section 4.2.4.1), multivariate analysis for feeding function was the Bray-Curtis coefficient, MDS, ANOSIM and the SIMPER routine (Clarke & Gorley, 2006).

4.2.4.3 Comparison of approaches

As a primary test of the compatibility of species and functional approaches, the relationship between feeding function diversity (H’) and species diversity (H’) was explored. The data conformed to a normal distribution (Kolmogorov Smirnov test, $p>0.05$) and variances could be considered equal (Levene’s test, test statistic=0.717, $p>0.05$). As variances were equal and data normally distributed, parametric Pearson’s Product Moment correlation and Method of Least Squares Regression were used (Fowler *et al.*, 1998). The overall relationship between functional and species diversity was first tested, followed by further regression analysis for individual sites. The regression slopes were added to the scatterplot of species diversity (H’) against functional diversity (H’).

To statistically compare the similarity of the communities between the species and feeding function approaches, a 2nd-stage MDS was used to compare the two similarity matrices (Clarke & Warwick, 2001). The resulting test statistic indicated the strength of the correlation with values closer to 1 or -1 indicating a stronger correlation than those closer to zero (Clarke *et al.*, 2006).

4.2.4.4 Environmental variables

The environmental factors that were important in determining the feeding function structure of the communities were identified using Canonical Correspondence Analysis (CCA), as not only does CCA relate composition to measured environmental variables, but also performs effectively if there are multiple important environmental gradients affecting composition and works well with data sets where taxa are not evenly distributed (Palmer, 1993; Zuur *et al*., 2007). The CCA was also displayed using a triplot, the proximity of sites to the environmental variable arrows signifying the influence of such variables, and the length of arrows showing the overall influence of the environmental factor (Palmer, 1993; Zuur *et al*., 2007). Due to the increased likelihood of achieving an artificially significant result due to the multiple tests undertaken in the analysis, Bonferroni correction was applied, with the α set at 0.05 (Moran, 2003).

4.3 Results

4.3.1 Species approach

Figure 4.2 shows the species diversity (H') for each sampling site. The highest diversity (~1.4) was found at Portholland and Trebarwith Strand, the sites classified as intermediately exposed. Conversely, the lowest diversity pair (~0.75) was at the sheltered sites, Llandudno and Filey.

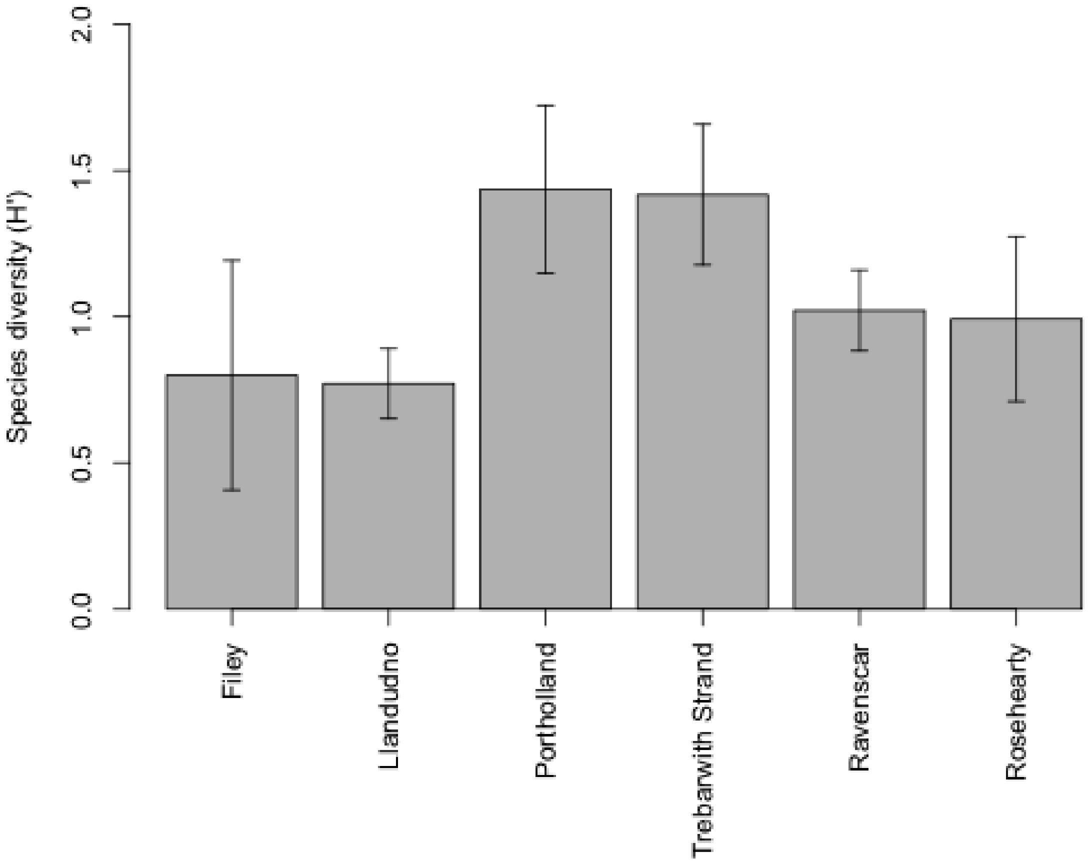

Figure 4.2: Species diversity (H') at six UK intertidal sample sites, order along the x-axis determined by increasing exposure of site

There was a significant difference in species diversity (H') between sites (ANOVA, $F_{5,24}$=6.258, P<0.001). Post-hoc testing (Tukey) indicated that diversity was significantly higher at both Portholland (mean=1.436, s.d.=0.288) and Trebarwith Strand (mean=1.417, s.d.=0.282) than at Llandudno (mean=0.771, s.d.=0.120) and Filey (mean=0.800, s.d.=0.392). There was no significant difference in species diversity between Ravenscar (mean=1.021, s.d.=0.240) or Rosehearty (mean=0.992, s.d.=0.138) and any other site (P>0.05).

There was a significant difference in mean species richness between sites (ANOVA, $F_{5,24}$=4.731, P<0.01). Mean species richness at Filey (mean=4.8, s.d.=0.836) was significantly lower than at Ravenscar (mean=10.6, s.d.=1.816), Portholland (mean=11.4, s.d.=3.131), Trebarwith Strand (mean=10.2, s.d.=2.049) and Rosehearty (mean=10.8, s.d.=3.962) (Tukey, P<0.05). There was no significant difference in species richness between Llandudno (mean=9.0, s.d.=1.871) and the other sites (Tukey, P>0.05).

Figure 4.3 illustrates the results of Multidimensional Scaling (MDS) of assemblage similarity between sites. There appears to be three groups, the sites being divided by exposure (sheltered, intermediate and exposed). The stress value of 0.07 suggests that Figure 4.3 is good representation of assemblage similarity (Clark & Warwick, 2001).

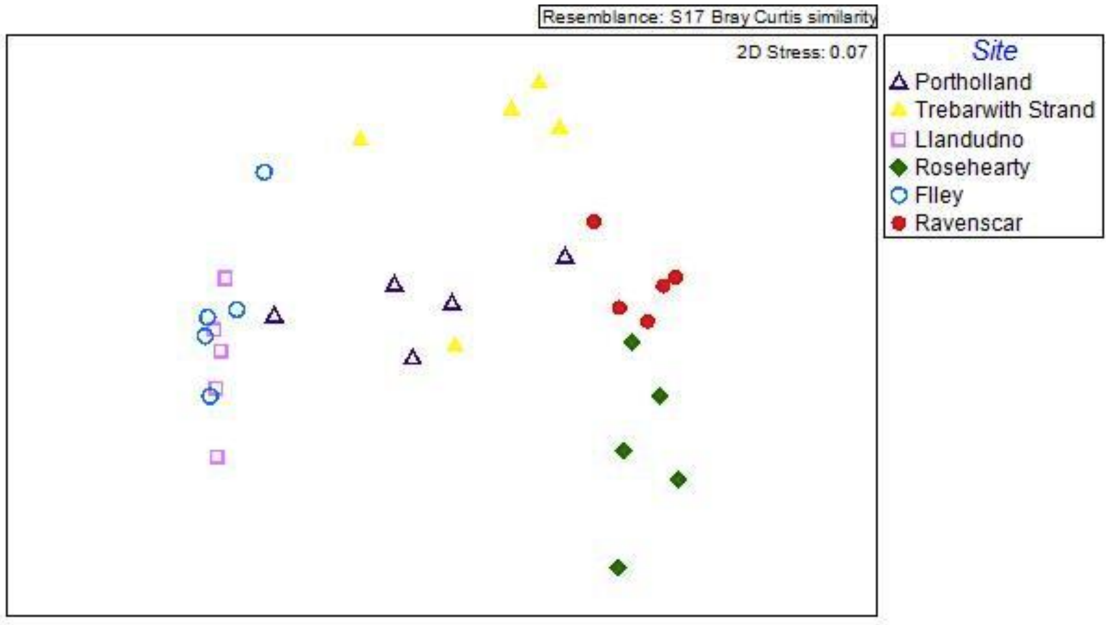

Figure 4.3: MDS plot for six UK intertidal mussel patch sites

There was a significant difference in assemblage similarity (ANOSIM, Global R= 0.742, P<0.05) between all pairwise site comparisons (P<0.05) except for that between the sheltered (Filey and Llandudno) sites (P>0.05).

Three taxa accounted for 86.49% of the overall 48.18% similarity between the samples from Portholland. Two key contributors were *Lasaea rubra* (average abundance= 68.80) and Oligochaete sp. (average abundance= 60.80), which contributed 35.67% and 34.17% respectively to the overall similarity. *Rissoa parva* has an average abundance of 49.40 and contributed 16.65%.

The 42.88% overall similarity between the Trebarwith Strand samples was mainly contributed by one species, *L. rubra* (average abundance= 55.80) with a 65.93% similarity contribution. Likewise, the 59.60% similarity between the Llandudno samples had one main contributing species, Oligochaete sp. (average abundance=147.20), which contributed 88.29% towards overall sample similarity.

There was a 53.06% overall similarity in the samples collected from Rosehearty. The highest contributor to this was *H. nilssoni*, which contributed 51.87% to overall similarity and had an average abundance of 415.60. One other species (*L. rubra*) had a very high average abundance of 687.00 and contributed 42.86%. The same two species contributed 94.37% to the 69.80% overall similarity between Ravenscar samples. At the Ravenscar site, *H. nilssoni* (average abundance= 152.80) contributed 67.42% and *L. rubra* (average abundance= 73.20) contributed 26.95% towards overall similarity.

Oligochaete sp. and *Littorina littorea* contributed a cumulative 93.35% to the overall 64.19% similarity between the Filey assemblage samples. Oligochaete sp. had an average abundance of 94.20 and contributed 76.60% while *L. littorea* had an average abundance of 15.20 and contributed 16.76% to overall sample similarity at Filey.

Site		Sheltered	Intermediate		Exposed	
		Filey	Portholland	Trebarwith Strand	Ravenscar	Rosehearty
Sheltered	Llandudno	40.10% Oligochaete (40.10)	66.46% Oligochaete (31.55) *L. rubra* (25.57) *R. parva* (17.09)	86.88% Oligochaete (54.40) *R. parva* (22.46)	95.96% *H. nilssoni* (38.05) *L. rubra* (18.16)	97.23% *L. rubra* (42.21) *H. nilssoni* (35.40) Oligochaete (14.20)
	Filey		64.80% *L. rubra* (29.65) Oligochaete (23.90) *R. parva* (20.13) *H. nilssoni* (10.89)	85.07% Oligochaete (44.43) *R. parva* (27.00)	95.71% *H. nilssoni* (42.36) Oligochaete (25.37) *L. rubra* (20.54)	96.54% *L. rubra* (44.59) *H. nilssoni* (37.60) Oligochaete (10.00)
Intermediate	Portholland			67.65% Oligochaete (25.82) *L. rubra* (24.84) *R. parva* (20.72) *H. nilssoni* (11.56)	67.85% *H. nilssoni* (40.24) Oligochaete (18.64) *L. rubra* (14.76) *R. parva* (14.10)	80.36% *L. rubra* (40.82) *H. nilssoni* (37.86)
	Trebarwith Strand				74.45% *H. nilssoni* (59.58) *R. parva* (20.19)	86.11% *L. rubra* (44.10) *H. nilssoni* (43.43)
Exposed	Ravenscar					57.53% *L. rubra* (55.28) *H. nilssoni* (32.30)

Table 4.1: SIMPER results for contributory taxa to the overall dissimilarity between each UK site pair (%) and the percentage contribution of each taxa. Only taxa with >10% contributions were included.

Table 4.1 shows the key contributors to the dissimilarity between the six sites, and the overall percentage dissimilarity between each site pair. One key comparison was Filey & Llandudno (average dissimilarity 40.10%) where the site was dominated by Oligochaetes with high average abundances at each (Llandudno=147.20, Filey=94.20). The more exposed sites of Ravenscar and Rosehearty (average dissimilarity = 57.5%) had similar infaunal communities with two taxa characteristic of the more exposed sites, *H. nilssoni* (Ravenscar=152.80, Rosehearty=415.60) and *L. rubra* (Ravenscar=73.20, Rosehearty=687.00). The intermediate shores of Portholland and Trebarwith Strand had communities with a similar composition to the exposed Ravenscar and Rosehearty but had higher numbers of Oligochaetes.

The results of the SIMPER analysis (Table 4.1) show clearly that there were four taxa that were the main contributors towards assemblage similarity/dissimilarity. These taxa were (in no particular order); the bivalve *L. rubra*, gastropod *R. parva*, amphipod *H. nilssoni* and Oligochaete sp.

4.3.2 Feeding function approach

As shown in Figure 4.4, the proportion of each feeding function in each sample varied between sites. There was a general increase in the proportion of grazers and active suspension feeders with increased exposure, though the proportion of detritivores was higher in sheltered sites and lowest in exposed sites.

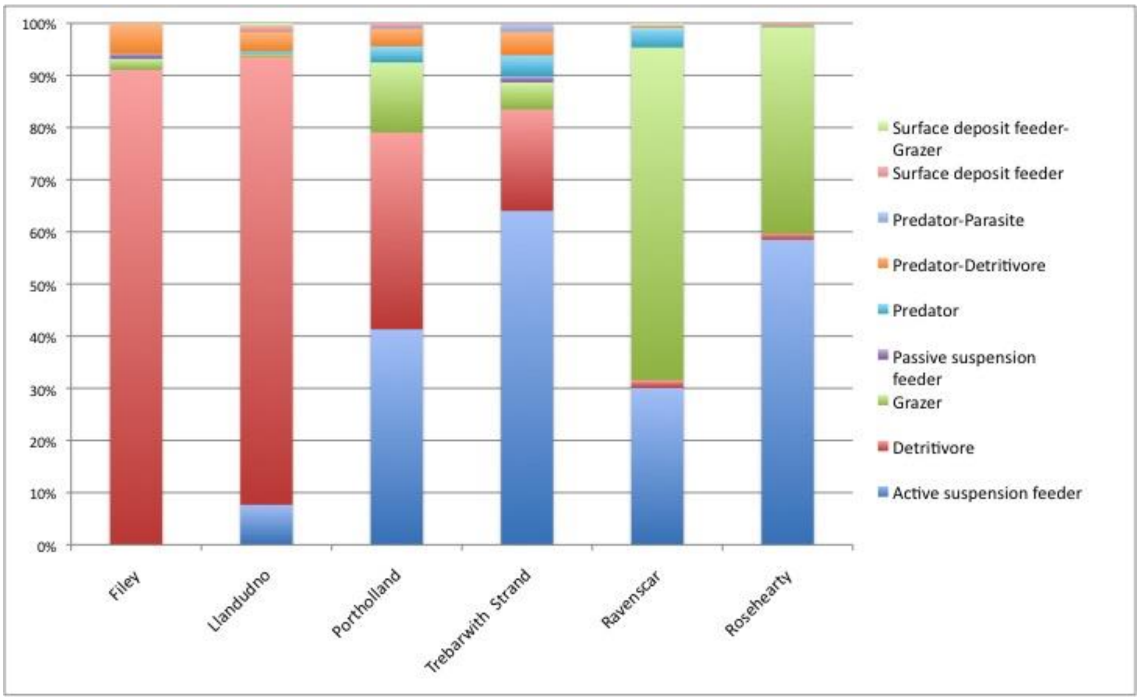

Figure 4.4: Percentage barplot of contributory feeding functions in infaunal communities from six UK sites.

Figure 4.5 displays the Shannon-Weiner diversity (H’) measure for feeding function at each site. Overall, there was highest feeding function diversity at the intermediate sites (Portholland, Trebarwith Strand), followed by exposed (Ravenscar, Rosehearty). The lowest diversity was to be found in the sheltered samples (Filey, Llandudno).

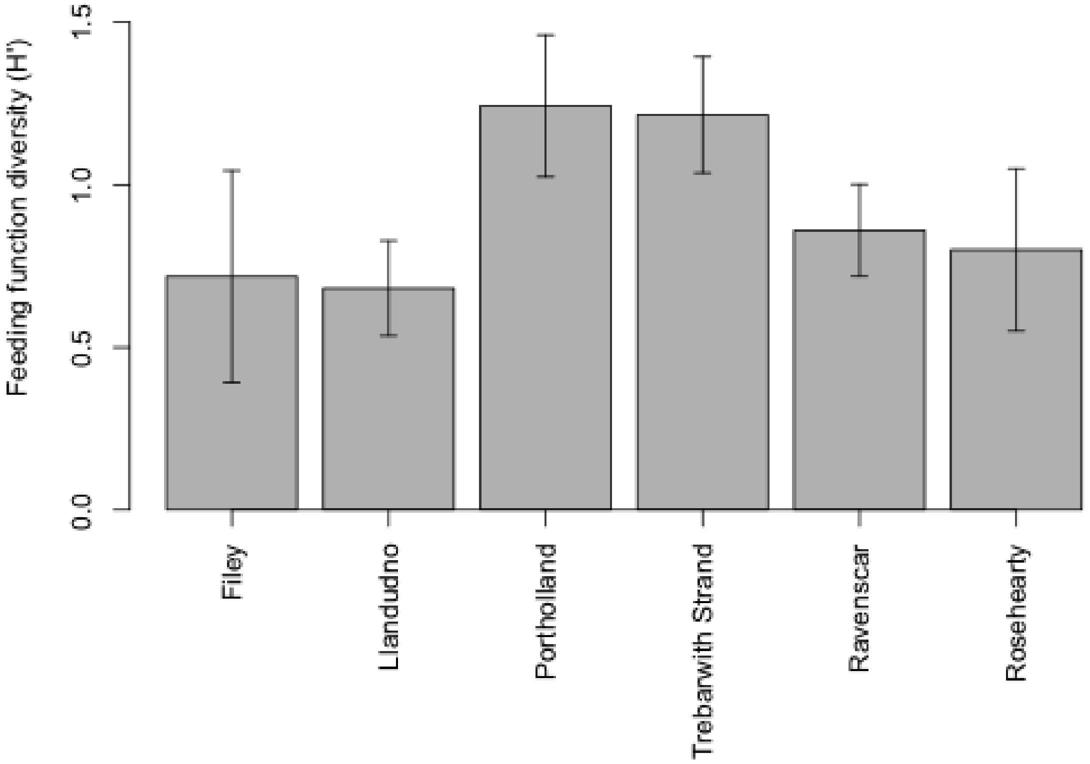

Figure 4.5: Feeding function diversity (H’) at six UK sample sites, order along the x-axis determined by increasing exposure of site

There was a significant difference in feeding function diversity between sites (ANOVA, $F_{5,24}$=6.361, P<0.001). Post-hoc testing (Tukey) indicated that diversity was significantly higher at both Portholland (mean=1.243, s.d.=0.219) and Trebarwith Strand (mean=1.215, s.d.=0.249) than at Llandudno (mean=0.682, s.d.=0.145) and Filey (mean=0.718, s.d.=0.326). Portholland also had a significantly higher functional diversity than Rosehearty (mean=0.800, s.d.=0.141). There was no significant difference in feeding function diversity between Ravenscar (mean=0.859, s.d.=0.179) and any other site (P>0.05).

Figure 4.6 shows the results of MDS plot analysis for similarity between site communities classed into feeding functions, the stress value (0.09) suggesting that it was a good representation of the similarity. There are three main clusters, corresponding to the main divisions of exposure; sheltered, intermediate and exposed sites.

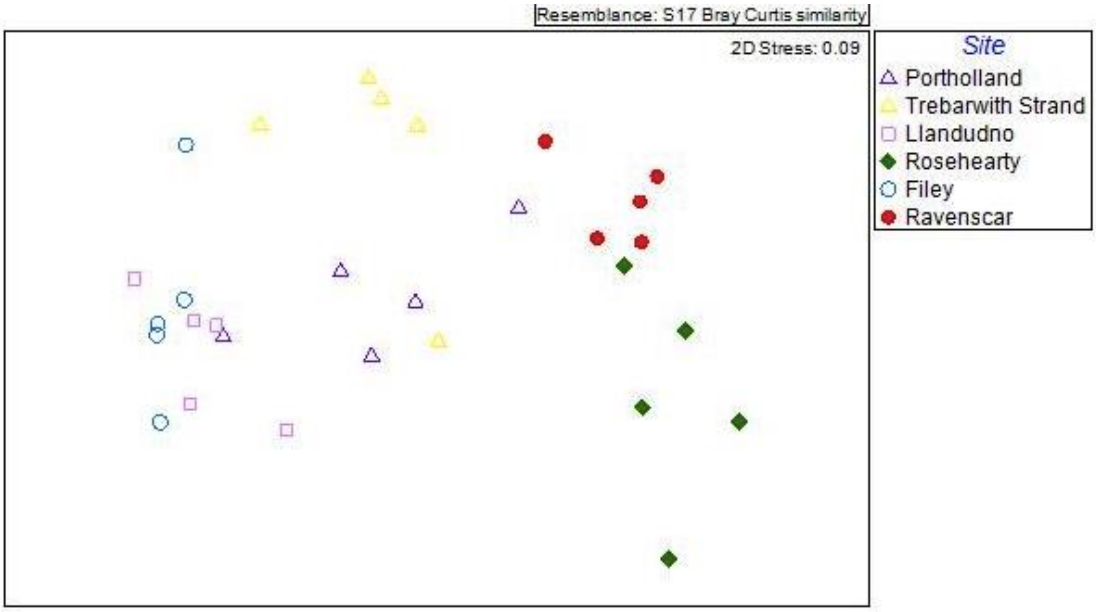

Figure 4.6: MDS plot for assemblage feeding function at six UK sites

There was a significant difference in feeding function assemblage overall similarity (ANOSIM, Global R= 0.715, P<0.05), although pairwise comparison of sites revealed that all sites were significantly different (P<0.05) with the exception of Filey and Llandudno (P>0.05), suggesting that the two sheltered sites are similar.

There was a 51.57% similarity by feeding function between the Portholland samples, 89.35% of which was contributed by three functions. Detritivores (average abundance=63.40) were the highest contributors (34.47%) with the second being active suspension feeders (average abundance=69.40), contributing 33.32% to overall similarity. Grazer-detritivores had an average abundance of 57.40 in the Portholland samples and contributed 21.56% to the overall 51.57% similarity.

The Trebarwith Strand samples had an overall functional similarity of 48.75%. Active suspension feeders (average abundance=56.60%) contributed 58.41% to the overall similarity, while grazer-detritivores (average abundance=9.00) contributed 11.36%.

Between the Llandudno samples, a 62.01% overall functional similarity was present, the only major contributor being detritivores with an average abundance of 148.20 and contributing 85.72%. Detritivores were also a major contributor (75.45%) to the 65.17% overall similarity at Filey, having an average abundance of 94.20. However, at Filey, grazer-detritivores (average abundance= 17.00) contributed an additional 18.26%.

Both active suspension feeders and grazers were the key contributors towards overall functional similarity at the two exposed sites. At Rosehearty, grazers (average abundance=465.20) contributed 56.66% to the 54.56% overall similarity, while active suspension feeders (average abundance=687.40) contributed 41.68%. There was an overall feeding function similarity of 72.39% at Ravenscar, grazers (average abundance=157.40) contributing 68.24% and active suspension feeders (average abundance=74.20) contributing 26.80%.

As shown in Table 4.2, there was often a high percentage of dissimilarity between sites, by feeding function. The two intermediate sites had a relatively high overall dissimilarity of 61.22% with grazers, active suspension feeders and grazer-detritivores being key contributors. Overall, there was a lower dissimilarity between intermediate and sheltered sites than between intermediate and exposed sites.

Sheltered sites were characterized by high abundances of detritivores (Filey=94.20, Llandudno=148.20), having a low overall dissimilarity of 36.93% in feeding function. However, the two exposed sites were characterized by high abundances of grazers and active suspension feeders. Exposed sites were both at least 90% dissimilar (overall) to the two sheltered sites, the key contributors to the dissimilarity being active suspension feeders, grazers and detritivores.

Site		Sheltered	Intermediate		Exposed	
		Filey	Portholland	Trebarwith Strand	Ravenscar	Rosehearty
Sheltered	Llandudno	36.93% DET (70.60) GRA-DET (10.37)	57.67% DET (36.12) ASF (26.13) GRA-DET (21.79) GRA (11.12)	72.48% DET (64.59) ASF (23.00)	90.09% GRA (41.67) DET (35.70) ASF (16.99)	94.08% ASF (42.34) GRA (40.74) DET (14.61)
	Filey		57.59% ASF (33.59) DET (26.16) GRA-DET (21.77) GRA (12.78)	72.48% DET(51.75) ASF (32.09)	93.92% GRA (44.67) DET (25.71) ASF (21.34)	95.61% ASF (45.04) GRA (42.37)
Intermediate	Portholland	57.59% ASF (33.59) DET (26.16) GRA-DET (21.77) GRA (12.78)		61.22% DET (29.32) ASF (27.77) GRA-DET (24.63) GRA (13.17)	70.31% GRA (43.00) DET (20.20) GRA-DET (16.82) ASF (15.50)	78.25% GRA (43.59) ASF (41.88)
	Trebarwith Strand	72.48% DET(51.75) ASF (32.09)	61.22% DET (29.32) ASF (27.77) GRA-DET (24.63) GRA (13.17)		70.31% GRA (63.73) ASF (21.68)	84.37% GRA (49.24) ASF (45.28)
Exposed	Ravenscar	93.92% GRA (44.67) DET (25.71) ASF (21.34)	70.31% GRA (43.00) DET (20.20) GRA-DET (16.82) ASF (15.50)	70.31% GRA (63.73) ASF (21.68)		56.31% ASF (56.32) GRA (38.17)

Table 4.2: SIMPER results for contributory feeding function to the overall dissimilarity between each UK site pair (%) and the percentage contribution of each function (ASF=Active Suspension Feeder; DET=Detritivore; GRA=Grazer; GRA-DET=Grazer-detritivore). Only functions with >10% contributions were included.

4.3.3 Comparison of species level and feeding function level approaches

Figure 4.7 displays a scatter plot of species diversity (x-axis) against feeding function diversity (y-axis), the points separated by tint according to site. As shown in the figure, there is an overall trend of increased feeding function diversity as species diversity increased, at all sites. There was an overall significant positive correlation between species diversity and feeding function diversity (Pearson's Product Moment, r = 23.20, df = 28, P<0.001).

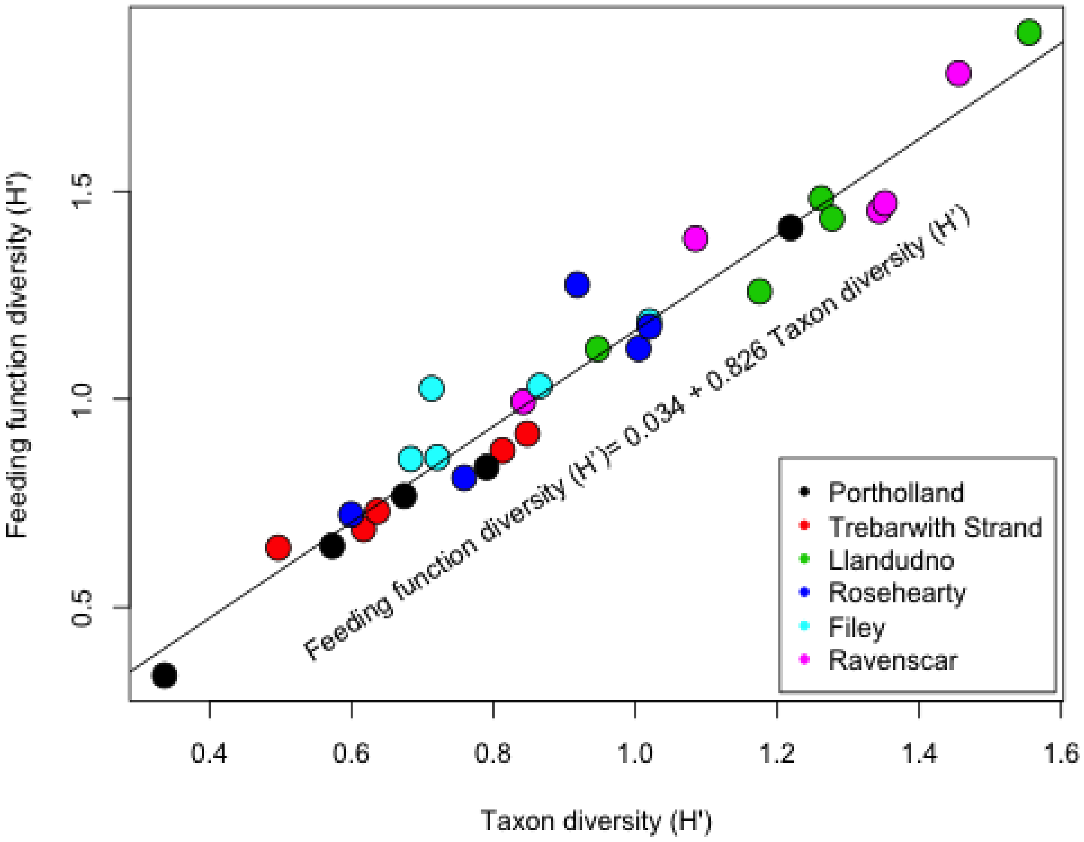

Figure 4.7: Scatterplot for species diversity (H') (x-axis) and feeding function diversity (H') (y-axis) at six sample sites

There was a significant relationship determined by Method of Least Squares Regression between species diversity (x-variable) and feeding function diversity (y-variable) (Regression ANOVA, $F_{1,28} = 538.4$, $P<0.001$). The equation for the line of fit through the points was feeding function diversity (H') = 0.034 + 0.826 species diversity (H') which accounted for 94.89% (R^2) of the variation in the y variable.

