

THE UNIVERSITY OF HULL

BENTHIC COMMUNITY STRUCTURE AND FUNCTION ALONG SALINITY AND  
ELEVATION GRADIENTS IN THE HUMBER ESTUARY

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## **Abstract**

Biological Traits Analysis (BTA) is increasingly being applied together with taxonomic and structural analysis in marine and estuarine studies of the benthos, to link species characteristics to ecosystem function. An investigation was made of benthic community structure and function along salinity and elevation gradients in the Humber Estuary, UK. The project aim was to establish whether community structure and function changed along either gradient. Samples were taken at three sites from inner to outer estuary and analysed in terms of abundance, biomass, diversity, species richness and taxonomic composition. Biological Traits Analysis (BTA) was applied to the same data, selecting thirteen traits with links to ecosystem functioning. Most aspects of community structure differed with change in abiotic gradient, particularly species richness, biomass and taxonomic composition. BTA results were similar, showing different profiles of trait expression along the salinity gradient, and along elevation gradients at two sites. Traits that showed clear sensitivity to abiotic factors, as well as links to function, were bioturbation, feeding traits, habitat, body size and reproductive traits. Although trait profiles changed, a loss of function was not always apparent as differences were in terms of proportions rather than presence or absence. Potential functional loss was indicated in some cases, particularly where traits with links bioturbatory activities were absent. Overall, BTA did not give a particularly different result to taxonomic analysis but it did show potential, with development, to increase understanding of benthic community links to ecosystem function.



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## **List of Abbreviations Used**

BTA: Biological Traits Analysis

BIOTIC: Biological Traits Information Catalogue

IECS: Institute of Estuarine and Coastal Studies

MR: Managed Realignment

PSA: Particle Size Analysis

FM: Feeding Mode

FA: Feeding Apparatus

FT: Food Type

AM: Adult Mobility

LH: Living Habitat

BL: Body Length (Adult)

L: Longevity

B: Bioturbatory Mode

RF: Reproductive Frequency

S: Salinity Preference

P: Living Position

F: Fecundity

M: Age at Maturity



# CHAPTER 1

## 1. Introduction

### 1.1 Background

Estuaries are complex environments, under stress due to constantly fluctuating physical conditions (Elliott and Whitfield, 2011). Typically, estuaries have fine grained sediments, rich in organic material, but factors such as high turbidity and low oxygen content combine with varying salinity to result in an environment that many species find too challenging to live in. The consequence of this is an ecosystem that supports a relatively small number of species that often exist in great abundance (Little, 2000; Elliott and McLusky, 2002; Elliott and Quintino, 2007); specialised species that have adapted to the environment to take advantage of high levels of nutrients found in estuaries. Many of these are opportunistic species and are typified by a small body size, short life-cycle and a high level of fecundity, colonizing an area very quickly when conditions become suitable, but have a low competitive ability and are unable to sustain high population densities over time once more effective competitors appear (Gray, 1979; Rosenberg et al., 2004). These benthic animals are normally found either on the sediment surface or in the top 5-10 cm and play a key role in the functioning of the estuarine ecosystem (Bremner et al, 2006), from driving nutrient and chemical cycles, to providing a vital energy link between primary producers and all faunal components (McLusky, 2000), supporting high numbers of migrating, and local, birds and fish populations (Atkinson et al., 2001; Atkinson, 2003; Mander et al., 2007).

This project considers an estuarine benthic ecosystem and examines three sites in the Humber Estuary in order to determine the impact of abiotic factors on community structure and functioning. Standard assessment of the health of a site often focuses on measuring biodiversity based on the taxa present, producing community structure information based on these species. An increasing number of studies are now also focussing on ecological function when assessing a site (Bremner et al., 2006a and 2008; Marine Ecological Surveys Ltd, 2008; Verissimo, 2012; Paganelli et al., 2012,). The idea behind this is that the functional roles of the species present – what the animals identified actually *do* in the community- could be a useful measure of ecosystem health and give an idea of the practical, functional, level of diversity that exists there. A popular approach to this is Biological Traits Analysis (BTA), in which aspects of an animal's life history and behaviour that relate to ecosystem functions are selected and scored for all taxa recorded at a sampling site. These characteristics, or traits, are analysed and used to build a picture of benthic ecological functioning across the site under consideration (Bremner et al., 2006 and 2006a).

Potential changes in benthic functioning will be examined here, using BTA, along two environmental gradients: salinity and elevation. The distance between sites along the estuary provides the salinity gradient, and the elevation gradient runs from lower to middle shore at each site. Access to the true lower shore was not feasible for this project, but the gradient was extended in distance and variability of terrain by selecting three sites that had been the subject of managed realignment, where the removal and setting back of flood defences now allows tidal inundation at a higher elevation.

## **1.2 Natural Stressors and Anthropogenic Activities**

Natural stressors in estuarine environments are present due to their nature as transitional waters (Little, 2000; Elliott and McLusky, 2002; Elliott and Whitfield 2011) and include tidal pressures, associated broad variation in salinity and oxygen levels, and dynamic flow regimes. Regular fluctuation between saline and freshwater within estuaries means species living in this type of environment need to be well adapted to highly variable conditions that would exclude the presence of more delicate animals. Estuarine invertebrates are often effective osmoregulators, able to sustain a suitable level of salt and water in their bodies despite changing concentrations in surrounding fluid (Willmer, 2006). They are generally euryhaline, able to exist at a wider range of salinities than most true marine or freshwater animals. Along with this, there is a great deal of sediment movement within estuaries, with fast changes in mudflat level and sediment composition taking place with the action of waves, tidal cycle, river run-off and seasonal change (Christe et al., 1999). This modifies habitats and can affect an organism's presence or absence at a site (JNCC, 2004). The consequence of this is that for studies examining anthropogenic impacts on the benthos, and generally in the estuary, there can be background 'noise' in the data, due to this environmental variability, making it challenging to distinguish some natural stressor from man-made ones (Elliott and Quintino, 2007).

Anthropogenic activity in most large estuaries is high and is characterised by industry, shipping, and more recently, recreation (Conley et al., 2000; McLusky and Elliott, 2004). In some estuaries industrial output has a very serious impact, such as the Baixada Santista estuary in Brazil, where a wide range of untreated organic and chemical contaminants threaten both the biota and human health (Braga et al., 2000), while in others, such as the Scheldt estuary on the borders of the Netherlands and Belgium, some contaminants, such as heavy metals, are still an issue but have decreased in recent decades due to improved water quality control regulations (Baeyens et al., 1998; McLusky, 2001). The demands of shipping require maintenance and development of port facilities and can include expansion on to natural estuarine habitat as well as regular dredging in some estuaries to sustain depth along shipping channels, which cause changes to morphology and flow regime (Cave et al., 2003; Cox et al., 2003; Humber Management Scheme, 2013). Dredging can also impact on benthic organisms and while some communities can recover quickly, it may take up to a year for a heavily dredged area to fully re-establish a population and resume natural functioning (Guerra-García et al., 2003; Lokkeborg, 2005, Marine Ecological Surveys, 2008, Bolam et al., 2011). Dredging can also be carried out for commercial fishing purposes and, together with trawling, can alter community composition in the sediment (Casey et al 2013, Handley et al, 2014). A further disturbance caused by shipping is the potential for invasive species to enter the ecosystem. Organisms of all kinds can be transported globally in the ballast water of ships and can occasionally make their way in to ecosystems far from the port of origin. Some can have serious consequences, both environmental and economic, as seen with the zebra mussel (Vitousek et al., 1997), and the phenomenon is regarded as a serious threat internationally, as well as to local benthic and pelagic species (Mario, 2002; Endresen, 2004; Hayes and Sliwa, 2003).

Other human uses of the estuary include land claim, which can radically altered the profile of the estuary over time, (Morris et al., 2004; Boyes and Elliott, 2006) along with the subsequent

building of hard sea defences to protect this claimed land and the low-lying land around it (JNCC, 2004).

A number of aspects of estuarine ecosystem processes are of benefit to human communities and are described in the literature as ecosystem services (Portman, 2013; Pinto, 2013; Lamarque, 2011). Benefits to humans include flood defence; land drainage; nutrient cycling and recreation and are important considerations in estuarine monitoring and management (French, 1997).

### **1.3 Estuarine Ecosystem Functions**

Examining ecosystem function is useful because it assesses processes taking place not just within, but also beyond the study site, which are still intrinsically connected to it. The functional approach considers the biota, but also the geochemical properties of the ecosystem, acknowledging the holistic nature of the systems and linking, in this case, the benthos to processes taking place across the whole estuary. Biological Traits Analysis does not measure functioning directly; rather it selects species characteristics that have an established link to measurable functional processes and uses these proxies to extrapolate ecosystem function at a given location.

The terms 'function' and 'functioning' and their exact definition for the purposes of empirical studies are still the subject of debate. There are a number of overlapping definitions, varying in detail, and at the root of this is the general way in which the terms are used. From definitions covering simple predator-prey interactions, to those encompassing the intricacies of full ecosystem processes, 'function' is applied at many levels of ecology activity, incorporating the biological, physical and chemical (Diaz and Cabido 2001; Jax 2005, Bremner 2008; Solan et al., 2012). Functioning is distinct from structure as it is measured as processes over time (e.g. secondary benthic production  $\text{m}^{-2}/\text{yr}^{-1}$ ), while structural studies consider assemblages at a specific moment in time. Definitional accuracy of the term is important; the nature of this study, examining estuarine benthic functional traits, would not be directly comparable with a study that, for instance, considered 'function' in terms of ecosystem services provided to humans by the same environment. The latter would examine practical political, economic or social outcomes, while the former would be concerned with biological interactions and various rate processes taking place at a relatively minute scale within the sediment. While these two studies could perhaps be compared the link would be a complicated one and not readily apparent (Pinto et al., 2014) so a clear definition is needed at the outset.

Although the broad socio-political and economic definitions of functioning outlined above are acknowledged by this study, the focus here is on benthic community functioning and this means the definition used here needs to be one more readily relatable to the benthos. Therefore, this project will consider the ecosystem processes that cycle energy and substances through the estuary, or are linked to perpetuating these cycles and maintaining natural estuarine systems (Naeem and Wright, 2003; Bremner, 2005).

These include:

- The cycling of chemicals and nutrients – the movement, use, or sequestration of substances (e.g. - nitrate, nitrite, phosphate, ammonia, carbon, oxygen, or contaminants) through the ecosystem.
- Food chain support - primary production, decomposition, nutrient export and the transfer of this energy through estuarine food webs.
- Sediment and hydrology – sediment modification, transport, coastal protection and flood water storage.
- Habitat provision – nursery role for fish, feeding and nesting habitat for birds and support of mammal species.

Detail of these functions is given in Chapter 2.1.2. Selection of taxa traits for analysis will be made with these processes in mind and should link the characteristics of benthic animals to these wider ecosystem functions. Analysis of trait composition at different points along the salinity and elevation gradients should then indicate if a functional change has occurred with a change in abiotic factors.

#### **1.4 Monitoring and Management in Estuaries**

Effective environmental management relies on accurate information from the field, and realistic site assessment is of particular importance in estuarine/transitional waters as they are areas of significant long-term financial investment (Wolfe et al., 1987; Humber Management Scheme, 2013). Government spending of £92 million over a four-year period was allotted to improve aspects of the quality of UK bodies of water, in line with the Water Framework Directive (WFD), and included significant spending in estuaries (DEFRA, 2012). Overall spending on the WFD has been estimated at £7 billion (Professor Mike Elliott, IECS, pers.comm 2014). Meeting the targets of the WFD meant bodies of water achieving a water quality status of 'good' by 2015, although this deadline has now been extended to 2027 (Hering et al., 2010). This status is reliant on both chemical content of the water and the ecological status of whole water body (which includes structure and functioning) meeting WFD guidelines. Assessing these conditions requires collection of biological, chemical and physical data and subsequent regular monitoring to ensure WFD guidelines are being met or being moved towards. The cost of these management and monitoring schemes is high, but is a necessary requirement under EU law (European Commission, 2000).

Flood defence is also a key management issue in estuaries. There is widespread scientific consensus that sea levels are rising (Hulme et al., 2002), and one of the consequences of this is new pressure on old flood defences. As sea levels rise the margin between the low tide point and sea wall defences becomes narrower, resulting in a greatly reduced intertidal zone. This process is known as coastal squeeze and occurs because hard coastal defences prevent a natural response to sea level rise, which would normally mean the gradual inland movement of the intertidal zone (JNCC, 2004). As increasing rises are predicted over the coming years the management of natural mudflat and intertidal habitat is becoming vital to flood defence strategy (Mazik, 2007), as traditional 'hard' sea wall defences are often no longer seen as

viable long term solutions (EA, 2013). Feedback on the success of a project or on the validity of a proposed undertaking can have a profound impact on the estuarine landscape and on its future management.

Other regular monitoring in estuaries includes surveys of wildlife. Estuaries are particularly important for birds, as they are a rich source of food, and most UK estuaries with significant or protected bird populations take regular record of species composition and population densities (Mander et al., 2007; Spencer, 2010; RSPB, 2014; Natural England, 2014).

### **1.5 Estuarine Communities and Designations**

Estuaries support significant communities of fish, birds and mammals and are an important resource in terms of feeding and providing a safe environment for breeding and development of juveniles, not just in temperate estuaries, but globally (Henderson and Bird, 2010; Donglai et al., 2011; Blaber, 2013). Estuaries are not only important for sustaining wildlife but are essential for maintaining many commercial fisheries stocks (Henderson and Seaby, 1994; McLusky, 2001). Estuaries are characterised by mudflat and salt marsh and these habitats have important functions for animal and human communities; from feeding and nesting grounds to the provision of natural flood defences. Intense anthropogenic use means that natural estuarine habitats have become reduced or rare and are now subject to designations to protect what remains. These designations may include: Special Protection Area (SPA), Special Area of Conservation (SAC), Site of Special Scientific Interest (SSSI), depending on the nature and importance of the site. If the site is of international importance it may be designated a Ramsar site and protected under European law. SPAs and SACs that contain either birds or other animals and habitats that are considered special or threatened in Europe may also be listed as European Marine Sites (EMS) under the EU Habitats and Birds Directive (Natural England, 2014). Over seventy sites in the UK are listed under these international designations, including, the Humber Estuary, the Severn Estuary and the Blackwater Estuary (JNCC, 2008 a, b and c). This means accurate monitoring and management of these sites is essential. The BTA approach used in this project is a monitoring tool that is still developing and shows potential promise for improving future assessment of ecosystem health.

### **1.6. Environmental Gradients**

Environmental landscapes naturally show differing measurable variables as they change from one type of terrain to another. These variables often show a clear gradient as two different habitats come to meet each other, and the estuary is a typical example of this occurring. Transitional ecosystems like this see freshwater and estuarine conditions meet and form ecotones – areas in which two distinct landscapes meet and elements of both may be observed alongside each other. Since a link exists between an environment and the community it supports it is reasonable to suppose that studying communities along such gradients could indicate how composition changes with changing abiotic conditions. The applications for understanding community response to environmental change are wide ranging, but chiefly it allows predictions to be made about the type of community that is likely to exist in a given set of ecosystem conditions. Both the gradients here present a potentially challenging range of living conditions, with extremes of immersion, emersion, and salinity fluctuation, making them ideal for a study concerning aspects of community change.

### 1.6.1 Elevation

Elevation along the profile of a shoreline, from sub-tidal to littoral fringe, is a well-studied gradient in the literature regarding the study of changing community composition (Scroati and Heaven, 2007, Little, 2009; Gray and Elliott, 2009). Many early ecological studies consider elevation, from as early as the 1800s on rocky shores, and it has been a subject of interest for ecologists ever since (Benson, 2002; Little 2000). This is almost certainly due to its accessibility and the often clear visual zonation of organisms that can be easily observed in many intertidal areas.

The distribution of organisms over an elevation gradient is one that is controlled by the tolerances of individual species. In an intertidal mudflat environment animals can be left exposed for hours at a time when the water retreats. This can have consequences such as desiccation, excessive inundation, lack of oxygen and exposure to predation. Ability to survive these conditions requires suitable adaptations. For example, some species of *Collembola*, which are mainly terrestrial, are found in the upper littoral zone and are able to trap air with their leg hairs and survive underwater for hours (BIOTIC, 2013). The inverse problem exists for aquatic animals in the same environment where the need is to maintain enough moisture to survive at low water. In soft sediment environments burrowing below the sediment surface, and keeping any siphons or palps retracted until covered by the tide again, is a common solution. These stressors and related adaptations are a factor in the distribution of organisms along the vertical gradient of the shoreline, making it an ideal abiotic factor along which to study community structure and functioning.

### 1.6.2 Salinity

Salinity has a strong effect on the distribution of organisms (Jones, 1988; Smyth, 2011; Crain et al., 2004; Bulger et al, 1993), and salinity preference has also been reported as a significant functional trait (Van der Linden et al., 2012). Changes occur in species composition along an estuarine/brackish water gradient from marine to freshwater (JNCC, 2004; Whitfield et al, 2012). There are typical patterns in type of animals sampled and species diversity along salinity gradients. Examples in the Humber include species at the seaward end that are not generally found below salinities of 20 (e.g. *Retusa obtusa*) while at the fresh water end species sampled may be almost fresh water, for example the *Planorbis.sp* of gastropod found at Alkborough. Between these, typical estuarine species such as *Macoma balthica* and *Corophium volutator* can be found in habitats subject to significant saline fluctuation.

An organism's level of tolerance to fluctuating saline concentration is a strong abiotic factor for species distribution (Smyth, 2011; Van der Linden et al., 2012; Fenchel, 1975) and is a reliable gradient along which change in taxonomic composition may be expected. Some animals are able to osmoregulate successfully over large saline gradients (euryhaline animals); while others may do so only within a small range (stenohaline animals) and this is a factor in variation of benthic community composition. Salinity preference is also an important trait and will be used as a factor in the BTA analysis.

The Humber salinity gradient is quite marked along the length of the estuary and ranges from almost fully marine near the mouth to salinities of as low as 11 at Paull and up to 25 at Welwick, down to salinities of 3-5 at some parts of the Alkborough site ((figures at height of tidal inundation. Freestone et al., 1987; Mazik et al 2007). This makes it very suitable for a study of this type. Although there is a distinct gradient along the length of the estuary, the vertical mixing of the saline and fresh water is quite thorough in the Humber, varying only slightly between the top and bottom of the water column (Freestone et al, 1987).



## **1.7 Biological Traits Analysis**

This project sets out to apply BTA to determine which functional traits are being expressed and to see if this changes along two environmental gradients. By examining samples along these two gradients there should be a change in environmental conditions that will allow a test of whether or not functional composition alters with this change. It is typical at these sites to see differing species composition with significant differences in elevation (Mazik 2010) and salinity (Freestone, 1987) and this may be reflected in changes to community structure and function.

The BTA approach has been used in plant and freshwater biology for a number of years (Chevenet, 1994; Statzner et al., 2004; Diaz and Cabido, 2001) and has increasingly been used to describe marine assemblages (Petchey and Gaston, 2006; Bremner et al., 2006). Recent examples of studies along estuarine gradients, examining benthic organisms and their functional traits include Verissimo et al (2012) and Paganelli et al. (2012), in the Mondego Estuary, Portugal and along the Emilia-Romagna coastline, Italy, respectively. However, BTA has yet to be applied across multiple sites in the Humber.

The traits analysis approach focuses not just on species composition, but on the array of functional traits that species assemblage represents. There are a multitude of behaviours and morphological characteristics exhibited by organisms that have a link to ecosystem function. BTA gives scores to determine the level to which a behaviour, or trait, is expressed by an animal and then removes the taxonomic information to leave a traits profile for the area sampled, representing the functional structure of the community (Bremner et al., 2006a and 2008; Chevenet, 1994; Loreau et al., 2001; Paganelli, 2012). Changes in the pattern of trait expression within assemblages could indicate the impact of differing environmental regimes (Charalampos, 2010), such as the gradients explored here.

Traits analysis is not offered here as an alternative to community structural studies based on biodiversity; rather it is an enhancement of knowledge, a more complete picture of the community. Biodiversity and ecosystem function are linked in the simple sense that the activity of organisms in a benthic environment can impact on aspect of ecosystem functions (Naeem and Wright, 2003; Bremner et al., 2006). Functional diversity, as expressed by the functional traits profile of the biota, can be a fuller examination of how well a given ecosystem is functioning, compared to taxonomic indices alone (Sigla et al., 2012).

## **1.8 Project Aims and Objectives**

This project considers the questions “Does benthic community structure alter along the gradients under consideration? And ‘Does benthic community function alter along these same gradients? The aim is to examine structural and functional changes in the benthos with these questions in mind and to then answer the overall question: ‘If structure changes, does function change too’?

This project will consider smaller (<500 µm) benthic animals in order to include nematoda, copepoda, amongst others, that are often present in high numbers. This study aims to consider

their contributions to community functioning as they have been routinely excluded by sieve size in the methodology of previous surveys at these sites (Mazik et al, 2007, 2010 and 2013)

A summary of the project's objectives is given below:

- To give a concise summary of the literature on the study sites and their wider context.
- To provide an overview of the literature on estuarine ecological functioning and BTA.
- To consider the benthic species sampled and summarise essential literature concerning their functional traits, including meiofaunal species.
- To look for community structural changes, if any, in the benthic community data along the salinity and elevation gradients. Examine species abundance, richness, evenness ('J) and diversity ('H) and biomass to determine this. Apply univariate and multivariate tests to sampling sites, sampling stations, and their abiotic factors.
- Use resulting data to reject or confirm null hypothesis regarding community structure.
- Use BTA process to produce data on community function, applying the same tests and statistical processes used in the structural analysis to see if functional change occurs over the same salinity and elevation gradients.
- Use the resulting output for this to reject or confirm null hypothesis regarding community function.

### Hypotheses

As community structure changes with differing environmental conditions it is reasonable to suppose that communities sampled at the littoral fringe will be different from those sampled at the low shore. Salinity is also known to be a key factor in benthic distribution.

Null hypothesis: no change community structure will be observed over the two environmental gradients within the structural variables considered.

Changes in species composition could mean a change in functional traits expressed and it is likely that there will be differences in the trait profiles of sites and sampling stations that are separated by abiotic gradients. Although it is possible that two different assemblages could express highly similar functional profiles, it is most likely that some changes will be observed.

Null hypothesis: no change in community function will be observed over the two environmental gradients based on the traits considered.

## 1.9. The Study Site

The sites examined in this study are located on the north and south banks of the Humber estuary, in North East England. The Humber is one of the largest estuaries in England, with a catchment area draining around 20% of the country's land surface. Major rivers such as the Ouse, Trent and Derwent flow in to the Humber and it is also notable for its large tidal range. This is over 7m at some sites and up to 6m at the study sites- defining it as macro-tidal (Humber Management Scheme, 2013; Wymer, 1997). Around one third of the estuary is exposed as mud or sand flats at low tide (JNCC, 2013). Site location national and locally are shown below in Fig.1.1.

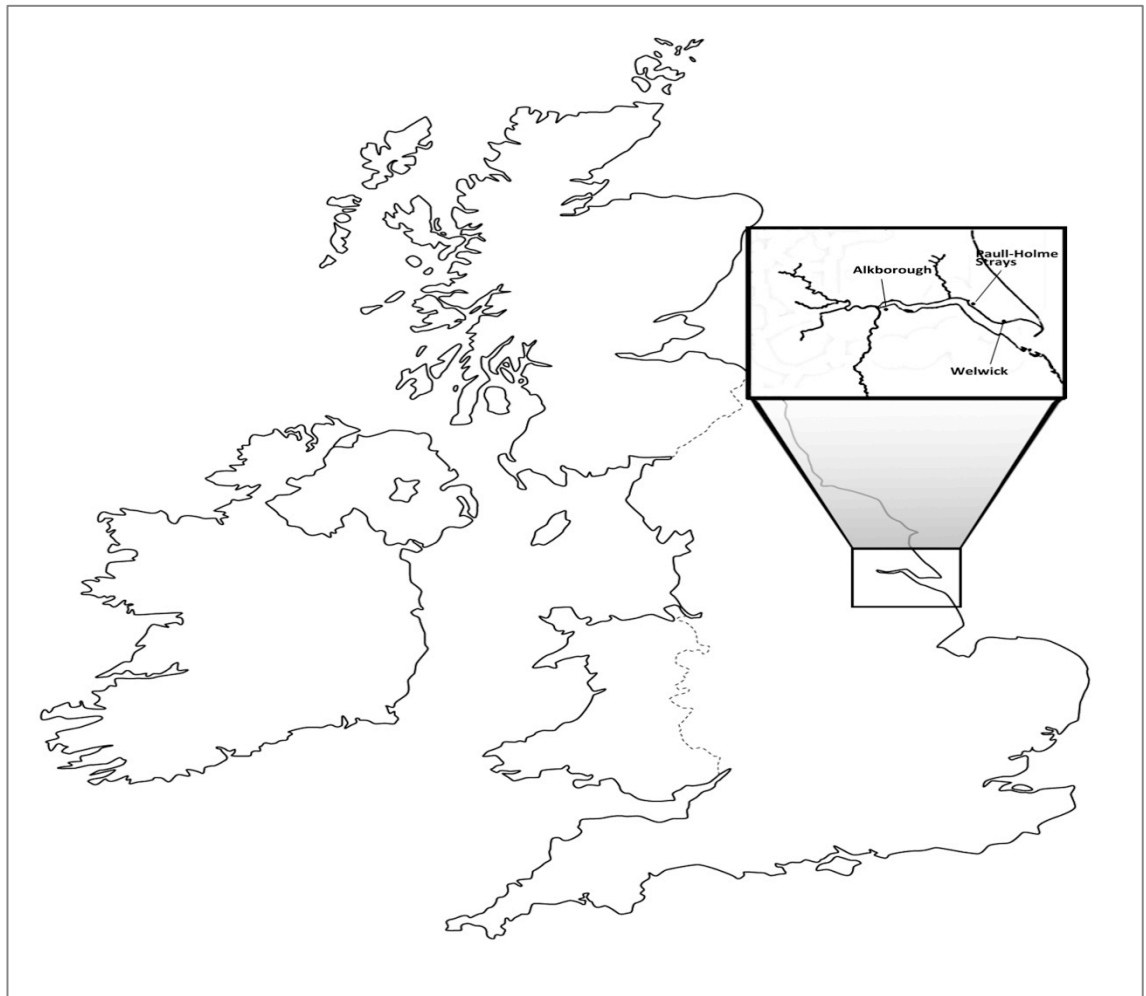


Figure 1.1. The location of the Humber estuary and three study areas on a national scale. (Based on templates available at [www.d-maps.com](http://www.d-maps.com)).

The Humber is characterised by extensive mudflats, as well as salt marsh and reed bed areas, and some sand flats, which are recognised nationally and internationally for their importance to water birds (Mander et al., 2007). These habitats also provide significant carbon storage, retaining high levels of organic matter (Natural England, 2012; Gribsholt and Kristensen, 2003). There is a significant longitudinal salinity gradient in the Humber, particularly on the north bank (Cave et al., 2003). The length of estuary is 62 km from freshwater (at a salinity of about 3) at Trent Falls to 33-34 at high water at Spurn Head (Freestone et al., 1987, Grant and

Middleton, 1993; Sanders et al., 1997). The sites in this study are along the line of the gradient and are located at the outer, middle and inner sections of the estuary (Fig 1.1)

A further point of note regarding the salinity regime in the Humber is the difference recorded across the width of the estuary. The difference is slight, but the north bank sites have a consistently higher salinity level than corresponding sites on the south side of the estuary. The body of water is large enough to be influenced by coreolis effect, causing inflowing seawater to make its ingress along the north bank. Vertically, the Humber is a shallow, well-mixed estuary; this is a weak salinity gradient in the water column, with a difference of between 3 and 5 between surface and bed (Freestone et al., 1987).

The region has long anthropogenic associations. Significant human populations making use of the estuary and its intertidal zones date back to the Bronze Age (Van de Noort and Fletcher, 2000; Natural England, 2012). The population of the total catchment area of the estuary is approximately 10.5million (Cave et al., 2005) while the nearest major city of Hull supports a population of around 263,900 (Hull City Council, 2010). Long use by large populations has had an impact on the estuary and its environs, significantly land claim and industrial use. The Humber still bears traces of heavy industry and mining, either directly on the estuary or from its large catchment. This is evident in the sediment in the form of trace metals and minerals (Cave et al., 2005; Grant and Middleton, 1990; Rees et al., 1999). The impact of land claim has been such that it has radically altered the profile of the river over the centuries it has taken place, with 8,184 ha of intertidal and salt marsh area having been taken, piece-by-piece, since the 17<sup>th</sup> Century (Boyes and Elliott, 2006; Morris et al., 2004)

There is also shipping activity, particularly on the south bank at Port of Immingham. This is one of the UK's biggest port in terms of tonnage, handling around 55million tonnes annually (Associated British Ports, 2013). The demands of heavy shipping require maintenance and development of port facilities and include expansion on to natural estuarine habitat, as well as regular dredging across the estuary to sustain depth along shipping channels (Humber Management Scheme, 2013, Cave et al., 2003).

The estuary encompasses a wide range of habitats, including mudflat, salt marsh, sand dunes and saline lagoons. From a geology and geomorphology perspective the Pleistocene sediments at North Ferriby are of particular note, as well as the sand spit formation at Spurn Head. In terms of important wildlife there are over 30 species of birds that use the estuary over winter or migrating; two species of lamprey are supported; a large breeding colony of grey seals and a number of rare vascular plants (Natural England, 2013).

These rare natural features, habitats, and the biota they support mean the Humber is protected by a number of designations. The Humber is recognised internationally by its designation as a European Marine Site and within this designation, its habitats are acknowledged as Special Areas of Conservation (SAC). It is also a Special Protection Area (SPA) under the EU Bird Directive (Humber Management Scheme, 2013; JNCC 2008a) as well as a Ramsar site, which also recognises it as being of special interest internationally (JNCC, 2008a). Monitoring is carried out regularly across the Humber estuary. Avian populations are monitored (Mander et al., 2007; Spencer, 2010; RSPB 2014) as well as fish and mammal populations (Humber Management Scheme, 2013; Lincolnshire Wildlife Trust, 2013).

Landscape surveys, sediment and flow studies, assessment of pollutants and other inputs and outputs are all part of on going monitoring in the estuary (Freestone et al., 1987; Mazik and Elliott, 2000; Burdon et al, 2004; Cave, 2005; Humber Management Scheme, 2013).

### 1.9.1 Managed Realignment: Paull and Welwick and Alkborough

Two sites in this study are on the north bank of the Humber, around 20km apart from each other, east of the city of Hull. The third, Alkborough, is much further upriver on the south bank, close to the Humber Bridge, west of Hull (See Fig 1.1).

Each site has been developed on the upper shore using a managed process to relinquish agricultural land and allow inundation by the tide. This strategy is known as managed realignment (MR), also called habitat creation, de-poldering, set back, and land claim (Mazik et al, 2010). The MR strategy is an approach to flood defence management and is linked to an increasing acceptance that hard flood defences are becoming costly and unsustainable in the face of predicted sea level rise (EA, 2013). An MR site is created when the existing engineered defences are deliberately breached, the line of defence moved back significantly, and the land in between these two points is open to the tidal effects of the river, allowing the water to migrate inland (Andrews, 2008; Winn et al, 2003). This took place at the Paull site in 2003 and at Welwick and Alkborough in 2006 (ABP Marine Environmental Research, 2013).



Figure 1.2 View of the main breach (top left) in the original sea wall at Paull, taken from Site 2.

There are a number of roles fulfilled by the process: compensation for habitat lost to land claim and port development in other parts of the Humber (Mander et al., 2007; Hull City Council, 2012) flood defence, allowing the rising river to move inland in a controlled manner. It is also a management option in the case of coastal squeeze- the setting back of the defences allowing the establishment of a more naturally functioning shoreline despite sea level rise (DEFRA, 2010; Winn et al., 2003)) The creation of compensation habitat for that lost to development is a requirement in the Humber (Mazik et al., 2010) due to its multiple protective designations, and the Environment Agency require replacement at a ratio of 1:3 for land lost to defence upgrades (Mazik, 2010; DEFRA 2010). This was the case Paull, providing compensation for improved defences on the south bank, while Welwick was part of a multi-site habitat compensation package negotiated with Associated British Ports (ABP) for port extensions on the south bank (Hull City Council, 2012). The project at Alkborough is a flood management

scheme, with the aim of storing excess water in extreme weather situation, lessening the impact of flood surges on the Humber and Trent (EA, 2013)

The physical development of MR sites is characterised by sediment accretion and a gradual colonisation of flora and fauna as the sites make a gradual transition from farmland to intertidal habitat (Watts et al 2003; Mazik et al., 2007; Luisetti et al., 2010). Accretion and associated salt marsh plant colonisation push the upper shore limit towards the land, expanding ecologically valuable habitat and alleviating potential flood risks. This aspect of MR makes it suited to the Humber due to its high sediment content, and significant levels of accretion have been recorded at MR sites here, including Paull Holme Strays (Mazik et al., 2010). This makes it particularly suited to this study as it's increased upper shore provides a longer, more accessible gradient than sites that have not been subject to the same alteration. Monitoring of the development of MR sites means that there is a great deal of information available from a range of long term studies (Edwards and Winn, 2006; Mazik et al., 2007 and 2010), and this has proved useful for this project. The third site at Alkborough could be added to this project without the extra cost and time constraints of sampling it personally, due to the comprehensive nature of the work already carried out there. There is also data from other studies and papers, many referenced above, to give this study support and context in terms of species lists, sediment properties, wider ecology and morphological development of the sites.

## CHAPTER 2

### 2. Literature Review

#### 2.1 Ecosystem Function

##### 2.1.1 Biodiversity and Ecosystem Function

Functioning in ecosystems is linked to biodiversity, although the nature of this link is the subject of debate (Loreau et al., 2002). Functioning is defined in terms of rate processes (measurable environmental processes such as chemical cycling), whereas 'biodiversity' can refer to several attributes: it may be used ecologically, in terms of landscapes, ecosystems and populations; genetically, in terms of populations or individuals, as well as in terms of diversity of organisms (Negrete, 2007). It often concerned with the range of species that exist in any given environment; from highly localised communities to global levels; within species and between species (de Long, 1996; Natural England, 2013). Biodiversity reflects the variability in assemblages, from bacteria to megafauna. Here the diversity of the benthic community is considered as an essential component of community structure, as well as a basis for the creation of functional trait profiles. The connection between biodiversity and ecosystem function may imply that changes in levels of species diversity can influence functional processes in the ecosystem (Naeem and Wright, 2003; Savage et al., 2007), however this connection has not been explored in a reliable, detailed, or predictive way.

Many studies do not consider natural assemblages, but rather construct experimental assemblages that look as a single aspect, such as grasses or vascular plants, and adjust biodiversity in these artificial assemblages to examine changes in function (e.g. Fornara and Tilman, 2008). While this provides some understanding, it is not of value for application in complex field systems, for further scientific study, or for policy makers, and this has led to some criticism of the usefulness of such work (Mooney in, Loreau et al., 2002).

The study of biodiversity in relation to ecosystem functioning is a relatively new field and more research is needed before it answers the main questions demanded of it (Mooney in, Loreau et al., 2002). Studies relating to biodiversity and ecosystem functioning began in the early 1990s (Chaplin et al, 1992; Petchey and Gaston, 2004), but there is still a lack of integration between specific areas of study, and there is still some discussion regarding the precise nature of the links between the two (McCann, 2000; Mooney in, Loreau et al., 2002; Loreau et al in, Loreau et al., 2002).

It has been discussed that functional diversity could be more important than species diversity for understanding ecosystems. For example, if the removal of a rare species has no real impact on healthy ecosystem function, many conservation efforts could be questioned (Schwartz et al., 2000; Loreau et al., 2001). The aim of identifying 'irreplaceable species and functional types' (Grimes, 1997) implies that there are 'replaceable' species, a questionable concept that raises a number of moral issues.

A main area of debate in the BTA approach is correct traits selection (Petchy and Gaston 2004), together with the limited scope of some studies (Colas et al., 2014) and also the appropriate tools for analysis (Bremner et al 2006). Fuzzy correspondence analysis, co-inertia analysis and non-metric multidimensional scaling are all suitable options, but trade-offs exist between their analytical power and ease of interpretation. Bremner et al. (2006a) suggest that non-metric multidimensional scaling could be relevant for any study that aims to give a general picture of ecosystem function, while fuzzy correspondence analysis and co-inertia analysis may be better to study human impacts such, as point source pollution. How trait profiles are weighted is also an issue – some studies use abundance data, some use biomass data and some use both (Bolam and Eggleton, 2014).

### 2.1.2 An Overview of Functioning in Estuaries

Biological, chemical and physical systems are important in driving estuarine ecosystem functioning. A concise overview of this wider estuarine functioning is given here to place the following work in its broader environmental context. This study defines ecosystem function as encapsulating all physical, chemical and biological ecosystem processes (Paterson et al. in Solan et al., 2012), but with a particular focus on the interactions of benthic biota on the physical environment of an estuarine mudflat.

Functioning in estuaries can be view at different scales. At the widest scale are landscape level processes, for example tidal transport of sediment, accreting in some areas or eroding in others. The morphology of the estuary, its beaches, mudflats, channels and sandbanks are changed or sustained by the dynamics of flow regime and associated sediment transport, thus affecting estuarine functioning.

Mudflats and saltmarsh are key functional habitats in estuaries, which are influenced by physical, chemical and biological factors.

- Biologically: predation changes population densities and composition. Bioturbation modifies sediment physically and chemically. Primary and secondary production forms the basis of estuarine food webs.
- Chemically: nutrient load levels can vary, causing eutrophication; oxygen, salinity and pH levels can determine the presence or absence of species. Organic matter decomposition is important in chemical and nutrient cycling.
- Physically: tidal regimes and associated sediment transport influence sediment characteristic such as composition, or interstitial drainage rate, both of which can influence the presence or absence of infaunal animals (JNCC, 2004, Hiscock and Marshall, 2006).

There are various categories of functioning in estuaries:

#### ***Substance Cycling – Nutrients, Chemical and Contaminants***

Nutrients, chemicals, pollutants, together with freshwater and marine biota are influence by tidal and freshwater regimes in the estuarine environment (Cave, 2005; Freestone et al, 1987). For instance, substances such as nitrate, nitrite, ammonia and phosphorus may enter the system, perhaps as land run-off or a riverine input, and are cycled though the water column



and the sediment (Falkowski, 1997; McLusky and Elliott, 2004). The cycling/regeneration of these nutrients is an important function (Jones and Frid, 2009), as they form the basis for primary production. In estuaries these nutrients have a number of sources, those mentioned above, but also decomposing organic matter and run-off (Morelock et al., 2005). Once in the estuarine system these substances are subject to use and change. The microbial loop uses and converts nutrients: – for example, ammonia is converted to nitrite, and nitrite to nitrate with different types of bacteria fulfilling different roles in the decomposition of materials and associated regeneration nutrients (Kemp and Boynton, 1984). These can then be utilised by microalgae and other plants in growth (McLusky and Elliott, 2009). Substances can also be moved straight through the estuary and drained in to the open ocean, or be carried out of the sediment and relocated through tidal or flow activity. For example, some organic matter is held in the sediment (see below), but it may be oxidised to produce carbon dioxide, bicarbonate and other dissolved organic carbon and can move in to the water column with suspended sediment and be transported elsewhere (Kathilankal et al., 2008).

Another area of major chemical activity is at the freshwater/saltwater interface, where ionic changes occur as marine or brackish water meets freshwater, altering the composition of substances in the water such as chloride and cadmium, changing the chemical profile of the water, including its salinity levels. (McLusky and Elliott, 2004).