Table 4.3: Significant results of Pearson's Product Moment correlation and Regression ANOVA for feeding function diversity (FF) and species diversity (Sp)

Site	Pearson's, df=3		Regression ANOVA			
	r	P	$F_{1,3}$	P	R^2 (%)	Equation of line
Portholland	0.974	0.005	55.78	0.005	93.20	FF 0.181+0.740 Sp
Trebarwith Strand	0.930	0.022	19.26	0.021	82.03	FF 0.049+0.823 Sp
Llandudno	0.986	0.002	108.0	0.002	96.40	FF -0.244 +1.200 Sp
Filey	0.997	<0.001	518.4	<0.001	99.23	FF 0.055+0.828 Sp
Ravenscar	0.888	0.044	11.19	0.044	71.81	FF 0.185+0.661 Sp

Table 4.3 shows that there was a significant positive relationship between feeding function diversity and species diversity at all but one site. There was no significant relationship between feeding function diversity and species diversity at Rosehearty (Pearson's Product Moment, r=0.878, df=3, P>0.05).

The test statistic of the 2nd-Stage MDS was 0.956, indicating that a very strong correlation existed between the similarity matrices at a species and feeding functional level within *M. edulis* patches across the UK.

4.3.4 Environmental variables

As shown in Figure 4.8, the percentages of different sediment grades varied between sites of different exposure, with no apparent trends across exposures. However, there was an overall trend of higher mean sediment weight in sheltered site samples (Filey=0.139kg+/-0.044, Llandudno=0.432kg+/-0.267) than in exposed sites (Ravenscar=0.001+/-0.001, Rosehearty=0.014kg+/-0.007).

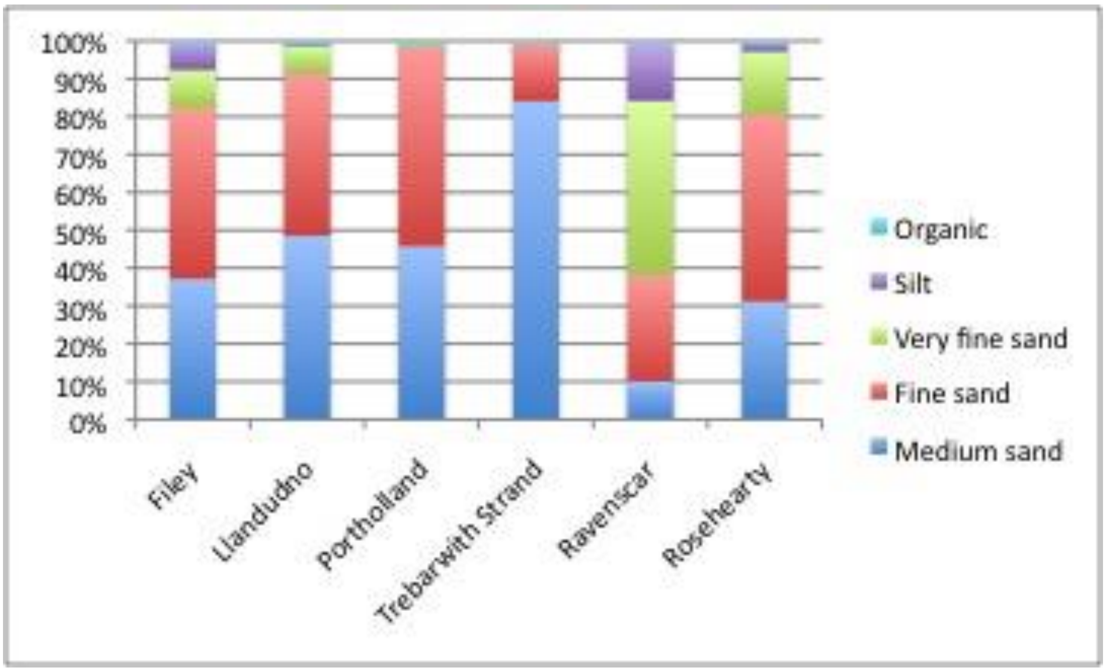

Figure 4.8: Barplot of percentage per sample of sediment grades and types (PMED, PFINE, PVFINE, PSILT, PORG) at six UK sites

Figure 4.9 shows that the percentage of small mussels (PSMALL) was highest in exposed sites, but also higher in sheltered site samples than in those from intermediate exposures. There was an absence of large mussels (PLARGE) in samples from the two exposed sites, with the highest percentages being in samples from sheltered sites. The two intermediate sites had highest percentages of medium sizes mussels (PMEDIUM). Additionally there was significant inverse relationship between PSMALL and total weight of sediment (Pearson's Product Moment, r = -3.66, df = 28, P<0.05) and a positive significant releationship between PLARGE and total sediment weight (Pearson's Product Moment, r = 4.53, df = 28, P<0.001). There was no significant correlation between PMEDIUM and total sediment weight (P>0.05).

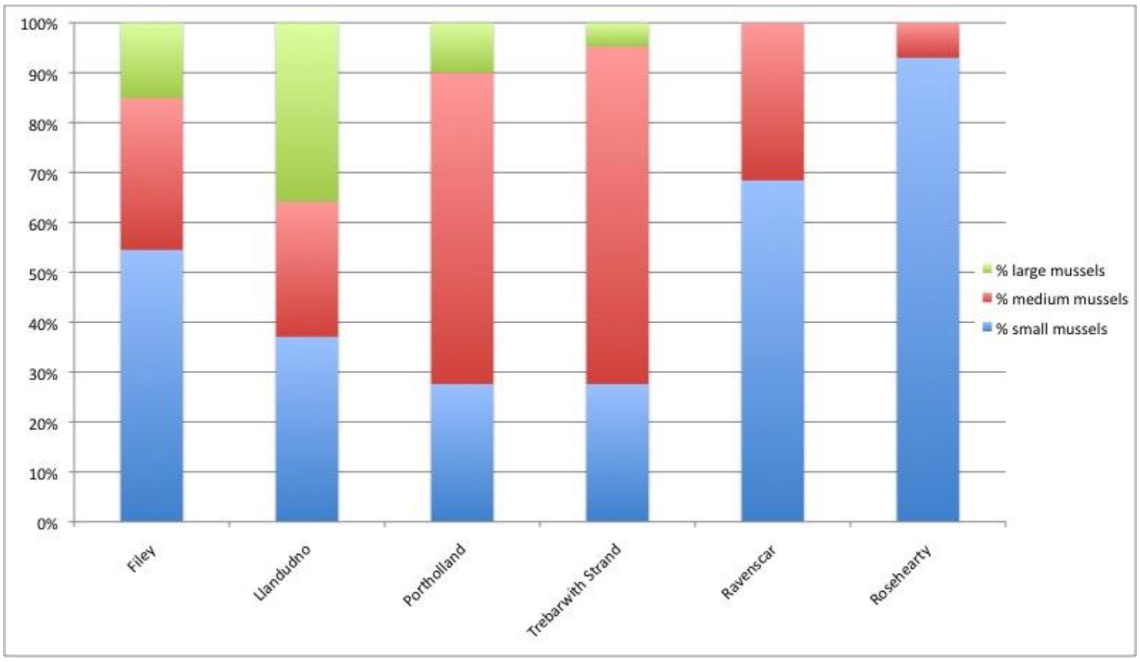

Figure 4.9: Barplot of percentage per sample of three mussel size classes (PSMALL, PMEDIUM, PLARGE) at six UK sites

Figure 4.10 displays the results of CCA analysis for the UK assemblage, using feeding functions and the environmental variables PSMALL, PMEDIUM, PLARGE, PMED, PFINE, PVFINE, PSILT, PORG and EXP. The sites Portholland (P1-5) and Trebarwith Strand (TS1-5) tend to correspond with higher proportions of medium sized mussels (PMEDIUM) and medium sand (PMED). These sites and environmental variables appear to be associated with higher proportions of, Grazer-detritivores and Predator-detritivores. The sheltered sites of Filey (F1-5) and Llandudno (L1-5) appear, in Figure 4.8, to be associated with the proportion of fine sand (PFINE) and higher proportions of detritivores typify the communities at the sheltered sites. The sites Rosehearty (RO1-5) and Ravenscar (RV1-5) were associated with higher proportions of organic sediment (PORG) and higher exposure (EXP) and a higher prevalence of Grazers.

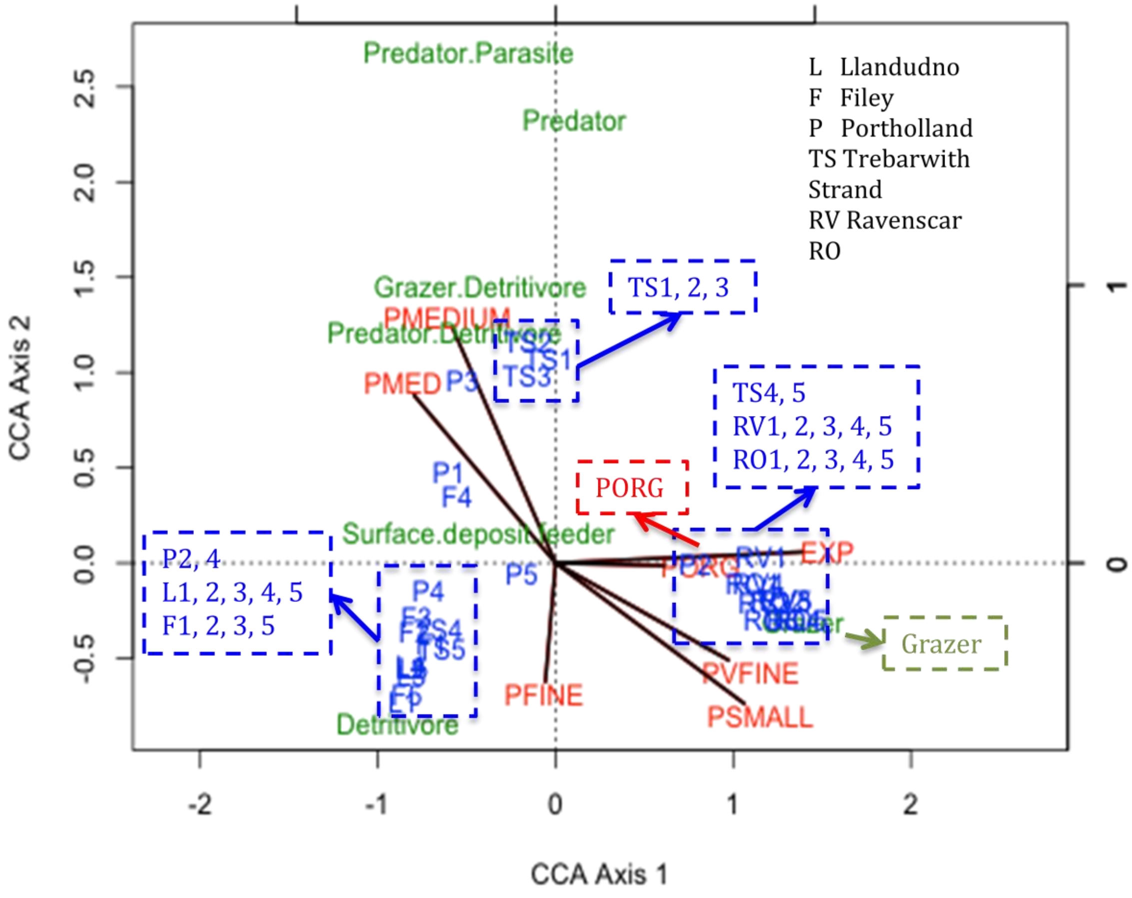

Figure 4.10: CCA triplot of UK sites, feeding functions and environmental factors

CCA analysis showed that CCA1 accounted for 74.3% of the variation in the model, and CCA2 for 17.8%, resulting in environmental variables accounting for 92.1% of the overall variation between the sites. Table 4.4 displays the relative contribution that each environmental variable had towards the CCA.

Table 4.4: Contribution of environmental variables to CCA1 and CCA2

Environmental variable	CCA1	CCA2
Exposure (EXP)	0.9371	0.1524
% small mussels (PSMALL)	0.5597	0.5638
% medium mussels (PMEDIUM)	-0.1749	-0.7581
% medium sand (PMED)	-0.3349	-0.8282
% fine sand (PFINE)	-0.2212	0.2804
% very fine sand (PVFINE)	0.5437	0.6349
% organic sediment (PORG)	0.2975	0.2910

CCA analysis further showed that 70% of the overall inertia was explained by all the environmental variables between sites, 95% of this being explained by the first two CCAs, a combination of CCA1 and CCA2. Following Bonferroni Correction, there was a significant influence on the site communities by several environmental variables, as shown in Table 4.5.

Table 4.5: Permutation testing for environmental variables in CCA model

Environmental variable	$F_{1,28}$	P
Exposure	25.7933	<0.001
% large mussels	12.9515	<0.001
% very fine sand	9.4718	<0.001
% small mussels	12.8818	<0.001
% medium sand	7.5062	<0.001
% medium mussels	6.0041	0.003

There was no significant influence of percentage organic sediment, percentage silt or percentage fine sand on the CCA model (PERMANOVA, p>0.05). From these results it was inferred that the structure of an assemblage at a feeding function level was most influenced by the environmental variables; exposure, proportions of mussel sizes, and the proportion of fine and very fine sand.

4.4 Discussion

It might be expected that species diversity be related to wave exposure, as stated by Ballantine (1961). The patterns of species diversity with highest diversity at the intermediate exposure sites matches the findings of other rocky shore studies, including Bustamante & Branch (1996); Prado & Castilla (2006) and Scrosati & Heaven (2007).

In lower exposure sites, where physical disturbances are low or infrequent events, species and populations will be excluded by competitively superior species or be unable to resist predation pressure (Cornell, 1978; Dial & Roughgarden, 1998). Conversely, at high level or frequent disturbance events only species tolerant to environmental effects, or efficient at recolonising habitats will thrive (Cornell, 1978; Lenz *et al*., 2004). This may be indicated by the dominance and high abundances of a few species at the sheltered sites, such as Oligochaete sp., a trend reflected in the overall rocky shore study by Healy (1996). The dominance of the exposed sites by a few organisms such as *L. rubra* and amphipods matched the results of the study by Lintas & Seed (1994). The distinct communities found at intermediately exposed sites (Figure 4.4) might suggest equilibrium between the sheltered and exposed communities, and also prevent exclusion of competitively inferior or low-tolerance species. In effect, local influences are effectively mitigated and so richness from the regional species pool is maximized (Ricklefs, 1987; Cornell & Lawton, 1992; Loreau, 2000; Wieters, 2001; Heads, 2005; Witman, 2013).

Figure 4.7 and associated regression and 2nd Stage MDS testing suggests that, overall, adopting a functional group level approach based on the dominant feeding function of a species is appropriate. The exception of Rosehearty in showing no significant relationship between functional and species diversity may be explained by the extremely high abundances of *L. rubra* at the site. *L. rubra* is a small, filter-feeding bivalve that is often found in large abundances attached to *M. edulis* byssal threads, usually associated with low rates of sedimentation (Crisp & Standen, 1998). This high abundance matches the findings of Bustamante & Branch (1996) and Ricciardi & Bourget (1999) that macrofaunal biomass on rocky shores increases with wave action. The population of *L. rubra* at Rosehearty may be outcompeting juvenile or very small *M. edulis* for secondary byssal space and the resulting high abundances may be skewing the results of the analysis. This matches the domination by active suspension feeders in the assemblage analysis at Rosehearty.

The significant difference in both species and functional diversity between sites, together with the highest diversities being found at the sites with an intermediate level of exposure (Figures 4.3 and 4.5) fits well with the curve predicted by the intermediate disturbance hypothesis (IDH). The well studied, and widely accepted, IDH suggests that the assemblage exists at equilibrium at sites where biological and biotic disturbances are balanced and so long-term diversity may be maintained (Cornell, 1978; Dial & Roughgarden, 1998; Lenz *et al*., 2004; Roxburgh *et al*., 2004). However, the IDH has been criticized for being over-simplistic in encompassing an array of complex mechanisms (Roxburgh *et al*., 2004) and notably refuted by Fox (2013), both empirically and theoretically. Despite this, the findings of this study support the IDH, the highest diversities being found at intermediate level exposures (Portholland and Trebarwith Strand) and assemblage similarity being significantly different between sites of different exposures (Figures 4 and 6).

The results of the feeding function ANOSIM show dominance by detritivores in the three lowest exposure sites. This could be attributed to higher rates of sedimentation either by physical deposition with lower water activity, or biodeposition by the mussels present (Tsuchiya, 1980; Bustamante & Branch, 1996a; Widdows & Brinsley, 2002; Prathep et al., 2003). It might be expected that larger mussels would be present at the sheltered sites due to the reduced risk of dislodgement by the lower water action (Seed, 1976; Tam & Scrosati, 2014). These larger mussels might be expected to produce and retain higher amounts of organically rich sediment (Levinton, 1972; Tsuchiya, 1980). The high abundances of grazers at the two most exposed sites (Ravenscar and Rosehearty) refutes the general rocky shore predictions of Ricciardi & Bourget (1999), although this may be attributed to increased epiphytic growth on the smaller, less algal-competitive mussels at the exposed sites.

The potential competition between small *M. edulis* and other active suspension feeders (predominantly *L. rubra*) may explain the lack of association between the two exposed sites and the proportions of small mussels (PSMALL) shown by CCA analysis and displayed in Figure 4.8. Competition between the two small bivalves might result from their similar suspension feeding behaviour (Seed, 1969; Crisp & Standen, 1988) or use of byssal matrices as secondary substrate (Lintas & Seed, 1994), in both instances competing for resources. However, this association could also be due to low levels of *M. edulis* recruitment, driven by larger ecological processes, which were not quantified or investigated in the course of this study. It has, for example, been speculated that mussel spatfall may be linked to annual fluctuations in seasonal climatic conditions (Seed, 1976). However, it must also be considered that sessile marine invertebrates frequently show negative correlation between body size and density (Petraitis, 1995), particularly in species that do not change growth form (Guinez & Castilla, 1999). This is often related to reduced availability of both food and space per organism, reducing body size (Petraitis, 1995). This occurrence may be termed as "self-thinning" (Hughes & Griffiths, 1988) and the negative relationship between size and density may be complicated by multilayering, as found in beds of intertidal mussels (Guinez & Castilla, 1999; Guinez, 2005). While the self-thinning and packing theories have been criticized for their apparent simplicity (Hughes & Griffiths, 1988), experimental populations of *M. edulis* have shown that self thinning is evident in mussel populations (Frechette *et al*., 1992). The research conducted by Frechette *et al*. (1992) indicated that small mussels were more susceptible to the negative effects than larger ones, with a steeper slope of the space-limited self-thinning relationship. This was likely to have influenced the ratios of PLARGE, PMEDIUM and PSMALL, with PSMALL being more limited by the presence of other mussel sizes within patches. The association between the exposed sites and percentage of organic sediment (PORG) may be related to the dominance by active suspension feeders and the consequential accumulation of pseudofaeces and faecal aggregates (Bayne *et al*., 1993; Haven & Morales-Alamo, 1966). Association between medium mussels (PMEDIUM) and assemblage structure at intermediate sites might be expected as the habitat forming benefits of the mussels (secondary space and biodeposits) may be balanced with the competitive costs of mussel presence (competition with sessile organisms and other suspension feeders). The two sheltered sites are shown in Figure 8 to be most closely associated with fine (PFINE) and very fine (PVFINE) sediment, which may explain the very high abundances of detritivores as a rich matrix within the mussel bed may be created. However, the lack of association with organic sediment suggests that there may other environmental variables or ecological processes occurring at the sheltered sites that were not revealed by this study. One possible explanation might be that at the sheltered sites the organics were consumed by high abundances of detritivores, unlike in the detritivore-poor exposed sites. This may indicate the association of the two exposed sites with PORG if the organic content of the sediments was not consumed.

It might be expected that exposure (EXP) was a significant environmental contributor both as a direct controller of diversity and as a primary influence on other environmental variables such as sediment transport (Levinton, 1972; Prathep *et al*., 2003) and mussel size (Seed, 1976; Tam & Scrosati, 2014). The resulting proportion of different mussel sizes was an important factor in determining assemblage structure both as a competitor species (with other active suspension feeders) and as an ecosystem engineer creating secondary space and substrate. This secondary substrate and space may serve as settlement surfaces for sessile infauna or serve as refuge from predation (Santelices & Martìnez, 1988; Valdivia & Thiel, 2006). As shown by Prathep *et al*. (2003), exposure is a key determinant of the composition of sediment deposited in intertidal habitats. The results of the environmental variable analysis follow the findings of Ricciardi & Bourget (1999) and Prathep *et al*. (2003) who found a significant influence of sediment grain size and exposure in determining assemblage structure in temperature intertidal habitats.

Analysis in this chapter has shown that the feeding function approach is representative of overall assemblage structure and is appropriate method. It may be practical to conclude that *M. edulis* infaunal communities on intertidal rocky shores in the UK do not share a common functional pattern. Therefore, while the feeding function approach did not reveal a fundamental structure underlying all mussel infaunal communities, it is a useful tool for comparing communities between sites. By identifying environmental factors and determining their influence on an assemblage it may be also possible to predict assemblage structure at a functional level. These findings are certainly intriguing, and offer possibilities for much further study at large geographical scales. However, it would be prudent to further analyse the approaches tested in this chapter in a similar habitat but in a distinct geographic region (Chapter 5).

Chapter 5 – Infaunal communities in Falkland Island mussel beds

5.4 Introduction

The Patagonia region of continental South America and outlying archipelagos contain a significant proportion of the world's sub-Antarctic coastal habitat, although studies are rare, particularly in the intertidal zone (Benedetti-Cecchi & Cinelli, 1997; Ríos & Mutschke, 1999; Escribano *et al*., 2003; Newcombe & Cárdanas, 2011). Broadly speaking, this area may be divided into two distinct zones, roughly divided between the Atlantic and Pacific oceans, with the western Humbolt region having a higher marine biodiversity (Miloslavich *et al*., 2011). The Atlantic coast of the region is dominated by the Patagonian Shelf, still considered as one of the most productive marine regions on the planet (Miloslavich *et al*., 2011). This productivity is generated and maintained by large oceanographic processes and features in the southern ocean (Cheung & Pitcher, 2005). The driving force behind these processes is the Falklands current, a northward flowing stream of cold water spurring off the Antarctic circumpolar current (Agnew, 2002; Arkhipkin *et al*., 2006; Broom *et al*., 2010). The upward movement of the Falklands current upon meeting the Patagonian Shelf creates an upwelling of oxygen- and nutrient-rich cold water, which allows particularly high marine productivity (Bisbal, 1995; Gibb *et al*., 2000; Agnew, 2002; Arhan *et al*., 2002). This high productivity supports an extremely valuable, mixed-stock fishery (Croxall & Wood, 2002; Cheung & Pitcher, 2005).

The Patagonian Shelf is home to the Falklands Islands (Figure 5.1), an archipelago consisting of two main islands (East and West Falkland) and several hundred smaller islands lying between latitudes of 50°-53° S (Cheung & Pitcher, 2005; Broom *et al.*, 2010). Despite being approximately 400 miles east of the South American continent, the Falkland Islands are often considered to be part of the Magellanic ecoregion which spans the Humbolt-Patagonian gap and also includes southern Chile and Argentina (Barnes & Lehane, 2001; Spalding *et al.*, 2007; Miloslavich *et al.*, 2011). Coastal habitats in this region are usually characterised by dry winds and cold-temperate marine waters (Bisbal, 1995; Bertness *et al.*, 2006; Silliman *et al.*, 2011).

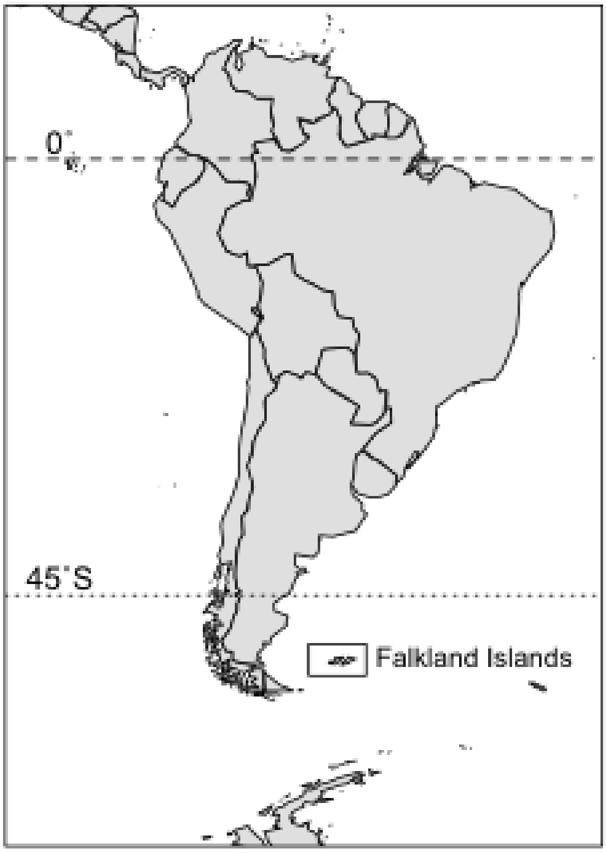

Figure 5.1 Regional position of the Falkland Islands

Extensive research has occurred in temperate, rocky intertidal habitats but this has often been restricted to the northern hemisphere or else to areas subject to moist maritime winds (Hidalgo *et al*., 2007). However, few studies have been done on rocky intertidal communities in the Magellan region (Ríos & Mutsche, 1999; Hidalgo *et al*., 2007). What research has occurred has mainly centred around certain areas, such as the shores at Mar del Palata, Argentina, in the far north of the region in which Vallarino *et al*. (1997), Vallarino & Elías (2002) and Elías *et al*. (2003) studied intertidal assemblage structure and the effects of pollution. Further to the south, Rico & Gappa (2006) and Silliman *et al*. (2011) also conducted intertidal community studies on the Argentinean coast. Another key study area in the region is the Strait of Magellan, Chile where Dayton (1985), Benedetti-Cecchi & Cinelli (1997) and Ríos & Mutsche (1999) also studied intertidal communities, including patch infauna studies.

While marine research in the Falkland Islands has a history spanning back to at least the mid-19th Century (Broom *et al*., 2010), the majority of studies have surrounded high–level predatory species such as penguins, albatross and pinnipeds (Barton, 2002; Bingham, 2002). There are some exceptions, however, where studies have investigated the intertidal and shallow sublittoral zone, including van Tussenbroek (1989; 1989a), Barnes & Lehane (2001), Waller (2008) and Broom *et al*. (2010). The rocky intertidal habitats of the Falkland Islands are dominated by mussel-barnacle mosaics with extensive macroalgae in the lower reaches and shallow sublittoral (Gray *et al*., 1997; Barnes & Lehane, 2001; Waller, 2008).

Elsewhere in the Magellan ecoregion, Silliman *et al*. (2011) demonstrated that habitat-creating sessile species are important for maintaining intertidal community richness. Thus it may be inferred that intertidal mussel patches are important habitats in the Falkland Islands. Despite this, studies on intertidal mussels in the Falkland Islands are scarce and those that exist focus upon mussel physiology and single species associations; growth and reproductive rate (Davenport & Davenport, 1984; Gray *et al*., 1997), algal parasitism (Gray *et al*., 1999; Rodríguez *et al*., 2008) and associations with a commensal isopod (Gray *et al*., 1997a).

Considering recent concerns and degree of research on the effects of climate change and other anthropogenic influences on biodiversity (Cheung *et al*., 2009), an understanding of effects in all geographical areas may be required. However, understanding the structure and functioning of communities is vital when attempting to predict future change (Newcombe & Cárdenas, 2011). As evidenced by the scarcity of research in published literature, there is a gap in the knowledge of intertidal communities across much of the Magellan ecoregion. In the Falklands this certainly extends to the description and analysis of the regionally important mussel bed habitat (Silliman *et al*., 2011). This study investigated infaunal community structure of mussel beds on Falkland Island rocky shores both at a taxonomic level, and a functional group level. The functional group approach and analysis of various environmental variables sought to identify the key environmental influences and indicate the subsequent effect on the infaunal community.

5.5 Methods

5.5.1 Site description

All sample sites for this study were on East Falkland, part of the Falkland Islands group lying approximately 400 miles due east of continental South America. The Falkland Islands were selected as a sample location as they lay along the route of a larger scientific expedition by the British Antarctic Survey vessel the RRS James Clark Ross, in November-December 2013. The position of the sample sites, in relation to the island of East Falkland, is displayed in Figure 5.2. Maps were generated using the 'maps' (http://cran.r-project.org/web/packages/maps/index.html), 'mapproj' (http://cran.r-project.org/web/packages/mapproj/index.html) and 'GISTools' (https://cran.r-project.org/web/packages/GISTools/index.html) packages in R.