#### ***Sequestration – Carbon and Contaminants***

Some substances that enter the estuary are not entirely cycled through it or used within it. Amounts are retained, stored or sequestered, often for long periods of time. Estuaries are known to be carbon ‘sinks’– a significant functional role in a carbon-sensitive era (Cacador et al., 2003). Carbon is trapped in salt marsh and mudflat environments in large amounts as they accrete and bury estuarine sediments rich in organic matter, and the rate of sediment accumulation is linked to carbon sequestration capacity (Kathilankal et al., 2008). Estuarine wetlands retain particularly high levels of carbon, and can have a carbon sequestration capacity (per unit area) of an order of magnitude higher than other wetland systems (Howe et al., 2009) due to typically high rates of vertical sediment accretion (Chmura et al., 2003). Once buried in estuarine sediment this carbon can remain there for millennia if undisturbed (Roulet, 2000). Carbon is also exchanged between the atmosphere and surface water, with the direction of the exchange being governed by latitude. In temperate areas coastal and estuarine water bodies act as a carbon sink, while in more tropical regions coastal and estuarine waters are a source of CO<sub>2</sub> to the atmosphere (Howe et al., 2009). Contaminants can also be sequestered quite readily in estuarine sediment. Examples include metals such as cadmium, mercury and lead which bind strongly with suspended sediment and contaminate mudflats and saltmarshes when these sediments settle there (Hiscock and Marshall, 2006). The activities of the benthos can have an impact on these processes via disturbance of the sediment, contribution to burial or re-suspension of substances in the sediment (Cardoso et al., 2008).

### ***Sediment Transport and Coastal Protection***

The regular movement and redistribution of sediment within estuaries is an important function in terms of maintaining natural morphological properties. Large amounts of sediment arrive in estuaries via riverine input and a great deal of this settles and is accreted within the estuary before reaching coastal waters (Morelock et al., 2005), but this is dependent on the nature of flow regimes. The two main causes of sediment movement in an estuary are from the catchment and tidal currents. These interact to create distinct transport pathways for sediment within the estuary, determining the characteristic of different areas in terms of grain size, as the size of particle settling on the sediment bed alters with flow rate (Dalrymple and Choi, 2005). The turbidity maximum is the area of an estuary where suspended sediment concentrations are highest and it is these areas that are likely to see significant mud deposits when particles flocculate and settle in contact with saline water (Schubel, 1968; Dalrymple and Choi, 2005), forming and sustaining mudflat habitat.

The maintenance of classic estuarine habitat, such as mudflat and salt marsh, via sediment transport, also has a role in coastal protection (Barbier, 2011). Storage of floodwater is a natural function of estuarine wetlands, as well as dissipating erosive forces. The size of the wetland is important for this, but the texture of the substratum is also a factor in the controlling of floodwaters (Sather and Smith, 1984), linking it to sediment transport functions as well as bioturbation activity in the sediment (see below).

### ***Bioturbation***

Bioturbation is the reworking of the sediment by organisms, either through ingestion, manipulation (burrow or tube construction) or disturbance via movement through it (Naeem et al., 1994; Gilbert, et al., 1998; Mazik and Elliott, 2000; Duchene and Rosenberg 2001; Rosenberg, 2001; Marie et al., 2008; Cardoso et al., 2008; Braeckman et al., 2010). Bioturbatory mode is an important functional category in any sediment-based ecosystem and its direct functional role in re-working the sediment is well established (Naeem et al., 1994). The extent of its impact depends on the array of species present and the range of bioturbatory traits they express, including those that link to bioturbation potential, such as body size and mobility (Herringshaw and Solan, 2008). Bioturbation is also linked to traits such as feeding method/apparatus, living habitat and living position (e.g. epifaunal or infaunal) as each of these may modify the sediment.

The mode of bioturbation varies between species and an individual species can display multiple modes, crossing different functional groups (Chevenet, 1994; Bremner et al., 2003; Bremner, 2008). For example, *Macoma balthica* disturbs the sediment through its feeding behaviour, capturing particles in the water column and also re-suspending them when they expelled are as faecal matter (Willows et al., 1998). It also displaces, oxygenates and irrigates the sediment as it constructs burrows (Michaud et al., 2005). This places it in the categories 'blind burrow ventilator', 'downward conveyer' and 'surficial biodiffuser' (See Methods 3.6). The burrowing action of *Hediste diversicolor* increases the sediment-water interface area, oxygenating significantly more of the sediment than in an un-burrowed area, while *Nephtys sp.* slowly homogenizes the top few cm of sediment as it moves through it, constantly hunting for prey animals (Davey and Partridge, 1998). *Hediste diversicolor* is classed as a gallery

bioturbators - in which diffusive mixing of particles occurs in the vicinity of intense burrowing activity and includes transport downwards of surface particles to the lower reaches of the burrow or tube (Kristensen et al., 2005). Species such as *Pygospio elegans* construct and live in permanent tubes and where they are found together in large numbers, forming beds that can have a stabilising effect on the sediment (Green, 1968), protecting the sediment bed from erosion and encouraging biodeposition (Graf & Rosenberg, 1997). These activities are functionally important as they increase the surface area of the sediment that is exposed to the water column, where nutrient and chemical exchanges take place. This alters the physical, chemical and biological properties of the sediment – in terms of the flux of nutrients, contaminants and organic matter exchange is increased between the sediment and the water column and also within the sediment itself (Freidrichs et al., 2000; and Fernandes, 2003). Bioturbation is also important in the decomposition of organic matter; downward conveyers draw matter deeper in to the sediment where it is processed by bacteria and subject to microbial decomposition, linking to biogeochemical cycles outlined above (Gerino et al., 2007; Braeckman et al., 2010). The depth of bioturbatory activity varies, but for some species it may be several centimeters deep. This can mean oxygenation of the sediment at much greater depth than in an area where no bioturbation has taken place, lowering the redox potential discontinuity layer considerably in some cases (Graf & Rosenberg, 1997; Cardoso, 2008; Duchene and Rosenberg, 2001). This increases the habitable area of the sediment significantly for many benthic animals and influences taxonomic composition, which in turn determines functional composition. Hence, changes in community structure could affect the levels of bioturbation and so impact on ecosystem function (Mazik and Elliott, 2000).

#### ***Trophic Interactions and Food Provision***

Food chain support is another key ecosystem function. High levels of organic matter and nutrients, in the sediment and the water column, are utilised by bacteria, zooplankton or microorganisms in the estuary and these are then cycled through the estuarine food web, as described above. The trophic behaviours of the benthos are important drivers of this ecosystem function, linking primary production at the base of the food chain to higher trophic levels (Ferren et al., 2014). The productive nature of estuaries means that high population densities are common at all trophic levels. Trophic structure is known to play a role in the biogeochemical balance of ecosystems (Naeem, in Solan et al., 2012). Influence can come from the top down in terms of predation and consumption levels controlling populations (Gray and Elliott, 2009), but also from the bottom up. Phytoplankton and zooplankton levels have been shown to control some fish population (Ware and Thomson, 2005) and benthic macrofauna trophic structure has been shown to have an impact on sediment biogeochemistry (Waldbusser and Marinelli, 2006).

Estuaries also have an important economic function in terms of food provision. The morphology and high organic content of estuaries make them ideal nursery and breeding grounds for commercially caught fish and crustacean species (Turner 1984; Henderson and Seaby, 1994), sustaining human food supply.

### **Habitat Provision**

Estuarine function includes habitat provision. For larger animals, such as birds and seals, they function as important feeding, breeding, nursery and refuge areas (Edwards and Winn, 2006; Mander et al., 2007). Fish also make use of the richly productive estuarine environment and some species, for example, *Pleuronectes platessa* along with other flat fish species, use estuaries as a nursery site in the early years of development (Jones, 1988; Henderson and Seaby, 1994; Elliott and Hemingway, 2002). At a smaller scale, estuarine mudflat and salt marsh are habitats typically rich in organic matter and are able support high density invertebrate population in, and on, the sediment (Kathilankal et al., 2008)

By definition, an ecosystem is a network of many aspects of biogeochemical components that link to form a working system. While this project is focussed on benthic processes, no part of the ecosystem is isolated and all of these functions, from sediment/water interface exchanges to coastal flood defence, are fundamentally connected to the workings of the entire estuarine landscape, from microalgae to flood defences.

#### 2.1.3 Approaches to Assessing Ecological Function

Describing the range of functioning that exists in a given ecosystem can be challenging (Petchey and Gaston, 2002; Diaz and Cabido, 2001). Biological Traits Analysis is used here, but there are many other approaches to studying ecosystem function and a brief consideration of some of these is given here.

Calculating production, either primary or secondary, is a well- established method for assessing function in aquatic environments (Emmerson and Huxman 2006; Gray and Elliott 2009). For instance, primary production, in terms of amount of carbon produced  $\text{m}^{-2}.\text{yr}^{-1}$ , can describe functions relating to nutrient cycling and the growth of organisms in the ecosystem by measuring how much carbon has been used in a given area – e.g. how much was buried in the sediment, how much was consumed by species in the water column, and how much by species in the benthos (Gray and Elliott, 2009). Other approaches measure aspects of functioning in terms of chemical flux, for example a study by Grenz et al. (1991) recorded changes in benthic nutrient and oxygen flux to assess the impact of biodeposition by mussels. Calculating rates of bioturbation in another approach to studying functioning; a study by Gerino et al. (2007) used tracer particles placed in the sediment to establish the rate of different modes of bioturbation (e.g. biodiffusion, conveying) directing measuring the amount and speed of sediment movement.

Some other approaches are similar to BTA, or at least have their roots in the same principle. BTA has a basis in habitat template theory, which is the idea that the behavioural characteristics of species (what this study terms 'traits') have evolved around the constraints of their habitat (Southwood, 1977). This implies an intrinsic, circular, relationship between evolved traits due to environmental pressures and an organism's modification of the environment due to behavioural traits. The links between organisms and the condition of their environment and, to an extent, vice versa, has been well studied.

Contemporary to BTA are approaches such as functional group analysis. This approach places animals in to groups, according to a few attributes that are considered to key to functional processes (Steneck and Dethier, 1994). For example, Steneck and Watling (1982) divided the animals in their samples into just four functional groups, based on their feeding activities. Although trophic mechanisms are considered to be a key component in the structuring of assemblages (Pearson and Rosenberg, 1987), the lack of consideration of other traits suggests functionally significant species characteristics could be omitted, leading to an incomplete view of community functioning (Bremner et al., 2003).

Another system that attempts to describe function is the ecological evaluation index, often shortened to EEI. This uses a pre-selected group of traits and applies them to aquatic ecosystems to assess ecological status, dividing sites in to two main categories – pristine and degraded (Orfanidis et al., 2003). Its emphasis is on traits that are ecological indicators, ones that can give an idea of an ecosystem's resilience, or otherwise, to potential changes. This emphasis is due to it originally being developed to support the aims of the Water Framework Directive with its water classifications of 'good' or 'poor' (European Commission, 2000; Orfanidis et al., 2001).

Some other ideas that relate to this are the concept of functional guilds, and niches. The functional guilds approach is similar to BTA, and the functional group approach, in that it takes animals in a community, and groups them according to resource use (Elliott et al., 2007). This is often by trophic group, in terms of a shared food source, and is a simple way of examining direct competition in a community, as guilds are defined as groups of species that exploit the habitat in the same particular way (Little, 2009). While this is similar to traits approaches at a glance it is really concerned with answering questions about competitive coexistence in communities. The focus is not on behaviour that relates to processes and their associated functions, but it merits mention here as the term 'functional guild' is often used almost interchangeably with 'functional group' in the literature (Blondel, 2003).

The niche approach has been applied at population, rather than community, level, in combination with traits analysis. Niches were an early idea in animal ecology (Elton, 1927) and species are still defined in studies by their realised and fundamental niches. Colas et al. (2014) linked this concept to a trait based approach at the population level, with the idea that this will show a more sensitive response to stressors than at community level, when species niches are analysed alongside selected, relevant, functional traits.

A further approach that measures the functional role of biodiversity in the ecosystem considers trophic relationships. Duffy et al. (2007) considered the impact of broad areas of biodiversity on ecosystem function. This approach considered 'horizontal' functional diversity, which it defined as the species richness and evenness that exist in a given ecosystem, plus its functional diversity and breadth of niches. This was examined together with 'vertical' diversity, which was represented by the length of the food chain, from top to bottom. Trophic interactions are established as having an impact on ecosystem functioning (Borer et al., 2006) so this, combined with the horizontal aspect, was used to answer questions about how changes in this type of diversity could impact on ecosystem function. This is similar to some

other studies which also consider depth and breadth of trophic interactions as measurements of functioning; some considering the total branch length of a dendrogram illustrating community trophic function (Petchey and Gaston, 2002), while others focus on the width of trophic traits distribution (Norberg, 2004). It is not uncommon to find studies that focus purely on trophic interactions (Maurer and Leathem, 1981; Desrosiers et al., 2000; Peng et al., 2013) and omit other aspects of benthic ecosystem functioning, and this links back again to debates regarding correct trait selection in BTA, or any study of ecosystem functioning.

The range of approaches is necessarily a large one, as ecosystem functioning is assessed in all fields of ecology, from plant, soil, freshwater, marine or estuarine, and the result is an array of experimental ideas that cannot all be considered in detail here. Average functional distinction, for instance, gives a measure of functional resemblance that exists between species (Sommerfeld, 2008), and was applied to a marine benthic assemblage, while other studies use traits for different purposes. The assembly rules approach, for example, uses functional traits as a basis for a set of rules concerning community organisation patterns, and has been applied in communities of tropical lichens (Koch et al., 2013).

Although many of these approaches have their own merits, BTA has been chosen here it has been used successfully in a number of recent studies of estuarine and marine environments (Bremner, 2008; Marchini et al., 2008; Van der Linden et al., 2012, Verissimo et al., 2012; Oug et al., 2012). It has also been applied across differing environmental conditions in some studies (Jones and Frid, 2009; Paganelli et al., 2012; Van der Linden et al., 2012), confirming its suitability for this project. Finally, despite the debate concerning trait selection, its broader approach to functional traits, beyond trophic group, is comprehensive and is ideal for building a solid trait profile across sites and stations considered here.

## **2.2. Biological Traits Analysis**

### **2.2.1 Background**

Biological Traits Analysis (BTA), in common with the methods outlined above in section 2.1.3, moves away from the purely species based approaches and focuses on the distribution and biological characteristics of the animals, grouping them according to their activities and behaviours (Chevenet et al., 1994; Bremner 2003; Bremner et al., 2006a). These groupings are based on selected traits in animals that relate to ecosystem processes. These could be behaviours, such as bioturbatory mode or feeding methods, which modify the sediment and aid in nutrient cycling, carbon fixing or oxidisation of the sediment. The consideration of the value and range of these traits has been suggested to be much more significant than species numbers in the determination of ecosystem functioning (Diaz and Cabido, 2001) and is potentially a powerful tool for ecosystem analysis.

### **2.2.2 Application**

BTA has been widely applied in the fields of plant and freshwater ecology (Chevenet, 1994; Diaz and Cabido, 2001; Bremner, 2003) but has been increasingly used by marine and estuarine ecologists over the last decade (Bremner, 2008). It is less common as an ecological

assessment tool for transitional waters, but is emerging as a complimentary addition to the traditional species based approach (Van der Linden et al., 2012, Verissimo et al., 2012; Marchini et al., 2008). The BTA system examines a larger number of functional traits and allows the selection of a range of traits that are suitable to the current study. One of the advantages of applying traits analysis to an estuarine or brackish water environment is that rather than concentrating on biodiversity in assemblages, as a majority of studies elect to do, it examines functional diversity to gauge the health of a given ecosystem. This is useful in estuarine/brackish water systems where taxonomic diversity is naturally low, but abundance is high and the relatively small number of species present could achieve healthy ecosystem functioning. Examining traits can describe ecosystem functioning more reliably in such cases, despite low species diversity (Marchini et al., 2008) making it a good choice for the study sites in this project and for estuarine conservation and shoreline management generally (Bremner, 2008)

The selection of traits depends on the species present and on the goals of the study being carried out. A large study was undertaken at 20 sites around the English coast to predict recolonisation/ recovery rates of the benthos in dredged areas (Marine Ecological Services Ltd, 2008) so the traits selected were those that related to the ability, or otherwise, of individual species to move back in to a disturbed area and regain previous levels of biomass. The relevant traits selected for this were fecundity, adult mobility, larval mode, age at reproductive maturity, and life span and size. These particular traits allowed for predictions to be made regarding the likely timespan for complete recovery of an area, providing essential information for the management of dredging activity. Other studies are more broad- spectrum and consider as many relevant traits as possible to describe community assemblages and their links to ecosystem processes (Van der Linden et al., 2012; Marchini et al., 2008; Verissimo et al., 2012; Paganelli et al., 2012) generating a list of traits that include feeding mode; body size; adult longevity; reproductive strategy; reproductive frequency; larval mode; mobility; body flexibility, habitat preference; morphology or growth form; salinity tolerance and bioturbation mode. Paganelli et al. (2012) also consider the sensitivity or tolerance of species to adverse conditions but this is not particularly appropriate in an estuarine habitat as the nature of the environment precludes the presence of particularly sensitive species. This project is primarily looking at possible changes in ecological functioning over abiotic gradients so traits must also be selected to reflect this. Sanders et al. (2007) suggested that the traits of bioturbation and body size were most effective in showing relations between biotic and abiotic datasets so these will certainly merit inclusion.

### 2.2.3 Trait selection: literature and links to function

Selecting traits for BTA provides challenges beyond judging the relevance of any given trait to a project. A number of studies mention the paucity of information in the literature (Marine Ecological Services Ltd, 2008; Verissimo et al. 2012) and there are gaps in our current knowledge of some species (Tyler, 2011) that are a potential hindrance to the easy selection and analysis of desired species traits. However, a further advantage to using BTA in an estuarine environment is that many estuarine species are well studied due to ease of access to sampling sites. There is certainly a core of keystone species such as *Hediste diversicolor*, *Macoma balthica*, *Nephtys hombergii*, for which there is a great deal of reference work available (Fauchald and Jumars, 1979; Fish and Fish 1989; Barnes 1994; Ciutat et al., 2006;

Marine Ecological Surveys Ltd 2008; BIOTIC, 2013). Selection of traits for this project will include an examination of aspects such as body size, bioturbation mode, feeding guild, mobility and reproductive techniques, life span and habitat and salinity preferences, linking these to ecosystem processes. This clear link between biological traits selected for study and ecosystem functions is critical. Each characteristic displayed by a species needs to be connected to functions such as resource movement (the cycling of energy and nutrients) or to habitat modification within the ecosystem (Chapin et al., 1997; Bremner, 2008). A large number of traits analysed might show more redundancy in the functioning of the ecosystem than a study of the same assemblage that selected carefully for a smaller number, potentially giving an inaccurate picture of ecosystem health. Therefore it is essential to select traits with a great deal of consideration to ensure that only relevant, functionally important, traits are included in the dataset (Petchey and Gaston, 2006; Bremner, 2008)

#### 2.2.4. Modalities and Traits scoring.

Once a list of suitable traits has been selected the BTA system then divides each biological trait into a number of trait modalities (Bremner et al., 2006a and 2008; Van der Linder et al., 2012). Each of these trait sub-categories specifies a permutation of each trait that is expressed by one or more animal in the assemblage under consideration. The trait of 'trophic group', for example, would produce modalities such as 'filter feeding; 'predator; surface deposit feeder' and so forth (Bremner, 2008; Paganelli et al., 2012; Bremner 2006a and b). As much information as possible is needed to complete the modalities in all traits for all species and it is not always possible to gather all the data required (Paganelli et al., 2012). In the event of absent information on a modality for a particular species it is recommended that the species concerned is not included in the final analysis so as to avoid bias or inaccurate weighting towards the traits they are represented in (Chevenet et al., 1994).