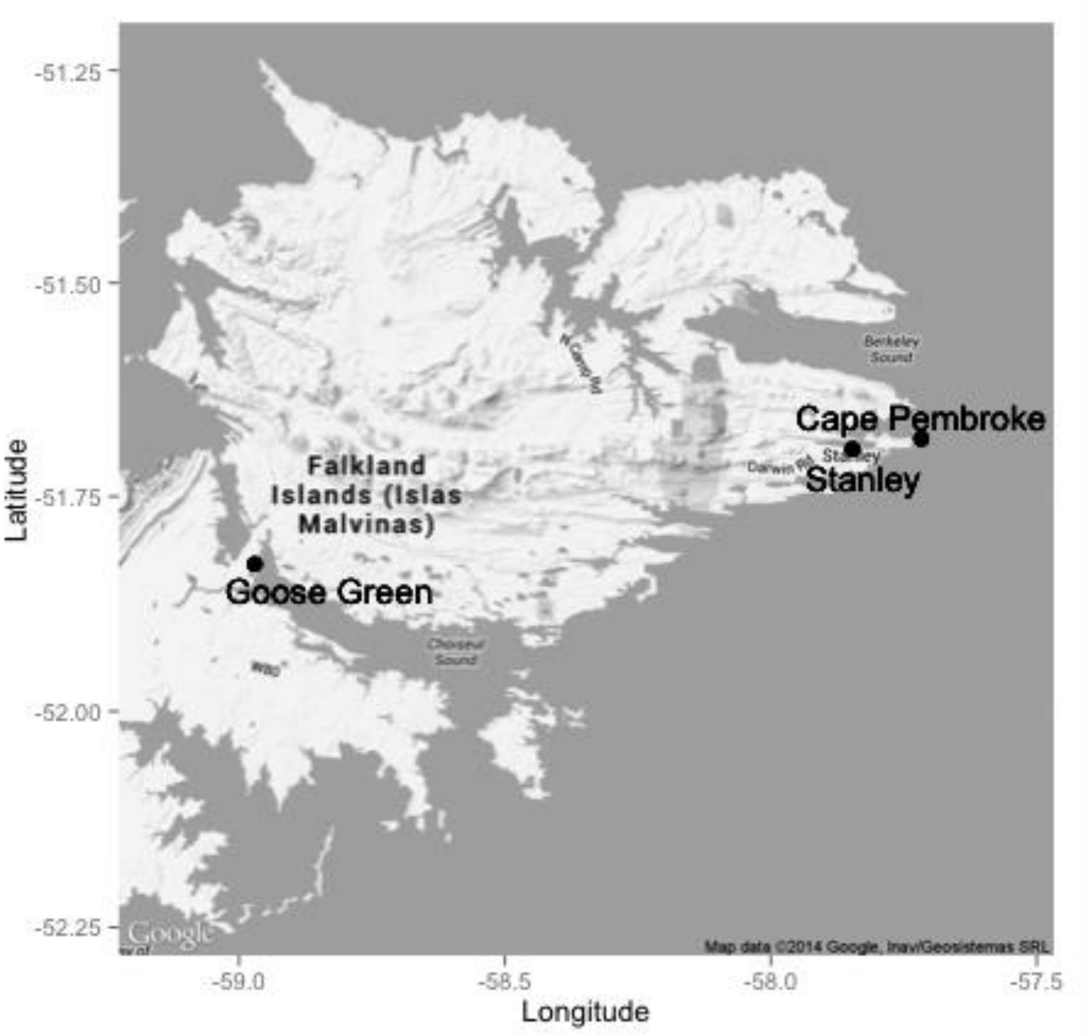

Figure 5.2: Position of sample sites within East Falkland

Cape Pembroke (Plate 4) (51°40.93’ S, 57°43.04’ W) lies on the tip of a peninsula on the far east of East Falkland. Having a Baardseth Index (Dring, 1992) value of 28, it was classified as “exposed.” Stanley (51° 41' 22.721" S, 57° 53' 23.57" W) was determined to be “sheltered,” having a Baardseth Index of 2 and was situated approximately 1.5km from the main settlement of Stanley, the territory capital. The second “sheltered” site was at Goose Green (51°49.64’ S, 58°58.19’ W) and had a Baardseth Index of 1, lying on the eastern shore of the East Falkland north-south isthmus. No sites of intermediate exposure were accessible during the sampling time period, thus restricting sampling to exposed and sheltered shores. All of the sample sites had intertidal rocky substrates with mussel patches. The intertidal mussel patches at all three sites were a mosaic of two species, the blue mussel *Mytilus edulis chilensis* and the ribbed mussel *Aulacomya ater*. Both of these bivalves are widespread on South American temperate shores, form intertidal patch habitats and fulfil a similar niche to *Mytilus* genera on rocky shore (Davenport & Davenport, 1984; Castilla & Guiñez, 2000; Robinson *et al.*, 2007).

5.5.2 Sampling method

5.2.2.1 Infaunal assemblage

This study followed the same sampling protocol as described in Section 4.2.2 and 4.2.3. All sites were sampled during the austral summer, at low tide during daylight hours. Water temperature at all sites was ~6°C, tides were in the period shortly after spring tides (3-4 days).

Due to the complexity of identifying, and lack of taxonomic keys for, many South Atlantic species and genera, fauna were not identified species level. Using high-magnification, specimens were identified to at least family level, with the exception of Oligochaeta (class), Coleoptera (order) and the echinoderm Spinulosa (order). Where more than one taxon of a family was present, each taxon was assigned a number. A list of the identified taxa from the Falkland Island samples is displayed in Table 5.1. A list of the samples and associated codes is included in Appendix 3 and voucher specimen codes are shown in Appendix 4.

5.2.2.2 Environmental variables

During the extraction of the macrofaunal assemblage from samples, all sediment larger than 38 microns was retained; allowing sediment characteristics for each sample to be identified. The sediment was oven dried at a temperature of 100°C for a period of 8 hours (Bale & Kenny, 2005), after which it was then passed through a series of sieves and graded according to the Udden/Wentworth scale (Wentworth, 1922). The dry weight of each of these divisions per sample was measured using an electronic balance to an accuracy of 0.01g and converted a weight in kilograms. Once the sediment profile was established the dried sediment was heated to 400°C for 6 hours (Bale & Kenny, 2005) to determine total organic sediment content per sample through loss on ignition (LOI) by reweighing and converting to kilograms. The organic content was calculated by subtracting the LOI weight from the original total dry weight (Bale & Kenny, 2005).

In addition to the taxon assemblage data, additional environmental variables were collected; exposure (EXP), percentage of small (PSMALL), medium (PMEDIUM) and large (PLARGE) mussels, percentage of medium sand (PMED), fine sand (PFINE), very fine sand (PVFINE) and silt (PSILT) as well as the percentage of organic sediment content (PORG). The mussel classes were assigned according to the measurements, small (<14.99mm), medium (15-29.99mm) and large (>30mm).

5.5.3 Data analysis

5.5.3.1 Taxon assemblage analysis

To compare assemblage diversity between the three sites, Shannon-Weiner (H') indices (Fowler *et al.*, 1998; Zar, 1999) were used as sampling area was equal in size from comparable populations and, additionally, it considers measures of abundance and richness (Fowler *et al.*, 1998; Zar, 1999) Additionally, the application of morphological classification made a multivariate calculation of taxonomic distinctiveness unsuitable (Clark & Warwick, 1998). Diversity indices generated richness (S), Shannon-Weiner index (H') and total abundance (N) in the statistical package PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke & Warwick, 2001).

Taxon diversity conformed to a normal distribution (Kolmogorov Smirnov test, P>0.05) and had variances that could be considered equal (Levene's test, test statistic = 3.455, P>0.05). Richness also conformed normal distribution (Kolmogorov Smirnov test, P>0.05) and had variances were considered equal (Levene's test, test statistic = 5.435, P>0.05). Analysis of Variance (ANOVA) was performed to determine where a significant difference was present between individual sites (Clarke & Gorley, 2006). Post-hoc (Tukey) tests identified where a significant difference in taxon diversity existed between sites (Clarke & Gorley, 2006).

To determine if there were significant differences in assemblage similarity between the sites the Bray-Curtis coefficient (Clarke & Warwick, 2001) was chosen. The Bray-Curtis similarity index (in PRIMER) generated a similarity matrix for all samples, which was then used to perform a non-parametric ordination using Multi Dimensional Scaling (MDS), producing a plot to visualise the similarity between the samples from different sites (Clarke & Gorley, 2006). To test the null hypothesis that there was no significant difference in overall assemblage similarity between the samples of different sites, an Analysis of Similarity (ANOSIM) was used (Clarke & Gorley, 2006).

To determine which taxa contributed the most to assemblage similarity or dissimilarity between sites, the Similarity Percentages Routine (SIMPER) was used (Clarke & Gorley, 2006). Only taxa that contributed more than 10% towards overall similarity or dissimilarity were reported in the results (Clarke & Gorley, 2006).

5.5.3.2 Feeding function assemblage analysis

The assemblage data for assigning feeding function was sourced as described in section 5.2.2.1 above. The functional approach followed the protocol as described in Chapter 3 of this thesis. The dominant feeding function was assigned to each identified taxon, as described in Section 3.2.1.1. However, due to the lack of species information and identification, dominant feeding method for each taxon was hypothesised using indications from the UK intertidal communities. For example, errant polychaetes in the UK study (*Eulalia viridis* etc.) were classed as predators and so Polychaete 1, a Falkland Islands errant polychaete was also classed as predatory. This approach led to the feeding function designations as displayed in Table 5.1.

Table 5.1: Assigned feeding functions for Falkland Island taxa

Active suspension feeder	**Grazer-Detritivore**	**Detritivore**
Lasaeidae	Littorinidae	Gammaridae 1
Carditidae	**Predator-Detritivore**	Gammaridae 2
Mactridae	Pilumnidae	Coleoptera
Grazer	Muricidae	Hydrobiidae
Hyalidae	**Surface deposit feeder**	Cerithiidae
Onchidiidae	Spinulosida	Munnidae
Predator-Parasite	Terebellidae	Sphaeromatidae
Acarina	**Predator**	Oligochaete sp
	Nereididae	

To establish feeding function diversity, Shannon-Weiner (H') indices were used. Feeding function diversity conformed to a normal distribution (Kolmogorov Smirnov test, P>0.05) and had variances that could be considered equal (Levene's test, test statistic = 2.905, P>0.05).

As the feeding function diversity data conformed to a normal distribution and had equal variances, a one-way ANOVA was used (Clarke & Gorley, 2006) to test the null hypothesis that there was no significant difference in feeding function diversity between sites. The post-hoc Tukey test was used to identify significant differences in diversity between specific sites (Clarke & Gorley, 2006).

The Bray-Curtis coefficient (in PRIMER) was used to compare similarity between samples (Clarke & Warwick, 2001), which was then used to perform an MDS plot, illustrating the similarity between samples (Clarke & Gorley, 2006). An Analysis of Similarity (ANOSIM) was used to test the null hypothesis that there was no significant difference in assemblage similarity between different sites, (Clarke & Gorley, 2006). The Similarity Percentages Routine (SIMPER) was used to identify which feeding functions contributed most to assemblage similarity or dissimilarity between each site (Clarke & Gorley, 2006).

5.2.3.3 Testing the functional approach

In order to test the effectiveness of the functional approach in representing the taxonomic level communities, the relationship between functional diversity (H') and species diversity (H') was tested. The data conformed to a normal distribution (Kolmogorov Smirnov test, $P>0.05$) and variances could be considered equal (Levene's test, test statistic=0.174, $p>0.05$). As variances were equal and data conformed to a normal distribution, parametric tests (Pearson's Product Moment correlation and Method of Least Squares Regression) were used (Fowler *et al.*, 1998). The relationship between functional and taxonomic diversity at each site was tested, followed by a test of the overall relationship across all sites.

To statistically compare the MDS analyses of the communities at taxon and feeding function level, a 2nd-stage MDS was used to compare the two similarity matrices (Clarke & Warwick, 2001). The resulting test statistic (r) indicated the strength of the correlation, values closer to 1 or -1 indicating a stronger correlation (Clarke & Warwick, 2001).

5.2.3.4 Environmental variables

To identify the environmental factors important in determining the feeding function assemblage structure, using the factors described in 5.2.2.2, Canonical Correspondence Analysis (CCA) was used. CCA was suitable as there were multiple important environmental gradients affecting composition and there was not an even distribution of taxa in the data set (Gauch & Wentworth, 1976; Palmer, 1993; Zuur *et al.*, 2007). The influence of each variable was displayed by proximity to, and length of, arrows on a triplot (Palmer, 1993; Zuur *et al.*, 2007). Due to the increased likelihood of achieving an artificially significant result due to the multiple tests undertaken in the analysis, Bonferroni correction was applied, with the α set at 0.05 (Moran, 2003). The effect of the significant variables was determined by permutated analysis of variance (PERMANOVA) as this test does not assume normal distribution of error between ecological variables (Anderson & Ter Braak, 2003).

5.6 Results

5.6.1 Taxon assemblage analysis

As shown in Figure 5.3, there was a difference in apparent evenness between assemblages from the three sites. Goose Green was dominated by one group of organisms, Oligochaetes, while Cape Pembroke appeared to have four or more dominant taxa. Samples from Stanley also showed high abundance and dominance of Oligochaetes but also Lasaeidae and Hyalidae.

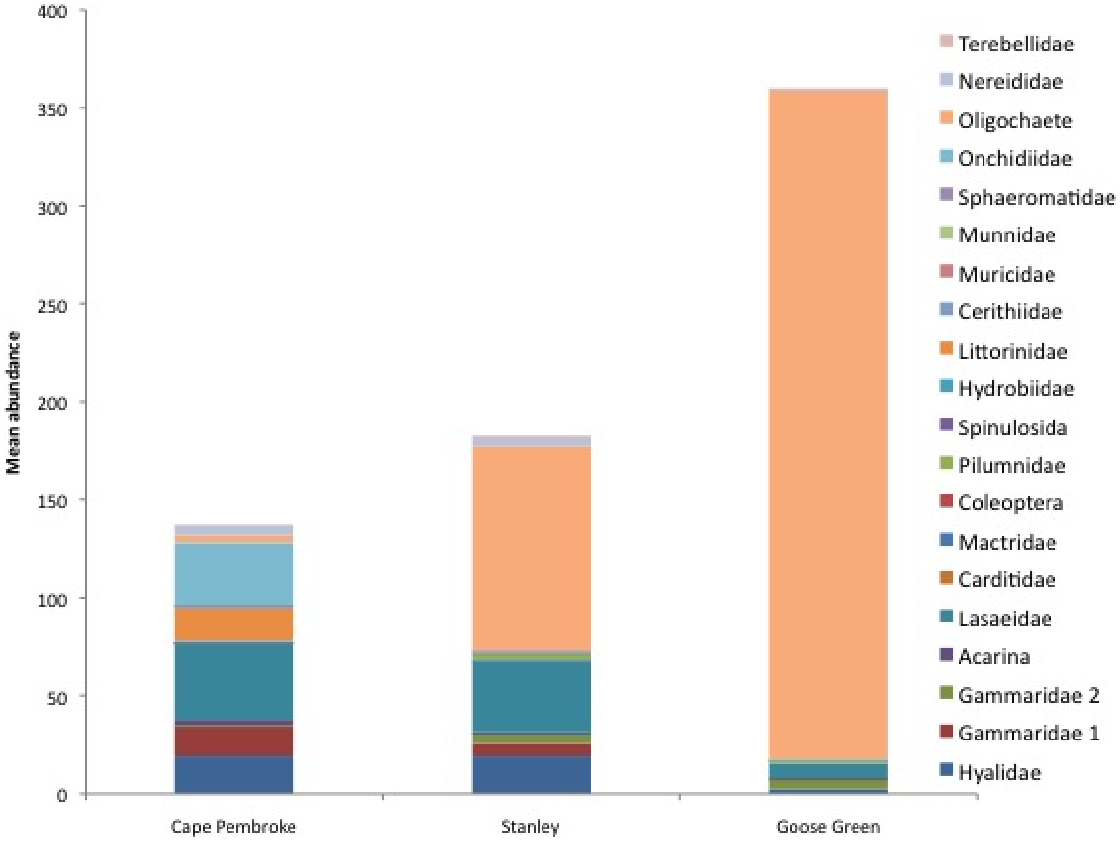

Figure 5.3: Mean abudance of taxa in infaunal samples from mussel beds at three intertidal sites on the East Falkland

There was a significant difference in taxon diversity (Figure 5.4) between the three sites (ANOVA, $F_{2,27}$=72.63, P< 0.001). Diversity at Cape Pembroke (mean=1.42, s.d.=0.27) was significantly higher than Stanley (mean=1.04, s.d.=0.25) and Goose Green (mean=0.27, s.d.=0.09)(Tukey, P<0.05). Diversity at Stanley was also significantly higher than at Goose Green (Tukey, P<0.05).

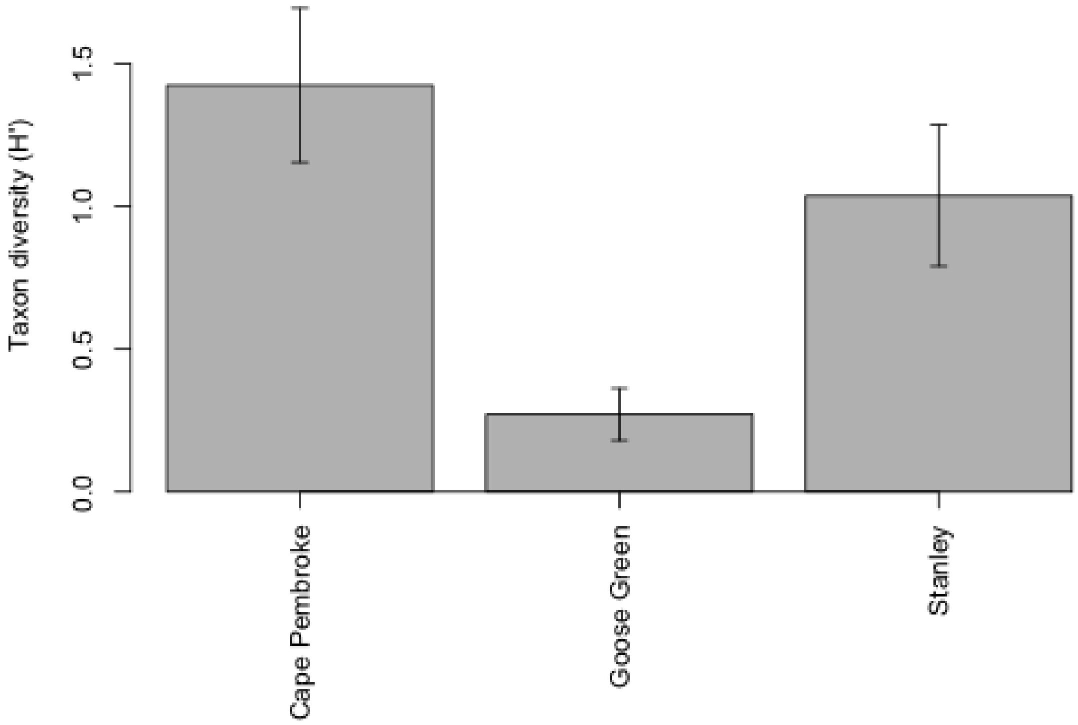

Figure 5.4: Mean (+/- sd) taxon diversity at three intertidal sites

There was a significant difference in mean taxon richness between the three sites (ANOVA<, $F_{2,27}$=5.435, P<0.05). Mean richness was significantly lower at Goose Green (mean=5.9, s.d.=1.371) than Cape Pembroke (mean=8.3, s.d.1.418) (Tukey, P<0.05). There was no significant difference between richness at Stanley (mean=6.5, s.d.=2.173) and Goose Green, or between Stanley and Cape Pembroke (Tukey, P>0.05)

Figure 5.5 displays the results of MDS analysis on a Bray-Curtis similarity matrix. There are three clusters of points, each corresponding to a different site with intertidal mussel patches. The stress value was 0.09, suggesting that this was a good representation of the sample similarity (Clarke & Warwick, 2001). There was a significant difference in assemblage similarity between the different sites (ANOSIM, Global R=0.71, P<0.001). Pairwise comparisons between sites showed that the communities at all sites were significantly different (in all cases, P<0.001).

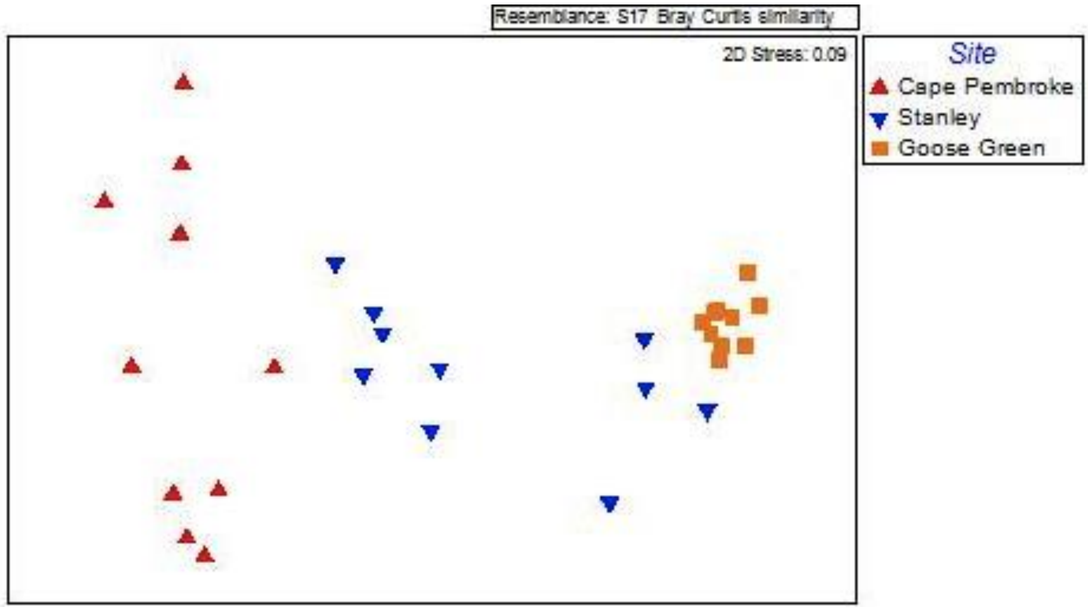

Figure 5.5: MDS analysis for three Falkland Island taxon communities

Three taxa accounted for 76.07% of the 41.00% overall similarity between the Cape Pembroke samples. Lasaeidae had an average abundance of 39.10 and contributed to 43.49% of the sample similarity, Onchidiidae was the next most important taxon (average abundance =31.70, contributing 16.45% to overall similarity). Hyalidae had an average abundance of 19.00 and contributed 16.04% of the overall similarity between Cape Pembroke samples.

At the Stanley site, three taxas accounted for 95.42% of the overall 52.18% similarity between samples. The most important taxon was Oligochaete sp. (average abundance =104.60), which contributed 60.97% to the overall similarity. Lasaeidae (average abundance= 36.60) and Hyalidae (average abundance=19.00) contributed 22.43% and 12.03% respectively to the overall similarity.

One species accounted for 96.43% of the overall 88.15% similarity between the Goose Green patch samples; Oligochaete sp. had an average abundance of 341.40.

Table 5.2: Taxas contributing to the 72.68% dissimilarity between Cape Pembroke and Stanley samples

Taxon	Average abundance Cape Pembroke	Average abundance Stanley	% Contribution to dissimilarity between sites
Oligochaete sp.	3.8	104.60	41.31
Lasaeidae	39.10	36.60	14.20
Onchidiidae	31.70	0.00	11.46
Hyalidae	19.00	19.00	8.64
Gammaridae 1	15.60	6.50	8.24
Littorinidae	17.90	0.00	7.70

Table 5.2 displays the taxas that contribute highest to the average dissimilarity (72.38%) between the Cape Pembroke and Stanley samples. Onchidiidae and Littorinidae were present at Cape Pembroke but absent at Stanley. Average

abundance of Gammaridae 1 was higher at Cape Pembroke than Stanley, although Oligochaete sp. were far more abundant at Stanley.

Table 5.3: Taxas contributing to the 94.00% dissimilarity between Cape Pembroke and Goose Green samples

Taxon	Average abundance Cape Pembroke	Average abundance Goose Green	% Contribution to dissimilarity between sites
Oligochaete sp.	3.8	341.40	72.99
Lasaeidae	39.10	7.60	6.53
Onchidiidae	31.70	0.00	5.88

There was an average dissimilarity of 94.00% between Cape Pembroke and Goose Green samples; Table 5.3 illustrates the taxa that contributed most to this. Onchidiidae (absent at Goose Green) and Lasaeidae were much higher in abundance at Cape Pembroke. However, Oligochaete sp. were greatly higher in abundance at Goose Green than Cape Pembroke.

Table 5.4: Taxas contributing to the 58.58% dissimilarity between Stanley and Goose Green samples

Taxon	Average abundance Stanley	Average abundance Goose Green	% Contribution to dissimilarity between sites
Oligochaete sp.	104.60	341.40	76.38
Lasaeidae	36.60	7.60	10.63
Hyalidae	19.00	2.20	5.79

One taxa, Oligochaete sp., accounted for 76.38% of the overall 58.58% dissimilarity between Stanley and Goose Green, being far more abundant in Goose Green samples (Table 5.4). At Stanley, however, Lasaeidea had a higher abundance (contributing 10.63%) and Hyalidae were also higher in abundance (contributing 5.79%).

5.6.2 Feeding function assemblage analysis

There was a significant difference in feeding function diversity (Figure 5.6) between the three intertidal sites (ANOVA, $F_{2,27}$=58.07, P< 0.001). There was significantly higher feeding function diversity at Cape Pembroke (mean=1.03, s.d.=0.20) than at Stanley (mean=0.63, s.d.=0.24) and also Goose Green (mean=0.16, s.d.=0.04)(Tukey, P<0.05). Diversity at Goose Green was significantly lower than at Stanley (Tukey, P<0.05).

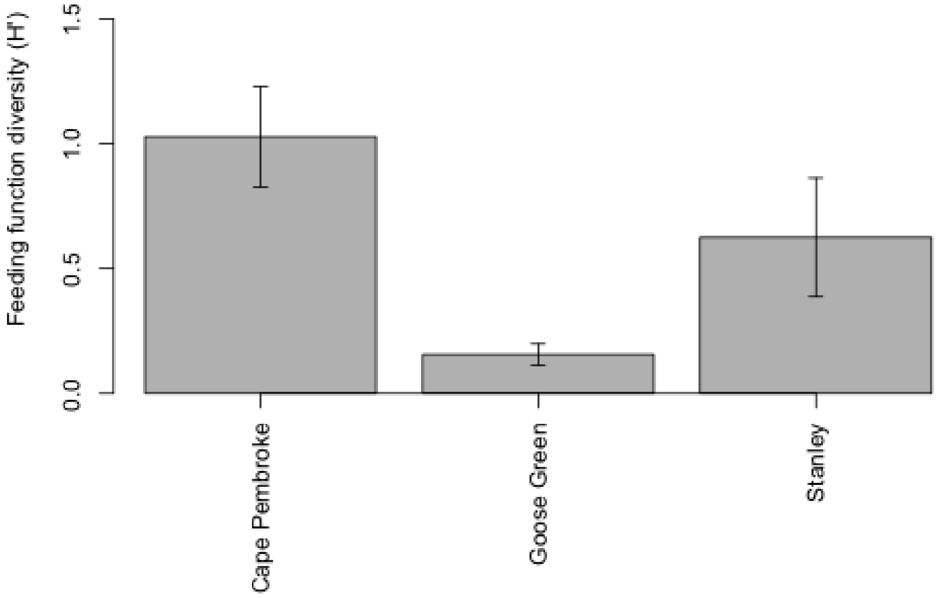

Figure 5.6: Mean (+/- sd) feeding function diversity at three intertidal sites

The stress value of 0.06 suggests that Figure 5.7 is a good representation of the sample similarity through a Bray Curtis matrix (Clarke & Warwick, 2001). The sites grouped into three clusters, Cape Pembroke being distinct from Goose Green, with Stanley transitional between them. There was a significant difference in assemblage similarity between the sites (ANOSIM, Global R=0.603, P<0.001), with pairwise comparison between sites showing that the communities at all sites were significantly different (in all cases, P<0.05).

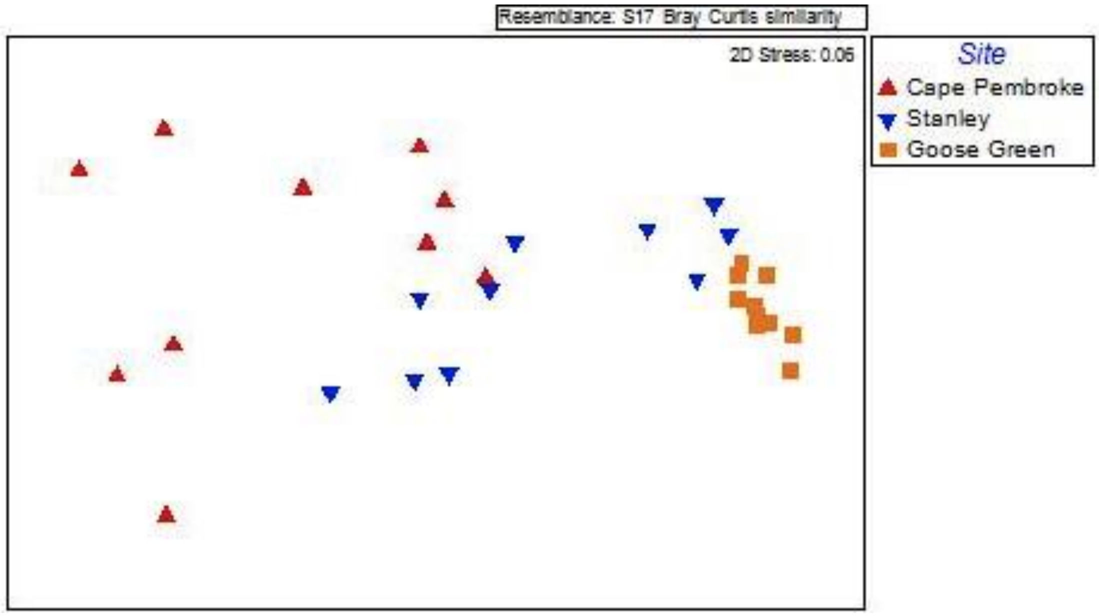

Figure 5.7: MDS analysis for feeding function assemblage similarity at three sites

Three feeding functions accounted for 95.65% of the 49.52% overall similarity between the Cape Pembroke samples. Active suspension feeders had an average abundance of 39.20 and contributed 36.47% of the overall similarity. Grazers (average abundance= 49.60) and detritivores were the remaining major contributors, accounting for 29.65% and 29.53% of the overall similarity.

The 61.40% overall similarity between Stanley samples was accounted for by two feeding functions. Detritivores had an average abundance of 136.40 and contributed 77.28%, while active suspension feeders (average abundance= 36.70) contributed 19.20% to the overall similarity.

Detritivores had an average abundance of 349.30 and contributed 97.76% to the overall 89.11% similarity between the Goose Green samples.

Table 5.5: Feeding functions contributing to the 58.52% dissimilarity between Cape Pembroke and Stanley samples

Feeding function	Average abundance Cape Pembroke	Average abundance Stanley	% Contribution to dissimilarity between sites
Detritivore	40.00	136.40	52.38
Grazer	49.60	0.00	23.69
Active suspension feeder	39.20	36.70	17.48

The overall dissimilarity between Cape Pembroke and Stanley, shown in Table 5.5, was 58.52%. Detritivores contributed 52.38% to this dissimilarity and were far more abundant at Stanley than at Cape Pembroke. Conversely, Cape Pembroke had a much higher abundance of grazers and marginally more active suspension feeders.

Table 5.6: Feeding functions contributing to the 79.87% dissimilarity between Cape Pembroke and Goose Green samples

Feeding function	Average abundance Cape Pembroke	Average abundance Goose Green	% Contribution to dissimilarity between sites
Detritivore	40.00	349.30	78.64
Grazer	49.60	0.00	11.33
Active suspension feeder	39.20	7.60	7.71

Between Cape Pembroke and Goose Green, there was 79.87% dissimilarity between communities (Table 5.6). Grazers and active suspension feeders were considerably more abundant at the exposed site than at the sheltered, however the abundance of detritivores was many times higher at Goose Green.

Table 5.7: Feeding functions contributing to the 48.19% dissimilarity between Stanley and Goose Green samples

Feeding function	Average abundance Stanley	Average abundance Goose Green	% Contribution to dissimilarity between sites
Detritivore	136.40	349.30	83.73
Active suspension feeder	36.70	7.60	12.96

Table 5.7 displays the two feeding functions that contributed to the 48.19% overall dissimilarity between the Stanley and Goose Green samples. Goose Green had a

higher abundance of detritivores, while Stanley had a higher abundance of active suspension feeders.