Having generated a comprehensive list of traits and modalities with strong links to ecosystem function the BTA approach then uses the literature to assign species to the appropriate modalities. In some cases this may be straightforward as species may clearly express just one modality within the trait. If a species is known to display a number of characteristics within a trait then they are given a score divided within the trait category to reflect this, with the weighting of the division referring to the frequency with which a particular modality is expressed. Using trophic group as an example, an animal that primarily surface deposit feeds may also occasionally filter feed opportunistically when environmental conditions make it viable, a behaviour seen in *Macoma balthica* (O'Brien, 1997). In this case the most part of the total score for this species in this trait would go to the 'surface deposit' modality while the smaller remainder would go to 'filter feeding'.

The system for scoring traits in this manner shows slight variation in the literature. Some studies award a score of up to 3 for each modality (Statzner et al., 2004), with the option to split the score in the manner described above when an affinity to multiple characteristics exists. Therefore no affinity for a modality would score 0 and a complete affinity to a single category would score the full 3. Some studies in freshwater biology use the same system with a score of 1- 5 (Biss and Usseglio-Polatera, 2004) but this does not appear to have been adopted in marine or estuarine projects. Another emergent scoring system gives a value out of



1 for each modality, effectively expressing the trait affinity as a proportion. Fundamentally, all these scoring systems can be expressed as a percentage, or fraction, of the range of values chosen to express degrees of affinity (Chevenet, 1994) and this study has adopted the procedure of scoring affinity for each modality out of 1. This avoids the need to justify an arbitrary scale of affinity such as the 0-3 and 0-5 scales mentioned above.

The traits and modalities used in this study are outlined below and detail of the selection processes is given in Methods 3.6, together a table summarising them (Table 3.1).

## 2.3 Trait Categories and Modalities

### 2.3.1 Bioturbation Modalities: Diffusers, Regenerators, Conveyers and Ventilators

**Biodiffusers** - Biodiffusing species are those that mix the sediment with their movement and cause it to become homogenised locally. Biodiffusers can also be grouped according to their living position -**Surficial biodiffusers** and **Gallery biodiffusers**. Surficial biodiffusers have a lower impact on sediment reworking and may cause some particle redistribution as they move across its surface, while gallery biodiffusers may have a significant impact e.g. *Hediste diversicolor* (Nereis Park, 2013; BIOTIC, 2013). Some species move freely in the sediment without forming tunnels or burrows, particularly *Nematode sp.* and for this study organisms of this type are classified as **Burrowing Biodiffusers**.

**Upward conveyers** are species that position themselves head down in the sediment. They feed at the bottom of their burrow and rework the sediment by depositing waste at the surface. A well-known example of an upward conveyer is the lugworm *Arenicola marina* (Cadee, 1976).

**Downward Conveyers** are species positioned vertically in the sediment with the head near to the surface. Particles are ingested near the surface and egested in the lower limits of the burrow; a number of polychaetes in this study that do so including *Pygospio elegans* and *Manayunkia aestuarina*.

**Blind burrow ventilators** inhabit burrows that are 'I' or 'J' shaped, with one entrance/exit. These species draw water in for respiratory purposes and in doing so oxygenate the surrounding sediment. Bivalves (e.g. *Macoma balthica*) fall in to this category.

**Regenerators** - dig and maintain burrows, bringing sediment from depth to surface. Additional mixing takes place when burrows are filled with surface sediment or when they eventually collapse. An example species is the amphipod *Corophium volutator*.

**Open burrow ventilators** - pull oxygenated water through a burrow with more than one opening, usually Y or U shaped, via body undulation/ cilia movement, oxygenating the sediment within.

### 2.3.2 Feeding Method, Food Type and Feeding Apparatus

#### **Feeding method**

For this study the trait 'Feeding Method' has been divided into 5 modalities, broadly covering the approaches to nutrient capture utilised by the species in this study. Many of these species express more than one trait per category, reflecting the adaptable, opportunistic, nature of many estuarine species.

**Deposit Feeders (Surface)** - Feed on particles found on the sediment surface, or any other surface the environment provides. These particles could be detritus, such as decaying animal matter, plant matter and the bacteria therein, or could be living matter such as microalgae or diatoms. Species feeding in this way disturb the sediment surface, mixing and re-suspending particles as well as cycling nutrients to higher trophic levels.

**Deposit Feeders (Sub-Surface)** - Organisms in this feeding modality consume a similar range of food items to those outlined above, but in doing so will move below the surface of the sediment. This causes diffusive mixing of particles below the surface, deepening the level of diffusive mixing taking place.

#### **Filter Feeding/Particle Selection**

Filter feeders trap particles suspended in the water column, using a range of appendages to capture them. Species such as these are important in sediment mixing and sequestration of substances as these particles are ingested and carried down deeper into the sediment at the base of a tube or burrow.

**Opportunistic Scavenger** - Organisms expressing this modality are generally mobile and are able to take advantage of a range of food sources when presented with them. Such species are adaptable, and this modality is often expressed alongside another more specific type of feeding that is a first preference. For instance, *Eteone longa/flava* is predatory, but is known to scavenge when presented with an opportunity to.

**Predator** - Predators can influence community assemblage in the trophic levels below them and their presence is an important determining factor in species composition (Borer et al., 2006).

#### **Feeding Apparatus**

Feeding Apparatus concerns the physical mechanisms used to carry out the feeding behaviours outlined above. These link to function in the sense that all involve some form of sediment

movement, and with it movement of chemicals, nutrients and other measurable aspects of the ecosystem. This relates to 'Food Type', discussed below, and is also linked to bioturbation in some modalities.

**Jaws/Mandibles** -This is a broad modality and covers organisms that have relatively complex mouthparts that can support a sophisticated set of operations when feeding. These species are distinct from those in the 'Simple Mouth' category in that they may have an array of appendages; such as those seen in amphipods, or complicated pharynx arrangements, such as the eversible jaws of *Hediste diversicolor*.

**Siphon** - Siphons are used only by bivalves in this study, and are extended to the surface from burrows in order to capture food particles from the sediment surface or directly from the water column. This means that such species can score for surface bioturbation, but unlike other surficial bioturbators that tend to be epifaunal, will also score as downward conveyers of particles and blind burrow ventilators, oxygenating the sediment.

**Radula** - Radula are present in three species in this study and are used for grazing on surfaces. The plates of the radula move and perform a scraping action that removes and collects particles from the grazing surface.

**Tentaculated** - This modality includes any organism that uses soft appendages to capture particles. Spionid polychaetes are included in this modality due to the grooved anterior palps used to collect food, as well as *Manayunkia aestuarina*.

**Simple Mouth** - This modality covers organisms with uncomplicated mouthparts and is suitable for a number of oligochaete species as well as the flat worm Turbellaria (indt.sp). An example from this study is *Enchytraeidae sp.*, which moves through the sediment, consuming bacteria. These bacteria merely need to fit in to the feeding aperture and require no sophisticated jaw or complicated arrangement of the pharynx.

### **Food Type**

The category 'Food Type' is concerned with the kind of substances being ingested by the animals in this study. This category is important when forming trait profiles for a community; diversity in trophic behaviour is an important indicator of healthy ecosystem functioning

**Microorganisms/Diatoms**- Microalgae and bacteria are also included in this category, which covers very small-scale, living, food sources.

**Detritus** - The modality 'Detritus' refers to any organic material, normally in some state of decay, found anywhere in the sediment, from the surface to deep within. Detritivores have an important functional role in recycling energy/nutrients through the food web.

**Suspended Particles** - Any particles of material, floating or being carried by water, that pass over the sediment bed within reach of an organism's capacity to capture it. Relates to sediment mixing, nutrient capture/cycling and sequestration of substances.

**Invertebrates** - Any species in the 'Predator' Feeding Method modality is likely to prey on other invertebrates in the community. Predatory species are an important link in moving energy up the food chain and in to the wider estuarine community. Predatory invertebrates in this study are likely to be a food source for larger, pelagic or avian species.

**Bacteria** - This modality refers to the trophic preference of species that select bacteria. Examples include *Enchytraeidae* sp. and Nematode Type C, both fulfilling important roles in terms of trophic interactions (see 2.3 Benthic Species list, below).

### 2.3.3 Habitat and Living Habitat

The position of species within the sediment, and the type of living habitat they develop there can have a significant impact on the surrounding area.

#### **Position Infaunal/Epifaunal**

This is a simple category and is included as it can give a quick insight in to the type of functional assemblages. An upper shore community with a large number of epifaunal species will almost certainly be expressing different traits to lower shore benthic communities.

**Epifaunal** - Epifaunal organisms live and feed on the sediment surface, impacting only on the upper few millimetres of the sediment as they move across it. There is some potential for this modality score to be split with infaunal, as some species may also burrow occasionally.

**Infaunal** - Infaunal organisms spend the majority of their time buried in the sediment. They may come to the surface for a time, or extend feeding apparatus up to it, but are generally within a tube, burrow or free living in the body of the sediment. Infaunal organisms play a significant role in ecosystem function, as they are often involved in bioturbatory activity that modifies or oxygenates the sediment.

#### **Living Habitat**

This relates to the category above but defines the use an organism makes of its surrounding in order to function successfully. This distinction is important as, for instance, free -living species can be both infaunal and epifaunal, and the impact an infaunal organism has can be variable depending on its characteristics.

**Tube Dwelling** - Species that construct a tube around their own bodies, often a mixture of mucus and surrounding sedimentary material; these tubes can form large beds in some socially gregarious species and have a stabilising effect on the surrounding sediment (See Chapter 2.1.2.).

**Permanent Burrow** -Some organisms construct burrows and leave them rarely, or perhaps only when a new one is necessary. Regular oxygenation caused by inflow in to these burrows can create microhabitats in the immediate area and enrich benthic biodiversity.

**Semi-Permanent Burrow** - These burrows are temporary, forming networks that will collapse in time as the organism moves on to a new area. *Hediste diversicolor* is an example of this kind of burrower – forming a short-term series of tunnels lined with a mucus excretion, that are eventually abandoned for newly created ones.

**Free Living** - This modality covers species with no building or burrowing behaviours that move freely through the sediment. This kind of behaviour can keep the sediment well mixed, but can also potentially be destabilising, depending on level of disturbance.

#### 2.3.4 Size, Mobility and Life span

##### **Adult Body Length**

The size of an organism is important as it relates to its bioturbation potential and its overall impact on the sediment. Modalities are given in the table below (Table 3.1) and relate to the body lengths of the organisms sampled.

##### **Adult Mobility**

In a similar manner to Body Size, above, the range and speed of movement of an organism is also important in terms of bioturbation, and, for less mobile creatures, increased sediment stability.

**Sessile** - Sessile species do not move from where they are located. As indicated above, in the case of some species this can mean the construction of permanent tubes from which the animal both feeds and reproduces.

**Low** - This modality covers organisms that move rarely but are not truly sessile. *Cyathura carinata* is one example from this study; it is almost always within its tube, but will emerge suddenly and briefly to capture a prey item.

**Medium** - This is a broad modality and is scored for species that are not known to be sedentary but are neither renowned for high- speed movement. An errant polychaete, such as *Eteone longa/flava*, would be placed in this modality.

**High** -This modality is reserved for species that have the capacity to move very quickly. They are largely epifaunal species in this study and include *Isotomurus palustris* and the copepod genus *Tachidius*.

##### **Longevity**

Long -lived organisms tend to imply stability in an ecosystem, while short-lived species can be opportunistic, and sometimes representative of unhealthy, polluted or anoxic sediment. There are, of course, exceptions to this, particularly since this study included meiofaunal species. These have limited longevity, often less than six months, alongside some traits that might typically be associated with larger macrofaunal predators. Modalities for this are given below in Table 3.1.

### 2.3.5 Salinity Preference

A key trait in some of studies in estuaries (Van der Linden et al., 2012; Verissimo et al., 2012), showing as a significant factor in species distribution. The salinity conditions in a given area strongly dictate which species are present and the animals present in the ecosystem impact upon it and modify it, as established above. The physiological ability of an organism to exist at various degrees of salinity is critical in determining the distribution of species in an estuarine environment (Jones, 1988, Smyth 2011, Crain et al., 2004, Bulger et al., 1993). Modalities here are given across the whole range of salinities sampled here, with some flexibility either side to account for particularly euryhaline species ranges, plus those at extreme ends of the spectrum (See Table 3.1).

### 2.3.6 Fecundity, Reproductive Frequency and Reproductive Maturity

Reproductive traits are included here as they can indicate ability of a community to sustain itself over time, an important aspect of healthy long-term functioning and stability.

#### **Fecundity**

There are six modalities in this category and they are quite broad, in order to accommodate the range of fecundity levels encompassed by the benthic assemblage in this study (See Table 3.1). Expressed as number of eggs laid in a single breeding episode, fecundity is an indicator of ability of an organism to replace itself and potentially expand the representation of its species in the community.

#### **Reproductive Frequency**

Due to a paucity of information on the subject this is simplified to just two modalities, semelparous and iteroparous. Although more reproductive detail would be ideal is still helpful to account for two quite different reproductive strategies; one putting all resources in to a single reproductive opportunity, and the other spreading this energy expenditure out over time in repeated breeding seasons.

#### **Age at Maturity**

The age at which an organism reaches reproductive maturity can be indicator of reproductive strategy, as well as linking to potential longevity. Species that take longer to mature (*e.g. Macoma balthica*) are associated with well-established, stable benthic communities implying a wide range of biogeochemical interactions between species and environment.

## CHAPTER 3

### Methods

#### 3.1. Site location and Survey Design

##### Paull and Welwick

Sampling was carried out at two sites on the North bank of the Humber estuary. The first was at Welwick in July 2010 and the following year Welwick was sampled again in July together with a second site at Paull Holme Strays in August (Figure 3.1). Samples were taken along an elevation gradient from upper to lower shore. The upper shore at both sites had salt marsh characteristics and was largely dry, cracked mud with vegetation encroaching at the landward edge, broken by muddy creeks (see figure 3.5). The area outside the MR site at Welwick was typical mudflat in both years; while at Paull the terrain remained similar to upper shore salt marsh until after station 5 (Figure 3.4). In 2010 three stations were sampled within the realignment site at Welwick and a further seven were sampled outside it at 100m intervals along a high to mid shore. An adjustment was made to the sampling design in 2011 due to the excessive amount of time required to process the 2010 samples. In this year three samples were still taken within each realignment site but only three were taken outside, at wider intervals to provide similar coverage from upper to lower shore. Beyond this only three stations out of the six, at each site, were subject to replicates in a further effort to reduce processing time to that manageable within this project's time frame. Taking a single sample at half the sites represented a compromise between spatial coverage of the site and replicates that would have been ideal with no time constraints. The three stations with replicates provide statistically useful data while the additional non-replicated sites build a wider picture of the surrounding habitat and species.

Due to these differences in sampling between years the 2010 data was not used in the final BTA analysis but are included in all data sets in the appendices for reference.

##### Alkborough

The third site analysed was Alkborough and was added using data collected by the Institute of Estuarine and Coastal Studies (Mazik et al., 2012). There were more samples taken at Alkborough (Fig.3.6), but the sampling methodology used was the same, with identical coring equipment used (see below) and triplicate samples for invertebrate analysis were taken at each station, as well as for PSA.

At all sites the elevation gradient was provided by the natural slope of the shore, and extended at the landward end by the presence of a managed realignment area at each site. The distance between sites and tidal regime of the Humber estuary provided the salinity gradient. Salinity values were based on those established in the literature for the for these sites, which are well-studied (Freestone et al., 1987; Mazik et al., 2007; Mazik et al., 2012. See 1.6.2) and confirm a clear difference between sites. Throughout the results the difference between sites is representative of changes in salinity regime.

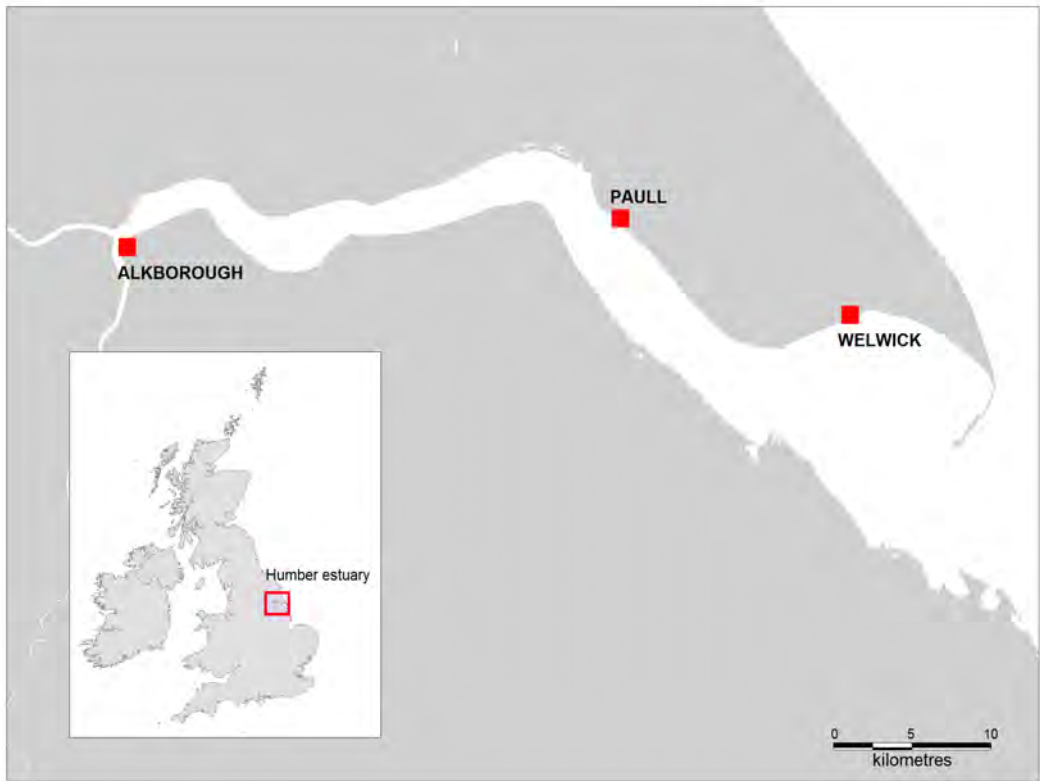


Figure 3.1. Sampling sites and location of Humber Estuary in the UK.



Figure 3.2. Sampling locations at Welwick, 2010. (Images from Google Earth). Data not ultimately presented in final BTA analysis due to difficulties sampling at the same locations the following year.





Figure.3.3 Sampling locations at Welwick 2011, illustrating the change in sampling design (Images from Google Earth).



Fig 3.4. A view across Welwick realignment area, covering sites 1-3 and illustrating level of vegetative growth compared to natural mudflat area.

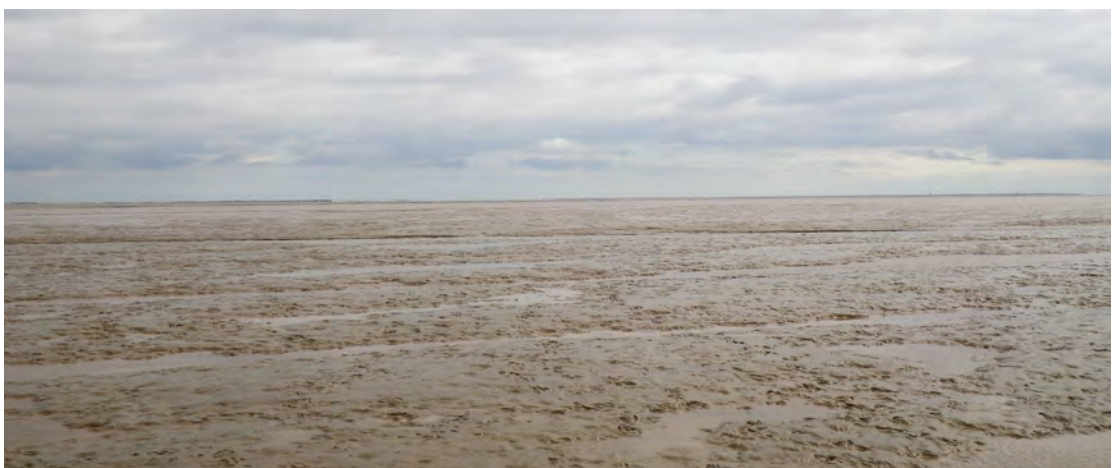


Fig 3.5. Typical estuarine mudflat taken outside the breach at Welwick, between S2 and S4.