5.3.3 Testing the functional approach

As shown in Figure 5.8, there was an overall positive relationship between feeding function diversity and taxon diversity across all sites. There was a significant correlation between feeding function diversity and taxon diversity, averaged across all sites (Pearson's Product Moment, $r = 0.91$, $df = 28$, $P < 0.001$). There was a significant positive relationship determined by Method of Least Squares Regression between taxon diversity (x-variable) and feeding function diversity (y-variable) (Regression ANOVA, $F_{1,28} = 146.1$, $P<0.001$). The equation for the line of fit through the points was Feeding function diversity (H') = 0.182 + 1.208 Taxon diversity (H') which accounted for 83.3% (R^2) of the variation in the y variable.

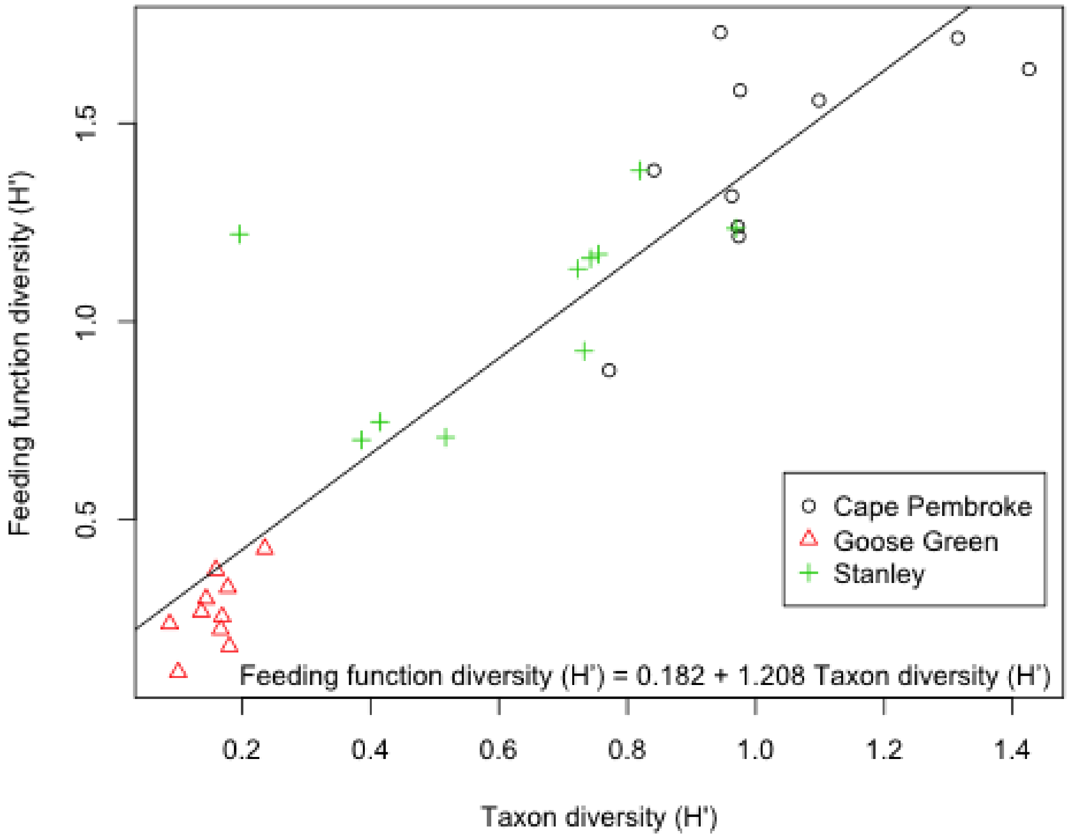

Figure 5.8: Scatterplot for taxon diversity (x-axis) and feeding function diversity (y-axis) at three sample sites.

The test statistic of the 2nd-Stage MDS was 0.935, suggesting that there was a very strong correlation between the similarity matrices at taxon and functional levels. This indicated that the feeding function approach was representative of the changes in communities between Falkland Island sites.

5.3.4 Environmental variables

Figure 5.9 displays the results of CCA analysis for the FI mussel infaunal communities, using feeding functions and various environmental variables. The sheltered sites of Stanley (ST1-10) and Goose Green (GG1-10) appear, in Figure 5.9, to be associated with the proportion of medium sand (PMED) and higher proportions of detritivores are prevalent in these sheltered communities. The exposed site, Cape Pembroke (CP1-10), was associated with higher proportions of organic sediment (PORG), fine sand (PFINE), medium sized mussels (PMEDIUM) and higher exposure (EXP) and a higher proportion of Grazers, Predators and Predator-parasites.

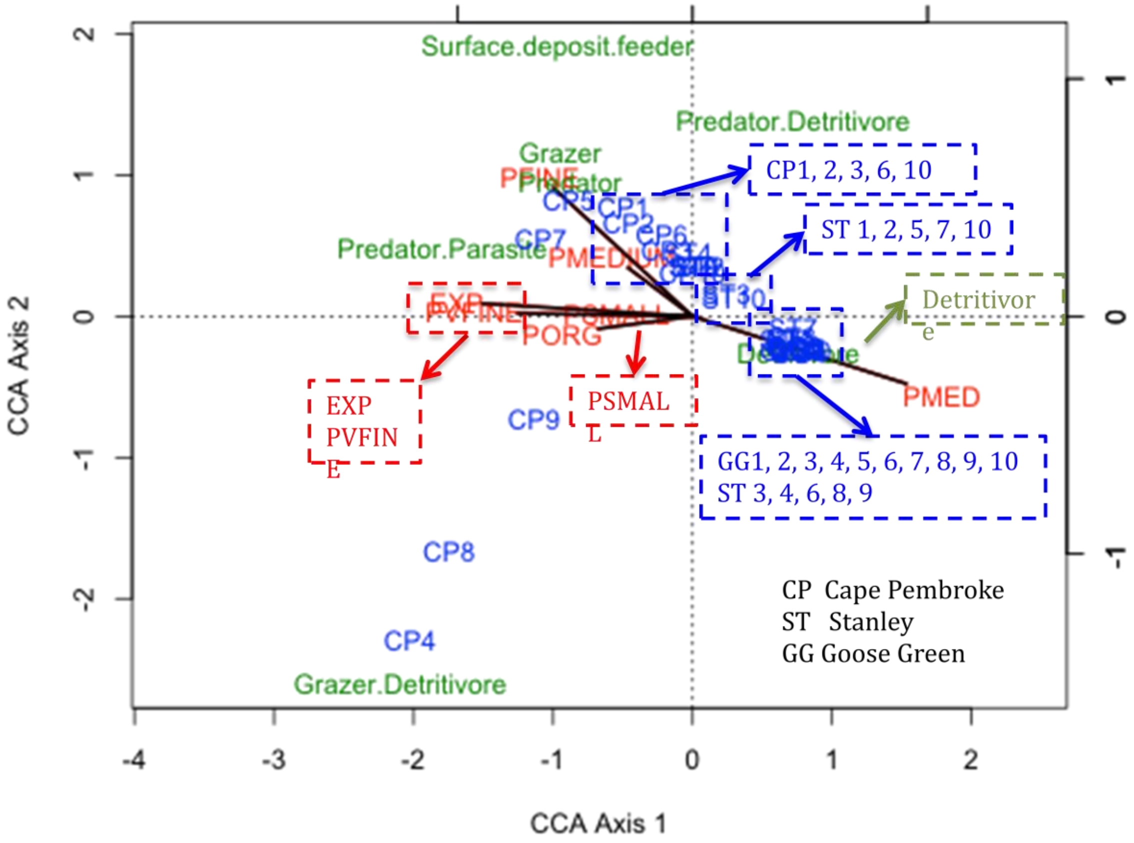

Figure 5.9: CCA analysis of FI sites, feeding functions and environmental factors

CCA analysis showed that CCA1 accounted for 81.2% of the variation in the site model, while CCA2 accounted for 12.8%, resulting in environmental variables accounting for 94.0% of the overall variation between the sites. Table 5.8 displays the relative contribution that each environmental variable had towards the CCA.

Table 5.8: Contribution of environmental variables to CCA1 and CCA2

Environmental variable	CCA1	CCA2
Exposure (EXP)	-0.8948	0.0538
% small mussels (PSMALL)	-0.1216	0.0046
% medium mussels (PMEDIUM)	-0.2751	0.2045
% medium sand (PMED)	0.9104	-0.2837
% fine sand (PFINE)	-0.5930	0.5413
% very fine sand (PVFINE)	-0.7458	0.0131
% organic sediment (PORG)	-0.4005	-0.0518

CCA analysis further showed that 52% of the overall inertia was explained by all the environmental variables between sites, 94% of this being explained by the first two CCAs, a combination of CCA1 and CCA2. After the application of Bonferroni Correction, there was a significant influence on the site communities by several environmental variables, as shown in Table 5.9.

Table 5.9: Permutation testing for environmental variables in FI CCA model following Bonferroni Correction

Environmental variable	$F_{1,28}$	P
Exposure	14.5638	<0.001
% medium sand	15.5760	<0.001
% very fine sand	8.8224	<0.001
% large mussels	9.0500	<0.001
% fine sand	5.8558	0.003
% silt	8.0686	0.003

There was no significant influence of percentage organic sediment (PORG), or percentage medium (PMEDIUM) and small mussels (PSMALL) on the CCA model (PERMANOVA, $p>0.05$). From these results it was inferred that the feeding function structure of an assemblage was most influenced by the following environmental variables; exposure, proportion of large mussels, and the proportion of various sediment grades.

5.4 Discussion

In another intertidal study in the Patagonian region, Silliman *et al.* (2001) found higher diversity of fauna in the presence of mussel beds. This was attributed to higher protection from desiccation and heat stress. The significantly higher diversity at the higher exposure site of Cape Pembroke compared to the sheltered Stanley and Goose Green sites is supported by the findings of studies outside the

Patagonian region such as Bustamante & Branch (1996) who found intertidal species diversity to be higher at exposed locations than at sheltered sites. Increased wave exposure can clear ecological space, further influencing communities by variations in biological interactions such as competition (Dayton, 1971). However, reugosity remains an important factor in maintaining higher diversity (Commito & Rusignuolo, 2000), particularly in exposed locations. In areas of high physical (wave) exposure species that are less tolerant to environmental effects may be excluded by physical factors (Cornell, 1978; Lenz *et al.*, 2004). However, in sheltered sites with low frequency or intensity of physical disturbance, biotic disturbance may become a key influence with only the most effective competitor species being successful (Cornell, 1978; Dial & Roughgarden, 1998). This may explain the lower diversity at Goose Green and Stanley where competitively superior or sediment tolerant organisms such as Oligochaete sp. were dominant in the communities. It might be expected that a site subject to intermediate levels of disturbance, where biological and biotic disturbances are balanced, would have the highest diversity (Connell, 1978; Lenz *et al.*, 2004) but this type of site was not sampled in this particular study.

Bertness *et al.* (2006) found higher fluxes in larval recruitment in wave-exposed shores in the southwestern Atlantic, contributing to variations in assemblage structure between sites. Variations in exposure may influence recruitment directly by altering the transport of larvae suspended in the water column (Gaines & Bertness, 1992), or may also affect the retention of larvae by clustering distribution or altering biological structures of the habitat (Fairweather, 1991;

Webb *et al*., 2009). This supply-side factor may also drive variations in assemblage structure between the Falkland sites in this study.

Results showed high abundance of *Lasaea* sp. and amphipods at Cape Pembroke, a pattern reflected in high abundances of Oligochaete sp. at Stanley and Goose Green. This pattern of dominance by only one or two species was also present in the study of other sub-Antarctic intertidal communities including the Strait of Magellan (Ríos & Mutschke, 1999). The high abundance of Oligochaete sp. may be due to higher sedimentation at the lower exposure sites, as similar patterns have been found in high-sediment mussel beds in other studies (Commito, 1987). Equally, the considerably lower abundance at Cape Pembroke may be a result of reduced sedimentation due to exposure (Prathep *et al*., 2003). This might explain the high abundance of detritivores, associated with higher rates of sedimentation either by biodeposition or by physical forces (Bustamante & Branch, 1996a; Widdows & Brinsley, 2002; Prathep et al., 2003), creating a nutritionally rich matrix for the infaunal assemblage (Seed, 1996).

Unlike the two sheltered sites, grazers were extremely abundant at Cape Pembroke, which may be facilitated by higher abundance of intertidal benthic diatom films in exposed locations Thompson *et al*. (2005), which would provide more food resources for intertidal grazers. The high abundances of grazers in the Cape Pembroke communities may also be attributed to increased epiphytic growth on the mussels at the exposed site (Bustamante & Branch, 1996). While a higher abundance of active suspension feeders might be expected only in the exposed location if organic sediment is kept in suspension by higher water movement

(Madsen *et al.*, 2001), there was also a similar abundance in the Stanley communities. As with the complexities of significant differences in diversity shown by the results of this study, the higher presence of active suspension feeders at Stanley over Goose Green may imply that exposure is not the only influential factor.

Proportions of several sediment grades were shown to be significantly influential by permutation testing, matching the results of Ricciardi & Bourget (1999) and Prathep *et al*. (2003) who both ascertained that sediment grain size significantly influenced assemblage structure in the intertidal zone. In addition to directly controlling diversity (under the IDH), exposure was shown to be a direct influence on assemblage structure, as shown by permutation testing. However, it may also be an influencing factor in determining other environmental variables, including mussel sizes (Seed, 1976) and sediment profile and transport (Levinton, 1972; Prathep *et al*., 2003). Mussel size profiles may be influenced by exposure, as larger mussels may have a higher probability of being dislodged by wave action and water movement than smaller specimens (Seed, 1976; Tam & Scrosati, 2014). The changing proportions of large mussels as a result of exposure may alter the amount of secondary space and substrate available for infaunal species (Dayton, 1971; Arribas *et al*., 2014), thus altering the amount of refuge space available for prey species and settlement area for sessile infaunal species (Santelices & Martinez, 1988; Valdivia & Thiel, 2006).

Equally, water movement may affect sediment sorting and deposition (Prathep *et al*., 2003; Sundblad *et al*., 2014). A further consequence of the effect of exposure upon mussel size is that different sizes of mussel deposit varying amounts of pseudofaeces and organic matter (Seed, 1996), thus indirectly influencing the profile of patch sediment. One result of this variation in biodeposition could be the effect on resource availability for detritivores as high abundances may be dependent upon the organic material in the sediment (Bonsdorff & Pearson, 1999; Commito, 1987).

The results of regression testing and 2nd-Stage MDS suggest that a feeding function approach is an appropriate alternative to taxonomic analysis of intertidal Falkland Island mussel infauna communities. Both the strong 2nd-stage MDS value of >0.9 and strong positive relationship leave little doubt as to the effectiveness of this approach. This positive result for the analysis is especially important, as this is the first evaluation of a functional group approach in intertidal assemblage classification in the Falkland Islands.

Chapter 6 – General discussion

6.1 General discussion

Mussels are major ecosystem engineers in rocky shores around the world (Seed, 1969; 1976; Lintas & Seed, 1994; Robinson & Griffiths, 2002). The complex matrix created by mussel beds is frequently habitat for communities of molluscs, annelids, amphipods and decapods (Tsuchiya & Nishihira, 1985; Santelices & Martínez, 1988; Peake & Quinn, 1993; Seed, 1996; Svane & Setyobudiandi, 1996; Ragnarsson & Raffaelli, 1999; Valdivia & Thiel, 2006). As such they have been the topic of many studies, specifically infaunal communities (Lintas & Seed, 1994).

Despite this, there is little or no consensus on a suitable sample size for intertidal mussel infaunal studies. As discussed previously, while existing literature offered several examples of how many sample replicates should be taken, there was little testing of appropriate sample area. It was important that an optimal sample size be established into order that the further methodology was effective to achieving further aims of the study (Length, 2001; Underwood & Chapman, 2005). The initial data analysis of this thesis aimed to establish an appropriate, optimal and efficient sample size for further study of intertidal mussel infaunal communities. The results suggested that samples of 0.04-0.0625m^2 were the most representative of the communities than the other smaller sample sizes, based on the generated species-area curve. Dissimilarity and multivariate testing also indicated that the communities in the two largest sample sizes were significantly dissimilar form those of the smaller sizes. The importance of this early chapter should not be underestimated, being the first critical evualation for appropriate sample size (area) for intertidal mussel infaunal studies, a study topic that continues to to important in descriptive, monitoring and experimental research.

The importance of this habitat to infaunal populations, as explained in Chapter 1 (Section 1.5), may be the creation of refuges from physical and biotic stresses for other species living within the engineer populations (Witman & Suchanek, 1984; Gutierrez *et al*., 2003). Communities within mussel beds may experience protection from dessication as the habitat patches may retain a higher level of humidity than surrounding bare substrate (Seed, 1969). The irregular topography and complex structure of mussel beds alters the rate and profile of sediment deposition within the patch and surrounding area (Commito *et al*., 2005). Additionally, biodeposition processes are enhanced by the production of of pseudofaeces, together with faecal aggregates (Haven & Morales-Alamo, 1966; Seed, 1996; van Broekhoven *et al*., 2015).

However, differences in environmental conditions between intertidal sites may contribute towards heterogeneity in infaunal communities. At locations with higher wave exposure the increased intensity of physical disturbance may exclude organisms with lower tolerances (Cornell, 1978; Lenz *et al*., 2004). At locations with low levels of physical disturbance only the most effective competitors species may become successful as biotic disturbance (in the form of competition) becomes a principal influence (Cornell, 1978; Dial & Roughgarden, 1998). The contrasting high levels effects of biotic and physical disturbances may result in dominance by only one or two species in intertidal communities (Ríos & Mutschke, 1999). One group of organisms, Oligochaete sp., was consistently present in high abundances in samples from sheltered sites, both in local and mesoscale studies. This may be explained by higher sedimentation in areas of lower water movement (Commito, 1987; Commito *et al*., 2005) resulting in higher incidence of Oligochaete sp. in the sheltered locations shown in the analyses of Chapters 3, 4 and 5. Similar patterns have also been found in high-sediment mussel habitats (Commito, 1987). Equally, reduced rates of sedimentation may have contributed to the lower abundance of Oligochaetes at exposed sites (Prathep *et al*., 2003). Additionally, increased pseudofaeces deposition by the higher abundance of mussels in sheltered locations may increase resource availability to detritivores such as Oligochaetes. At the exposed sites, however, there was an overall pattern of high abundance of *Lasaea* sp. and amphipod species, the dominance of exposed sites by a few species being similar to results from Lintas & Seed (1994).

Across the range of exposures, the highest species diversity was present at the intermediately exposed sites, with lower diversity at the lower and higher ends of the exposure scale. However, diversity was often higher in exposed sites than sheltered sites. The general pattern of highest species diversity in this study corresponds with similar patterns in rocky shore studies by Bustamante & Branch (1996); Prado & Castilla (2006) and Scrosati & Heaven (2007). This fits with general trends in ecology where habitats subject to an intermediate level of physical and biotic disturbance might be expected to support a higher diversity of organisms (Connell, 1978; Lenz *et al*., 2004). Conversely, at sites where disturbance is low or infrequent, diversity may be reduced as communities are chiefly composed of a few competitive or environmentally tolerant organisms

(Connell, 1978; Dial & Roughgarden, 1998). While this pattern of diversity fits well with the established Intermediate Disturbance Hypothesis (IDH) (Connell, 1978), this theory has been disputed in recent years. Both Svensson *et al*. (2012) and S Fox (2013) dismiss the IDH as being over-simplistic and an attempt to generalise a complex issue, stating that it has been unsupported, both empirically and theoretically. The complexity arises from the possibility that heterogeneity in levels of diversity between habitats is due to a combination of both disturbance and productivity, something not considered by the IDH (van Denderen *et al*., 2014).

Fox (2013) also describes inaccuracy in the application of the IDH as while higher disturbances may decrease organism densities, competition should also decrease. However, this reduced competition would also include the weakening of competitive exclusion, thus maintaining higher numbers of species in areas of higher disturbance (Fox, 2013). Sheil & Burslem (2013) defend the IDH as being supported in several empirical examples, particularly in areas of low disturbance. However, both sides of the debate agree that the IDH may be too simplistic to account for all variability in diversity across all spatial scales but that while the IDH may not be an ideal explanation of diversity differences, it is a useful underlying mechanism (Fox, 2013; Sheil & Burslem, 2013; van Denderen *et al*., 2014). Svensson et al. (2012) also note that the effectiveness of the IDH in studying variation in diversity may depend on the strict definition of diversity, the coexistence of effective competitors and colonisers predicted at intermediate disturbance levels might be supported if diversity is based on peak species richness, with lower emphasis on evenness and abundances. Despite the ongoing debate using metadata and theoretical evidences in the wider ecological community, the results of the data chapters in this thesis would appear to support the IDH, showing an overall U-shaped curve in Shannon-Weiner diversity (H') with a peak at sites with intermediate levels of physical exposure.

Using an alternative functional grouping approach removes inherent dissimilarities resulting from geographically distinct taxonomic assemblages; reduces the requirement for detailed taxonomic identification skills (Fagerstrom, 1991; Zak *et al*., 1994; Gall & Le Duff, 2014) and can also reveal assemblage interactions and dynamics (Bustamante & Branch, 1996b, Ieno, 2006; Tyler *et al*., 2012). When the functional group approach based on feeding method was applied, there was a significant difference in feeding functional diversity between sites of different exposure. As with the taxonomic species approach to assemblage analysis, highest feeding function diversity was present at sites with intermediate levels of exposures. Analysis of community structure between sites matched the findings of some other studies, such as McQuaid & Branch (1985) and Bustamante & Branch (1996), in showing that grazers and detritivores are often key components of infaunal communities in mussel beds. Often these groups were the main contributors towards dissimilarity between sites, possibly resulting from variations in exposure. It is likely that exposure would influence the availability of different resources within the habitat, so directly affecting the feeding structure of the associated communities (Santelices & Martínez, 1988).

One possible consequence of higher exposure, and therefore higher water movement, might be reduction in biodeposition and sedimentation that may result in lower resource availability for detritivores at higher exposure sites (Bonsdorff & Pearson, 1999; Commito, 1987). The opposite situation is indicated by the dominance of detritivores in the sites with low degrees of exposure where deposition of sediment and biodeposits is likely to be higher due to lower water activity (Bustamante & Branch, 1996a; Widdows & Brinsley, 2002; Prathep et al., 2003).

The reduction in deposition of organic material at higher wave exposures may also be expected to support higher numbers of active suspension feeders (Madsen *et al*., 2001), as demonstrated by the higher abundances of these organisms at higher exposure sites in Chapters 3, 4 and 5. Equally, different levels of exposure may alter the availability or suitability of substrate for algal growth, resulting in variations in resources available to grazers (Bustamante & Branch, 1996b; Tomanova *et al*., 2006; Kim *et al*., 2014). For example, Thompson *et al*. (2005) and Kim *et al*. (2014) suggest that higher abundances of diatom films might be associated with higher levels of wave exposure, which may subsequently support higher abundances of grazers.

However, the percentage of organic sediment was not shown to be significantly influential in determining functional assemblage structure. Determining key environmental variables that may drive assemblage patterns is important (Haila, 2002); Canonical Correspondence Analysis being used to indicate such environmental factors. The significant influence of mussel sizes (proportion of small, medium and large) was likely due to the varying availability of secondary substrate and habitat that these provide, particularly for sessile species (Dayton, 1971). Similarly, different sizes of mussels might alter the availability of suspended or deposited organic material (Jungerstam *et al*., 2014), thus influencing the availability of food resources to several feeding functional groups, including active suspension feeders and detritivores (Tsuchiya, 1980; Dahlback & Gunnarsson, 1981; Crisp & Standen, 1988; Hatcher *et al.*, 1994). Differences in some sediment grade proportions were also shown to be significant environmental factors, trapped sediment increasing the amount of habitat available to burrowing organisms but there may also be a negative influence if sedimentation results in habitat instability and layer anoxia (Prathep *et al.*, 2003).

Nevertheless, it is extremely likely that the key environmental variable influencing the structure of infaunal communities at a feeding function level is that of exposure. As discussed previously, wave exposure affects the availability of resources within a habitat (Santelices & Martínez, 1988; Arribas *et al*., 2014; Bryson *et al*., 2014) and therefore may influence other environmental variables. An example of this is the proportion of different sediment grades as different volumes and types of sediment may be deposited or suspended at different wave exposures, including organic compounds (Bonsdorff & Pearson, 1999). Additionally, the degree of wave exposure might influence the size profiles of mussels present (Seed, 1976; Garner & Litvaitis, 2013), thus indirectly altering both the amount of secondary substrate available and volume of biodeposits (Commito, 1987; Widdows & Brinsley, 2002; Prathep *et al.*, 2003).

An understanding of assemblage patterns at biogeographic scales may assist in the study of larger-scale ecosystem processes such as organic energy flows and system functioning (Underwood *et al.*, 2000; Rex *et al.*, 2005; Watson *et al.*, 2011). The majority of biogeographical studies have occurred in the terrestrial environment, and those that do exist in marine systems are frequently limited to using literature metadata (Blackburn & Gaston, 1998; 2001; Brown, 1999).

It might be considered that a grouping approach based on dominant feeding function is appropriate for identifying variations in infaunal assemblage structure both at local and also mesoscales. This has been indicated by the successful application of the feeding function approach in assemblage analysis in Chapters 3, 4 and 5 of this thesis. It was sensible to test the approach at a variety of spatial scales as a species' niche may change across large ranges (Paine, 2010) or else mesoscale patterns might be eclipsed by large-scale changes in ecosystem processes (Rex *et al.*, 2005; Bryson *et al.*, 2014). However, it is also important to consider that within any taxonomic grouping higher than genus, species may have different feeding functions. For example while many chitons (class Polyplacophora) are herbivorous grazers upon algae, there are some species that are highly carnivorous upon arthropods (Latyshev et al., 2004), demonstrating that an understanding of taxonomic group biology is important when assigning feeding functions.

In addition to assemblage analysis, correlation and 2nd Stage MDS testing also indicated that trends in feeding functional assemblage structure were representative of those at a species level at all spatial scales considered in this study. Furthermore, when compared to another functional grouping approach, based on Reproductive mode method, feeding function was shown to be more representative at local scales. In conclusion, the results of Chapters 3, 4 and 5 suggest that a feeding function approach to assemblage analysis of mussel infauna is suitable and representative at local, and regional scales.

The strong correlation shown in both UK and Falkland Islands samples between taxonomic and feeding functional diversity does suggest further implications to understanding of system dynamics. Several studies have discussed the linear relationship between species richness and niche availability within ecosystems, systems with higher richness often having more ecological spaces or niches (Fox, 1981; Duncan *et al*., 1998); Dimitrakopoulos & Schmid, 2004). Whether the increased richness is a consequence of a higher amount of ecological space being available or whether niche space is facilitated by the presence of higher numbers of taxa is unclear and further demonstrates the complexities that arise when studying ecosystem functioning (Duncan *et al*., 1998; Rangel *et al*., 2007). There may also be further implications for ecosystem processes such as colonisation, succession and facilitation of settlement, as discussed by Margalef (1963). It may also not be inappropriate to suggest that this potential for a linear relationship has implications not only for studies of infaunal assemblages but also in the wider context of larger ecological questions, such as the debate between neutral and niche theories (Hubbell, 2001; Krebs, 2006). The convergence of influences on infaunal assemblages shown in this study might even go so far as to support an integrated ecological theory (Watson *et al*., 2011), combining factors that would appear to maintain niche theory (see Leibold, 1995), such as feeding functional groups and environmental variables, and components closer to neutral theory (see

Hubbell, 2001) including those which may influence over larger-scales such as reproductive mode.

6.2 Opportunities for further work

To quote the poet Paul Valéry, "A work is never completed except by some accident" (Valéry. 1964). Logistical limitations are always present in research and so the sites sampled and the communities analysed within this thesis were to the maximum extent that proved practical. However, there are obvious avenues for further investigation into the topics covered in this thesis, particularly with reference to the feeding functional grouping approach. Additional sample sites with low-intermediate or intermediate-high exposures might be beneficial in identifying transitional patterns in heterogeneity between sites. The inclusion of an intermediate site in the Falkland Islands would have been advantageous, particularly to identify whether a distinct assemblage structure might be present between high and low exposures, as possibly suggested by the spread of MDS points for Stanley (Figures 5.4 and 5.6). Despite the potential advantages that such a site might afford in understanding infaunal assemblage structure in Falkland Islands mussel beds, constraints on time and access during the field sampling made using such a site quite unfeasible. As a temperate marine assemblage, it is also likely that Falkland Island infaunal assemblage structure experiences seasonal variation, as seen in UK samples (Section 2.3.1), but logistical constraints also prevented seasonal sampling. A similar argument might be made for additional sample sites in the UK, perhaps including sheltered, intermediate and exposed locations in the north, south, east and west of the region but, as with the Falkland Islands, sampling opportunities were limited and sample processing time remains considerable.

Given the flexibility of the feeding function approach in studying assemblage structure, there are palpable opportunities for it to be employed in the wider ecological context. The infaunal communities of other ecosystem engineers in the intertidal zone, such as macroalgae have been studied extensively, including Colman (1939); Everett (1991); Kelaher *et al.* (2001) and Christie *et al.* (2009). The methodologies used in these studies when describing communities are often comparable to that used in this thesis, suggesting that a feeding functional approach might be suitable for other engineered habitats. The potential for this may be seen in the expansion of feeding functional groupings in soft sediment assemblage studies such as Pinn & Robertson (2003); Thrush *et al*. (2006) and MacDonald *et al*. (2010).