Figure 3.6 Sampling locations at Paull Holme Stray 2011 (Images from Google Earth).



Figure. 3.7 Paull, August 2011, taken between stations 1 and 2 (see figure 3.4 above) showing a reduced central creek and encroaching salt marsh flora. Below, Fig 3.8 shows natural mudflat area at Paull S4.







Figure 3.9 Sampling locations at the Alkborough site (Mazik et al., 2012). Images from Google earth.



Fig 3.10 Alkborough, July 2011, showing dense vegetation in more elevated areas.



Fig 3.11. A second view of Alkborough 2011, showing saltmarsh flora encroaching on to former mudflat.

### **3.2. Benthic Sampling Method.**

Three benthic core samples 15cm deep and 11.5cm in diameter and 0.001m<sup>2</sup> were taken to sample infaunal invertebrates. A 5cm diameter core was used to collect a single sediment sample for particle size analysis (PSA). Each sample was carefully removed from its core in the field and stored in pre-labelled, sealable, plastic bags for transportation. Each station location was logged on a Garmin GPS device; although due to equipment failure in 2010 not all the stations could be logged using GPS and a 25m measuring chain was used to measure the distance between sites as accurately as possible. Field notes were also taken to record a general description of the habitat.

### **3.3. Laboratory Methods**

Infaunal samples were sieved through a 250 $\mu$  mesh to retain animals in the upper half of the meiofaunal size range of 63 $\mu$ -500 $\mu$ , along with macrofaunal species, defined as 500 $\mu$ -5cm (Elliott and Gray, 2009). The retained portion was preserved in 4% formalin with a Rose Bengal vitalstain. Samples were sorted under a binocular microscope at x10 magnification. Identification was carried out under a binocular microscope at x20 magnification and where necessary a compound microscope at up to x1000 magnification was used. Where possible animals were identified to species level, if not, to the lowest taxonomic level practical. This was achieved using a range of taxonomic keys (Hayward and Ryland, 2003; Brinkhurst and Jamieson, 1971; Thompson and Brown 1976) and the expertise of laboratory staff. These sorted, identified and preserved animals were then subject to biomass measurement. These sorted, identified, preserved animals were then subject to biomass measurement. Tissue dry-wet weight biomass was recorded using laboratory scales (Mettler -Toledo Delta Range PB3002), with readings taken to four decimal places. In the event of the scales giving a reading of 0.000 a biomass of <0.0001 was recorded.

### **3.4. Particle Size Analysis**

Particle size analysis was carried out using a Malvern Mastersizer and using GRADISTAT v.8.0 (Blott and Pye, 2010), a macro enabled Excel-based programme, to arrange data output. Secondary sieving was not needed for the majority of samples but was used on occasions where particle size exceeded 1mm. Anything less than 1mm was analysed using laser granulometry technique employed by the Malvern Mastersizer. Sediment particle size and the associated descriptive statistics were calculated using the Folk and Ward method using the phi ( $\phi$ ) scale.

### **3.5. Community Structure Analysis Methods**

All univariate and multivariate analyses for this project were carried out based on salinity (as represented by sites along the estuarine gradient) and elevation band. Within-site analysis examined variation between elevation band, and between-site variation (representing the salinity gradient) assessed differences along this gradient with elevation bands (<2.4m and >2.4m). The choice of 2.4m as the point between upper and lower shore bands was partly due to a lack of more detailed data at Welwick, but also as this was close to the height of the realignment breaches and a best fit for an upper/lower shore divide based on observation and

the experience of other studies (Mazik, 2010, 2012 and Mazik, pers.comm 2012-14). Multiple elevation bands were examined within Paull (three bands) and Alkborough (eight bands). Paull was analysed with three elevation bands but not included in the final results as the differences were negligible when compared to the <2.4m and >2.4m band analysis.

Univariate descriptors of community structure, including Abundance (N), Species Richness, biomass, Shannon-Wiener diversity ( $H'_{(\log_2)}$ ) and Pielou's Evenness ( $J'$ ) were calculated using PRIMER version 6 & PERMANOVA + $\beta$ 20 (Clarke and Gorely, 2006). Data were subject to Levene's test for homogeneity of variance with a view to performing ANOVA (using SPSS v20) but low P values (<0.05) for the majority of variable data (abundance, evenness, richness, diversity) meant this key assumption for ANOVA was not met. Transformations were attempted but were not effective. A Kruskal-Wallis test was performed and significant p-values (< 0.05) rejected the null of the same median in all groups. PERMANOVA was then considered as a suitable approach for non-parametric analysis of the univariate parameters (Anderson, 2001). Raw data was assembled in Excel (existing data was added at this point for the site at Alkborough) and processed in PRIMER v.6 (Clarke and Gorely, 2006).

Data were assigned factors within PRIMER: site (representing change in salinity) and elevation (height above chart datum based on LAT). Since measured elevation data for Welwick were limited, due to permission restrictions from data holders ABP, it was difficult to make direct comparison with the other sites that had more detailed elevation data. To overcome this Paull and Alkborough were assigned a broader elevation category of <2.4m and >2.4m which allowed direct comparison with the best elevation data available for Welwick. The data set for each variable was square root transformed and placed in a resemblance matrix prior to PERMANOVA analysis. Factors were added in the PERMANOVA test design and applied to the variables individually, and then to the combined multivariate data. Monte Carlo (MC) method was applied to ensure the most accurate estimation of the true p-value. PERMANOVA p-values given in the results are based on the MC method.

Welwick 2010 was sampled at three stations within the realignment site (S1, S2, S3 see Methods Fig 3.1) that could be considered upper shore and are above a height of 2.4m. The remainder are below this and can be broadly considered to be at a lower elevation (Dr. Krysia Mazik, IECS, pers. comm). This data was ultimately not presented in the results section as some necessary differences in sampling location in 2011 meant direct comparison between years was not possible.

For Welwick 2011 the same simple banding was applied, but in this instance there were three upper shore stations (W11S1, W11S2, W11S3) and only three lower shore stations (W11S4, W11S5, W11S6), reasons for this are outlined in 'Methods' above. Every effort was made to obtain more accurate elevation data but in the end permission to use certain data could not be sought in time and this simpler division of the gradient was used as the next best substitute.

The changes between sites and elevation bands were also considered using non-metric Multi-Dimensional Scaling (MDS). Plots were produced from a multivariate data sheet in which all variables were transformed and normalised. Euclidean distance was used instead of Bray-Curtis when constructing the resemblance matrix as the variables used different scales.

SIMPER analysis was also used for taxonomic composition to determine which species caused a distinction, if any, between sites and elevation bands.

## **3.6 BTA Methods**

### **3.6.1 BTA Methods: Selection of Traits**

The selection of traits used for this study aimed to ensure a meaningful traits matrix in which each trait was relatable to ecosystem functioning. This selection was informed by studies in the literature, with a consideration of the study environment in mind. Building a solid, relevant range of traits and modalities for the species and sites under consideration was approached with care as the 'correct number of traits' is still a subject of some debate across various BTA studies (Bremner 2006a, Petchey and Gaston 2006).

Some restrictions were imposed by the size of this study; it may have been interesting to explore a wider range of traits and to see which emerged as statistically relevant, but the intensive nature of the gathering of traits data means it is most sensible to select traits that are well established in the literature. Detailed reproductive information, for instance, was difficult to acquire for a large number of the species here, as well as being variable between areas for some species. Only basic reproductive data, available for all species, or at least for their genus, has been included in the final analysis under 'Fecundity', 'Age at Maturity' and the simple category 'Reproductive Frequency' that identifies either semelparous (single reproductive event) or iteroparous (multiple reproductive events) species.

The physical size of a benthic organism is significant in a study relating to ecosystem function, particularly in terms of bioturbation and nutrient cycling potential. Although the measurement of total body volume would have been preferred for this study, the additional work required was outside the timescale of this project, so body length is the trait used here instead.

Thirteen traits were selected in total, chosen on the basis of being realistic to research and relatable to ecosystem functioning. Some traits, such as the three feeding traits were used as they are found in numerous other studies; these traits are closely linked and it may be interesting to see if they are independently useful or generate overlap and are essentially redundant. A summary of these traits, modalities and shorthand codes for each (to be used in results) is given in the table that follows (Table 3.1).

Table 3.1 Functional Traits, Modalities and coding.

FUNCTIONAL TRAIT	MODALITY	CODE
<b>Feeding Method (FM)</b>	Deposit Feeder (Surface)	FM/D
	Subsurface Deposit Feeder	FM/SS
	Filter/Particle Selection	FM/FS
	Opportunistic scavenger	FM/OS
	Predator	FM/P
<b>Feeding Apparatus (FA)</b>	Jaws/Mandibles	FA/J
	Tentaculated	FA/T
	Radula	FA/R
	Siphon	FA/S
	Simple Mouth	FA/M
<b>Food Type (FT)</b>	Microorganisms /Diatoms	FT/M
	Detritus	FT/D
	Suspended Particles	FT/S
	Invertebrates	FT/I
	Bacteria	FT/B
<b>Adult Movement (AM)</b>	Sessile	AM/S
	Low	AM/L
	Medium	AM/M
	High	AM/H
<b>Habitat (H)</b>	Epifaunal	H/E
	Infaunal	H/I
<b>Living Habitat (LH)</b>	Tube Dwelling	LH/T
	Permanent Burrow	LH/PB
	Semi-Permanent Burrow	LH/SP
	Free Living	LH/F
<b>Bioturbatory Mode (B)</b>	Upward Conveyer	B/U
	Downward Conveyer	B/D
	Gallery Biodiffuser	B/GB
	Surficial Biodiffuser	B/SB
	Open Burrow Ventilator	B/OV
	Blind Burrow Ventilator	B/BV
	Burrowing Biodiffuser	B/BB
<b>Adult Body Length (BL)</b>	<2mm	BL/2mm
	2-5mm	BL/5mm
	5mm-1cm	BL/1cm
	1cm-2cm	BL/2cm
	2- >5cm	BL/5cm

Table 3.1 cont.

FUNCTIONAL TRAIT	MODALITY	CODE
<b>Longevity (L)</b>	<6mth	L/<6
	6-18mth	L/6-18
	18mth- 2yrs	L/18-2
	2-5yrs	L/2-5
	>5yrs	L/>5
<b>Salinity Preference (S)</b>	1-5	S/5
	5-10	S/10
	10-15	S/15
	15-20	S/20
	20-25+	S/25
<b>Fecundity (F)</b>	10-50	F/10
	50-100	F/100
	100-1000	F/1k
	1000-10,000	F/10K
	>10,000	F/>10K
<b>Reproductive Frequency (RF)</b>	Iteroparous	RF/I
	Semelparous	RF/S
<b>Age at Maturity (M)</b>	<6mth	M/<6
	≥6mth	M/6
	6mth-1yr	M/6mth-1
	1-2yr	M/1-2

### 3.6.2 Exclusions and Generalisations.

Not every animal collected is included in the final traits matrix. In some cases a species only occurs at one site and only one individual is present. Given the intensive amount of research needed to compile a full traits score a practical decision has been made to exclude the species in these instances (Bremner, 2005). An example of this is a species of Collembola of the genus *Sminthurides* of which one individual appeared once across the whole survey; this animal is a true freshwater collembolan, unlike the multitude of marsh springtails found across the sampling stations and is not typical of the habitat. A small Arachnid was found in one sample along with an Acarina (indt.sp.) and a Coeleoptera (indt.sp), all appearing in isolation, and these were also excluded from the traits scoring and analysis

A number of Dolichopodidae (Diptera), and other fly larvae, were considered for potential exclusion. Although they are only benthic for a stage of their life cycle they are part of the benthic community for that stage and some literature is available on their feeding habits – mainly scavenging and predation. However, many trait categories in this study are based on adult animals and include aspects of reproduction as well as lifespan and it would only be possible to accurately score these larvae for a fraction of categories. With this in mind the animals are scored only in the areas they directly contribute to while in their benthic phase, and in all non-relevant categories they are scored a zero. Chevenet (1994) suggests that animals without a full set of traits scores should be excluded completely, but the particular nature of *Diptera dolichopodidae* larvae and the important role that such animals play in the



trophic dynamics of the benthic community (LaSalle and Bishop, 1990) have strongly suggested inclusion here. For categories 'Adult Body Length' and 'Longevity' larval body length is given and approximate length of larval phase is applied instead of total lifespan. A number of other fly larvae were noted at Alkborough and these were treated in the same manner.

In some instances it has not been possible to identify an animal to species level. The animal may have been damaged or there was a lack of available expertise to identify more precisely. Where this has occurred generalised traits for the genus have been given and where possible weight has been given to the traits of animals of the same genus that have been successfully identified to species level and found in the vicinity. For example, *Nephtys hombergii* is the only *Nephtys* recorded in this region of the Humber estuary, so in the instance that an animal was damaged beyond reliable identification to species, generalised traits have favoured those of *N.hombergii*. *Nephtys cirrosa* is present elsewhere in the Humber, but not at the study sites, so it seems more sensible to select traits from a species that is known to be present specifically at the sites and stations under consideration. Generalising traits for a genus does contain the potential for some inaccuracy, or for the need to place small scores in numerous modalities, but it is a better choice overall than excluding a contributing member of the community all together.

### 3.6.3 Statistical Approaches.

Traits data were scored using fuzzy coding (Chevenet, 1994), using a trait affinity score of 0-1. A score of 0 equally no affinity for a modality and a score of 1 represented full affinity to the modality. Where a species expressed multiple modes the score was split to reflect this. E.g.- for Feeding Mode a predatory animal that also opportunistically scavenged would score 0.5 in each modality. To link the completed traits data to the sampled benthic assemblage both biomass and abundance data were used. Each sampling station trait score, for each taxon, was multiplied by the relevant abundance or biomass data to produce a figure indicating the degree to which traits are expressed. Traits were weighted by both abundance and biomass as the presence of high-abundance meiofaunal animal alongside relatively large bivalves and polychaetes appeared to cause each to produce a skewed perspective when used in isolation. Both approaches are presented next to each other in the results for traits analysis below in Chapter 4.3. Stacked column charts are used to visually compared the two versions of the results, biomass-weighted and abundance-weighted. In some instances error bars were removed from these charts as the difference in biomass or abundance values between samples were so large that parts were difficult to read. Removing the error bars increased the clarity and allowed traits with smaller numerical representation to be discerned.

As in the community structure statistical methods, PERMANOVA (PRIMER 6+ (Clarke and Gorely, 2006)) were used to analyse variance between sites along the salinity gradient and the within-site elevation gradient, as well as a year on year comparison at Welwick. Bray–Curtis similarity was calculated on square root-transformed data and used to create the resemblance matrix. For multivariate analysis, non-metric Multi Dimensional Scaling (MDS) was used, and SIMPER analysis was carried out on the data to observe the contribution individual traits, also in PRIMER 6+ (Clarke and Gorely, 2006). For some MDS plots two outliers, PS5R1 and ALK 102B, caused serious clustering effects for a number of traits due to containing a very small

number of animals. The effect was such that data was represented as two points, the outlier and everything else. Where this was the case these outliers were removed to allow relationships between the other samples to be discerned. Where this has occurred it is noted in the chart legend.

# CHAPTER 4

## 4. Results

### 4.1 Physical Aspects: Particle Size Analysis Results

At Welwick in 2011 there was a slightly higher sand content in samples from the lower shore when compared to the upper shore; less than 20% at all three >2.4m stations, compared to between 22% and 39% at upper shore stations. Mean values for upper and lower elevation band were not significantly different.

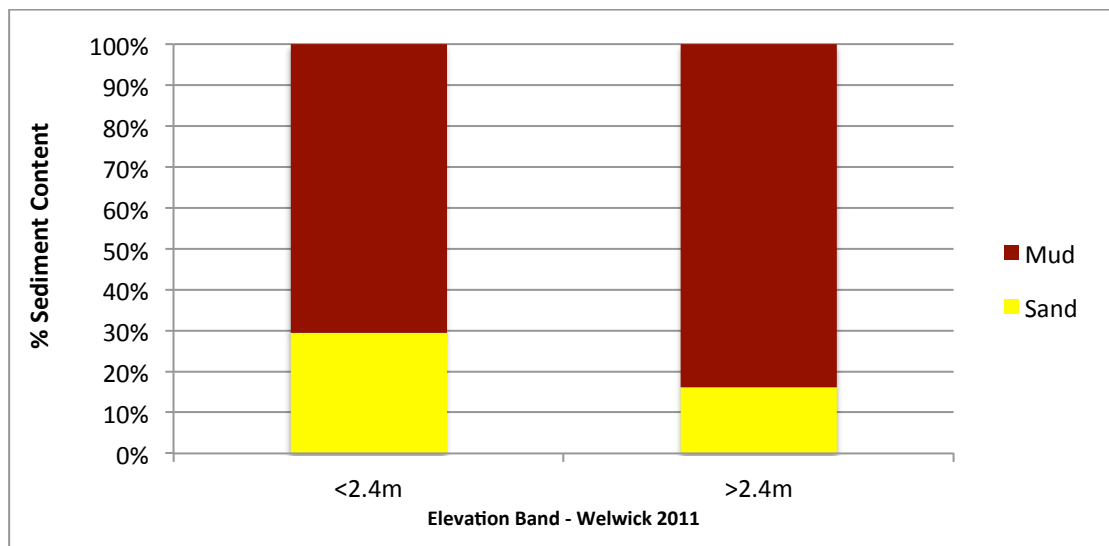


Figure 4.1.1. Sediment composition at Welwick 2011.

Table 4.1.1 Summary of particle size and composition of sediment sampled at Welwick 2011

Elevation	Mean Grain Size (Phi)	Mean Sand %	Mean Mud %	Mean Gravel %	Folk and Ward Description	Mean Sorting (Phi)
<2.4m	5.803	16.10	83.9	0.00	Coarse Silt	1.909
>2.4m	5.382	29.50	70.5	0.00	Coarse Silt	1.919

At Paull 2011 there was a slight trend of less sand content in the lower elevation bands, with only 15% present at S6 (the lowest elevation station), compared to >20% at all other stations. Mean values for upper and lower shore sites suggested no significant difference in sediment composition across the gradient. See Fig 4.1.2.

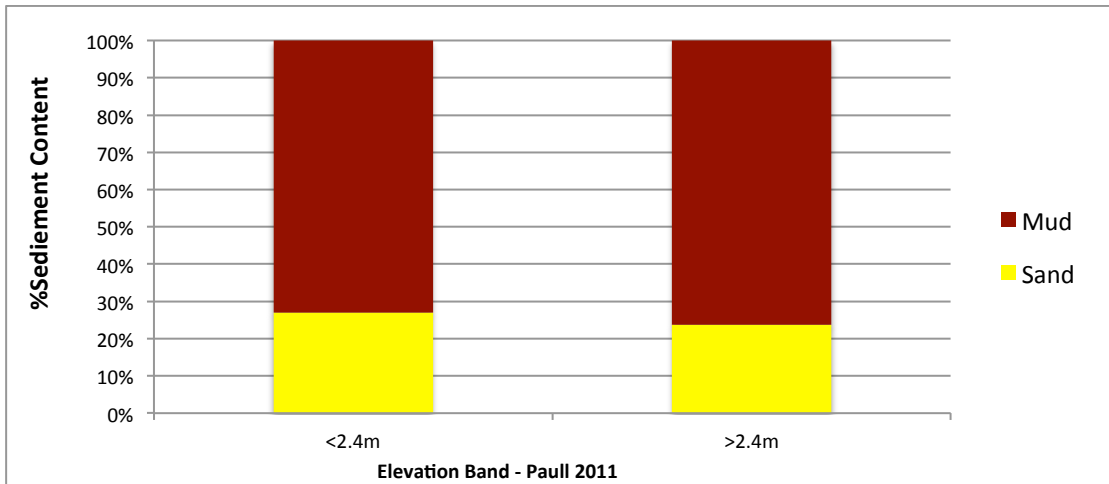


Figure. 4.1.2. Sediment composition at Paull 2011.

Table 4.1.2 Summary of particle size and composition of sediment sampled at Paull 2011.

Elevation	Mean Grain Size (Phi)	Mean Sand %	Mean Mud %	Mean Gravel %	Folk and Ward Description	Mean Sorting (Phi)
<2.4 m	5.348	26.96	73.04	0.00	Coarse Silt	1.873
>2.4 m	5.578	23.75	76.2	0.00	Coarse Silt	1.878

Alkborough had higher levels of mud content than both Paull and Welwick, particularly in the >2.4 m band. This area is heavily vegetated which could be a confounding factor in an elevation based analysis.

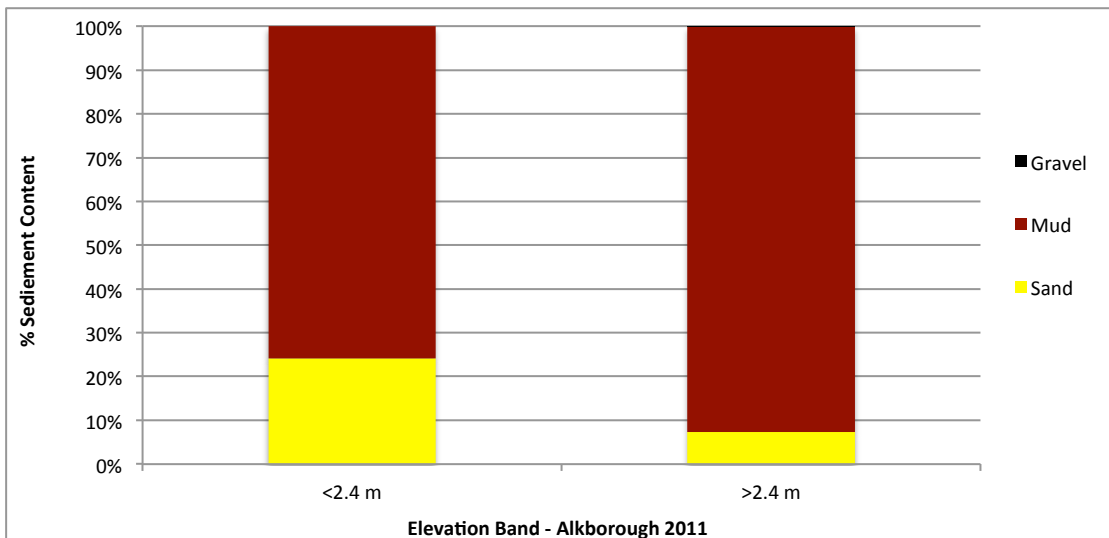


Fig 4.1.3. Alkborough sediment content across two elevation bands.

Table. 4.1.3. Mean values within Elevation Bands Alkborough 2011.

Elevation	Mean Grain Size (Phi)	Mean Sand %	Mean Mud %	Mean Gravel %	Folk and Ward Description	Mean Sorting (Phi)
<2.4m	6.572	7.31	96.6	0.1	Medium Silt	0.016
>2.4m	5.542	24.18	75.8	0.0	Coarse Silt	1.906

The upper shore (>2.4 m) had higher mud content than the lower shore (<2.4 m) and was a finer silt with a smaller mean grain size ( $p < 0.05$ ) (see Table 4.1.4). A comparative between upper and lower shore gave a significant p-value of 0.0042.

#### *Between Sites*

Site is used throughout this study as a proxy for the salinity gradient in the Humber, based on site location and established differences in salinity regime. Tests between sites, within elevation band, indicated there was no significant difference in sediment composition in the <2.4m elevation band. However, in the >2.4m band Paull was significantly different to both Alkborough ( $p < 0.01$ ) and Welwick ( $p < 0.05$ ). (Table 4.1.5 and 4.1.6).

Table 4.1.4 Comparative test (sediment) at <2.4 m, between sites

Within <2.4 m Elevation Band	P-Value (MC)
Welwick 2011/Paull	0.1712
Welwick 2011/ Alkborough	0.2074
Paull/Alkborough	0.419

Table 4.1.5 Comparative test (sediment) at >2.4 m, between sites.

Within >2.4 m Elevation Band	P-Value (MC)
Welwick 2011/ Paull	0.0268
Welwick 2011/ Alkborough	0.0608
Paull/Alkborough	0.0008

#### *Alkborough Elevation Detail*

Samples at Alkborough contained over 70% of mud at all stations. There was a trend towards higher sand content at lower shore sites (>3 m), where sand content increased to a maximum of 27.5% at Station A13 at 0 m elevation. See Fig 4.1.4. The spread of sites within the Alkborough alignment area, compared with the smaller number of samples over a narrower area outside, may be a confounding factor here.

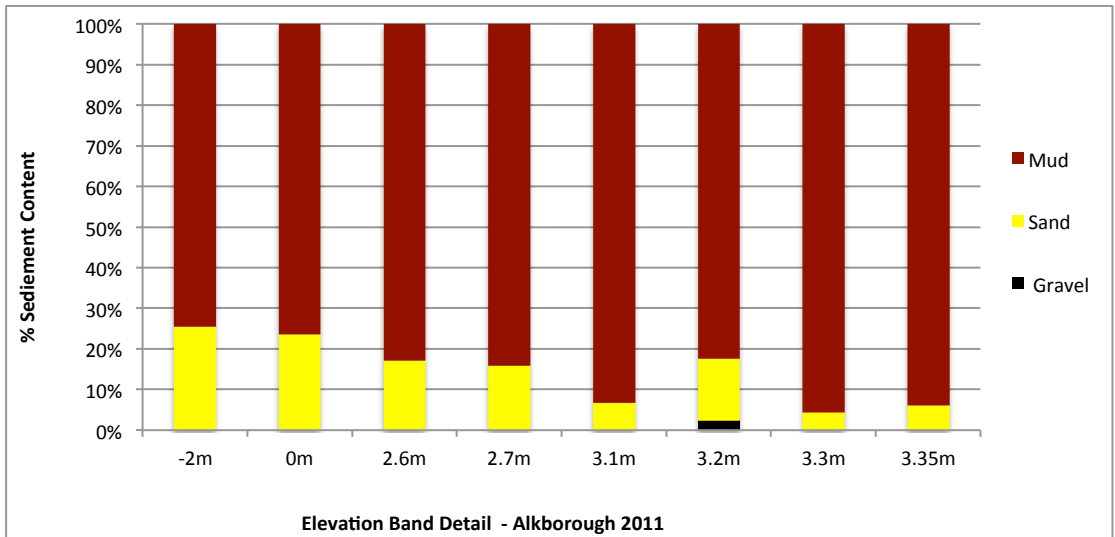


Figure. 4.1.4. Sediment composition at Alkborough 2011 over eight elevation bands. Sand content drops off past 0 m but rises briefly again at 3.2 m. The wide spread of sampling stations inside the realignment area could contribute to this variation as they cover both highly vegetative and creek/mud habitats.

## 4.2 Community Structure Results

### 4.2.1 Multivariate Analysis

MDS ordination for all community structure variables showed the separation of Alkborough from the other two sites along the salinity gradient of the Humber ( $p < 0.01$  and Pseudo-F 28.4), as well between stations sampled on the upper and lower shore at Alkborough, with  $p < 0.01$  (Fig 4.2.9). One of the most distinct changes was in abundance and this is illustrated in the MDS ordination and 2D bubble plot in Fig. 4.2.10 A and B, below. Welwick showed some difference in community structure between upper and lower elevation bands ( $p < 0.01$ ), while at Paull there was little separation between the two bands and changes were not significant (Fig. 4.2.9). Between Paull and Welwick significant differences in community structure were only observed in the  $< 2.4$  m band ( $p < 0.05$ ).

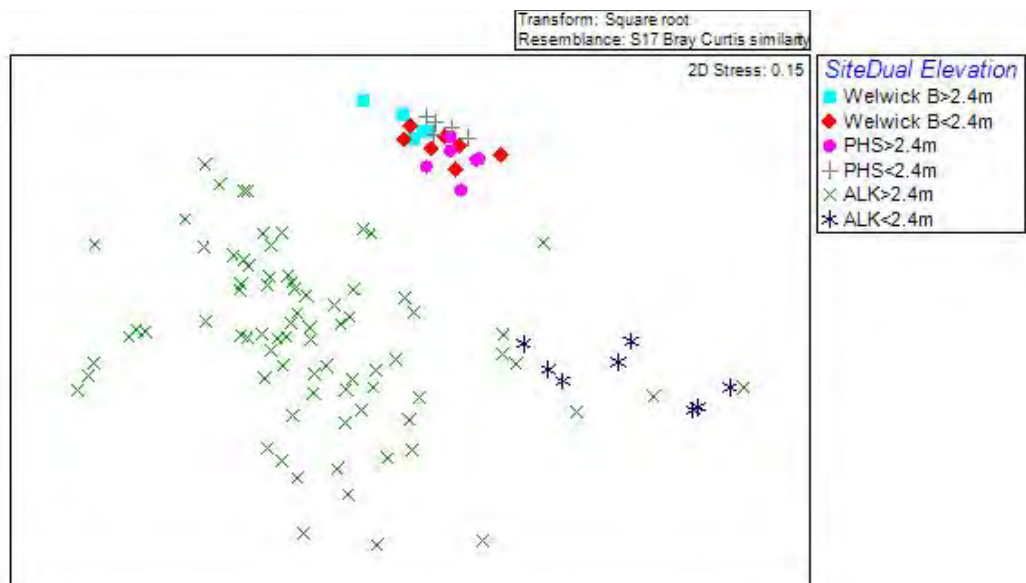


Figure 4.2.1. MDS square root transformed for 2011, site/elevation band. Taxonomic composition.

PERMANOVA results for taxonomic composition showed clear change between sites along the salinity ( $p < 0.001$  and  $F = 14.3$ ) and elevation gradients ( $p < 0.01$  and  $F = 3.8$ ). Tests within each site, between the two elevation bands, showed significant differences at Welwick and Alkborough ( $p < 0.01$ ), but not at Paull. Tests within two elevation bands ( $< 2.4$  m and  $> 2.4$  m), along the salinity gradient between sites, indicated Alkborough was different in taxonomic composition to both Paull and Welwick in both bands, at  $p < 0.01$ . In the  $> 2.4$  m elevation band Welwick and Paull were different ( $p < 0.01$ ), but not in the  $< 2.4$  m band.

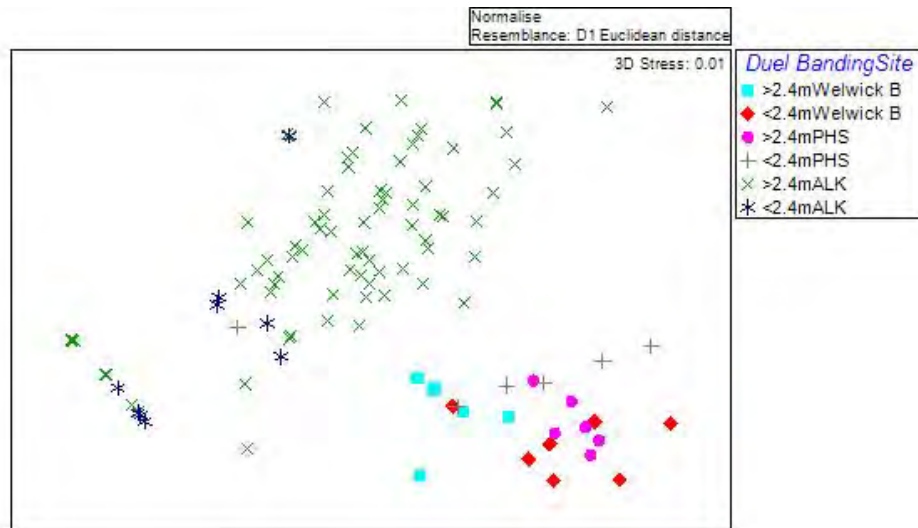


Figure 4.2.2.A. MDS plot showing abundance data with two factors, 'Site' (representing changing salinity) and 'Elevation band'.

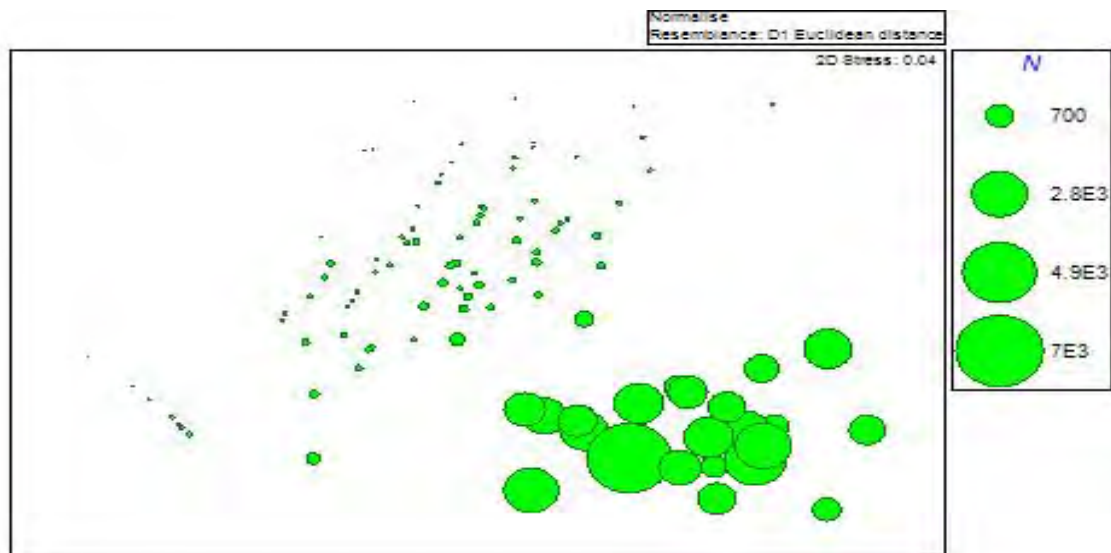


Figure 4.2.2 B. 2D Bubble Plot of the data shown in the MDS plot 4.2.10A, above.

Species composition data was subject to SIMPER analysis, highlighting the species responsible for the discrimination between upper and lower shore samples. At Welwick and Paull Nematode sp. made significant contributions to all elevation bands, but at Welwick definition between bands was provided by species with lower %contributions. At Welwick <2.4 m, bivalves (*Macoma balthica*) polychaetes (*Eteone longa/flava*) and oligochaetes (*Tubificoides benedii*) contributed to the composition, while at Welwick >2.4 m large contributions were made by Collembola sp. and *Manayunkia aesturina*, neither of which were found on the lower shore. Overall, the average dissimilarity between the two elevation bands at Welwick was 52.16% (Table 4.2.2. See Appendix 7.1 for full Average. Dissimilarity tables).



At Paull, the distinction was less clear and the three Nematoda types dominated both elevation bands, along with *Manayunkia aestuarina* and Enchytraeidae (Table 4.2.1, below). This was reflected in the average dissimilarity between elevation bands, which returned a result of 44.79% (Table 4.2.2. See Appendix 4.1 and 4.2 for full Average similarity and dissimilarity tables).

At Alkborough, there was a distinct difference in species composition across the two elevation bands, with *Baltidrilus costatus* (*Heterochaete costata*) completely dominating the lower shore. Within the <2.4m band there was a relatively high average similarity across the samples at 64.03%, especially in comparison to the upper shore band with an average similarity of 24.31%, suggesting strong heterogeneity between samples taken on the lower shore. However, this is likely to be affected by there being fewer stations in the lower band, spread across a smaller area, and is not necessarily conclusive. Species composition at >2.4m was characterised by oligochaetes (*Paranais littoralis* and Enchytraeidae) and Collembola sp. and Diptera larvae. Between the two elevation bands there was a very high average dissimilarity of 93.14%, supporting the MDS and PERMANOVA output above (Fig 4.2.9 and Table 4.2.15).

Detailed elevation band analysis, over three bands, <2.4 m, 2.4 m-2.6 m and 2.61-2.8 m, at Paull did not show any significant differences in community structure components. Each band was dominated by *Manayunkia aestuarina* and at least one of the Nematode types; only the <2.4m band indicated a low within-band similarity at 48.55%. This likely to be related to the broad parameters of this band, which includes any station at <2.4 m, and it is likely that PS6 was much lower than PS5. (See Discussion for elevation band/gradient issues at Paull).

Table 4.2.1 Average Similarity, between elevations (<2.4 m and >2.4 m), for all sites 2011

Average Similarity - % Species Contribution by Elevation Band									
Elevation	Welwick 2011	% Contribution	Paull 2011	% Contribution	Alkborough 2011	% Contribution			
<2.4 m Elevation	Nematode Type B	24.94	Nematode Type B	20.53	<i>Baltidrilus costatus</i> ( <i>Heterochaete costata</i> )	95.03			
	Nematode Type A	20.62	Nematode Type A	16.30					
	Nematode Type C	15.42	<i>Manayunkia aestuarina</i>	13.78					
	Tellinacea Sp.	6.67	Nematode Type C	13.09					
	<i>Tubificoides benedii</i>	6.00	Copepoda <i>Tachidius</i>	8.48					
	Copepoda <i>Tachidius</i>	4.95	Enchytraeidae	5.31					
	<i>Macoma balthica</i>	4.28	Tellinacea sp.	4.06					
	<i>Hydrobia ulvae</i>	2.30	<i>Macoma balthica</i>	3.79					
	<i>Eteone longa/flava</i>	2.19	<i>Hydrobia ulvae</i>	2.97					
	Enchytraeidae	2.13	<i>Isotomurus palustris</i>	2.73					
	Ostracoda sp.	2.07							
		Average Similarity%	68.67	Average Similarity%			48.55	Average Similarity%	64.03
	>2.4 m Elevation	Nematode Type B	27.58	<i>Manayunkia aestuarina</i>			26.28	<i>Paranais littoralis</i>	32.57
Nematode Type A		17.41	Nematode Type A	16.82	Enchytraeidae	28.17			
<i>Isotomurus palustris</i>		13.41	Nematode Type B	12.54	Collembola sp.	14.33			
Enchytraeidae		12.11	Nematode Type C	9.42	<i>Diptera dolichopodidae</i>	11.01			
<i>Manayunkia</i>		11.22	<i>Enchytraeidae</i>	8.34	<i>Corophium volutator</i>	4.98			
<i>aestuarina</i>		10.92	Copepod <i>Tachidius</i>	6.32					
Nematode Type C			<i>Hediste diversicolor</i>	3.56					
			<i>Hydrobia ulvae</i>	3.22					
			Tellinacea sp.	3.19					
			<i>Eteone long/flava</i>	2.07					
	Average Similarity %	63.01	Average Similarity %	67.44	Average Similarity%	24.31			

Table 4.2.2 % Average Dissimilarity, all sites 201

% Dissimilarity Between Elevation Band/Sites Along the Salinity Gradient						
Site/Elevation	Welwick <2.4 m	Paull <2.4 m	Alkborough <2.4 m	Welwick >2.4 m	Paull >2.4m	Alkborough > 2.4m
Welwick <2.4 m						
Paull <2.4 m	46.49					
Alkborough <2.4 m	98.60	99.11				
Welwick >2.4 m	52.16	50.79	98.91			
Paull >2.4 m	44.20	44.79	98.16	45.27		
Alkborough >2.4 m	94.84	96.29	93.14	95.00	94.77	

### Alkborough- Elevation Detail

Multi-Dimensional Scaling showed the clear separation of lower shore band from >2.4 m samples in terms of community structure, particularly stations sampled outside the realignment area (Fig 4.2.11).