As discussed previously, knowledge of the functional diversity and structure of assemblages might allow for the development and modeling of energy flow through the systems (Steneck & Dethier, 1982; Polis & Strong, 1996). However, it must be remembered that the complexity of energy flows within ecosystems makes such modeling far from simple (Zak & Visser, 1996). Despite this, further work to establish biomass and quantify energy within each trophic level (Polis & Strong, 1996) might allow for the mapping of energy flows through a system, following a structure as displayed in the example in Figure 6.1

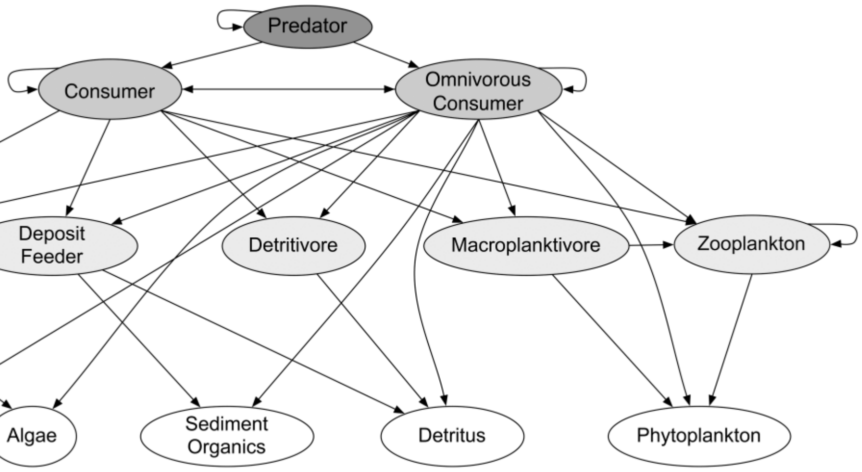

Figure 6.1: From Byrnes *et al*. (2007), food web showing connections between all trophic functional groups. Arrows represent one group consuming the group to which the arrow points. Shading indicates trophic level (none = 1, light = 2, moderate = 3, dark = 4)

Once expanded into other engineered habitats within rocky shores, there is the prospective for implications of a feeding functional grouping for rocky shore communities to be developed into an ecological monitoring system. Precedent for this kind of outcome has already been set in soft-sediment systems by programs such as the Ecological Evaluation Index (Orfanidis *et al*., 2003). Beyond satisfying scientific curiosity and detecting variations at local scales, such monitoring systems can have importance within global ecological issues. Various groups of researchers have concerns over future ecological issues on the global perspective, one of the forerunners being negative anthropomorphic influences (Cheung *et al.*, 2009). Such influences may include pollution, including oil spills (Fukuyama *et al.*, 2014); climate change (Helmuth *et al.*, 2006; Schückel & Kröncke, 2013); invasive organisms (Arenas *et al.*, 2009; Bax *et al.*, 2003) and aquaculture (Wilding & Nickell, 2013). Coastal systems are often considered susceptible to these events, often due to their proximity to human activity (Cheung *et al.*, 2009). Monitoring coarse changes in assemblage patterns at a functional level may not only show variations in assemblage structure but also indicate changes in ecosystem processes (MacNeil *et al.*, 1997; Petchey & Gaston, 2006) and feed into wider monitoring of marine biodiversity.

In conclusion, while strict patterns of assemblage structure were not shown to be constant across local and regional scales, a novel method based on dominant feeding functional grouping has been identified. Additionally, the results both supported and questioned several ecological theories, presenting opportunities for future exploration of theories such as the IDH and niche versus neutral theory using a functional grouping approach. The suitability of the feeding functional grouping approach has been established in communities separated by thousands of miles and almost entirely dissimilar at a traditional species level. The ecological data collected in the course of this study has also provided entirely new information on the infaunal assemblage of Falkland Island intertidal mussel beds, an assemblage not before studied. It is hoped that the results of this investigation may contribute to the future of research into the richness and diversity of intertidal ecosystems.

References

Aarset, A.V. & Zachariassen, K.E. (1982) Effects of oil pollution on the freezing tolerance and solute concentration of the blue mussel *Mytilus edulis. Marine Biology* **72**:45-51

Abele, L.G. & Walters, K. (1979) Marine benthic diversity: a critique and alternative explanations. *Journal of Biogeography* **6**:115-126

Adrianov, A.V. & Maiorova, A.S. (2010) Reproduction and development of common species of peanut worms (Sipuncula) from the Sea of Japan. *Russian Journal of Marine Biology* **36**:1-15

Agnew, D.J. (2002) Critical aspects of the Falkland Islands pelagic ecosystem: distribution, spawning and migration of pelagic animals in relation to oil exploration. *Aquatic Conservation: Marine and Freshwater Ecosystems* **12**:39–50

Aldred, N., Ista, L.K., Callow, M.E., Callow, J.A., Lopez, G.P. & Clare, A.S. (2006) Mussel (*Mytilus edulis*) byssus deposition in response to variations in surface wettability. *Journal of The Royal Society Interface* **3**:37-43.

Alheit, J. & Niquen, M. (2004) Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography* **60**:201-222

Allen, J.A., Cook, M., Jackson, D.J., Preston, S. & Worth, E.M. (1976) Observations on the rate of production and mechanical properties of the byssus threads of *Mytilus edulis* L. *Journal of Molluscan Studies* **42**:279-289

Alonso, D., Etienne, R.S. & McKane, A.J. (2006) The merits of neutral theory. *Trends in Ecology and Evolution* **21**:451-457

Anderson, D.R. (2001) The need to get the basics right in wildlife field studies. *Wildlife Society Bulletin* **29**:1294-1297

Anderson, M. & Ter Brakk, C.J.F. (2003) Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* **73**:85–113

Anestis, A., Portner, H.O., Lazou, A. & Michaelidis, B. (2008) Metabolic and molecular stress responses of sublittoral bearded horse mussel *Modiolus barbatus* to warming sea water, implications for vertical zonation. *Journal of Experimental Biology* **21**:2889-2898

Arenas, F., Sanchez, I., Hawkins, S.J. & Jenkins, S.R. (2006) The invasibility of marine algal assemblages: role of functional diversity and identity. *Ecology* **87**:2851–2861

Arhan, M., Naveira Garabato, A.C., Heywood, K.J. & Stevens, D.P. (2002) The Antarctic Circumpolar Current between the Falkland Islands and South Georgia. *Journal of Physical Oceanography* **32**:1914-1931

Arkhipkin, A.I., Laptikhovsky, V.V., Sirota, A.M. & Grzebielec, R. (2006) The role of the Falkland Current in the dispersal of the squid *Loligo gahi* along the Patagonian Shelf. *Estuarine, Coastal and Shelf Science* **67**:198-204

Arribas, L.P., Donnarumma, L., Palomo, M.G. & Scrosati, R.A. (2014) Intertidal mussels as ecosystem engineers: their associated invertebrate biodiversity under contrasting wave exposures. *Marine Biodiversity* **44**:203-211

Ashford, J.R., Fach, B.A., Arkhipkin, A.I. & Jones, C.M. (2012) Testing early life connectivity supplying a marine fishery around the Falkland Islands. *Fisheries Research* **121-122**:144–152

Asmus, H. (1987) Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. *Marine Ecology Progress Series* **39**:251-266

Asmus, R.M. & Asmus, H. (1991) Mussel beds: limiting or promoting phytoplankton? *Journal of Experimental Marine Biology and Ecology* **148**:215-232

Ayre D.J., Minchinton, T.E. & Perrin, C. (2009) Does life history predict past and current connectivity for rocky intertidal invertebrates across a marine biogeographic barrier? *Molecular Ecology* **18:**1887–1903

Bairati, A. & Zuccarello, L.V. (1976) The ultrastructure of the byssal apparatus of *Mytilus galloprovincialis*. *Cell and tissue research* **166**:219-234

Baker, H.G. (1972) Seed weight in relation to environmental conditions in California. *Ecology* **53**:997-1010

Bale, A.J. & Kenny, A.J. (2005) *Sediment Analysis and Seabed Characterisation*. In: Methods for the Study of Marine Benthos. 3rd Edition. Eleftheriou, A. & McIntyre, A. eds. Blackwell Science Ltd. – Oxford, UK

Ballantine, D. & Morton, J.E. (1956) Filtering, feeding, and digestion in the lamellibranch *Lasaea rubra. Journal of the Marine Biological Association of the United Kingdom* **35**:241-274

Ballentine, W. J. (1961) A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies* **1**:1–19

Barnes, D.K.A. & De Grave, S. (2001) Ecological biogeography of southern polar encrusting faunas. *Journal of Biogeography* **28**:359-365

Barnes, D.K.A. & Lehane, C. (2001) Competition, mortality and diversity in South Atlantic coastal boulder communities. *Polar Biology* **24**:200-208

Barnes, D.K.A. & Griffiths, H.J. (2008) Biodiversity and biogeography of southern temperate and polar bryozoans. *Global Ecology and Biogeography* **17:**84–99

Barrell, J. & Grant, J. (2015) High-resolution, low-altitude aerial photography in physical geography: A case study characterizing eelgrass (*Zostera marina* L.) and blue mussel (*Mytilus edulis* L.) landscape mosaic structure. *Progress in Physical Geography* doi: 10.1177/0309133315578943

Barton, J. (2002) Fisheries and fisheries management in Falkland Islands conservation zones. *Aquatic Conservation: Marine and Freshwater Ecosystems* **12**:127-135

Bax, N., Williamson, A., Aguero, M., Gonzalez, E. & Geeves, W. (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy* **27**:313-323

Bayne, B.L. (1964) Primary and Secondary Settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* **33**:513-523

Bayne, B.L. (1976) *The Biology of Mussel Larvae* In: Marine Mussels: Their Ecology and Physiology (Bayne, B.L., ed.). pp.81-115 Cambridge University Press-Cambridge, UK

Bayne, B.L., Holland, D.L., Moore, M.N., Lowe, D.M. & Widdows, J. (1978) Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom* **58**:825-841

Bayne, B.L. & Worrall, C. M. (1980) Growth and production of mussels *Mytilus edulis* from two populations. *Marine Ecology Progress Series* **3**:317-328

Bayne, B.L., Salkeld, P.N. & Worrall, C.M. (1983) Reproductive effort and value in different populations of the marine mussel, *Mytilus edulis* L. *Oecologia* **59**:18-26

Bayne, B.L., Iglesias, J.I.P., Hawkins, A.J.S., Navarro, E., Heral, M. & Deslous-Paoli, J.M. (1993) Feeding behaviour of the mussel, *Mytilus edulis*: responses to variations in quantity and organic content of the seston. *Journal of the Marine Biological Association of the United Kingdom* **73**:813-829

Beaumont, A.R. & Budd, M.D. (1982) Delayed growth of mussel (*Mytilus edulis*) and scallop (*Pecten maximus*) veligers at low temperatures. Marine Biology **71**:97-100

Bell, E. & Gosline, J. (1996) Mechanical design of mussel byssus: material yield enhances attachment strength. *Journal of Experimental Biology* **199**:1005-1017

Bell, G. (2001) Neutral Macroecology. *Science* **293**:2413-2418

Bellwood, D.R., Hughes, T.P. & Hoey, A.S. (2006) Sleeping Functional Group Drives Coral-Reef Recovery. *Current Biology* **16**:2434-2439

Benedetti-Cecchi, L. & Cinelli, F. (1997) Spatial distribution of algae and invertebrates in the rocky intertidal zone of the Strait of Magellan: are patterns general? *Polar Biology* **18**:337-343

Bengtsson, J. (1998) Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Applied Soil Ecology* **10**:191-199

Bertness, M.D. & Grosholz, E. (1985) Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* **67**:192-204

Bertness, M.D. & Leonard, G.H. (1997) The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* **78**:1976-1989

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R. & Ingraham, A.O. (1999a) Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* **80**:2711–2726

Bertness, M.D., Crain, C.M., Silliman, B.R., Bazterrica, M.C., Reyna, M.V., Hidalgo, F. & Farina, J.K. (2006) The community structure of western Atlantic Patagonian rocky shores. *Ecological Monographs* **76**:439-460

Biggs, B.J.F. (1995) The contribution of flood disturbance, catchment geology and land use to the habitat template of periphyton in stream ecosystems. *Freshwater Biology* **33**:419-438

Bingham, M.I.K.E. (2002) The decline of Falkland Islands penguins in the presence of a commercial fishing industry. *Revista Chilena de Historia Natural* **75**:805-818

Bisbal, G.A. (1995) The Southeast South American shelf large marine ecosystem: evolution and components. *Marine Policy* **19**:21-38

Blackburn, T.M. & Gaston, K.J. (1998) Some methodological issues in macroecology. *The American Naturalist* **151**:68-83

Blackburn, T.M. & Gaston, K.J. (2001) Linking patterns in macroecology. *Journal of Animal Ecology* **70:**338–352

Blanchette, C.A., Miner, C.M., Raimondi, P.T., Lohse, D., Heady, K.E.K. & Broitman, B.R. (2008) Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. *Journal of Biogeography* **35**:1593–1607

Blondel, J. (2003) Guilds or functional groups: does it matter? *OIKOS* **100**:223–231

Bongers, T. & Bongers, M. (1998) Functional diversity of nematodes. *Applied Soil Ecology* **72**:453-559

Bonsdorff, E. & Pearson, T.H. (1999) Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional-group approach. *Australian Journal of Ecology* **24**:312–326

Booth, J.D. (1977) Common bivalve larvae from New Zealand: Mytilacea. *New Zealand Journal of Marine and Freshwater Research* **11**:407-440

Borja, A., Elliott, M., Carstensen, J., Heiskanen A-S. & van der Bund, W. (2010) Marine management- towards an integrated implementation of the European Marine Strategy Framework and Water Framework Directive. *Marine Pollution Bulletin* **60**:2175-2186

Borthagaray, A.I. & Carranza, A. (2007) Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. *Acta Oecologica* **31**:243-250

Bosman, A.L., Hockey, P.A.R. & Siegfried, W.R. (1987) The influence of coastal upwelling on the functional structure of rocky intertidal communities. *Oecologia* **72**:226-232

Bostrom, C., Jackson, E.L. & Simenstad, C.A. (2006) Seagrass landscapes and their effects on associated fauna: A review. *Estuarine, Coastal and Shelf Science* **68**: 383-403

Bowden, D.A., Rowden, A.A. & Attrill, J.A. (2001) Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. *Journal of Experimental Marine Biology and Ecology* **259**:133-154

Branch, G.M., Odendaal, F. & Robinson, T.B. (2008) Long-term monitoring of the arrival, expansion and effects of the alien mussel *Mytilus galloprovincialis* relative to wave action. *Marine Ecology Progress Series* **370**: 171–183

Bremner, J., Rogers, S.I. & Frid, C.L.J. (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series* **254**:11-25

Bremner, J., Rogers, S.I. & Frid, C.L.J. (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators* **6**:609-622

Brenko, M.H. & Calabrese, A. (1969) The combined effects of salinity and temperature on larvae of the mussel *Mytilus edulis*. *Marine Biology* **4**:224-226

Bricelj, V.M., Lee, J.H., Cembella, A.D. & Anderson, D.M. (1990) Uptake kinetics of paralytic shellfish toxins from the dinoflagellate *Alexandrium fundyense* in the mussel *Mytilus edulis*. *Marine Ecology Progress Series* **63**:177-188

Briggs, J.C. (2007) Marine biogeography and ecology: invasions and introductions. *Journal of Biogeography* **34**:193–198

Broom, J.E.S., Nelson, W.A., Farr, T.J., Phillips, L.E. & Clayton, M. (2010) Relationships of the Porphyra (Bangiales, Rhodophyta) flora of the Falkland Islands: a molecular survey using rbcL and nSSU sequence data. *Australian Systematic Botany* **23**:27-37

Brown, J.H. (1971) Mammals on mountaintops: nonequilibrium insular biogeography. *The American Naturalist* **105:**467-478

Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science* **243:**1145–1150

Brown, J.H. (1999) Macroecology: Progress and Prospect. *Oikos* **87**:3-14

Bryson, E.S., Trussell, G.C. & Ewanchuk, P.J. (2014) Broad-scale geographic variation in the organization of rocky intertidal communities in the Gulf of Maine. *Ecological Monographs,* **84**:579-597

Buck, B. H., Thieltges, D. W., Walter, U., Nehls, G., Rosenthal, H. (2005) Inshore–offshore comparison of parasite infestation in *Mytilus edulis*: implications for open ocean aquaculture. *Journal of Applied Ichthyology* **21**:107-113

Buckley, H.L. & Freckleton, R.P. (2010) Understanding the role of species dynamics in abundance–occupancy relationships. *Journal of Ecology* **98**:645–658

Burnham, K.P. & Overton, W.S. (1979) Robust estimation of population size when capture probabilities vary among animals. *Ecology* **60**:927–936

Buschbaum, C., Dittman, S., Hong, J.S., Hwang, I.S., Strasser, M., Thiel, M., Valdivia, N., Yoon, S.P. & Reise, K. (2009) Mytilid mussels: global habitat engineers in coastal sediments. *Helgoland Marine Research* **63**:47-58

Bustamante, R.H. & Branch, G.M. (1996) Large Scale Patterns and Trophic Structure of Southern African Rocky Shores: The Roles of Geographic Variation and Wave Exposure. *Journal of Biogeography* **23**:339-351

Bustamante, R.H. & Branch, G.M. (1996a) The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *Journal of Experimental Marine Biology and Ecology* **196:**1-28

Bustamante, M., Tajadura, J., Gorostiaga, J.M. & Saiz-Salinas, J.I. (2014) Response of rocky invertebrate diversity, structure and function to the vertical layering of vegetation. *Estuarine, Coastal and Shelf Science* **147**:148-155

Byrnes, J.E., Reynolds, P.L. & Stachowicz, J.J. (2007) Invasions and Extinctions Reshape Coastal Marine Food Webs. *PLoS ONE* **2**:e295. doi:10.1371/journal.pone.0000295

Cabral-Oliveira, J., Mendes, S., Maranhão, P. & Pardal, M.A. (2014) Effects of sewage pollution on the structure of rocky shore macroinvertebrate assemblages. *Hydrobiologia* **726**:271-283

Cadotte, M.W., Murray, B.R. & Lovett-Doust, J. (2006) Ecological patterns and biological invasions: using regional species inventories in macroecology. *Biological Invasions* **8**:809–821

Cain, S.A. (1934) The Species-Area Curve. *American Midland Naturalist* **19**:573-581

Calderwood, J., O'Connor, N.E. & Roberts, D. (2016) Breaking and entering: Examining the role of stress and aerial exposure in predator–prey relationships between the common shore crab (*Carcinus maenas*) and cultivated blue mussels (*Mytilus edulis*). *Aquaculture* **452**:217–223

Camacho, A.P., Labarta, U. & Beiras, R. (1995) Growth of mussels (*Mytilus edulis galloprovincialis*) on cultivation rafts: influence of seed source, cultivation site and phytoplankton availability. *Aquaculture* **138**:349-362

Cao, Y., Williams, D.D. & Larsen, D.P. (2002) Comparison of Ecological Communities: The Problem of Sample Representativeness. *Ecological Monographs* **72**:41-56

Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R. & Largier, J.L. (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications* **13**:90-107

Carstensen, J., Conley, D.J. & Henriksen, P. (2004) Frequency, composition, and causes of summer phytoplankton blooms in a shallow coastal ecosystem, the Kattegat. *Limnology and Oceanography* **49**:190-201

Cartwright, S.R. & Williams, G.A. (2014) How hot for how long? The potential role of heat intensity and duration in moderating the beneficial effects of an ecosystem engineer on rocky shores. *Marine Biology* **161**:2097-2105

Casey, M.M. & Chattopadhyay, D. (2008) Clumping behavior as a strategy against drilling predation: Implications for the fossil record. *Journal of Experimental Marine Biology and Ecology* **367**:174-179

Castenholz, R.W. (1961) The effect of grazing on marine littoral diatom populations. *Ecology* **42**:783-794

Castilla, J.C. & Guiñez, R. (2000) Disjoint geographical distribution of intertidal and nearshore benthic invertebrates in the Southern Hemisphere. *Revista Chilena de Historia Natural* **75**:585-603

Catterall, C.P. & Poiner, I.R. (1987) The potential impact of human gathering on shellfish populations, with reference to some NE Australian intertidal flats. *OIKOS* **50**:114-122

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Díaz, S. (2000). Consequences of changing biodiversity. *Nature* **405**:234-242

Chapman, M. G., Tolhurst, T. J., Murphy, R. J. & Underwood, A. J. (2010) Complex and inconsistent patterns of variation in benthos, micro-algae and sediment over multiple spatial scales. *Marine Ecology Progress Series* **398**:33-47

Chappuis, E., Terradas, M., Cefalì, M.E., Mariani, S. & Ballesteros, E. (2014) Vertical zonation is the main distribution pattern of littoral assemblages on rocky shores at a regional scale. *Estuarine, Coastal and Shelf Science* **147**:113-122

Cheung, W.W.L. & Pitcher, T.J. (2005) A mass-balance model of the marine ecosystem and fisheries of the Falkland Islands. In: Palomares, M.L.D., Pruvost, P., Pitcher, T.J. & Pauly, D. (eds.) Modeling Antarctic marine ecosystems. *Fisheries Centre Research Reports* **13**:65-84

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K, Watson, R. & Pauly, D. (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**:235–251

Chiba, S. & Noda, T. (2000) Factors maintaining topography-related mosaic of barnacle and mussel on a rocky shore. *Journal of the Marine Biological Association of the U.K.* **80**:617-622

Chipperfield, P.N.J. (1953) Obseravtions on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *Journal of the Marine Biological Association of the United Kingdom.* **32**:449-476

Christie, H., Norderhaug, K.M., & Fredriksen, S. (2009) Macrophytes as habitat for fauna. *Marine Ecology Progress Series* **396**:165–306

Clarke, A. & Lidgard, S. (2000) Spatial patterns of diversity in the sea: bryozoan species richness in the North Atlantic. *Journal of Animal Ecology* **69:**799-814

Clarke, A., Griffiths, H.J., Linse, K., Barnes, D.K.A. & Crame, J.A. (2007) How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs. *Diversity and Distributions* **13**:620–632

Clarke, K.R. (1990) Comparisons of dominance curves. *Journal of Experimental Marine Biology and Ecology* **138**:143–157

Clarke, K.R. & Warwick, R.M. (2001) *Change in Marine Communities: An approach to statistical analysis and interpretation*. 2nd Edition. PRIMER-E Ltd.-Plymouth

Clarke, K.R., Somerfield, P.J., Airoldi, L. & Warwick, R.M. (2006) Exploring interactions by second-stage community analysis. *Journal of Experimental Marine Biology and Ecology* **338**:179-192

Clarke, K.R., Chapman, M.G., Somerfield, P.J. & Needham, H.R. (2006a) Dispersion-based weighting of species counts in assemblage analyses. *Marine Ecology Progress Series* **320**:11-27

Coates, M. (1998) A comparison of intertidal assemblages on exposed and sheltered tropical and temperate rocky shores. *Global Ecology and Biogeography Letters* **7**:115–124

Cochran, W.G. (1963) *Sampling techniques*. 2nd Edition. John Wiley & Sons - New York

Cole, V.J. & McQuaid, C.D. (2010) Bioengineers and their associated fauna respond differently to the effects of biogeography and upwelling. *Ecology* **91:**3549-3562

Commito, J.A. (1987) Adult-larval interactions: predictions, mussels and cocoons. *Estuarine, Coastal and Shelf Science* **25**:599-606

Commito, J.A. & Boncavage, E.M. (1989) Suspension-feeders and co-existing infauna: an enhancement counterexample. *Journal of Experimental Marine Biology and Ecology* **125**:33-42

Commito, J.A. & Rusignuolo, B.R. (2000) Structural complexity in mussel beds: the fractal geometry of surface topography. *Journal of Experimental Marine Biology and Ecology* **255**:133–152

Commito, J.A., Celano, E.A., Celico, H.J., Como, S. & Johnson, C.P. (2005) Mussels matter: postlarval dispersal dynamics altered by a spatially complex ecosystem engineer. *Journal of Experimental Marine Biology and Ecology* **316**:133–147

Connell, J.H. (1972) Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* **3**:169-192

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *The American Naturalist* **111**:1119-1144

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science* **199**:1302-1310

Connell, J.H. (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **93**:11-45

Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species-area relationship. *The American Naturalist* **113**:791-833

Coolidge, S. (1880) *On the Shore*. In: *Verses*. Roberts brothers, Boston

Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**:1-12

Côté, I.M. (1995) Effects of predatory crab effluent on byssus production in mussels. *Journal of Experimental Marine Biology and Ecology* **188**:233-241

Côté, I.M. & Jelnikar, E. (1999) Predator-induced clumping behaviour in mussels (*Mytilus edulis* Linnaeus). *Journal of Experimental Marine Biology and Ecology* **235**:201-211

Cowen, R.K. & Sponaugle, S. (2009) Larval Dispersal and Marine Population Connectivity. *Annual Review of Marine Science* **1**:443–66

Craeymeersch, J.A., Herman, P.M.J. & Meire, P.M. (1986) Secondary production of an intertidal mussel (*Mytilus edulis* L.) population in the Eastern Scheldt (S.W. Netherlands). *Hydrobiologia* **133**:107-115

Crain, C.M. & Bertness, M.D. (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. *BioScience* **56**:211-218

Creese, R., Hooker, S., De Luca, S. & Wharton, Y. (1997) Ecology and environmental impact of *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae) in Tamaki Estuary, Auckland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **31**:225-236

Crisp, D.J. & Standen, A. (1988) *Lasaea rubra* (Montagu) (Bivalvia : Erycinacea), an apomictic crevice-living bivalve with clones separated by tidal level preference. *Journal of Experimental Marine Biology and Ecology* **117**:27-45

Crooks, J.A. & Khim, H.S. (1999) Architectural vs. biological effects of a habitat-altering exotic mussel, *Musculista senhousia. Journal of Experimental Marine Biology and Ecology* **240**:53-75

Croxall, J. P., & Wood, A. G. (2002). The importance of the Patagonian Shelf for top predator species breeding at South Georgia. *Aquatic Conservation: Marine and Freshwater Ecosystems* **12**:101-118

Cummins, K.W (1973) Trophic relations of aquatic insects. *Annual Review of Entomology* **18**:183-206

Cummins, K.W. (1974) Structure and function of stream ecosystems. *BioScience* **24**:631-641

Cummins, K.W. & Klug, M.J. (1979) Feeding Ecology of Stream Invertebrates. *Annual Review of Ecology and Systematics* **10**:147-172

da Costa, F., Aranda-Burgos, J.A., Cerviño-Otero, A., Fernández-Pardo, A., Louzán, A.,, Nóvoa, S. & Martínez-Patiño, D. (2012) Clam reproduction. *Clam Fisheries and Aquaculture* **45**

Dahlback, B. & Gunnarsson, L.A.H. (1981) Sedimentation and sulfate reduction under a mussel culture. *Marine Biology* **63**:269–275

Damianidis, P. & Chintiroglou, C.C. (1998) Feeding guilds of polychaetes associated with *Mytilus galloprovincialis* (Lam.) assemblage in the north Aegean Sea. *Rapp. Comm. int. Mer Médit* **35**:416-417

Daneri, G., Dellarossa, V., Quinones, R., Jacob, B., Montero, P. & Ulloa, O. (2000) Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Marine Ecology Progress Series* **197**:41-49

Dare, P.J. & Davies, G. (1975) Experimental suspended culture of mussels (*Mytilus edulis* L.) in Wales using spat transplanted from a distant settlement ground. *Aquaculture* **6**:257-274

Darwin, C. & Wallace, A. (1858) On the tendency of species to form varieties, and on the perpetuation of varieties and species by natural means of selection. *Journal of the Proceedings of the Linnean Society of London, Zoology* **3**:45–62

Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*. John Murray - London

Davenport, J. & Davenport, J. (1984) A preliminary assessment of growth rates of mussels from the Falkland Islands (*Mytilus chilensis* Hupe and *Aulacomya ater* (Molina)). *J. Cons. int. Explor. Mer.* **41**:154-158

Davenport, J. & Stevenson, T.D.I. (1998) Intertidal colonization rates. A matched latitude, north *v*. south, remote v. near shore island experiment. *Diversity and Distributions* **4**:87–92

Day, R.W., Barkai, A. & Wickens, P.A. (1991) Trapping of three drilling whelks by two species of mussel. *Journal of Experimental Marine Biology and Ecology* **149:**109-122

Dayton, P.K. (1971) Competition, disturbance and community organisation: the provision and subsequent utilisation of space in a rocky intertidal community. *Ecological Monographs* **41**:351-389

Denny, M. (1995) Predicting Physical Disturbance: Mechanistic Approaches to the Study of Survivorship on Wave-Swept Shores. *Ecological Monographs* **65**:371-418

Desmond, A.J. (1979) Designing the Dinosaur: Richard Owen's Response to Robert Edmond Grant. *Isis* **70**:224-234

Dethier, M.N. (1994) The ecology of intertidal algal crusts: variation within a functional group. *Journal of Experimental Marine Biology and Ecology* **177**:37-71

Dial, R. & Roughgarden, J. (1998) Theory of marine communities: the intermediate disturbance hypothesis. *Ecology* **79**:1412-1424

Dimitrakopoulos, P.G., & Schmid, B. (2004) Biodiversity effects increase linearly with biotope space. *Ecology Letters* **7**:574-583

Dittmann, S. (1990) Mussel beds—amensalism or amelioration for intertidal fauna? *Helgoländer Meeresuntersuchungen* **44**:335-352

Dolmer, P. (2000) Feeding activity of mussels *Mytilus edulis* related to near-bed currents and phytoplankton biomass. *Journal of Sea Research* **44**:221-231

Dornelas, M., Connolly, S.R. & Hughes, T.P. (2006) Coral reef diversity refutes the neutral theory of biodiversity. *Nature* **440**:80-82

Dring, M.J. (1992) *The Biology of Marine Plants*. Cambridge University Press-Cambridge

Duffy, J.E. (1990) Amphipods on seaweeds: partners or pests? *Oecologia* **83**:267-276

￼￼Duffy, J.E. (2006) Biodiversity and the functioning of seagrass ecosystems. *Marine Ecology Progress Series* **311**:233-250

Duncan, R.P., Buckley, H.L., Urlich, S.C., Stewart, G.H., & Geritzlehner, J. (1998) Small-scale species richness in forest canopy gaps: the role of niche limitation versus the size of the species pool. *Journal of Vegetation Science* **9**:455-460

Edwards, D. (1998) Issues and Themes for Natural Resources Trend and Change Detection. *Ecological Applications* **8**:323-325

Eilertsen, H.C., Taasen, J.P. & WesIawski, J.M. (1989) Phytoplankton studies in the fjords of West Spitzbergen: physical environment and production in spring and summer. *Journal of Plankton Research* **11**:1245-1260

Eleftheriou, A. & Moore, D.C. (2005) Macrofauna Techniques, In: *Methods for the Study of Marine Benthos.* 3rd Edition. Eleftheriou, A. & McIntyre, A. Eds. Blackwell Science Ltd.- Oxford

Elías, R., Rivero, M.S. & Vallarino, E.A. (2003) Sewage impact on the composition and distribution of polychaeta associated to intertidal mussel beds of the Mar del Plata rocky shore, Argentina. *Iheringia, Sér. Zool., Porto Alegre* **93**:309-318

Elliott, M. & Dewailly, F. (1995) The structure and functioning of European estuarine fish assemblages. *Netherlands Journal of Aquatic Ecology* **29**:397-417

Elliott, M., Whitfield, A.K., Potter, I.C., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G. & Harrison, T.D. (2007) The guild approach to categorizing estuarine fish assemblages: a global review. *Fish and Fisheries* **8**:241–268

Elner, R.W. (1978) The Mechanics of Predation by the Shore Crab, *Carcinus maenas* (L.), on the Edible Mussel, *Mytilus edulis* L. *Oecologia* **36**:333-344

Elton, C.S. (1927) *Animal Ecology*. University of Chicago Press - USA

Emson, R.H. (1977) The feeding and consequent role of *Eulalia viridis* (OF Müller)(Polychaeta) in intertidal communities. *Journal of the Marine Biological Association of the United Kingdom* **57**:93-96

Engle, V.D. & Summers, J.K. (1999) Latitudinal gradients in benthic community composition in Western Atlantic estuaries. *Journal of Biogeography* **26:**1007–1023

Ensom, P. (2009) *Yorkshire Geology*. The Dovecote Press Ltd. – UK

Escribano, R., Fernández, M. & Aranís, A. (2003) Physical-chemical processes and patterns of diversity of the Chilean eastern boundary pelagic and benthic marine ecosystems: an overview. *Gayana* **67**:190-205

Etienne, R.S., Alonso, D. & McKanec, A.J. (2007) The zero-sum assumption in neutral biodiversity theory. *Journal of Theoretical Biology* **248**:522–536

Everett, R.A. (1991) Intertidal distribution of infauna in a central California lagoon: the role of seasonal blooms of macroalgae. *Journal of Experimental Marine Biology and Ecology* **150**:223-247

Eyster, L.S. & Pechenik, J.A. (1987) Attachment of *Mytilus edulis* L. larvae on algal and byssal filaments is enhanced by water agitation. *Journal of Experimental Marine Biology and Ecology* **114**:99-110

Fagerstrom, J.A. (1991) Reef-building guilds and a checklist for determining guild membership: a new approach for study of communities. *Coral Reefs* **10**:47-52

Fairweather, P.G. (1991) Implications of 'supply-side' ecology for environmental assessment and management. *TRENDS in Ecology & Evolution* **6**:60-63

Farrell, T.M. (1991) Models and mechanisms of succession: an example from a rocky intertidal community. *Ecological Monographs* **61**:95-113

Farrell, P. & Nelson, K. (2013) Trophic level transfer of microplastic: *Mytilus edulis* (L.) to *Carcinus maenas* (L.). *Environmental Pollution* **177**:1-3.