PERMANOVA results showed change in all community structure variables across the elevation gradient ( $p < 0.01$  and  $F=3.8$ ). In tests across the eight elevation bands, where each individual band was compared to others, 11 pairings out of 28 returned a significant value of  $p < 0.05$ . Some of these differences were between high shore and low shore bands, such as 3.35 m/-2 m and 3.3/-2 m but others showed a difference between much closer bands. The pairs 3.1 m/2.7 m, 3.1 m/2.6 m were all significantly different ( $p < 0.05$ ), despite being close to each other. Other lower shore pairings with the 3.1 m band (3.1 m/0 m, 3.1 m/-2 m) also showed differences ( $< 0.05$ ) and suggested that 3.1 m was elevation at which abiotic conditions changed enough to influence community structure and composition.

SIMPER analysis was also performed for the same data set and indicated that there was a difference between elevation bands at Alkborough. Within-band similarity varied along the gradient, with a very high average similarity in the lowest shore (-2 m) band of 73.93%, where the samples were dominated by *Heterochaete costata*, but a very low within band similarity of 25.88% in the highest (3.35 m) band, suggesting high heterogeneity of samples (Table 4.2.6). When bands were compared to each other there was a very high % Average Dissimilarity between many of the bands, supporting the PERMANOVA results, and the MDS plot below (Fig 4.2.11), with some bands showing as 100% dissimilar (3.2 m/0 m and 2.7 m/0 m – Table 4.2.5).

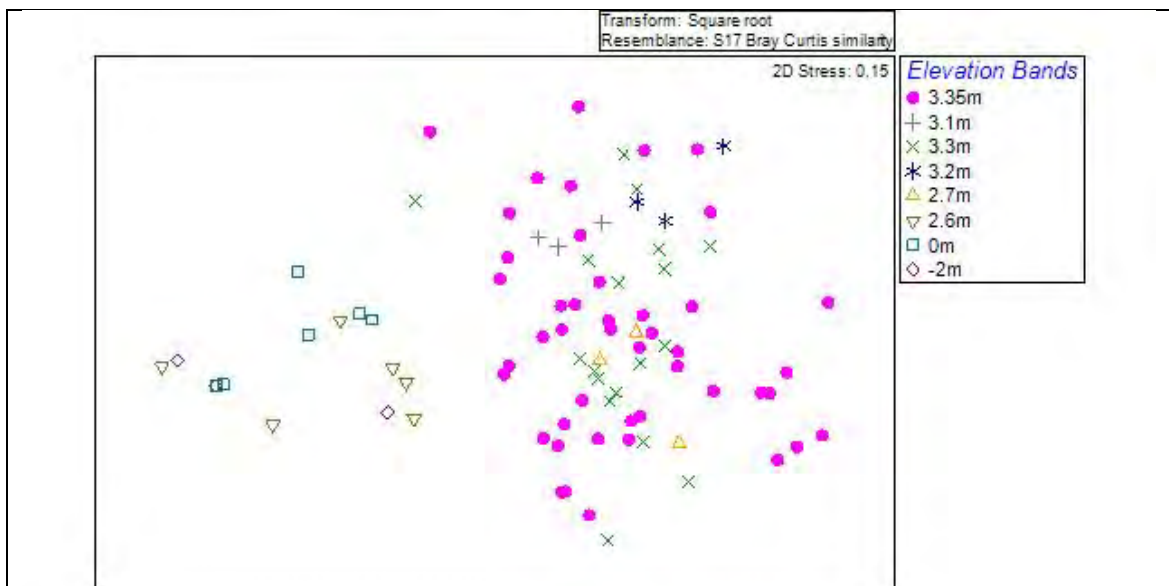


Fig. 4.2.3. MDS for Alkborough, taxonomic composition 2011.

Table 4.2.3 SIMPER % dissimilarity between eight elevation bands at Alkborough in 2010 and 2011

% Dissimilarity Between Elevation Bands – Alkborough 2011 Eight Bands								
Elevation	-2 m	0 m	2.6 m	2.7 m	3.1 m	3.2 m	3.3 m	3.35 m
-2 m								
0 m	36.88							
2.6 m	40.10	46.66						
2.7 m	92.58	100.00	89.88					
3.1 m	100.00	88.17	95.88	72.25				
3.2 m	98.67	100.00	98.61	79.20	71.74			
3.3 m	96.57	97.20	93.59	61.91	69.09	73.88		
3.35 m	96.84	97.60	93.52	68.78	77.17	82.10	71.78	

Table 4.2.4 SIMPER results showing % species contribution.

Average Similarity: Alkborough Elevation Detail - % Species Contribution Band		
Elevation	Alkborough 2011	% Contribution
-2 m	<i>Baltidrilus costatus</i> ( <i>Heterochaete costata</i> )	100.00
	Average Similarity%	73.93
0 m	<i>Baltidrilus costatus</i> ( <i>Heterochaete costata</i> )	87.91
	Average Similarity %	63.14
2.6 m	<i>Baltidrilus costatus</i> ( <i>Heterochaete costata</i> )	91.32
	Average Similarity %	49.31
2.7 m	Echytraeidae	56.50
	<i>Paranais littoralis</i>	22.33
	Average Similarity %	58.47
3.1 m	<i>Paranais littoralis</i>	32.27
	<i>Diptera dolichopodidae</i>	31.24
	Average Similarity %	69.41
3.2 m	Chironomidae Larvae	76.82
	Average Similarity %	67.52
3.3 m	<i>Paranais littoralis</i> Enchytraeidae	
	Average Similarity %	30.09
3.35 m	Enchytraeidae	28.57
	<i>Paranais littoralis</i>	27.15
	Collembola sp.	25.10
	Average Similarity %	25.88

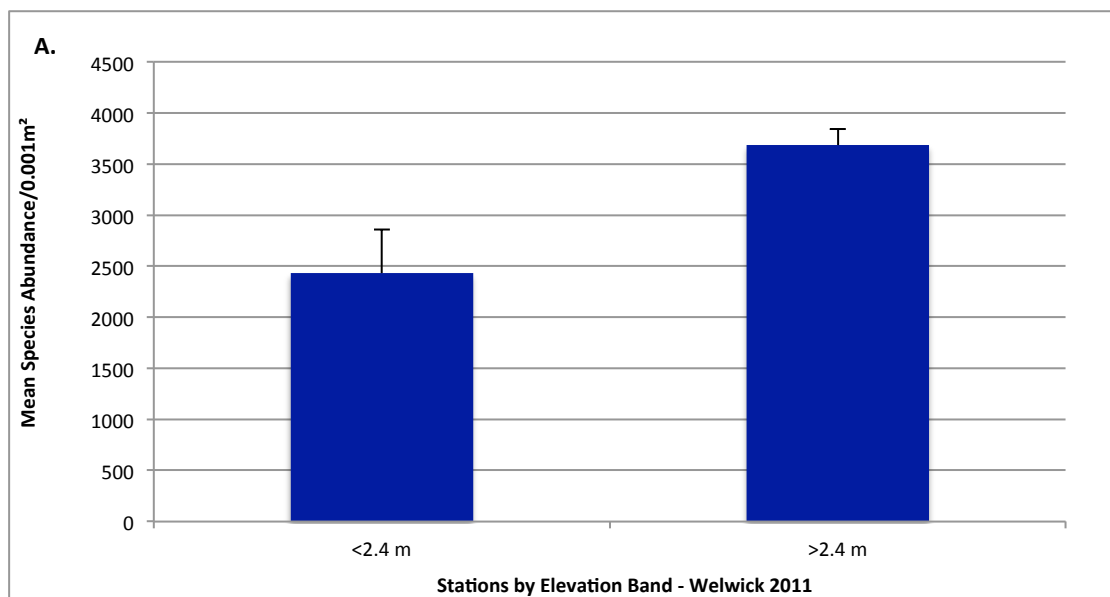
## 4.2.2 Univariate Analysis

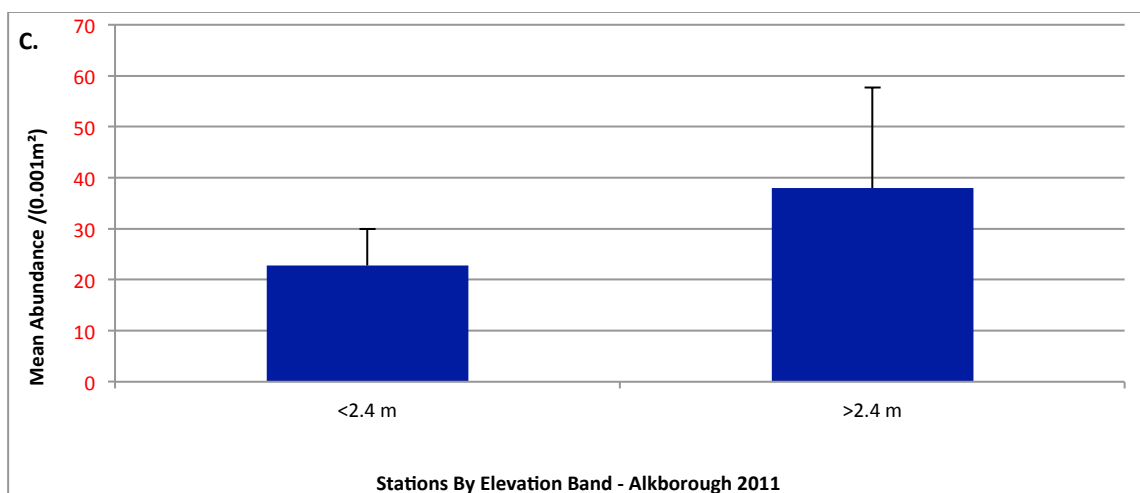
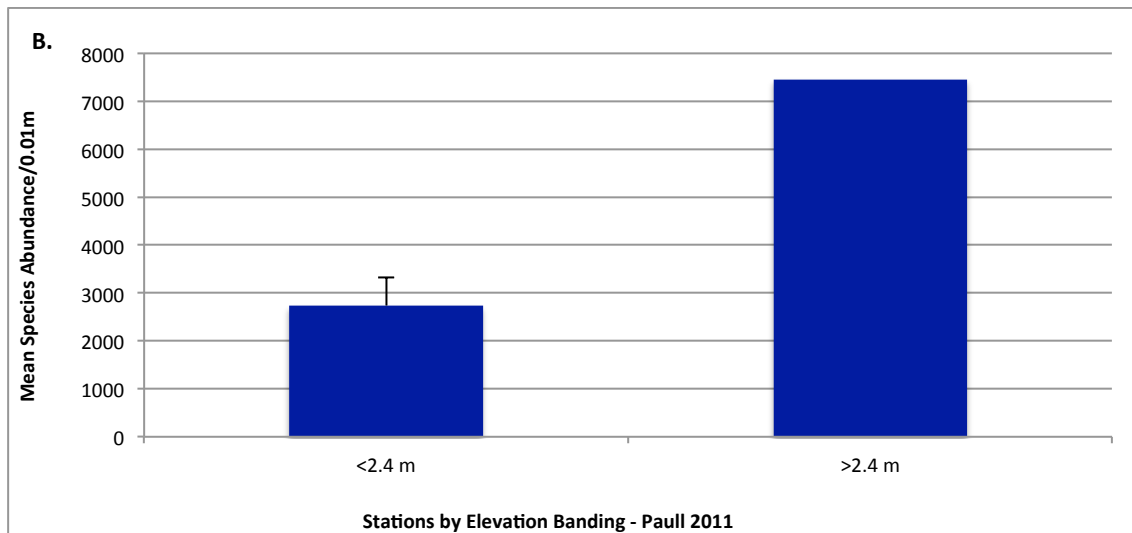
### **Abundance**

Abundance showed a significant difference in values between sites ( $p < 0.01$ ,  $F = 54.23$ ). Tests between sites, within elevation band (<2.4 m and >2.4 m), indicated that Alkborough was significantly different to Welwick and Paull in both bands ( $p < 0.01$ ), indicating that salinity was an important factor in changes in abundance. See Appendix (2) for MDS plot illustrating a much lower abundance levels at Alkborough, compared to the other two study sites.

A significant difference between high and low elevations was found at Welwick, where there was a higher overall level of abundance in the upper shore band ( $p < 0.05$ ). At Alkborough there was some variation visible across the gradient when all eight bands were analysed but it was not a consistent trend, reflecting the within-band variability of terrain and hydrographic regime at Alkborough above 2.4 m, and was not significant in tests. Between the <2.4 m and >2.4 m elevation bands Paull also showed no significant difference in abundance between <2.4m and >2.4m. See Table 4.2.1 for mean values.

A point of note in Fig 4.2.1 is the large drop in abundance levels at Alkborough. These are some two orders of magnitude lower and highlight the difference in conditions at Alkborough.





Figures 4.2.4. A-C. A. Mean abundance/0.001 m<sup>2</sup> at Welwick 2011. B. Mean abundance/0.001 m<sup>2</sup> at Paull 2011. C. Mean abundance /0.001 m<sup>2</sup> at Alkborough 2011. See Table 4.2.1 for Std. Dev. Note significantly lower N at Alkborough, highlighted in red.

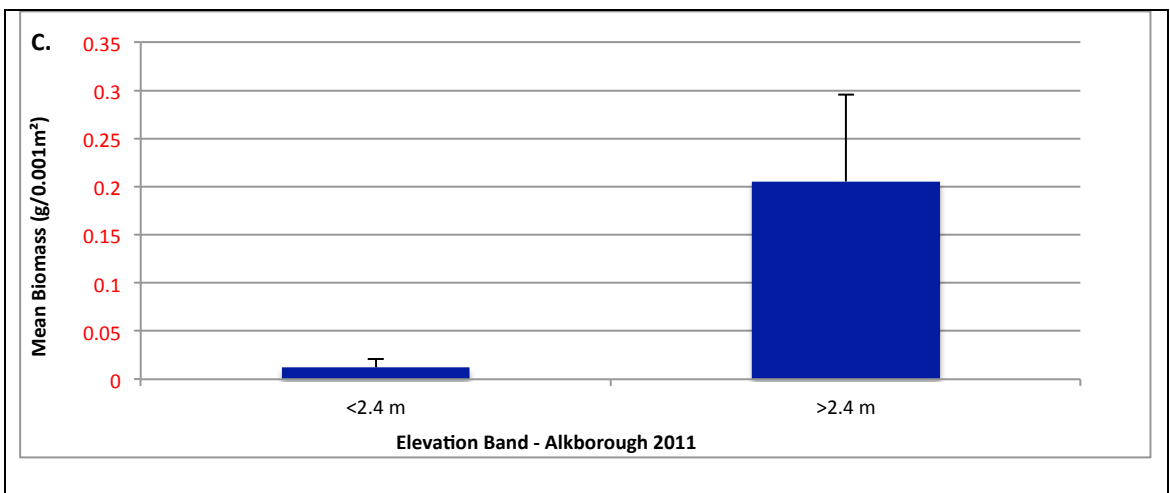
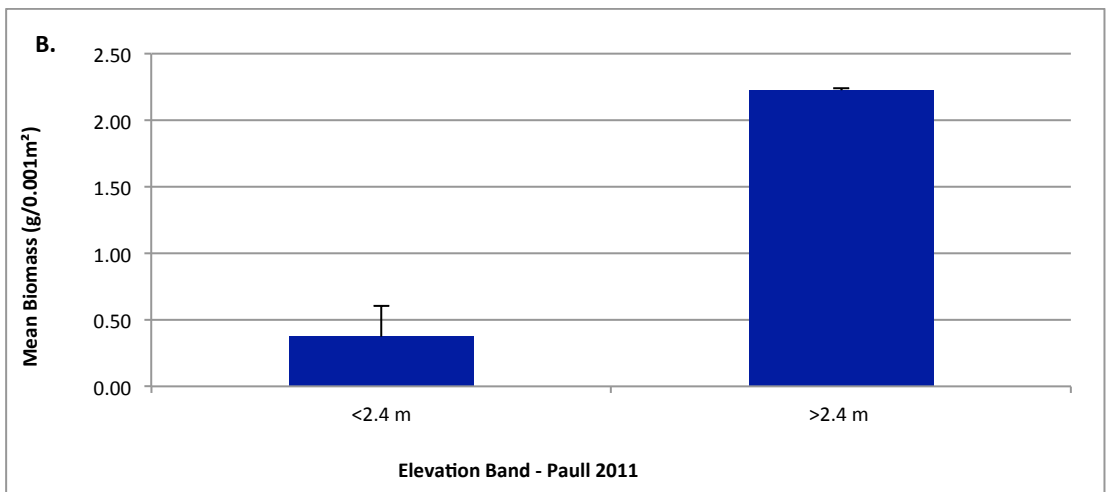
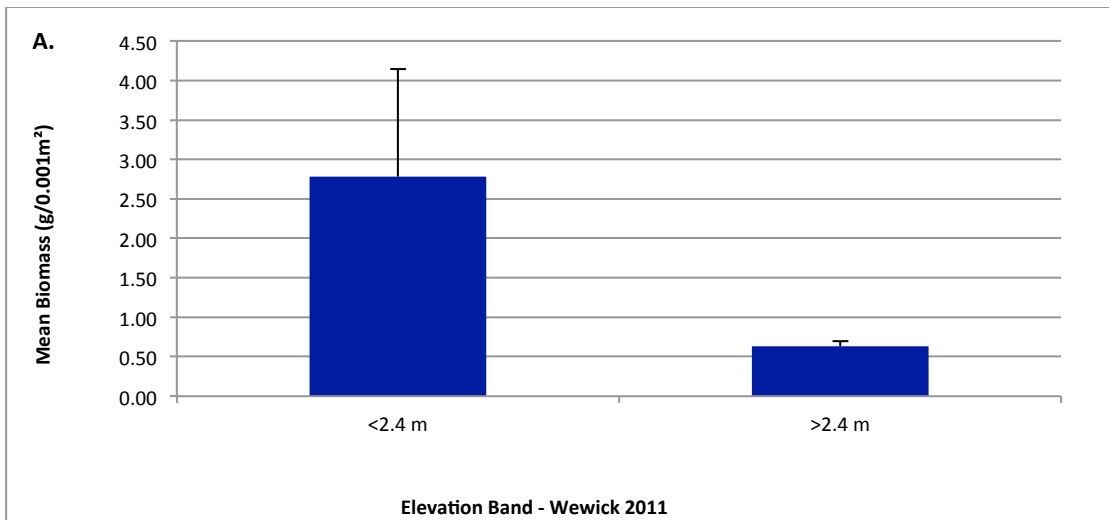
### Biomass

PERMANOVA results indicated significant changes between sites ( $p < 0.01$  and Pseudo-F 36.15) with increasingly lower levels as salinity decreased. Biomass also showed a change with elevation ( $p < 0.01$  and  $F = 9.5$ ).

At Welwick the higher levels were in the <2.4 m band, but at Paull and Alkborough the increased biomass levels were at >2.4 m (Fig.4.2.3 A-C). At Welwick there was also a noticeable trend within the <2.4 m band, with a gradient apparent from high to low shore, with biomass levels increasing between S4 and S6. This is likely to be due to the presence of larger species at the lower end of the band, such as *Cerastoderma edule*, which has a very high biomass compared to species sampled at higher elevations (e.g. *Isotomerus palustris*/Nematode sp.)

At Alkborough higher biomass values could be caused by higher abundance at >2.4 m, along with a higher number of samples taken. An analysis of the more detailed elevation banding at Alkborough did not show anything significantly different from the <2.4 m and >2.4m comparison. At Paull there were variations in the hydro graphic regime within the >2.4 m band that may have caused some with-in band sample stations to experience conditions more

typical of the lower shore, particularly Station 3 which lay on an inlet creek (See Methods Fig.3.4). There was also no variation when elevation was examined across three bands at Paull.



Figures 4.2.5 A,B and C . A. Mean biomass/0.001 m<sup>2</sup> at Wewick 2011. B. Mean biomass /0.001 m<sup>2</sup> at Paull 2011. C. Mean biomass /0.001 m<sup>2</sup> at Alkborough 2011. See Table 4.3.1 for S.D. Note again the very low biomass values for Alkborough, related to low abundance values above, highlighted in red.