Fauchald, K. & Jumars, P.A. (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanography & Marine Biology, an Annual Review* **17**:193-284

Feare, C.J. (1970) Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus* (L.). *Oecologia* **5**:1-18

Feio, M.J. & Dolédec, S. (2012) Integration of invertebrate traits into predictive models for indirect assessment of stream functional integrity: A case study in Portugal. *Ecological Indicators* **15**:236–247

Fenberg, P.B., Menge, B.A., Raimondi, P.T. & Rivadeneira, M.M. (2015) Biogeographic structure of the northeastern Pacific rocky intertidal: the role of upwelling and dispersal to drive patterns. *Ecography* **38**:83-95

Field, A., Miles, J. & Field, Z. (2012) *Discovering Statistics Using R*. Sage Publications Ltd. – London

Flemming, B.W. & Delafontaine, M.T. (1994) Biodeposition in a juvenile mussel bed of the East Frisian Wadden Sea (southern North Sea). *Netherland Journal of Aquatic Ecology* **28**:289-297

Folmer, E.O., Drent, J., Troost, K., Buttger, H., Dankers, N., Jansen, J., van Stralen, M., Millat, G. & Herlyn, M. (2014) Large-Scale Spatial Dynamics of Intertidal Mussel (*Mytilus edulis* L.) Bed Coverage in the German and Dutch Wadden Sea. *Ecosystems* **17**:550-566

Fowler, J., Cohen, L., & Jarvis, P. (2013). *Practical statistics for field biology*. John Wiley & Sons-London,UK

Fox, B.J. (1981) Niche parameters and species richness. *Ecology* **62**:1415-1425

Fox, J.W. (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology and Evolution* **28**:86-92

Franco, A., Elliott, M., Franzoi, P. & Torricelli, P. (2008) Life strategies of fishes in European estuaries: the functional guild approach. *Marine Ecology Progress Series* **354**:219–228

Frandsen, R. & Dolmer, P. (2002) Effects of substrate type on growth and mortality of blue mussels (*Mytilus edulis*) exposed to the predator *Carcinus maenas. Marine Biology* **141**:253-262

Frechette, M., Aitken, A.E. & Page, L. (1992) Interdependence of food and space limitation of a benthic suspension feeder: consequences for self-thinning relationships. *Marine Ecology Progress Series* **83**:55-62

Fretter, V. (1948) The structure and life history of some minute prosobranchs of rock pools: *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *Rissoella opalina* (Jeffreys). *Journal of the Marine Biological Association of the United Kingdom* **27**:597-632

Fuentes, M. (2004) Slight differences among individuals and the unified neutral theory of biodiversity. *Theoretical Population Biology* **66**:199–203

Fukuyama, A.K., Shigenaka, G. & Coats, D.A. (2014) Status of intertidal infaunal communities following the Exxon Valdez oil spill in Prince William Sound, Alaska. *Marine Pollution Bulletin* **84**:56–69

Fuller, S.C. & Lutz, R.A. (1989) Shell morphology of larval and post-larval mytilids from the north-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **69**:181-218

Gaines, S.D. & Bertness, M.D. (1992) Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* **360**:579-580

Gall, E.A. & Le Duff, M. (2014) Development of a quality index to evaluate the structure of macroalgal communities. *Estuarine, Coastal and Shelf Science* **139**:99-109

Garner, Y.L. & Litvaitis, M.K. (2013) Effects of wave exposure, temperature and epibiont fouling on byssal thread production and growth in the blue mussel, *Mytilus edulis*, in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology* **446**:52–56

Gauch, H.G. (1973) A Quantitative Evaluation of the Gray-Curtis Ordination. *Ecology* **54**:829-836

Gauch H.G. & Wentworth, T.R. (1976) Canonical Correspondence Analysis as an ordination technique. *Vegetatio* **33**:17-22

Gaylord, B. (1999) Detailing agents of physical disturbance: wave-induced velocities and accelerations on a rocky shore. *Journal of Experimental Marine Biology and Ecology* **239**:85–124

Gaylord, B. & Gaines, S.D. (2000) Temperature or Transport? Range Limits in Marine Species Mediated Solely by Flow. *The American Naturalist* **155**:769-789

Gee, J.M. & Warwick, R.M. (1996) A study of global biodiversity patterns in the marine motile fauna of hard substrata. *Journal of the Marine Biological Association of the UK* **76**:177-184

Gerino, M., Stora, G., François-Carcaillet, F., Gilbert, F., Poggiale, J.-C., Mermillod-Blondin, F., Desrosiers, G. & Vervier, P. (2003) Macro-invertebrate functional groups in freshwater and marine sediments: a common mechanistic classification. *Vie Milieu* **53**:221-231

Gestoso, I., Arenas, F., Rubal, M., Veiga, P., Peña, M. & Olabarria, C. (2013) Shifts from native to non-indigenous mussels: Enhanced habitat complexity and its effects on faunal assemblages. *Marine Environmental Research* **90**:85-95

Gherardi, F. & Vannini, M. (1993) Hermit crabs in a mangrove swamp: proximate and ultimate factors in the clustering of *Clibanarius laevimanus. Journal of Experimental Marine Biology and Ecology* **168**:167-187

Ghiselin, M.T. (1974) A Radical Solution to the Species Problem. *Systematic Biology* **23**:536-544

Gibb, S.W., Barlow, R.G., Cummings, D.G., Rees, N.W., Trees, C.C., Holligan, P. & Suggett, D. (2000) Surface phytoplankton pigment distributions in the Atlantic Ocean: an assessment of basin scale variability between 50°N and 50°S. *Progress in Oceanography* **45**:339-368

Gibbs, P.E., Langston, W.J., Burt, G.R. & Pascoe, P.L. (1983) *Tharyx marioni* (Polychaeta): a remarkable accumulator of arsenic. *Journal of the Marine Biological Association of the United Kingdom* **63**:313-325

Gifford, S., Dunstan, R.H., O'Connor, W., Koller, C.E. & MacFarlane, G.R. (2007) Aquatic zooremediation: deploying animals to remediate contaminated aquatic environments. *TRENDS in Biotechnology* **25**:60-65

Gillmor, R.B. (1982) Assessment of intertidal growth and capacity adaptations in suspension-feeding bivalves. *Marine Biology* **68**:277-286

Godwin, L.S. (2003) Hull fouling of maritime vessels as a pathway for marine species invasions to the Hawaiian Islands. *Biofouling* **19**:123-131

Goldberg, D.E. & Estabrook, G.F. (1998) Separating the effects of numbers of individuals sampled and competition on species diversity: an experimental and analytical approach. *Journal of Ecology* **86**:983-988

Golikov, A.N., Dolgolenko, M.A., Maximovich, N.V. & Scarlato, O.A. (1990) Theoretical approaches to marine biogeography. *Marine Ecology Progress Series* **63**:289-301

Gosling, E.M. (1994) *Speciation and wide-scale genetic differentiation*. In: Genetics and evolution of aquatic organisms. Chapman and Hall – London

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**:379-391

Grantham, B.A., Eckert, G.L. & Shanks, A.L. (2003) Dispersal potential of marine invertebrates in diverse habitats. *Ecological Applications* **13**:108-116

Gravel, D., Canham, C. D., Beaudet, M. & Messier, C. (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* **9**:399-409

Gray, A.P., Seed, R. & Richardson, C.A. (1997) Reproduction and growth of *Mytilus edulis chilensis* from the Falkland Islands. *Scientia Marina* **61**:39-48.

Gray, A.P., Richardson, C.A. & Seed, R. (1997a) Ecological Relationships Between the Valviferan Isopod *Edotia doellojuradoi* Giambiagi, 1925, and its Host *Mytilus edulis chilensis* in the Falkland Islands. *Estuarine, Coastal and Shelf Science* **44**:231–239

Gray, A.P., Lucas, I.A.N., Seed, R. & Richardson, C.A. (1999) *Mytilus edulis chilensis* infested with *Coccomyxa parasitica* (Chlorococcales, Coccomyxaceae). *Journal of Molluscan Studies* **65**:289–294

Griffin, J.N., Mendez, V., Johnson, A.F., Jenkins, S.R. & Foggo, A. (2009) Functional diversity predicts overyielding effect of species combination on primary productivity. *Oikos* **118**:37-44

Grinnell, J. (1917) The Niche-Relationships of the California Thrasher. *The Auk* **34**:427-433

Grizzle, R.E., Short, F.T., Newell, C.R., Hoven, H. & Kindblom, L. (1996) Hydrodynamically induced synchronous waving of seagrasses: 'monami' and its possible effects on larval mussel settlement. *Journal of Experimental Marine Biology and Ecology* **206**:165-177

Guinez, R. & Castilla, J.C. (1999) A Tridimensional Self-Thinning Model for Multilayered Intertidal Mussels. *The American Naturalist* **154**:341-357

Guinez, R. (2005) A review on self-thinning in mussels. *Revista de Biología Marina y Oceanografía* **40**:1–6

Günther, C-P. (1992) Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales. *Netherlands Journal of Sea Research* **30**:45-56

Gutiérrez, J.L., Jones, C.G., Strayer, D.L. & Iribarne, O.O. (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* **101**: 79–90

Haila, Y. (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* **12**:321-334

Hair, J.F., Money, A.H., Samouel, P. & Page, M. (2007) *Research Methods for Business*. Wiley & Sons Ltd - UK

Hammond, W. & Griffiths, C.L. (2004) Influence of wave exposure on South African mussel beds and their associated infaunal communities. *Marine Biology* **144**:547-552

Hatcher, A., Grant, J. & Schofield, B. (1994) Effects of suspended mussel culture (*Mytilus* spp.) on sedimentation, benthic respiration and sediment nutrient dynamics in a coastal bay. *Marine Ecology Progress Series* **115**:219–235

Haven, D.S. & Morales-Alamo, R. (1966) Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnology and Oceanography* **11:**487-498

Hawkins, A.J.S., Bayne, B.L. & Day, A.J. (1986) Protein Turnover, Physiological Energetics and Heterozygosity in the Blue Mussel, *Mytilus edulis*: The Basis of Variable Age-Specific Growth. *Proceedings of the Royal Society of London - Series B Biological Sciences* **229**:161-176

Hay, M.E., Renaud, P.E. & Fenical, W. (1988) Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. *Oecologia* **75**:246-252

Hayward, P.J. & Ryland, J.S. (Eds.) (1995) *Handbook of the marine fauna of North-West Europe*. Oxford University Press – Oxford, UK

Heads, M. (2005) Towards a panbiogeography of the seas. *Biological Journal of the Linnean Society* **84:**675–723

Healy, B. (1996) The distribution of Oligochaeta on an exposed rocky shore in southeast Ireland. *Hydrobiologia* **334**:51-62

Heaney, L.R. (2000) Dynamic Disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography* **9:**59-74

Heaven, C.S. & Scrosati, R.A. (2008) Benthic community composition across gradients of intertidal elevation, wave exposure, and ice scour in Atlantic Canada. *Marine Ecology Progress Series* **369:**13-23

Helmuth, B.S.T. & Hofmann, G.E. (2001) Microhabitats, Thermal Heterogeneity, and Patterns of Physiological Stress in the Rocky Intertidal Zone. *Biological Bulletin* **201**: 374–384.

Helmuth, B., Mieszkowska, N., Moore, P. & Hawkins, S.J. (2006) Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. *Annual Review of Ecology, Evolution, and Systematics* **37**:373–404

Hernandez, P.A., Graham, C.H., Master, L.M. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* **29**:773-785

Hidalgo, F.J., Silliman, B.R., Bazterrica, M.C. & Bertness, M.D. (2007) Predation on the Rocky Shores of Patagonia, Argentina. *Estuaries and Coasts* **30**:886–894

Highsmith, R.C. (1985) Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Marine Ecology Progress Series* **5**:169-179

Hilbish, T.J., Mullinax, A., Dolven, S.I., Meyer, A., Koehn, R.K. & Rawson, P.D. (2000) Origin of the antitropical distribution pattern in marine mussels (*Mytilus* spp.): routes and timing of transequatorial migration. *Marine Biology* **136**:69-77

Hilbish, T., Carson, E., Plante, J., Weaver, L. & Gilg, M. (2002) Distribution of *Mytilus edulis*, *M. galloprovincialis*, and their hybrids in open-coast populations of mussels in southwestern England. *Marine Biology* **140**:137-142

Hoehn, P., Tscharntke, T., Tylianakis, J.M. & Steffan-Dewenter, I. (2008) Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B* **275**:2283–2291

Hoeinghaus, D.J., Winemiller, K.O. & Birnbaumm, J.S. (2007) Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *Journal of Biogeography* **34:**324–338

Holland, A.F. & Polgar, T.T. (1976) Seasonal Changes in the Structure of an Intertidal Community. *Marine Biology* **37**:341-348

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of Biodiversity on Ecosystem Functioning: A consensus of current knowledge. *Ecological Monographs* **75**:3-35

Hooper, G.J. & Davenport, J. (2006) Epifaunal composition and fractal dimensions of intertidal marine macroalgae in relation to emersion. *Journal of the Marine Biological Association of the United Kingdom* **86**:1297-1304

Howe, H.F. & Smallwood, J. (1982) Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics* **13**:201-228

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press - Princeton, USA

Hubbell, S.P. (1997) A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral reefs* **16**:S9-S21.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press - Princeton, USA.

Hubbell, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* **19**:166-172

Hughes, R.N. & Griffiths, C.L. (1988) Self-Thinning in Barnacles and Mussels: The Geometry of Packing. *The American Naturalist* **132**:484-491

Hunt, H.L. & Scheibling, R.E. (2001) Patch dynamics of mussels on rocky shores: Integrating process to understand pattern. *Ecology* **82**:3213-3231

Ieno, E.N., Solan, M., Batty, P. & Pierce, G.J. (2006) How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Marine Ecology Progress Series* **311**:263–271

Innes, J.L. (1984) The Optimal Sample Size in Lichenometric Studies. *Arctic and Alpine Research* **16**:233-244

Iwasaki, K. (1995) Comparison of mussel bed community between two intertidal mytilids *Septifier virgatus* and *Hormomya mutabilis*. *Marine Biology* **123**:109-119

Jablonski, D. & Lutz, R.A. (1983) Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* **58**:21-89

Jenkins, S.R., Norton, T.A. & Hawkins, S.J. (1999) Interactions between canopy forming algae in the eulittoral zone of sheltered rocky shores on the Isle of Man. *Journal of the Marine Biological Association of the United Kingdom* **79**:341-349

Jenkins, S.R. & Hartnoll, R.G. (2001) Food supply, grazing activity and growth rate in the limpet *Patella vulgata* L.: a comparison between exposed and sheltered shores. *Journal of Experimental Marine Biology and Ecology* **258**:123–139

Jenkins, S.R., Moore, P., Burrows, M.T., Garbary, D.J., Hawkins, S.J., Ingolfsson, A., Sebens, K.P, Snelgrove, P.V.R., Wethey, D.S. & Woodin, S.A. (2008) Comparative ecology of North Atlantic shores: do differences in players matter for process? *Ecology* **89**:S3–S23

Johnson, M.P. (2006) Rocky intertidal invertebrates: the potential for metapopulations within and among shores. In: *Marine Metapopulations*. Kritzer, J.P. & Sale, P.F. (eds.). Elsevier Academic Press – London, UK

Joint Nature Conservation Committee (2011) *UK Biodiversity Action Plan Priority Habitat Descriptions* Maddock A. ed. http://jncc.defra.gov.uk/PDF/UKBAP_PriorityHabitatDesc-Rev2011.pdf

Joint Nature Conservation Committee (2014) UK biotope classifications. http://jncc.defra.gov.uk/marine/biotopes/biotope.aspx?biotope=JNCCMNCR00000461

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos* **69**:373-386

Jones, S.J., Mieszkowska, N. & Wethey, D.S. (2009) Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the East coast of the United States. *Biological Bulletin* **217**:73–85.

Jonsson, M. & Malmqvist, B. (2003) Importance of species identity and number for process rates within different stream invertebrate functional feeding groups. *Journal of Animal Ecology* **72**:453-459

Jørgensen, C.B., Larsen, P.S., Møhlenberg, F. & Riisgård, H.U. (1988) The mussel pump: properties and modeling. *Marine Ecology Progress Series* **45**:205–216

Jost, L. (2007) Partitioning Diversity into Independent Alpha and Beta Components. *Ecology* **88**:2427-2439

Jungerstam, J., Erlandsson, J., McQuaid, C.D., Porri, F., Westerbom, M. & Kraufvelin, P. (2014) Is habitat amount important for biodiversity in rocky shore systems? A study of South African mussel assemblages. *Marine Biology* **161**:1507-1519

Kanwisher, J.W. (1955) Freezing in intertidal animals. *Biological Bulletin* **109**:56-63

Kautsky, N. (1982) Growth and size structure in a Baltic *Mytilus edulis* population. Marine Biology **68**: 117-133.

Kearney, R., Farebrother, G., Buxton, C.D. & Goodsell, P. (2013) How terrestrial management concepts have led to unrealistic expectations of marine protected areas. *Marine Policy* **38**:304-311

Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**:157-264

Kelaher, B.P. (2003) Changes in habitat complexity negatively affect diverse gastropod assemblages in coralline algal turf. *Oecologia* **135**:431-441

Kenney, M.A., Sutton-Grier, A.E., Smith, R.F. & Gresens, S.E. (2009)
Benthic macroinvertebrates as indicators of water quality: The intersection of science and policy. *Terrestrial Arthropod Reviews* **2**:99–128

Kensler, C.B. & Crisp, D.J. (1965) The colonization of artificial crevices by marine invertebrates. *Journal of Animal Ecology* **34**:507-516

Kensler, C.B. (1967) Dessication resistance of intertidal crevice species as a factor in their zonation. *Journal of Animal Ecology* **36**:391-406

Killeen, I.J. & Light, J.M. (1998) Observations on *Onoba semicostata* and *O. aculeus* around British and northern French coasts. *Journal of Conchology* **36**:7-9

Kim, S., Kang, Y.H., Choi, C.J., Won, N.I., Seo, I.S., Lee, H.J., Jung, S. & Park, S.R. (2014) Effects of intensity and seasonal timing of disturbances on a rocky intertidal benthic community on the southern coast of Korea. *Ecological Research* **29**:421-431

King, P.A., McGrath, D., & Britton, W. (1990) The use of artificial substrates in monitoring mussel (*Mytilus edulis* L.) settlement on an exposed rocky shore in the west of Ireland. J*ournal of the Marine Biological Association of the United Kingdom* **70**:371-380

Knops, J.M., Tilman, D., Haddad, D.N., Naeem, S., Mitchell, C.E., Haarstad, J., M.E. Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E. & Groth, J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* **2**:286-293

Kohn, D.D. & Walsh, D.M. (1994) Plant Species Richness--The Effect of Island Size and Habitat Diversity. *Journal of Ecology* **82**:367-377

Kraan, C., van der Meer, J., Deking, A. & Piersma, T. (2009)Patchiness of macrobenthic invertebrates in homogenized intertidal habitats: hidden spatial structure at a landscape scale. *Marine Ecology Progress Series* **383**:211–224

Krebs, C.J. (2009) *Ecology; the experimental analysis of distribution and abundance*. 6th Edition. Benjamin Cummings – London, UK

Kruskal, W. & Mosteller, F. (1980) Representative Sampling, IV: The History of the Concept in Statistics, 1895-1939. *International Statistical Review / Revue Internationale de Statistique* **48**:169-195

Lane, D.J.W., Nott, J.A. & Crisp, D. J. (1982) Enlarged stem glands in the foot of the post-larval mussel, *Mytilus edulis*: adaptation for bysso-pelagic migration. *Journal of the Marine Biological Association of the United Kingdom* **62**:809-818

Lane, D.J.W., Beaumont, A.R., & Hunter, J.R. (1985) Byssus drifting and the drifting threads of the young post-larval mussel *Mytilus edulis*. *Marine Biology* **84**:301-308

Latyshev, N.A., Khardin, A.S., Kasyanov, S.P. & Ivanova M.B. (2004) A study on the feeding ecology of chitons using analysis of gut contents and fatty acid markers. *Journal of Molluscan Studies* **70**: 225–230

Lauzon-Guay, J.S., Hamilton, D.J. & Barbeau, M.A. (2005) Effect of mussel density and size on the morphology of blue mussels (*Mytilus edulis*) grown in suspended culture in Prince Edward Island, Canada. *Aquaculture* **249**:265-274

Lawrie, S.M. & McQuaid, C.D. (2001) Scales of mussel bed complexity: structure, associated biota and recruitment. *Journal of Experimental Marine Biology and Ecology* **257**:135-161

Lebour, M. V. (1938) Notes on the breeding of some lamellibranchs from Plymouth and their larvae. *Journal of the Marine Biological Association of the United Kingdom* **23**:119-144

Leibold, M.A. (1995) The Niche Concept Revisited: Mechanistic Models and Community Context. *Ecology* **76**:1371-1382

Lenth, R.V. (2001): Some Practical Guidelines for Effective Sample Size Determination. *The American Statistician* **55**:187-193

Lenz, M., Molis, M. & Wahl, M. (2004) Experimental test of the intermediate disturbance hypothesis: frequency effects of emersion on fouling communities. *Journal of Experimental Marine Biology and Ecology* **305**:247–266

Levinton, J. (1972) Stability and trophic structure in deposit-feeding and suspension-feeding communities. *The American Naturalist* **106**:472-486

Levinton, J.S. & Suchanek, T.H. (1978) Geographic variation, niche breadth and genetic differentiation at different geographic scales in the mussels *Mytilus californianus* and *M. edulis*. *Marine Biology* **49**:363-375

Lilley, S.A. & Schiel, D.R. (2006) Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia* **148**:672-681

Lima, F.P., Queiroz, N., Ribeiro, P.A., Hawkins, S.J. & Santos, A.M. (2006) Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. *Journal of Biogeography* **33**:812–822

Lin, J. (1991) Predator-prey interactions between blue crabs and ribbed mussels Living in clumps. *Estuarine, Coastal and Shelf Science* **32**:61-69

Lindberg, D.R. (1991) Marine Biotic Interchange Between the Northern and Southern Hemispheres. *Paleobiology* **17**:308-324

Lintas, C. & Seed, R. (1994) Spatial variation in the fauna associated with *Mytilus edulis* on a wave-exposed rocky shore. *Journal of Molluscan Studies* **60**:165-174

Little, C.: Williams, G.A. & Trowbridge, C. (2009) *The Biology of Rocky Shores*. 2nd Edition. Oxford University Press - UK

Littler, M.M. & Littler, D.S. (1984) Relationships between macroalgal functional form groups and substrata stability in a sub-tropical rocky-intertidal system. *Journal of Experimental Marine Biology and Ecology* **74**:13-34

Littorin, B. & Gilek, M. (1999) Vertical Patterns in Biomass, Size Structure, Growth and Recruitment of *Mytilus edulis* in an Archipelago Area in the Northern Baltic Sea Proper. *Ophelia* **50**:93-112

Logan, M. (2010) *Biostatistical Design and Analysis Using R: A Practical Guide*. Wiley-Blackwell – Oxford, UK

Lohse, D.P. (1993) The importance of secondary substratum in a rocky intertidal community. *Journal of Experimental Marine Biology and Ecology* **166**:1-17

Lomolino, M.V. (2000) A call for a new paradigm of island biogeography. *Global Ecology & Biogeography* **9**:1–6

Lopez Gappa, J.J., Tablado, A. & Magaldi, N.H. (1990) Influence of sewage pollution on a rocky intertidal community dominated by the mytilid *Brachidontes rodriguezi. Marine Ecology Progress Series* **63**:163-175

Loreau, M. (2000) Are communities saturated? On the relationship between α, β and γ diversity. *Ecology Letters* **3**:73-76

Lourie, S.A. & Vincent, A.C.J. (2004) Using biogeography to help set priorities in marine conservation. *Conservation Biology* **18**:1004-1020

Lowell, R.B. (1984) Dessication of intertidal limpets: effects of shell size, fit to substratum, and shape. *Journal of Experimental Marine Biology and Ecology* **77**:197-207

Lubchenco, J. & Menge, B.A. (1978) Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* **48**:67-94

Lubchenco, J. (1983) *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* **64**:1116-1123

Lucas, A. & Watson, J.J. (2002) *Bioenergetics of aquatic animals*. Taylor & Francis – UK

Lüning, K. (1984) Temperature tolerance and biogeography of seaweeds: The marine algal flora of Helgoland (North Sea) as an example. *Helgoländer Meeresunters* **38**:305-317

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press - Princeton

Macdonald, T.A., Burd, B.J., Macdonald, V.I. & van Roodselaar, A. (2010) Taxonomic and Feeding Guild Classification for the Marine Benthic Macroinvertebrates of the

Strait of Georgia, British Columbia. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2874**:1-69

MacNeil, C., Dick, J.T.A. & Elwood, R.W. (1997) The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. *Biological Review* **72**:349-364

Madeira, D., Narciso, L., Cabral, H.N. & Vinagre, C. (2012) Thermal tolerance and potential impacts of climate change on coastal and estuarine organisms. *Journal of Sea Research* **70**:32-41

Madsen, J.D., Chambers, P.A., James, W.F., Koch, E.W. & Westlake, D.F. (2001) The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* **444**:71-84

Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Science Ltd. – Oxford, UK

Mallet, A.L., Carver, C.E.A., Coffen, S.S. & Freeman, K.R. (1987) Winter growth of the blue mussel *Mytilus edulis* L.: importance of stock and site. *Journal of Experimental Marine Biology and Ecology* **108**:217–228

Margalef, R. (1963) On certain unifying principles in ecology. *The American Naturalist* **97**:357-374

Margalef, R. (1968) *Perspectives in Ecological Theory*. University of Chicago Press – Chicago, USA

Mason, J. (1976) *Cultivation*. In: Marine Mussels: Their Ecology and Physiology (Bayne, B.L., ed.). pp.13-65 Cambridge University Press-Cambridge, UK

Mason, N.W., Mouillot, D., Lee, W.G. & Wilson, J.B. (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* **111**:112-118

Mathieson, S., Cattrijsse, A., Costa, M.J., Drake, P., Elliott, M., Gardner, J. & Marchand, J. (2000) Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. *Marine Ecology Progress Series* **204**:225–242

Matias, M.G., Underwood, A.J. & Coleman, R.A. (2007) Interactions of components of habitats alter composition and variability of assemblages. *Journal of Animal Ecology* **76**:986–994

McBane, C.D. & Croker, R.A. (1984) Some observations on the life history of the amphipod crustacean, *Hyale nilssoni* (Rathke), in New Hampshire. Estuaries **7**:541-545

McCook, L.J. & Chapman, A.R.O. (1991) Community succession following massive ice-scour on an exposed rocky shore: effects of *Fucus* canopy algae and of mussels during late succession. *Journal of Experimental Marine Biology and Ecology* **154**:137-169

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *TRENDS in Ecology and Evolution* **21**:178-185

McGrorty, S., Clarke, R.T., Reading, C.J. & Goss-Custard, J.D. (1990) Population dynamics of the mussel *Myilus edulis*: density changes and regulation of the population in the Exe estuary, Devon. *Marine Ecology Progress Series* **67**:157-169

McKane, A.J., Alonso, D. & Sole, R.V. (2004) Analytic solution of Hubbell's model of local community dynamics. *Theoretical Population Biology* **65**:67–73

McMahon, R.F. (2002) Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:1235-1244

McQuaid, C.D. & Branch, G.M. (1985) Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Marine Ecology Progress Series* **22**:153-161

McQuaid, C.D. & Lindsay, T.L. (2000) Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom-up regulation of intertidal populations. *Marine Ecology Progress Series* **206**:147-154

McQuaid, C.D. & Phillips, T.E. (2000) Limited wind-driven dispersal of intertidal mussel larvae: in situ evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. *Marine Ecology Progress Series* **201**:211-220

Menge, B.A. (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* **46**:355-393

Menge, B.A. (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* **146**:69-100

Menge, B.A. (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* **65**:21-74

Menge, B.A., Allison, G.W., Blanchette, C.A., Farrell, T.M., Olson, A.M., Turner, T.A. & van Tamelen, P. (2005) Stasis or kinesis? Hidden dynamics of a rocky intertidal macrophyte mosaic revealed by a spatially explicit approach. *Journal of Experimental Marine Biology and Ecology* **314**:3–39

Mermillod-Blondin, F. & Rosenberg, R. (2006) Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic Sciences* **68**:434-442

Michaud, E., Desrosiers, G., Mermillod-Blondin, F., Sundby, B. & Stora, G. (2005) The functional group approach to bioturbation: The effects of biodiffusers and gallery-diffusers of the *Macoma balthica* community on sediment oxygen uptake. *Journal of Experimental Marine Biology and Ecology* **326**:77–88

Micheli, F. & Halpern, B.S. (2005) Low functional redundancy in coastal marine assemblages. *Ecology Letters* **8**:391-400

Miloslavich, P., Klein, E., Díaz, J.M., Hernandez, C.E., Bigatti, G., Campos, L., Artigas, F., Castillo, J., Penchaszadeh, P.E., Neill, P.E., Carranza, A., Retana, M.V., Diaz de Astarloa, J.M., Lewis, M., Yorio, P., Piriz, M.L., Rodríguez, D., Yoneshigue-Valentin, Y., Gamboa, L. & Martin, A. (2011) Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. *PloS one* **6**: e14631

Miyamoto, Y. & Noda, T. (2004) Effects of mussels on competitively inferior species: competitive exclusion to facilitation. *Marine Ecology Progress Series* **276**:293–298

Moeser, G.M., Leba, H. & Carrington, E. (2006) Seasonal influence of wave action on thread production in *Mytilus edulis. Journal of experimental biology* **209**:881-890

Moran, M.D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* **100**:403-405

Moreno, C.E. & Halffter, G. (2000) Assessing the completeness of bat biodiversity inventories using species accumulation curves. *Journal of Applied Ecology* **37**:149-158

Murphy, H.M., Jenkins, G.P., Hindell, J.S. & Connolly, R.M. (2010) Response of fauna in seagrass to habitat edges, patch attributes, and hydrodynamics. *Austral Ecology* **35**:535-543

Murray, L.G., Newell, C.R. & Seed, R. (2007) Changes in the biodiversity of mussel assemblages induced by two methods of cultivation. *Journal of Shellfish Research* **26**:153-162

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *TRENDS in Ecology and Evolution* **15**:278-285

Navarrete, S.A. & Castilla, J.C. (1990) Barnacle walls as mediators of intertidal mussel recruitment: effects of patch size on the utilization of space. *Marine Ecology Progress Series* **68**:113-119

Navarette, S.A., Broitman, B.R. & Menge, B.A. (2008) Interhemispheric comparison of recruitment to intertidal communities: pattern, persistence and scales of variation. *Ecology* **89**:1308–1322

Nehls, G. & Thiel, M. (1993) Large-scale distribution patterns of the mussel *Mytilus edulis* in the Wadden Sea of Schleswig-Holstein: Do storms structure the ecosystem? *Netherlands Journal of Sea Research* **31***:*181-187

Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography,* **26**:867–878

Newcombe, C.L. (1935) A Study of the Community Relationships of the Sea Mussel, *Mytilus edulis* L. *Ecology* **16**:234-243

Newcombe, E.M. & Cárdanas, C.A. (2011) Rocky reef benthic assemblages in the Magellan Strait and the South Shetland Islands (Antarctica). *Revista de Biología Marina y Oceanografía* **46**:177-188

Newell, R. (1965). The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proceedings of the Zoological Society of London* **144**:25-45

Newell, C.R., Short, F., Hoven, H., Healey, L., Panchang, V. & Cheng, G. (2010) The dispersal dynamics of juvenile plantigrade mussels (*Mytilus edulis* L.) from eelgrass (*Zostera marina*) meadows in Maine, USA. *Journal of Experimental Marine Biology and Ecology* **394**:45-52

Nicastro, K.R., Zardi, G.I., McQuaid, C.D., Pearson, G.A. & Serrão, E.A. (2012) Love thy neighbour: group properties of gaping behaviour in mussel aggregations. *PloS ONE* **7**:e47382

Nielsen, M.V. (1988) The effect of temperature on the shell-length growth of juvenile *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology* **123**:227–234

Norén, F., Haamer, J. & Lindahl, O. (1999) Changes in the plankton community passing a *Mytilus edulis* mussel bed. *Marine Ecology Progress Series* **191**:187-194

Nusser, S.M., Breidt, F.J. & Fuller, W.A. (1998) Design and Estimation for Investigating the Dynamics of Natural Resources. *Ecological Applications* **8**:234-245

O'Connor, N.E. & Crowe, T.P. (2008) Do mussel patches provide a refuge for algae from grazing gastropods? *Journal of Molluscan Studies* **74**:75–78

Occhipinti-Ambrogi, A. (2007) Global change and marine communities: Alien species and climate change. *Marine Pollution Bulletin* **55**:342–352

Olson, D.M. & Dinerstein, E. (1998) The Global 200: A Representation Approach to Conserving the Earth's Most Biologically Valuable Ecoregions. *Conservation Biology* **12**:502-515

Okamura, B. (1986) Group Living and the Effects of Spatial Position in Aggregations of *Mytilus edulis*. *Oecologia* **69**:341-347

Olive, P.J.W. (1995) Annual breeding cycles in marine invertebrates and environmental temperature: Probing the proximate and ultimate causes of reproductive synchrony. *Journal of Thermal Biology* **2**:79-90

Orfanidis, S., Panayotidis, P. & Stamatis, N. (2003) An insight to the ecological evaluation index (EEI). *Ecological Indicators* **3**:27–33

Padilla, D.K. & Allen, B.J. (2000) Paradigm lost: reconsidering functional form and group hypotheses in marine ecology. *Journal of Experimental Marine Biology and Ecology* **250**:207–221

Paganelli, D., Marchini, A. & Occhipinti-Ambrogi, A. (2012) Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): a study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). *Estuarine, Coastal and Shelf Science* **96**:245-256

Paine, R.T. (1969) Food web complexity and species diversity. *The American Naturalist* **100**:65-75

Paine, R.T. (1974) Intertidal Community Structure: Experimental Studies on the Relationship between a Dominant Competitor and Its Principal Predator. *Oecologia* **15**:93-120

Paine, R.T. & Levin, S.A. (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145-178

Paine, R.T. (2010) Macroecology: Does it ignore or can it encourage further ecological syntheses based on spatially local experimental manipulations? *The American Naturalist* **176**:385-393

Palmer, C., O'Keeffe, J., Palmer, A. (1993) Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River eastern Cape, South Africa. II. Functional morphology and behaviour. *Freshwater Biology* **29**:455-462

Palmer, M.W. (1993) Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* **74**:2215-2230

Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D.M., Kingsolver, J., Peterson, A.T. & Sagarin, R. (2005) Empirical Perspectives on Species Borders: From Traditional Biogeography to Global Change. *Oikos* **108:**58-75

Patterson, B.D. & Atmar, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnaean Society* **28**:65-82

Peake, A.J. & Quinn, G.P. (1993) Temporal variation in species-area curves for invertebrates in clumps of an intertidal mussel. *Ecography* **16**:269-277

Persson, L. (1999) Trophic Cascades: Abiding Heterogeneity and the Trophic Level Concept at the End of the Road. *Oikos* **85**:385-397

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters* **5**:402–411

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* **9**:741-758

Petersen, J.K., Hasler, B., Timmermann, K., Nielsen, P., Tørring, D.B., Larsen, M.M. & Holmer, M. (2014) Mussels as a tool for mitigation of nutrients in the marine environment. *Marine Pollution Bulletin* **82**:137-143

Petraitis, P.S. (1995) The Role of Growth in Maintaining Spatial Dominance by Mussels (*Mytilus Edulis*). *Ecology* **76**:1337-1346

Phillips, J.C., Kendrick, G.A. & Lavery, P.S. (1997) A test of a functional group approach to detecting shifts in macroalgal communities along a disturbance gradient. *Marine Ecology Progress Series* **153**:125-138

Pierce, R.W. & Turner, J.T. (1993) Global biogeography of marine tintinnids. *Marine Ecology Progress Series* **94**:11-26

Pieters, H., Kluytmans, J.H., Zandee, D.I. & Cadee, G.C. (1980) Tissue composition and reproduction of *Mytilus edulis* in relation to food availability. *Netherlands Journal of Sea Research* **14**:349-361

Pinn, E.H. & Robertson, M.R. (2003) Macro-infaunal biodiversity and analysis of associated feeding guilds in the Greater Minch area, Scottish west coast. *Journal of the Marine Biological Association of the U.K.* **83**:433-443

Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *The American Naturalist* **147**:813-846

Pollock, D.E. (1979) Predator-prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater* at Robben Island on the Cape West Coast of Africa. *Marine Biology* **52**:347-356

Prado, L. & Castilla, J.C. (2006) The bioengineer *Perumytilus purpuratus* (Mollusca: Bivalvia) in central Chile: biodiversity, habitat structural complexity and environmental heterogeneity. *Journal of the Marine Biological Association of the United Kingdom* **86**:417-421

Prathep, A., Marrs, R.H. & Norton, T.A. (2003) Spatial and temporal variations in sediment accumulation in an algal turf and their impact on associated fauna. *Marine Biology* **142**:381–390

Price, H.A. (1980) Seasonal variation in the strength of byssal attachment of the common mussel *Mytilus edulis* L. *Journal of the Marine Biological Association of the United Kingdom* **60**:1035-1037

Price, H.A. (1982) An analysis of factors determining seasonal variation in the byssal attachment strength of *Mytilus edulis. Journal of the Marine Biological Association of the United Kingdom* **62**:147-155

Pugh, P.J.A. & King, P.E. (1985) Vertical distribution and substrate association of the British Halacaridae. *Journal of Natural History* **19**:961-968

Pulfrich, A. (1996) Attachment and settlement of post-larval mussels (*Mytilus edulis* L.) in the Schleswig-Holstein Wadden Sea. *Journal of Sea Research* **36**:239-250

Purvis, A., & Hector, A. (2000) Getting the measure of biodiversity. *Nature* **405**:212–219

Qin, X & Waite, J.H. (1995) Exotic collagen gradients in the byssus of the mussel Mytilus edulis. *Journal of Experimental Biology* **198**:633-644

Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press - Cambridge

Raffaelli, D. (1985) Functional feeding groups of some molluscs defined by gut content analysis. *Journal of Molluscan Studies* **51**:233-239

Ragnarsson, S.Á. & Raffaelli, D. (1999) Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments*. Journal of Experimental Marine Biology and Ecology* **241**:31-43

Rangel, T.F.L., Diniz-Filho, J.A.F. & Colwell, R.K. (2007) Species richness and evolutionary niche dynamics: a spatial pattern–oriented simulation experiment. *The American Naturalist* **170**:602-616

Reimer, O. & Tedengren, M. (1997) Predator-induced changes in byssal attachment, aggregation and migration in the blue mussel, *Mytilus edulis. Marine and Freshwater Behaviour and Physiology* **30**:251-266

Reimer, O. & Harms-Ringdahl, S. (2001) Predator-inducible changes in blue mussels from the predator-free Baltic Sea. *Marine Biology*

Reish, D.J. (1964) Studies on the *Mytilus edulis* community in Alamitos Bay, California. II. Population variations and discussion of the associated organisms *Veliger* **6**:202-207

Rex, M.A., Crame, J.A., Stuart, C.T. & Clarke, A. (2005) Large-scale biogeographic patterns in marine molluscs: a confluence of history and productivity? *Ecology* **86**:2288–2297

Ricciardi, A. & Bourget, E. (1999) Global patterns of macro invertebrate biomass in marine intertidal communities. *Marine Ecology Progress Series* **185**:21-35

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science* **235**:167-171

Ricklefs, R.E. (2006) The Unified Neutral Theory of Biodiversity: Do the Numbers Add Up? *Ecology* **87**:1424-1431

Rico, A. & Gappa, J.L. (2006) Intertidal and subtidal fouling assemblages in a Patagonian harbour (Argentina, Southwest Atlantic). *Hydrobiologia* **563**:9–18

Riginos, C. & Nachman, M.W. (2001) Population subdivision in marine environments: the contributions of biogeography, geographical distance and discontinuous habitat to genetic differentiation in a blennioid fish, *Axoclinus nigricaudus. Molecular Ecology* **10:**1439–1453

Riisgard, H.U., Larsen, P.S. & Pleissner, D. (2014) Allometric equations for maximum filtration rate in blue mussels *Mytilus edulis* and importance of condition index. *Helgoland Marine Research* DOI 10.1007/s10152-013-0377-9

Rilov, G. & Schiel, D.R. (2006) Seascape-dependent subtidal-intertidal trophic linkages. *Ecology* **87**:731–744

Ríos, C. & Mutschke, E. (1999) Community structure of intertidal boulder-cobble fields in the Straits of Magellan, Chile. *Scientia Marina* **63**:193-201

Robinson, T.B. & Griffiths, C.L. (2002) Invasion of Langebaan Lagoon, South Africa, by *Mytilus galloprovincialis* – effects on natural communities. *African Zoology* **37**:151–158

Robinson, T.B., Branch, G.M., Griffiths, C.L., Govender, A. & Hockey, P.A.R. (2007) Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. *Marine Ecology Progress Series* **340**:163-171

Rodríguez, F., Feist, S.W., Guillou, L., Harkestad, L.S., Bateman, K., Renault, T. & Mortensen, S. (2008) Phylogenetic and morphological characterisation of the green algae infesting blue mussel *Mytilus edulis* in the North and South Atlantic oceans. *Diseases of Aquatic Organisms* **81**:231-240

Rosenberg, R. (2001) Marine benthic faunal successional stages and related sedimentary activity. *Scientia Marina* **65**:107-119

Rosindell, J., Hubbell, S.P. & Etienne, R.S. (2011) The Unified Neutral Theory of Biodiversity and Biogeography at Age Ten. *Trends in Ecology and Evolution* **26**:340-348

Roth, S. & Wilson, J.G. (1998) Functional analysis by trophic guilds of macrobenthic community structure in Dublin Bay, Ireland. *Journal of Experimental Marine Biology and Ecology* **222**:195-217

Roxburgh, S.H., Shea, K. & Wilson, J.B. (2004) The Intermediate Disturbance Hypothesis: Patch Dynamics and Mechanisms of Species Coexistence. *Ecology* **85**:359-371

Roy, K., Jablonksi, D. & Valentine, J.W. (2000) Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proceedings: Biological Sciences* **267**:293-299

139:959–965

Ruuskanen, A., Bäck, S. & Reitalu, T. (1999) A comparison of two cartographic exposure methods using *Fucus vesiculosus* as an indicator. *Marine Biology* **134**:139-145

Sagarin, R.D. & Gaines, S.D. (2002) Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography* **29**:985–997

Saier, B. (2002) Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna. *Helgol Mar Res* **56**:44–50

Sale, P.F., Hanski, I. & Kritzer, J.P. (2006) The merging of metapopulation theory and marine ecology: establishing the historical context. In: *Marine metapopulations*. Kritzer, J.P. & Sale, P.F. (eds.) Elsevier Academic Press – London, UK

San Martin, E., Harris, R.P. & Irigoien, X. (2006) Latitudinal variation in plankton size spectra in the Atlantic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography* **53**:1560-1572

Sanders, H.L. (1968) Marine Benthic Diversity: A Comparative Study. *The American Naturalist* **102**:243-282

Santelices, B. & Martínez, E. (1988) Effects of filter-feeders and grazers on algal settlement and growth in mussel beds. *Journal of Experimental Marine Biology and Ecology* **118**:281-306

Scheiner, S.M. (2003) Six types of species-area curves. *Global Ecology and Biogeography* **12**:441-447

Schiel, D.R. (2004) The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. *Journal of Experimental Marine Biology and Ecology* **300**:309–342

Schluter, D. (1982) Seed and patch selection by Galapagos ground finches: Relation to foraging efficiency and food supply. *Ecology* **63**:1106–1120

Schnute, J.T. & Richards, L.J. (2001) Use and abuse of fishery models. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:10-17

Schückel, U. & Kröncke, I. (2013) Temporal changes in intertidal macrofauna communities over eight decades: A result of eutrophication and climate change. *Estuarine, Coastal and Shelf Science* **117**:210-218

Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. & Van Mantgem, P.J. (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**:297-305

Scrosati, R. & Heaven, C. (2007) Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. *Marine Ecology Progress Series* **342**:1–14

Scrosati, R.A., van Genne, B., Heaven, C.S. & Watt, C.A. (2011) Species richness and diversity in different functional groups across environmental stress gradients: a model for marine rocky shores. *Ecography* **34**:151-161

Seed, R. (1968) Factors Influencing Shell Shape in the Mussel *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom* **48**:561-584

Seed, R. (1969) The Ecology of *Mytilus edulis* L. (Lamellibranchiata) on Exposed Rocky Shores I. Breeding and Settlement. *Oecologia* **3**:277-316

Seed, R. (1976) *Ecology* In: Marine Mussels: Their Ecology and Physiology (Bayne, B.L., ed.). pp.13-65 Cambridge University Press-Cambridge, UK

Seed, R. & O'Connor, R.J. (1981) Community organization in marine algal epifaunas. *Annual Review of Ecology and Systematics* **12**:49-74

Seed, R. (1996) Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biological Association of the United Kingdom* **76**:203-210

Seng, Y.P. (1951) Historical Survey of the Development of Sampling Theories and Practice. *Journal of the Royal Statistical Society. Series A* **114**:214-231

Sheil, D. & Burslem, D.F.R.P. (2013) Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox. *Trends in Ecology and Evolution* **28**:571-572

Shelford, V.E. (1935) The major communities. *Ecological Monographs* **5**:251-292.

Sigurdsson, J.B., Titman C.W. & Davies, P.A. (1976) The dispersal of young post-larval bivalve molluscs by byssus threads. *Nature* **262**:386-387

Silliman, B.R., Bertness, M.D., Altieri, A.H., Griffin, J.N., Bazterrica, M.C., Hidalgo, F.J., Crain, C.M. & Reyna, M.V. (2011) Whole-Community Facilitation Regulates Biodiversity on Patagonian Rocky Shores. *PloS one* **6**:e24502

Simberloff, D. (1974) Experimental Zoogeography of Islands: Effects of Island Size. *Ecology* **57**:629-648

Smith, J.E., Hunter, C.L. & Smith, C.M. (2002) Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. *Pacific Science* **56**:299-315

Smith, J.R., Fong, P. & Ambrose, R.F. (2006) Dramatic declines in mussel bed community diversity: response to climate change? *Ecology* **87**:1153-1161

Somerfield, P.J. & Clarke, K.R. (1995) Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series* **127**:113-119

Somero, G.N. (2002) Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integrative and Comparative Biology* **42**:780-789

Sorte, C.J.B., Williams, S.L. & Carlton, J.T. (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography* **19:**303–316

Sorte, C.J.B., Jones, S.J. & Miller, L.P. (2011) Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. *Journal of Experimental Marine Biology and Ecology* **400**:209–217

Sousa, W.P. (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**:1225-1239

Sousa, W.P. (1984) Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* **65**:1918-1935

Sousa, R., Gutierrez, J.L., Aldridge, D.C. (2009) Non-indigenous invasive bivalves as ecosystem engineers. *Biological Invasions* **11**:2367–2385

Southwood, T.R.E. (1966) *Ecological Methods*. Chapman & Hall Ltd. - London

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdana, Z.A., Finlayson, M., Halpern, B.S., Jorge. M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience* **57**:573-583

Statzner, B. & Higler, B. (1985) Questions and comments on the River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Science* **42**:1038-1044

Steneck, R.S. & Watling, L. (1982) Feeding Capabilities and Limitation of Herbivorous Molluscs: A Functional Group Approach. *Marine Biology* **68**:299-319

Steneck, R.S. & Dethier, M.N. (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* **69**:476-498

Stevenson, R.J. (1995) Scale-Dependent Determinants and Consequences of Benthic Algal Heterogeneity. *Journal of the North American Benthological Society* **16**:248-262

Stuart, V., Newell, R.C. & Lucas, M.I. (1982) Conversion of kelp debris and faecal material from the mussel *Aulacomya ater* by marine micro-organisms. *Marine Ecology Progress Series* **7**:47-57

Suchanek, T.H. (1978) The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **31**:105-120

Sukhotin, A.A., Abele, D. & Pörtner, H.O. (2002) Growth, metabolism and lipid peroxidation in *Mytilus edulis* L.: age and size effects. *Marine Ecology Progress Series* **226**:223-234

Sundblad, G., Bekkby, T., Isæus, M., Nikolopoulos, A., Norderhaug, K.M. & Rinde, E. (2014) Comparing the ecological relevance of four wave exposure models. *Estuarine, Coastal and Shelf Science* **140**:7-13

Sutherland, W.J., Clout, M., Cote, I.M., Daszak, P., Depledge, D.H., Fellman, L., Fleishman, E., Garthwaite, R., Gibbons, D.W., De Lurio, J., Impey, A.J., Lickorish, F., Lindenmayer, D., Madgwick, J., Margerison, C., Maynard, T., Peck, L.S., Pretty, J., Prior, S., Redford, K.H., Scharlemann, J.P.W., Spalding, M. & Watkinson, A.R. (2010) A horizon scan of global conservation issues for 2010. *Trends in Ecology and Evolution* **25**:1-7

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B* **278**:1823-1830

Svane, I. & Ompi, M. (1993) Patch dynamics in beds of the blue mussel *Mytilus edulis* L.: effects of site, patch size, and position within a patch. *Ophelia* **37**:187-202

Svane, I. & Setyobudiandi, I. (1996) Diversity of associated fauna in beds of the blue mussel *Mytilus edulis* L.: Effects of location, patch size, and position within a patch. *Ophelia* **45**:39-53

Svensson, J.R., Lindegarth, M., Jonsson, P.R. & Pavia, H. (2012) Disturbance–diversity models: what do they really predict and how are they tested? *Proceedings of the Royal Society of London B: Biological Sciences* rspb20112620

Swingland, I.R. (2001) Biodiversity, definition of. *Encyclopedia of Biodiversity* **1**: 377-391

Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* **47**:561–94

Szefer, P., Ikuta, K., Frelek, K., Zdrojewska, I. & Nabrzyski, M. (1999) Mercury and other trace metals (Ag, Cr, Co, and Ni) in soft tissue and byssus of *Mytilus edulis* from the east coast of Kyushu Island, Japan. *Science of the Total Environment* **229**:227-234

Tam, J.C. & Scrosati, R.A. (2014) Distribution of cryptic mussel species (*Mytilus edulis* and *M. trossulus*) along wave exposure gradients on northwest Atlantic rocky shores. *Marine Biology Research* **10**:51-60

Tanner, J.E. (2005) Edge effects on fauna in fragmented seagrass meadows*. Austral Ecology* **30**:210–218

Thiel, M. & Ullrich, N. (2002) Hard rock versus soft bottom: the fauna associated with intertidal mussel beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussel beds. *Helgoland Marine Research* **56**:21-30

Theisen, B.F. (1972) Shell cleaning and deposit feeding in *Mytilus edulis* L. (Bivalvia). *Ophelia* **10**:49-55

Thompson, R.C., Wilson, B.J., Tobin, M.L., Hill, A.S. & Hawkins, S.J. (1996) Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. *Journal of Experimental Marine Biology and Ecology* **202**:73-84

Thompson, R.C., Crowe, T.P. & Hawkins, S.J. (2002) Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation* **29**:168–191

Thompson, R.C., Moschella, P.S., Jenkins, S.R., Norton, T.A. & Hawkins, S.J. (2005) Differences in photosynthetic marine biofilms between sheltered and moderately exposed rocky shores. *Marine Ecology Progress Series* **296**:53–63

Thornley, B. & Adams, C. (1998) Content and quality of 2000 controlled trials in schizophrenia over 50 years. *British Medical Journal* **317**:1181-1184

Thrush, S.F., Hewitt, J.E. Gibbs, M., Lundquist, C & Norkko, A. (2006) Functional Role of Large Organisms in Intertidal Communities: Community Effects and Ecosystem Function. *Ecosystems* **9**:1029–1040

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300-1302

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. & Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**:1098-1103

Tjørve, E., Kunin, W.E., Polce, C. & Calf Tjørve, K.M (2008) Species-area relationship: separating the effects of species abundance and spatial distribution. *Journal of Ecology* **96**:1141-1151

Tokeshi, M. (1993) Species Abundance Patterns and Community Structure, In: *Advances in Ecological Research.* Begon, M. & Fitter, A.H. Eds. **24**:111-186

Tomanek, L. (2010) Variation in the heat shock response and its implication for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. *The Journal of Experimental Biology* **213**:971-979

Tomanova, S., Goitia, E. & Hele□ic, J. (2006) Trophic levels and functional feeding groups of macroinvertebrates in neotropical streams*. Hydrobiologia* **556**:251-264

Torp-Christensen, H, Dolmer, P., Hansen, B.W., Holmer, M., Dahl Kristensen, L., Poulsen, L.K., Stenberg, C., Albertsen, C.M., Støttrup, J. (2015) Aggregation and attachment responses of blue mussels, *Mytilus edulis*: impact of substrate composition, time scale and source of mussel seed. *Aquaculture* **435:**245-251

Trussel, G.C., Ewanchuk, P.J. & Bertness, M.D. (2003) Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. *Ecology* **84**:629-640

Tsuchiya, M. (1980) Biodeposit production by the mussel *Mytilus edulis* L. on rocky shores. *Journal of Experimental Marine Biology and Ecology* **47**:203-222.

Tsuchiya, M. & Nishihira, M. (1985) Islands of *Mytilus* as a habitat for small intertidal animals: effect of island size on community structure. *Marine Ecology Progress Series* **25**:71-81

Tsuchiya, M. & Nishihira, M. (1986) Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. *Marine Ecology Progress Series* **31**:171-178

Tsuchiya, M. & Retiere, C. (1992) Zonation of Intertidal Organisms and Community Structure of Small Animals Associated with Patches of the Mussel *Mytilus edulis* L. along the Rocky Coast of Dinard, Brittany, France. *Bull. Coll. Sci. Univ. Ryukyus* **54**: 47-81

Tsuchiya, M. (2002) Faunal structures associated with patches of mussels on East Asian coasts. *Helgoland Marine Research* **56**:31–36

Tyler, E.H.M., Somerfield, P.J., Berghe, E.V., Bremner, J., Jackson, E., Langmead, O., Lourdes, M., Palomares, D. & Webb, T.J. (2012) Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. *Global Ecology and Biogeography* **21**:922–934

Ugland, K.I., Gray, J.S. & Ellingsen, K.E. (2003) The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology* **72**:888-897

Ulrich, W. & Ollick, M. (2005) Limits to the estimation of species richness: The use of relative abundance distributions. *Diversity and Distributions* **11**:265–273

Underwood, A.J. & Fairweather, P.G. (1989) Supply-side ecology and benthic marine assemblages. *TRENDS in Ecology & Evolution* **4**:16-20

Underwood, A.J. (1997) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press – Cambridge, UK

Underwood, A.J. (2000) Experimental ecology of rocky intertidal habitats: what are we learning? *Journal of Experimental Marine Biology and Ecology* **250**:51–76

Underwood, A.J., Chapman, M.G. & Connel, S.D. (2000) Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* **250**:97–115

Underwood, A.J. & Chapman, M.G. (2005) Design and Analysis in Benthic Surveys, In: *Methods for the Study of Marine Benthos.* 3rd Edition. Eleftheriou, A. & McIntyre, A. Eds. Blackwell Science Ltd.- Oxford

Underwood, A.J. & Chapman, M.G. (2006) Early development of subtidal macrofaunal assemblages: relationships to period and timing of colonization. *Journal of Experimental Marine Biology and Ecology* **330**:221-233

Valdivia, N. & Thiel, M. (2006) Effects of point-source nutrient addition and mussel removal on epibiotic assemblages in *Perumytilus purpuratus* beds. *Journal of Sea Research* **56**:271–283

Vallarino, E.A. & Elias, R. (1997) The Dynamics of an Introduced *Balanus glandula* Population in the Southwestern Atlantic Rocky Shores. The Consequences on the Intertidal Community. *Marine Ecology* **18**:319-335

Vallarino, E.A., Rivero, M., Gravina, M.C. & Elías, R. (2002) The community-level response to sewage impact in intertidal mytilid beds of the Southwestern Atlantic, and the use of the Shannon index to assess pollution. *Revista de Biología Marina y Oceanografía* **37**:25-33

Valéry, P. (1964) *Selected Writings of Paul Valery*. New Directions Publishing

van Broekhoven, W., Jansen, H., Verdegem, M., Struyf, E., Troost, K., Lindeboom, H. & Smaal, A. (2015) Nutrient regeneration from feces and pseudofeces of mussel *Mytilus edulis* spat. *Marine Ecology Progress Series* **534**:107-120

Van Cauwenberghe, L. & Janssen, C.R. (2014) Microplastics in bivalves cultured for human consumption. *Environmental Pollution* **193**:65-70 van Denderen, P.D., Hintzen, N.T., Rijnsdorp, A.D., Ruardij, P. & van Kooten, T. (2014) Habitat-specific effects of fishing disturbance on benthic species richness in marine soft sediments. *Ecosystems* **17**:1216-1226

van Tamelen, P.G. (1996) Algal zonation in tidepools: experimental evaluation of the roles of physical disturbance, herbivory and competition. *Journal of Experimental Marine Biology and Ecology* **201**:197-231

van Tussenbroek, B.I. (1989) Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falkland Islands. *Marine Biology* **100**:419-430

van Tussenbroek, B.I. (1989a) Morphological variations of *Macrocystis pyriferain* the Falkland Islands in relation to environment and season. *Marine Biology* **102**:545-556

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980) The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Science* **37**:130-137

Varvio, S.L., Koehn, R.K. & Väinölä, R. (1988) Evolutionary genetics of the *Mytilus edulis* complex in the North Atlantic region. *Marine Biology* **98**:51-60

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. *Ecology* **89**:2290-2301

Volkenborn, N., Hedtkamp, S.I.C., van Beusekom, J.E.E. & Reise, K. (2007) Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. *Estuarine, Coastal and Shelf Science* **74**:331-343

Waite, J.H. (1983) Adhesion in byssally attached bivavles. *Biological Reviews* **58**:209-231

Wallace, J.C. (1980) Growth rates of different populations of the edible mussel, *Mytilus edulis*, in north Norway. *Aquaculture* **19**:303-311

Waller, C.L., Worland, M.R., Convey, P. & Barnes, D.K.A. (2006) Ecophysiological strategies of Antarctic intertidal invertebrates faced with freezing stress. *Polar Biology* **29**:1077-1083

Waller, C.L. (2008) Variability in intertidal communities along a latitudinal gradient in the Southern Ocean. *Polar Biology* **31**:809–816

Wallis, R.L. (1975) Thermal tolerance of *Mytilus edulis* of Eastern Australia. *Marine Biology* **30**:183-191

Ward, J.E. & Targett, N.M. (1989) Influence of marine microalgal metabolites on the feeding behavior of the blue mussel *Mytilus edulis*. *Marine Biology* **101**:313-321

Watson, H. C. (1835) *Remarks on the geographical distribution of British plants (etc.)* Longman – London

Watson, J.R., Hays, C.G., Raimondi, P.T., Mitarai, S., Dong, C., McWilliams, J.C., Blanchette, C.A., Caselle, J.E. & Siegel, D.A. (2011) Currents connecting communities: nearshore community similarity and ocean circulation. *Ecology* **92**:1193-1200

Watt, C.A. & Scrosati, R.A. (2013) Bioengineer effects on understory species richness, diversity, and composition change along an environmental stress gradient: experimental and mensurative evidence. *Estuarine, Coastal and Shelf Science* **123**:10-18

Webb, T.J., Tyler, E.H.M. & Somerfield, P.J. (2009) Life history mediates large-scale population ecology in marine benthic taxa. *Marine Ecology Progress Series* **396**:293–306

Webb, T.J. (2012) Marine and terrestrial ecology: unifying concepts, revealing differences. *Trends in Ecology and Evolution* **27**:535-541

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology* **30**:377-392.

Westerbom, M. & Jattu, S. (2006) Effects of wave exposure on the sublittoral distribution of blue mussels (*Mytilus edulis*) in a heterogeneous archipelago. *Marine Ecology Progress Series* **306**:191-200

White, G.E., Hose, G.C. & Brown, C. (2014) Influence of rock-pool characteristics on the distribution and abundance of inter-tidal fishes. *Marine Ecology* doi: 10.1111/maec.12232

Whittaker, R.H., Levin, S.A. & Root, R.B. (1973) Niche, Habitat, and Ecotope. *The American Naturalist* **107**:321-338

Widdows, J. (1978) Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom* **58**:109-124

Widdows, J., Fieth, P. & Worrall, C. (1979) Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis. Marine Biology* **50**:195-207

Widdows, J. & Brinsley, M. (2002) Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. *Journal of Sea Research* **48**:143–156

Wieters, E. (2001) Marine macroecology. *Trends in Ecology & Evolution* **16**:67-69

Wilding, T.A. & Nickell, T.D. (2013) Changes in Benthos Associated with Mussel (*Mytilus edulis* L.) Farms on the West-Coast of Scotland. *PLoS ONE* **8**: e68313

Williams, G. (1987) *Techniques and Fieldwork in Ecology*. Harper Collins - London

Willott, S.J. (2001) Species accumulation curves and the measure of sampling effort. *Journal of Applied Ecology* **38**:484-486

Witman, J.D. & Suchanek, T.H. (1984) Mussels in flow: drag and dislodgement by epizoans. *Marine Ecology Progress Series* **16**:259-268

Witman, J.D. (1985) Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecological Monographs* **55**:421-445

Witman, J.D. (2013) Are regional effects on local diversity more important in marine than in terrestrial communities? *Oikos* **122**:301–305

Word, J.Q. (1979) Classification of benthic invertebrates into infaunal trophic index feeding groups. *Coastal Water Research Project Biennial Report 1980* p.103-121

Yamada, S.B. & Boulding, E.G. (1998) Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology* **220:**191–211

Yonge, C.M. (1962) On the primitive significance of the byssus in the Bivalvia and its effects in evolution. *Journal of the Marine Biological Association of the United Kingdom* **42**:113-125.

Young, R.T. (1942) Spawning Season of the California Mussel, *Mytilus Californianus*. *Ecology* **23**:490-492

Youssef, N.H. & Elshahed, M.S. (2008) Species richness in soil bacterial communities: A proposed approach to overcome sample size bias. *Journal of Microbiological Methods* **75**:86-91

Yu, D.W., Terborgh, J.W. & Potts, M.D. (1998) Can high tree species richness be explained by Hubbell's null model? *Ecology Letters* **1**:193–199

Zacharias, M.A. & Roff, J.C. (2001) Explanations of patterns of intertidal diversity at regional scales. *Journal of Biogeography* **28**:471-483

Zak, J.C., Willig, M.R., Moorhead, D.L. & Wildman, H.G. (1994) Functional diversity of microbial communities: a quantitative approach. *Soil Biology and Biochemistry* **26**:1101-1108

Zak, J.C. & Visser, S. (1996) An appraisal of soil fungal biodiversity: the crossroads between taxonomic and functional biodiversity. *Biodiversity & Conservation* **5**:169-183

Zar, J.H. (1999) *Biostatistical analysis*. 4th Edition. Prentice-Hall - Upper Saddle River, NJ

Zuur, A.F., Ieno, E.N. & Smith, G.M. (2007) *Analysing Ecological Data*. Springer – New York

Plate 1: Sampling site at Rosehearty, Aberdeenshire

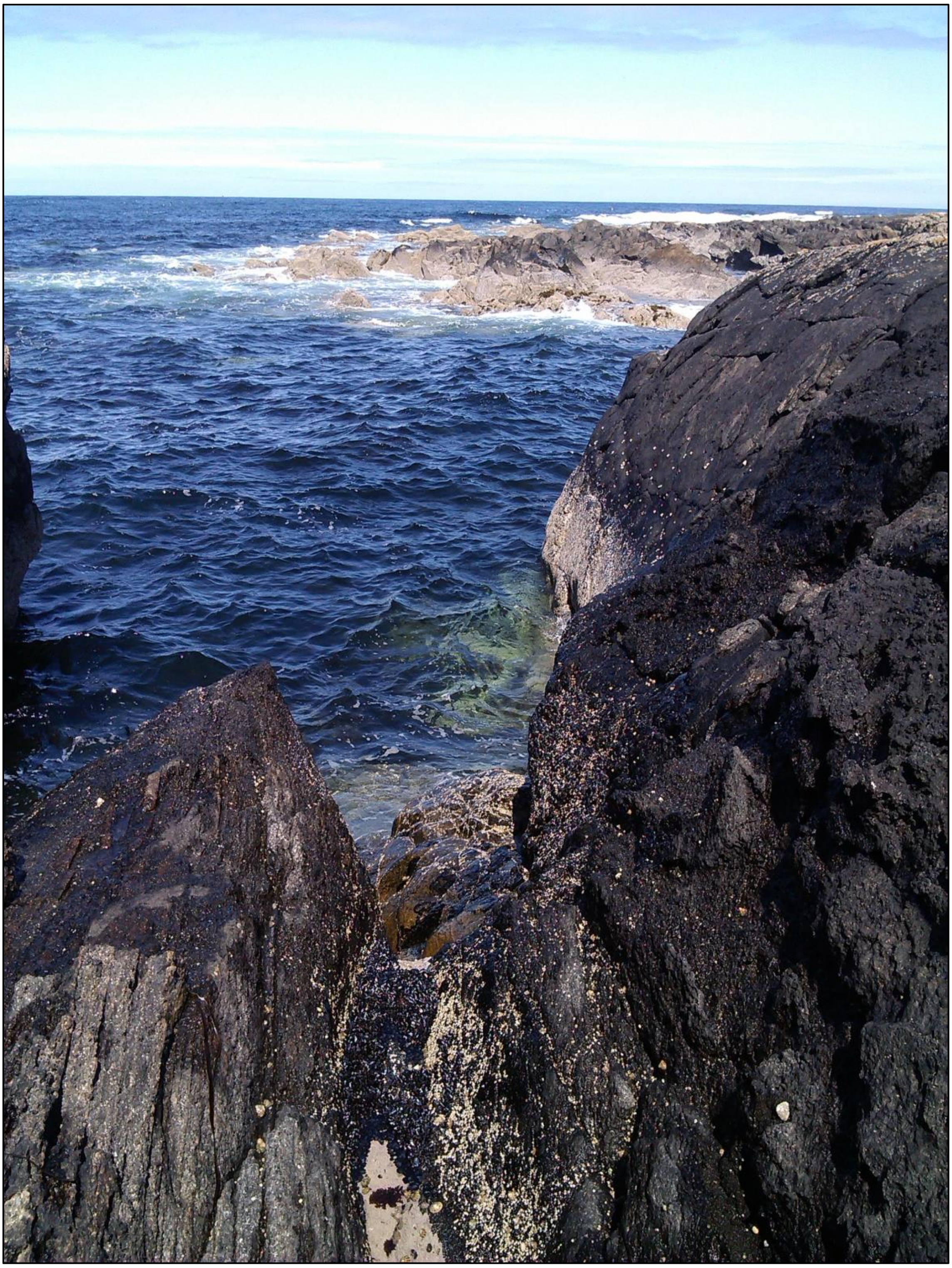

Plate 2: Sampling site at Portholland, Cornwall

Plate 3: Sampling site at Llandudno, Conwy

Plate 4: Sampling site at Cape Pembroke, East Falkland

Appendix 1: Synopses of the British Fauna

Published by The Linnean Society (Volume, Title, Author, Year of publication)

2: Molluscs: Prosobranch and Pyramidellid Gastropods Keys and Notes for the Identification of the Species

3: British Marine Isopods (Naylor, E.) 1972

8: Molluscs: Benthic Opisthobranchs (Mollusca: Gastropoda) (Thompson, T.E.) 1989

12: British Sipunculans (Gibbs, P.E.) 1978

21: British Other Marine Estuarine Oligochaetes (Brinkhurst) 1982

24: Nemerteans (Gibson, R.) 1982

25: Shallow Water Crabs Keys and notes for identification of the species (Ingle, R.W.) 1983

31: Earthworms (Sims, R.W. & Garard, B.M.) 1985

32: Polychaetes British Amphinomida, Spintherida and Eunicida (George, J.D. & Hartmann-Schroder, G.) 1985

36: Halacarid Mites (Green, J. & Macquitty, M.) 1987

37: Molluscs Caudofoveata, Solenogastres, Polyplacophora and Scaphopoda (Jones, A.M. & Baxtyer, J.M.) 1987

45: Polychaetes British Phyllodocoideans, Typhloscolecoideans and Tomopteroideans (Pleijel, F. & Dales, R.P.) 1991

54: Polychaetes: British Chrysopetaloidea, Pisionoidea and Aphroditoidea (Chambers S.J. & Muir, A.I.) 1998

55: Lobsters, Mud Shrimps and Anomuran Crabs (Ingle, R.W. &Christiansen, M.E.) 2004

56: Echinoderms (Southward, E.C. & Campbell, A.C.) 2005

Appendix 2: Taxonomic list of UK infauna from *M. edulis* patches and associated feeding function

Acanthochitona crinita (Pennant, 1777)	Grazer
Acanthodoris pilosa (Abildgaard in Müller, 1789)	Grazer
Alvania beanii (Hanley in Thorpe, 1844)	Detritivore
Amblyosyllis formosa (Claparède, 1863)	Predator
Amphinomidae sp. (Lamarck, 1818)	Predator
Amphipholis squamata (Delle Chiaje, 1828)	Surface deposit feeder
Amphiura chiajei (Forbes, 1843)	Surface deposit feeder
Amphiura filiformis (O.F. Müller, 1776)	Surface deposit feeder
Aphelochaeta filiformis (Keferstein, 1862)	Surface deposit feeder
Aphelochaeta marioni (Saint-Joseph, 1894)	Surface deposit feeder
Apherusa bispinosa (Bate, 1857)	Detritivore
Astarte sulcata (da Costa, 1778)	Active suspension feeder
Atelecyclus rotundatus (Olivi, 1792)	Predator
Bathyporeia guilliamsoniana (Bate, 1857)	Detritivore
Bdellidae	Predator-Detritivore
Brachystomia scalaris (MacGillivray, 1843)	Grazer
Buccinum undatum (Linnaeus, 1758)	Predator
Cancer pagurus (Linnaeus, 1758)	Predator-Detritivore
Carcinus maenas (Linnaeus, 1758)	Predator-Detritivore
Cephalothrix linearis (Rathke, 1799)	Detritivore
Cingula trifasciata (J. Adams, 1800)	Detritivore
Cirratulus cirratus (O. F. Müller, 1776)	Surface deposit feeder
Crissila semistriata (Montagu, 1808)	Detritivore
Cymodoce truncata (Leach, 1814)	Detritivore
Cyrtolaelapidae	Predator
Cythereis albomaculata (De Vos, 1957)	Detritivore
Cytherois fischeri (Sars, 1866)	Detritivore
Echinogammarus marinus (Leach, 1815)	Surface deposit feeder
Echinogammarus obtusatus (Dahl, 1938)	Surface deposit feeder
Ecrobia ventrosa (Montagu, 1803)	Surface deposit feeder-Grazer
Emplectonema gracile (Johnston, 1837)	Predator-Detritivore
Eulalia viridis (Linnaeus, 1767)	Predator
Eumida sanguinea (Örsted, 1843)	Predator
Gammarus zaddachi (Sexton, 1912)	Surface deposit feeder
Gibbula umbilicalis (da Costa, 1778)	Detritivore
Gitana sarsi (Boeck, 1871)	Detritivore
Halacaridae (Murray, 1877)	Predator-Parasite
Hexapoda	Detritivore
Hiatella arctica (Linnaeus, 1767)	Active suspension feeder
Hyale nilssoni (Rathke, 1843)	Grazer
Hydrobia neglecta (Muus, 1963)	Surface deposit feeder-Grazer
Idotea granulosa (Rathke, 1843)	Detritivore
Idotea neglecta (Sars, 1897)	Grazer

Idotea pelagica (Leach, 1815)	Detritivore
Inachus phalangium (Fabricius, 1775)	Detritivore
Iphimedia minuta (G.O. Sars, 1882)	Detritivore
Jaera albifrons (Leach, 1814)	Grazer
Jaera ischiosetosa (Forsman, 1949)	Grazer
Kellia suborbicularis (Montagu, 1803)	Active suspension feeder
Lacuna pallidula (da Costa, 1778)	Grazer
Lacuna parva (da Costa, 1778)	Grazer
Lacuna vincta (Montagu, 1803)	Grazer
Lasaea rubra (Montagu, 1803)	Active suspension feeder
Lepidochitona cinerea (Linnaeus, 1767)	Grazer
Leptochiton asellus (Gmelin, 1791)	Grazer
Lineus (Sowerby, 1806)	Predator
Liocarcinus depurator (Linnaeus, 1758)	Predator-Detritivore
Littorina fabalis (Turton, 1825)	Grazer
Littorina littorea (Linnaeus, 1758)	Detritivore
Littorina obtusata (Linnaeus, 1758)	Grazer
Littorina saxatilis (Olivi, 1792)	Detritivore
Lutraria lutraria (Linnaeus, 1758)	Active suspension feeder
Magelona mirabilis (Johnston, 1865)	Surface deposit feeder
Malacoceros fuliginosus (Claparède, 1870)	Active suspension feeder
Melarhaphe neritoides (Linnaeus, 1758)	Detritivore
Modiolus barbatus (Linnaeus, 1758)	Active suspension feeder
Modiolus modiola (Linnaeus, 1758)	Active suspension feeder
Myrianida prolifera (O.F. Müller, 1788)	Predator
Nannastacus unguiculatus (Bate, 1859)	Surface deposit feeder
Nassarius incrassatus (Strøm, 1768)	Predator
Nassarius reticulatus (Linnaeus, 1758)	Predator
Nematoda	Predator-Detritivore
Nemertean	Predator-Detritivore
Nephasoma minutum (Keferstein, 1862)	Passive suspension feeder
Nephtys caeca (Fabricius, 1780)	Predator
Neptunea antiqua (Linnaeus, 1758)	Predator-Detritivore
Nereimyra punctata (Müller, 1788)	Predator
Nereis pelagica (Linnaeus, 1758)	Predator
Nucella lapillus (Linnaeus, 1758)	Predator-Detritivore
Obtusella intersecta (S. Wood, 1857)	Detritivore
Oligochaeta	Detritivore
Onoba semicostata (Montagu, 1803)	Detritivore
Onychiuridae	Detritivore
Ophiothrix fragilis (Abildgaard, in O.F. Müller, 1789)	Passive suspension feeder
Ostracoda (Latreille, 1802)	Detritivore
Parvicardium pinnulatum (Conrad, 1831)	Active suspension feeder
Parvicardium scabrum (Philippi, 1844)	Active suspension feeder
Peringia ulvae (Pennant, 1777)	Surface deposit feeder-Grazer
Phyllodoce groenlandica (Örsted, 1842)	Predator
Phyllodoce maculata (Linnaeus, 1767)	Predator
Pisidia longicornis (Linnaeus, 1767)	Detritivore

Polititapes rhomboides (Pennant, 1777)	Active suspension feeder
Polychaete sp. (Grube, 1850)	Predator-Detritivore
Polydora ciliata (Johnston, 1838)	Passive suspension feeder
Porcellana platycheles (Pennant, 1777)	Detritivore
Pusillina inconspicua (Alder, 1844)	Detritivore
Pusillina sarsii (Lovén, 1846)	Detritivore
Rissoa parva (da Costa, 1778)	Detritivore
Sabellidae (Latreille, 1825)	Passive suspension feeder
Skeneopsis planorbis (O. Fabricius, 1780)	Grazer
Sphaeroma serratum (Fabricius, 1787)	Detritivore
Sunamphitoe pelagica (Milne Edwards, 1830)	Predator
Testudinalia testudinalis (O. F. Müller, 1776)	Grazer
Tonicella rubra (Linnaeus, 1767)	Grazer
Tryphosa nana (Krøyer, 1846)	Detritivore
Tubificidae (Vejdovský, 1884)	Detritivore
Urothoe marina (Bate, 1857)	Detritivore

Appendix 3: Sample codes for infaunal samples from UK and Falkland Islands intertidal mussel beds

Sample code	Date (yyyymmdd)	Site	Location
WF_25_25_1	20091214	Filey	UK
WF_25_25_2	20091214	Filey	UK
WF_25_25_3	20091214	Filey	UK
WF_20_20_1	20091214	Filey	UK
WF_20_20_2	20091214	Filey	UK
WF_20_20_3	20091214	Filey	UK
WF_15_15_1	20091214	Filey	UK
WF_15_15_2	20091214	Filey	UK
WF_15_15_3	20091214	Filey	UK
WF_15_10_1	20091214	Filey	UK
WF_15_10_2	20091214	Filey	UK
WF_15_10_3	20091214	Filey	UK
WF_10_10_1	20091214	Filey	UK
WF_10_10_2	20091214	Filey	UK
WF_10_10_3	20091214	Filey	UK
WF_10_5_1	20091214	Filey	UK
WF_10_5_2	20091214	Filey	UK
WF_10_5_3	20091214	Filey	UK
WF_5_5_1	20091214	Filey	UK
WF_5_5_2	20091214	Filey	UK
WF_5_5_3	20091214	Filey	UK
SF_25_25_1	20100322	Filey	UK
SF_25_25_2	20100322	Filey	UK
SF_25_25_3	20100322	Filey	UK
SF_20_20_1	20100322	Filey	UK
SF_20_20_2	20100322	Filey	UK
SF_20_20_3	20100322	Filey	UK
SF_15_15_1	20100322	Filey	UK
SF_15_15_2	20100322	Filey	UK
SF_15_15_3	20100322	Filey	UK
SF_15_10_1	20100322	Filey	UK
SF_15_10_2	20100322	Filey	UK
SF_15_10_3	20100322	Filey	UK
SF_10_10_1	20100322	Filey	UK
SF_10_10_2	20100322	Filey	UK
SF_10_10_3	20100322	Filey	UK
SF_10_5_1	20100322	Filey	UK
SF_10_5_2	20100322	Filey	UK
SF_10_5_3	20100322	Filey	UK
SF_5_5_1	20100322	Filey	UK
SF_5_5_2	20100322	Filey	UK
SF_5_5_3	20100322	Filey	UK
UF_25_25_1	20100612	Filey	UK
UF_25_25_2	20100612	Filey	UK
UF_25_25_3	20100612	Filey	UK
UF_20_20_1	20100612	Filey	UK

UF_20_20_2	20100612	Filey	UK
UF_20_20_3	20100612	Filey	UK
UF_15_15_1	20100612	Filey	UK
UF_15_15_2	20100612	Filey	UK
UF_15_15_3	20100612	Filey	UK
UF_15_10_1	20100612	Filey	UK
UF_15_10_2	20100612	Filey	UK
UF_15_10_3	20100612	Filey	UK
UF_10_10_1	20100612	Filey	UK
UF_10_10_2	20100612	Filey	UK
UF_10_10_3	20100612	Filey	UK
UF_10_5_1	20100612	Filey	UK
UF_10_5_2	20100612	Filey	UK
UF_10_5_3	20100612	Filey	UK
UF_5_5_1	20100612	Filey	UK
UF_5_5_2	20100612	Filey	UK
UF_5_5_3	20100612	Filey	UK
AF_25_25_1	20100927	Filey	UK
AF_25_25_2	20100927	Filey	UK
AF_25_25_3	20100927	Filey	UK
AF_20_20_1	20100927	Filey	UK
AF_20_20_2	20100927	Filey	UK
AF_20_20_3	20100927	Filey	UK
AF_15_15_1	20100927	Filey	UK
AF_15_15_2	20100927	Filey	UK
AF_15_15_3	20100927	Filey	UK
AF_15_10_1	20100927	Filey	UK
AF_15_10_2	20100927	Filey	UK
AF_15_10_3	20100927	Filey	UK
AF_10_10_1	20100927	Filey	UK
AF_10_10_2	20100927	Filey	UK
AF_10_10_3	20100927	Filey	UK
AF_10_5_1	20100927	Filey	UK
AF_10_5_2	20100927	Filey	UK
AF_10_5_3	20100927	Filey	UK
AF_5_5_1	20100927	Filey	UK
AF_5_5_2	20100927	Filey	UK
AF_5_5_3	20100927	Filey	UK
WR_25_25_1	20091218	Ravenscar	UK
WR_25_25_2	20091218	Ravenscar	UK
WR_25_25_3	20091218	Ravenscar	UK
WR_20_20_1	20091218	Ravenscar	UK
WR_20_20_2	20091218	Ravenscar	UK
WR_20_20_3	20091218	Ravenscar	UK
WR_15_15_1	20091218	Ravenscar	UK
WR_15_15_2	20091218	Ravenscar	UK
WR_15_15_3	20091218	Ravenscar	UK
WR_15_10_1	20091218	Ravenscar	UK
WR_15_10_2	20091218	Ravenscar	UK
WR_15_10_3	20091218	Ravenscar	UK
WR_10_10_1	20091218	Ravenscar	UK

WR_10_10_2	20091218	Ravenscar	UK
WR_10_10_3	20091218	Ravenscar	UK
WR_10_5_1	20091218	Ravenscar	UK
WR_10_5_2	20091218	Ravenscar	UK
WR_10_5_3	20091218	Ravenscar	UK
WR_5_5_1	20091218	Ravenscar	UK
WR_5_5_2	20091218	Ravenscar	UK
WR_5_5_3	20091218	Ravenscar	UK
SR_25_25_1	20100321	Ravenscar	UK
SR_25_25_2	20100321	Ravenscar	UK
SR_25_25_3	20100321	Ravenscar	UK
SR_20_20_1	20100321	Ravenscar	UK
SR_20_20_2	20100321	Ravenscar	UK
SR_20_20_3	20100321	Ravenscar	UK
SR_15_15_1	20100321	Ravenscar	UK
SR_15_15_2	20100321	Ravenscar	UK
SR_15_15_3	20100321	Ravenscar	UK
SR_15_10_1	20100321	Ravenscar	UK
SR_15_10_2	20100321	Ravenscar	UK
SR_15_10_3	20100321	Ravenscar	UK
SR_10_10_1	20100321	Ravenscar	UK
SR_10_10_2	20100321	Ravenscar	UK
SR_10_10_3	20100321	Ravenscar	UK
SR_10_5_1	20100321	Ravenscar	UK
SR_10_5_2	20100321	Ravenscar	UK
SR_10_5_3	20100321	Ravenscar	UK
SR_5_5_1	20100321	Ravenscar	UK
SR_5_5_2	20100321	Ravenscar	UK
SR_5_5_3	20100321	Ravenscar	UK
UR_25_25_1	20100607	Ravenscar	UK
UR_25_25_2	20100607	Ravenscar	UK
UR_25_25_3	20100607	Ravenscar	UK
UR_20_20_1	20100607	Ravenscar	UK
UR_20_20_2	20100607	Ravenscar	UK
UR_20_20_3	20100607	Ravenscar	UK
UR_15_15_1	20100607	Ravenscar	UK
UR_15_15_2	20100607	Ravenscar	UK
UR_15_15_3	20100607	Ravenscar	UK
UR_15_10_1	20100607	Ravenscar	UK
UR_15_10_2	20100607	Ravenscar	UK
UR_15_10_3	20100607	Ravenscar	UK
UR_10_10_1	20100607	Ravenscar	UK
UR_10_10_2	20100607	Ravenscar	UK
UR_10_10_3	20100607	Ravenscar	UK
UR_10_5_1	20100607	Ravenscar	UK
UR_10_5_2	20100607	Ravenscar	UK
UR_10_5_3	20100607	Ravenscar	UK
UR_5_5_1	20100607	Ravenscar	UK
UR_5_5_2	20100607	Ravenscar	UK
UR_5_5_3	20100607	Ravenscar	UK
AR_25_25_1	20100919	Ravenscar	UK

AR_25_25_2	20100919	Ravenscar	UK
AR_25_25_3	20100919	Ravenscar	UK
AR_20_20_1	20100919	Ravenscar	UK
AR_20_20_2	20100919	Ravenscar	UK
AR_20_20_3	20100919	Ravenscar	UK
AR_15_15_1	20100919	Ravenscar	UK
AR_15_15_2	20100919	Ravenscar	UK
AR_15_15_3	20100919	Ravenscar	UK
AR_15_10_1	20100919	Ravenscar	UK
AR_15_10_2	20100919	Ravenscar	UK
AR_15_10_3	20100919	Ravenscar	UK
AR_10_10_1	20100919	Ravenscar	UK
AR_10_10_2	20100919	Ravenscar	UK
AR_10_10_3	20100919	Ravenscar	UK
AR_10_5_1	20100919	Ravenscar	UK
AR_10_5_2	20100919	Ravenscar	UK
AR_10_5_3	20100919	Ravenscar	UK
AR_5_5_1	20100919	Ravenscar	UK
AR_5_5_2	20100919	Ravenscar	UK
AR_5_5_3	20100919	Ravenscar	UK
UK_F_1	20130605	Filey	UK
UK_F_2	20130605	Filey	UK
UK_F_3	20130605	Filey	UK
UK_F_4	20130605	Filey	UK
UK_F_5	20130605	Filey	UK
UK_RV_1	20130606	Ravenscar	UK
UK_RV_2	20130606	Ravenscar	UK
UK_RV_3	20130606	Ravenscar	UK
UK_RV_4	20130606	Ravenscar	UK
UK_RV_5	20130606	Ravenscar	UK
UK_P_1	20130602	Portholland	UK
UK_P_2	20130602	Portholland	UK
UK_P_3	20130602	Portholland	UK
UK_P_4	20130602	Portholland	UK
UK_P_5	20130602	Portholland	UK
UK_TS_1	20130602	Trebarwith Strand	UK
UK_TS_2	20130602	Trebarwith Strand	UK
UK_TS_3	20130602	Trebarwith Strand	UK
UK_TS_4	20130602	Trebarwith Strand	UK
UK_TS_5	20130602	Trebarwith Strand	UK
UK_RO_1	20130608	Rosehearty	UK
UK_RO_2	20130608	Rosehearty	UK
UK_RO_3	20130608	Rosehearty	UK
UK_RO_4	20130608	Rosehearty	UK
UK_RO_5	20130608	Rosehearty	UK
UK_L_1	20130613	Llandudno	UK
UK_L_2	20130613	Llandudno	UK
UK_L_3	20130613	Llandudno	UK
UK_L_4	20130613	Llandudno	UK
UK_L_5	20130613	Llandudno	UK
FI_CP1	20131103	Cape Pembroke	Falkland Is.

FI_CP2	20131103	Cape Pembroke	Falkland Is.
FI_CP3	20131103	Cape Pembroke	Falkland Is.
FI_CP4	20131103	Cape Pembroke	Falkland Is.
FI_CP5	20131103	Cape Pembroke	Falkland Is.
FI_CP6	20131103	Cape Pembroke	Falkland Is.
FI_CP7	20131103	Cape Pembroke	Falkland Is.
FI_CP8	20131103	Cape Pembroke	Falkland Is.
FI_CP9	20131103	Cape Pembroke	Falkland Is.
FI_CP10	20131103	Cape Pembroke	Falkland Is.
FI_ST1	20131103	Stanley	Falkland Is.
FI_ST2	20131103	Stanley	Falkland Is.
FI_ST3	20131103	Stanley	Falkland Is.
FI_ST4	20131103	Stanley	Falkland Is.
FI_ST5	20131103	Stanley	Falkland Is.
FI_ST6	20131103	Stanley	Falkland Is.
FI_ST7	20131103	Stanley	Falkland Is.
FI_ST8	20131103	Stanley	Falkland Is.
FI_ST9	20131103	Stanley	Falkland Is.
FI_ST10	20131103	Stanley	Falkland Is.
FI_GG1	20131104	Goose Green	Falkland Is.
FI_GG2	20131104	Goose Green	Falkland Is.
FI_GG3	20131104	Goose Green	Falkland Is.
FI_GG4	20131104	Goose Green	Falkland Is.
FI_GG5	20131104	Goose Green	Falkland Is.
FI_GG6	20131104	Goose Green	Falkland Is.
FI_GG7	20131104	Goose Green	Falkland Is.
FI_GG8	20131104	Goose Green	Falkland Is.
FI_GG9	20131104	Goose Green	Falkland Is.
FI_GG10	20131104	Goose Green	Falkland Is.

Appendix 4: Falkland Islands voucher specimen codes and information

Sample code	**Sample name**	**Identification to Class**
FI_CP2_AMP_1	Amphipod 1	Hyalidae
FI_CP5_AMP_2	Amphipod 2	Gammaridae 1
FI_CP5_AMP_3	Amphipod 3	Gammaridae 2
FI_CP8_ARA_1	Arachnid 1	Acarina
FI_ST1_BIV_1	Bivalve 1	Lasaeidae
FI_CP1_BIV_2	Bivalve 2	Carditidae
FI_CP1_BIV_3	Bivalve 3	Mactridae
FI_ST1_BIV_4	Coleoptera 1	Coleoptera
FI_CP2_DEC_1	Decapod 1	Pilumnidae
FI_GG3_ECH_1	Echinoderm 1	Spinulosida
FI_CP1_GAS_1	Gastropod 1	Hydrobiidae
FI_CP2_GAS_2	Gastropod 2	Littorinidae
FI_GG8_GAS_3	Gastropod 3	Cerithiidae
FI_CP2_GAS_4	Gastropod 4	Muricidae
FI_ST1_ISO_1	Isopod 1	Munnidae
FI_CP1_ISO_2	Isopod 2	Sphaeromatidae
FI_CP1_OPI_1	Nudibranch 1	Onchidiidae
FI_CP1_OLI	Oligochaete sp	Oligochaete sp
FI_CP4_POL_1	Polychaete 1	Nereididae
FI_CP9_POL_2	Polychaete 3	Terebellidae