### Species Richness

Species richness showed a significant change between sites along the salinity gradient ( $p < 0.01$  and  $F = 57.37$ ) Tests within each of the two elevation bands, along the salinity gradient, indicated Alkborough was significantly different to Welwick and Paull ( $p < 0.01$ ), with much lower species richness at Alkborough, in both elevation bands. A significant difference was also found between Paull and Welwick in the  $>2.4$  m band ( $p < 0.05$ ) with higher species richness at Welwick, but not in the  $<2.4$  m band. As with abundance and biomass the figures at Alkborough for species richness are significantly lower, with a maximum of three species found at any one station (See table 4.2.1).

At Welwick species richness was higher at  $<2.4$  m compared to  $>2.4$  m ( $p < 0.01$ , Fig.4.2.2, A), while at Paull the difference between elevation bands was not significant (Table 4.2.1). Alkborough there was no clear difference between  $<2.4$  m and  $>2.4$  m elevation, but species richness was generally lower further down the shore (Fig 4.2.2, B and C). At Alkborough species richness was higher at  $>2.4$  m ( $p < 0.01$  and  $F = 4.4513$ ). Examination of the detailed elevation data for Alkborough indicated this increase began in the 3.1 m band (See Appendix 2), although the values are still extremely low (See Table 4.2.1) Paull did not show any change in the detailed elevation band analysis. Mean values are given above in Table 2.4.1.

Table. 4.2.5 Mean values for  $<2.4$  m and  $>2.4$  m and Std.Dev. for Shannon Weiner Diversity ('H), Pielou's Evenness ('J), Biomass, abundance and species richness as Margalef's 'd', with standard deviation. (Mean values for  $<2.4$  m and  $>2.4$  m elevation are also given.)

Elevation	H'(log2)	S.D	'J	S.D	Biomass	S.D
W11 Mean <2.4 m	1.28	0.329	0.32	0.049	0.93	1.1818
W11 Mean >2.4 m	1.26	0.019	0.38	0.011	0.21	0.111
P11 Mean <2.4 m	1.69	0.691	0.48	0.0004	0.19	0.2164
P11 Mean >2.4 m	1.67	0.076	0.43	0.0011	0.56	0.373

Table 4.2.5 Continued

Elevation	Abundance	S.D	Species richness	S.D
W11 Mean <2.4 m	810.66	371.73	15.333	1.15
W11 Mean >2.4 m	3685.55	276.461	9.776	0.509
P11 Mean <2.4 m	1334.11	724.027	12.443	4.669
P11 Mean >2.4 m	2062.44	636.984	15.11	1.155

Elevation	Abundance	S.D	Species Richness	S.D
A11 Mean <2.4 m	22.77	7.21	1.66	0.034
A11 Mean >2.4 m	37.97	19.678	2.65	0.116

Elevation	H'(log2)	S.D	'J	S.D	Biomass	S.D
A11 Mean <2.4 m	0.56	0.133	0.47	0.148	0.00	0.0049
A11 Mean >2.4 m	1.39	0.348	0.70	0.132	0.01	0.0060

### *Evenness*

Evenness ('J) only showed significant change along the salinity gradient between Paull and Welwick in the <2.4 m band, with a lower 'J value at Welwick, indicating a slightly higher variation between species. Tests within the two elevation bands (<2.4 m and >2.4 m), between sites along the salinity gradient, showed no significant difference, with the exception of Welwick and Paull in the <2.4 m band ( $p < 0.01$ ). Within each site tests between upper and lower shore were significant at Alkborough ( $p < 0.01$ ), but not at Welwick or Paull. Generally, 'J did not appear show consistent significant variance across the two gradients.

### *Shannon-Weiner Diversity (H')*

PERMANOVA results for H' indicated significant changes between sites ( $p < 0.001$ ). Tests within elevation bands (<2.4 m and >2.4 m), between sites, showed Alkborough was different to Paull and Welwick in the <2.4 m band, with much lower values at Alkborough ( $p < 0.01$ ). In the >2.4 m band the difference was between Welwick and Paull, with higher values at Welwick ( $p < 0.05$ ), and no difference between Alkborough and the other two sites. Tests between the two elevation bands within each site showed a significant change in H' at Alkborough at  $p < 0.01$ , where values were much lower at <2.4 m, but not at Paull or Welwick.

## 4.3 Benthic Species in the Humber Estuary: Biology and Traits

### 4.3.1 Background

The general biology of species recorded, based on this study's research, is described in sections 4.3.2- 4.3.18 below. Information on traits for each species is summarised in Tables 2.1, 2.2 and 2.3, where the final traits score is also given (see Methods 3.3). Initially, as much information as possible was collated about each species to give a broad description of each type of animal; traits with links to functioning were then identified. Where reliable information was missing for a specific species careful consideration was used in applying traits from a near phylogenetic neighbour (Verissimo et al., 2012, Bolam et al., 2014). In cases where the animal could not be identified to species level, due to damage to key identifying features, they were placed in the next taxonomic group to which they could be reasonably identified – e.g. family level.

### 4.3.2 Polychaetes

#### ***Hediste diversicolor***

A Nereid polychaete, abundant in Humber Estuary mud flats, this animal has been observed utilising multiple modes of feeding (Fauchald and Jumars, 1979). It is an omnivore and may be predatory or deposit feeding. It may also switch to filter feeding if there is a high density of algae in the water (Riisgård, 1991; BIOTIC, 2013). This is unlikely to be a common feeding approach in the Humber due to high turbidity and low phytoplankton concentration (Dr K. Mazik, IECS pers.comm. 2013) but in the event that local conditions are suitable, captured phytoplankton is stored in a mucus bag secreted by the worm that is re-ingested with its additional nutrients at intervals (Fish and Fish, 1989; Scaps, 2002). When exhibiting predatory behaviour *H.diversicolor* targets meiofauna and some larger invertebrates such as *Corophium volutator* and juvenile *Macoma balthica* (Rönn et al., 1988). These are burrowing animals and their burrows are 'Y' shaped and semi-permanent (Davey, 1994). They are not confined to one burrow and may move freely when scavenging or selecting a new burrow site, classifying them as gallery biodiffusers in terms of their bioturbatory impact (Cardoso et al., 2008). Individuals grow to around 100 mm, or up to 120 segments (Fauchald and Jumars, 1979; Fish and Fish 1989). They have a lifespan of 1-2 years and reproduce only once (Green, 1968), with around 1000-10,000 eggs being produced (BIOTIC, 2013). They are an abundant mid-estuarine polychaete and are an important food source, together with other species, for many birds that use the estuary over winter or during migration (Kristensen, 1984; Ólafsson & Persson, 1986).

#### **Spionids**

*Pygospio elegans* and *Streblospio shrubsolii* are spionid polychaetes, found at the study sites. Spionids are tube-building polychaetes and are regular re-workers of the sediment. They are sedentary and filter feed from within a tube. Tubes are formed when mucus is secreted and combined with grains of sediment to construct a tube around the body. Feeding apparatus protrudes from this tube to capture particles from the water flow around them.

#### ***Pygospio elegans***

*P.elegans* is a slender, many segmented worm, up to 15 mm long with a life span of one year. It is sessile within its tube, where it filter feeds via two mobile appendages at its anterior end. *P.elegans* uses these grooved, ciliated tentacles to capture particles in the water or the

sediment, periodically drawing them back towards itself in order to collect food particles (Suspended particles, detritus, phytoplankton) for consumption (Green, 1968). In doing so the sediment surface is disturbed, material is cycled downwards at the end of the tube, and where large beds are present sediment can be stabilised (Dauer, 1981; BIOTIC, 2013).

Brooded (in tube) larvae or planktonic/leithotrophic larvae are produced, varying between populations, likely dependent on environmental conditions (Bolam, 1999). Reproduction can be sexual or asexual, and is continuous, producing between 46 and 2000 eggs at each breeding event (Rasmussen, 1953).

### ***Streblospio shrubsoli***

*S.shrubsoli* is a tube building spionid worm, using its tentacular appendages to feed on suspended particles or detritus at the sediment-water interface (Dauer, 2003). Its bioturbatory activities are similar to those for *Pygospio elegans* (see above), conveying material downward in to the sediment and stabilising the local sediment bed. *Streblospio shrubsoli* grows up to 10mm long and lives for up to a year. It is mature at 3 months and has highly variable reproduction techniques. Reproduction may be sexual or asexual, with larval development either planktotrophic or lecithotrophic, and all may occur within the same population. Reproduction occurs continuously, with peaks in the summer months (Levin and Creed, 1986; Sarda and Martin, 1993; Lardicci, 1997; Kevrekidis, 2005; BIOTIC, 2013).

### ***Manayunkia aestuarina***

*M.aestuarina* is a small (up to 6 mm), sedentary, tube -building worm, one of a number of species of sabellid polychaetes, commonly known as fan worms. Found in the surface of the mud at mid-estuarine salinities, *Manayunkia aestuarina* binds sand and mud together to form a tube around twice the length of its body (Hayward and Ryland, 2009; Encyclopaedia of Life, 2013). *M.aestuarina* filter feed using an array of anterior tentacles and palps, selecting suspended particles or detritus (Ballerstedt, 2005). Tube building modifies and stabilises the sediment and *M.aestuarina* is often found, in large numbers, forming dense beds of tubes. A fecundity figure for *M.aestuarina* could not be obtained, but generalised work on Sabellidae suggests the number is in the region of around 10,000- 20,000 (McHugh and Fong, 2002; Marine Ecological Surveys Ltd, 2008) and work on other species within the genus *Manayunkia* suggests eggs are brooded within the tube (Pettibone, 1953).

### **Cirratulidae**

A family of polychaete worms, often found in muddy estuarine environments. They are characterised by two patches of multiple palps at the anterior end (Fauchald and Rouse, 1997). Cirratulidae species are normally free living in the sediment, although a few species are tube building and feed primarily on subsurface deposits (Fauchald and Jumars, 1979). Mobility is low as they generally remain near a tube, semi-permanent burrow, or crevice (de Kluijver on ETI Bioinformatic 2013). They live between 1 and 5 years, depending on species and are mature at one year or less, reproducing annually and seasonally (Marine Ecological Services Limited, 2008).

### ***Eteone longa/flava***

Phyllodocid polychaetes that comprise a species complex; *Eteone longa* and *Eteone flava* are difficult to distinguish when preserved, as one of the key identification points is colour that can

only be observed in a live specimen, which was not possible in this study. There are some slight differences in chaetae detail and dorsal cirri morphology, but since they have a near identical trait score they were not separated in this study. *Eteone* is an errant polychaete and moves through the sediment as it hunts for other invertebrates, primarily spionids, as well as opportunistically deposit feeding and scavenging (Wolff, 1973; Fauchald and Jumars, 1979). They are tolerant of wide ranging salinities but prefer salinities around 25-30 (Barnes, 1994). Specimens have been recorded at between 30 mm and 120 mm (Hartmann-Schröder, 1996) and longevity is around 2 years. Reproduction is annual, in spring, with external fertilisation and fecundity levels of between 100 and 10,0000 eggs per breeding season (BIOTIC, 2013)

### 4.3.3 Oligochaeta

Oligochaetes are opportunistic worms and are able to thrive in conditions other benthic animals may find difficult, including polluted or low oxygen sediments. They are free-living and similar in appearance to the common earthworm. Oligochaetes are segmented and have a small number of chaetae bundles per segment, but no parapodia or tentacles (Barnes, 1994).

#### ***Tubificoides benedii***

Tubificids are abundant in most estuaries, including the Humber, and can reach high densities (Green, 1968; Barnes, 1994). They thrive in low oxygen and organic enrichment conditions, burrowing in fine estuarine mud and silt (Bagheri and McLusky, 1982). Distinct papillations and bidentate chaetae are key identification points for *Tubificoides benedii*, as well as a body length of up to 55 mm

*Tubificoides benedii* is unusual in that it is regarded as a classic opportunist, but has a life span of a few years and reproduces via internal fertilisation, discontinuously, and exhibits internal brooding, unlike many other oligochaetes (Giere, 2006). Exact fecundity figures could not be found for *T. benedii* specifically, but generalised traits for tubificoides suggest around 100-1000 (Seys et al., 1999; Marine Ecological Surveys Ltd, 2008). They live for around three years and burrow at depths of up to 10cm, biodiffusing the sediment as it moves through, consuming a mixture of bacteria, detritus and faeces of other oligochaetes (Giere, 2006; BIOTIC, 2013)

#### ***Baltidrilus costatus (Heterochaete costata)***

A tubificidae oligochaete worm found commonly in estuarine muddy sediment at salinities between 10-25. This species breeds once and dies after breeding. It is thought to take two years to reach full sexual maturity and measures up to 16 mm in length, subsurface deposit feeding on detritus within the sediment (Brinkhurst, 1964; Brinkhurst and Jamieson, 1971). This worm was previously known as *Tubifex costatus* and *Heterochaete costata* and has recently been renamed *Baltidrilus costatus* (Timm, 2013). No specific fecundity figures could be found for this species specifically so a generalized figure for *Tubificoides* of 100-1000 (Seys et al., 1999) has been given after the method given by Verissimo et al. (2012).

#### ***Nais elinguis***

A small oligochaete worm, tolerant of a wide range of condition, *N. elinguis* burrows diffusively through the sediment, selecting diatoms for preference (Bowker et al., 1985) and feeding generally on microalgae, using simple mouthparts. It is an infaunal animal, measuring from 2 mm to 12 mm, living typically less than a year and tolerating wide ranging salinities (Brinkhurst and Jamieson 1971). Reproduction is iteroparous, asexual, producing mini-adults via budding (Clifford, 2013).

#### ***Paranais littoralis***

*P. littoralis* is a challenging oligochaete species to trait score as many of its behaviours and characteristics vary according to population studies, location and available resources. Even body length is not consistent; migrating animals have been observed to lengthen considerably during a relocation period so a generalised figure is between 5 and 14 mm (Giere, 2006).

Populations can peak and trough according to algal blooms, in common with other Naid species (Giere, 2006). They are mainly epibenthic and free living, burrowing diffusively on occasion and feeding on microalgae for preference (Hayward and Ryland, 1993; Chapman and

Brinkhurst, 1980). They exist at a wide range of salinities, from 5-25, with a life span of up to one year. Reproduction is variable, but is asexual and via budding from posterior segments of adults, taking place through adult life when site and resources are advantageous (Brinkhurst and Jamieson 1971).

### ***Enchytraeidae***

Enchytraeidae are small, almost transparent oligochaetes occurring inter-tidally in estuaries. Identified to family level in this study, this large family has many terrestrial species as well as marine and brackish water ones and has the general appearance of an earthworm. (Barnes, 1994)

They are characterised by bundles of 5, simple pointed chaetae in a splayed, hand-like formation on either side of each segment. These animals burrow in sediment and are generally subsurface deposit feeders, using a simple mouth structure to select bacteria (Brinkhurst, 1973). Average body length is between 5 mm and 10 mm (Will Musk, Senior Taxonomist, pers. comm. IECS, 2013). Fecundity figures are not widely available but a study of four *Enchytraeidae* species by Learner (1972) suggested around 10-50 eggs per cocoon, with production of clutches taking place regularly over a number of months.

### **4.3.4 Nematoda**

Nematode worms are some of the most abundant worms and are found in most sedimentary habitats. They are difficult to identify to species level and this study has not been able to determine specific species. Nematodes sampled in the Humber tend to be small worms and all have the simple body shape of a typical nematode, no obvious chaetae, annulations, papillations or segmentation are present (Will Musk Senior Taxonomist, IECS pers.comm. 2013).

The nematode body is made up of two concentric tubes joined at either end of the animal, the inner tube forming a muscular oesophagus and intestinal tracts for processing ingested particles (Romeyn and Bouwman, 1983; University of Nebraska-Lincoln, 2013). Generally, nematodes feed on any organic matter living or dead, but specialisation in food type occurs at species level. Most species have separate sexes and the females produce either live young or eggs that hatch as mini adults. There is no larval phase (Fitter and Manuel, 1995). Nematodes are small worms but their high abundance means they may have an impact on the sediment. They are treated as meiofaunal in much of the literature but in studies that group by size many nematodes are listed in a macrofaunal size category (Hayward and Ryland, 1993). In most macrofaunal studies they are not identified to species level. Those sampled here are a range of sizes and it is evident that more than one species is present. Given that nematodes are so varied in both size and also in trophic preference an attempt has been made to broadly divide those present here.

Nematodes express a wide range of traits and sizes and there are a minimum of three species present here, based on morphology visible through a x20 microscope which allows the observation of differences in general appearance and robustness and also some differences in the terminal spine at the posterior of the animal, a key taxonomic feature. When a compound microscope was used the differences between animals was even clearer.

The length of estuarine nematodes varies from around 0.5- 5.0 mm. A wide variation is found in their morphological structures, especially in size and form of the buccal cavity that can be indicators of feeding strategy (Romeyn and Bouwman, 1983). Romeyn and Bouwman (1983) shows that some of the benthic species detailed in their study are similar morphologically to the three sampled for this study. Based on the appearance of the buccal parts it could be suggested that the feeding behaviour observed by Romeyn and Bouwman (1983) for these worms could be comparable to that of the Humber sample worms, with very similar feeding apparatus.

An investigation was made of the three morphological types sampled, under a binocular compound microscope. Where necessary lactophenol clearing agent was applied to the sample to clarify fine detail. At higher magnifications (40x/0.65 and 100x/1.25) increased detail was available and a clear difference between the types was apparent. There was some difference observed between the two species of the larger morphological type, but they were broadly similar in appearance and size compared to the third type, which was quite different. Lacking the taxonomic expertise to identify them they have been labelled Nematode Type A, Nematode Type B and Nematode Type C. Type A is given to the larger, more robust, nematode and with more complicated buccal armature (see Figs 4.3.1 and 4.3.3). This assemblage of feeding apparatus is nearly identical to that depicted in the 8<sup>th</sup> species of the Romeyn and Bouwman's (1983) study, *Sphaerolairnus balticus*, a nematode which selectively feeds on and ingests other nematodes, and it has been assigned to a predatory feeding modality accordingly.

Type B is of a similar length to Type A, perhaps typically a little longer, but is a much more slender animal and has less complicated mouthparts with no visible hairs or palps at the anterior end. These mouthparts bear very close resemblance to the species *Adoncholaimus thalassophygas* detailed in Romeyn and Bouwman (1983), which preys upon other nematodes, piercing and sucking out the contents rather than ingesting a full animal. The terminal spine is also quite distinctly different from other nematodes in this study (See Fig. 4.3.2) Type C is much smaller, generally not larger than 1 mm (see Fig.4.3.7), has simpler mouthparts and differing morphological detail around the terminal spine. The mouthparts suggest different feeding strategies to the other nematodes in this study, based on the work of Romeyn and Bouwman (1983) and earlier work by Weiser (1953).

Bacteria-consuming nematodes have the least modified or diversified structures around the pharynx and feeding cavity. The basic plan is a circular opening surrounded by six 'lips', sometimes fused into three or less 'lips'. The structures called 'lips' are cuticle-lined areas of the mouth, exposed to the outside. They open inwards into the buccal cavity, a triangular or cylindrical tube that can contain small structures with the appearance of teeth (University of Nebraska-Lincoln 2013). These simple structures are similar to those seen in Type C where it is likely that certain bacteria are preferred, or excluded, on grounds of size (Romeyn and Bouwman, 1983). Nematodes that feed on microorganisms or invertebrates tend to have more complicated mouthparts and are typically structure in a similar way to that seen in Nematode Type A (Fig.4.3.1).



Nematode samples were scrutinised for Welwick, Paull and Alkborough and all three types were present at all three sites, in roughly similar proportions, suggesting a wide ranging salinity tolerance.



Figure. 4.3.1 Nematode Type A showing details of mouthparts.



Figure 4.3.2 Type A - posterior.



Figure. 4.3.3 Type A shown next to a 1 mm graticule.





Figure 4.3.4 Type B, anterior, cleared with lactophenol to show detail.



Figure 4.3.5 Type B. Anterior, (un-cleared).



Figure 4.3.6 Type B –posterior.



Figure 4.3.7 Type B (middle) and Type C (top right) against a 1 mm graticule.





Figure 4.3.8. Type C, whole animal.

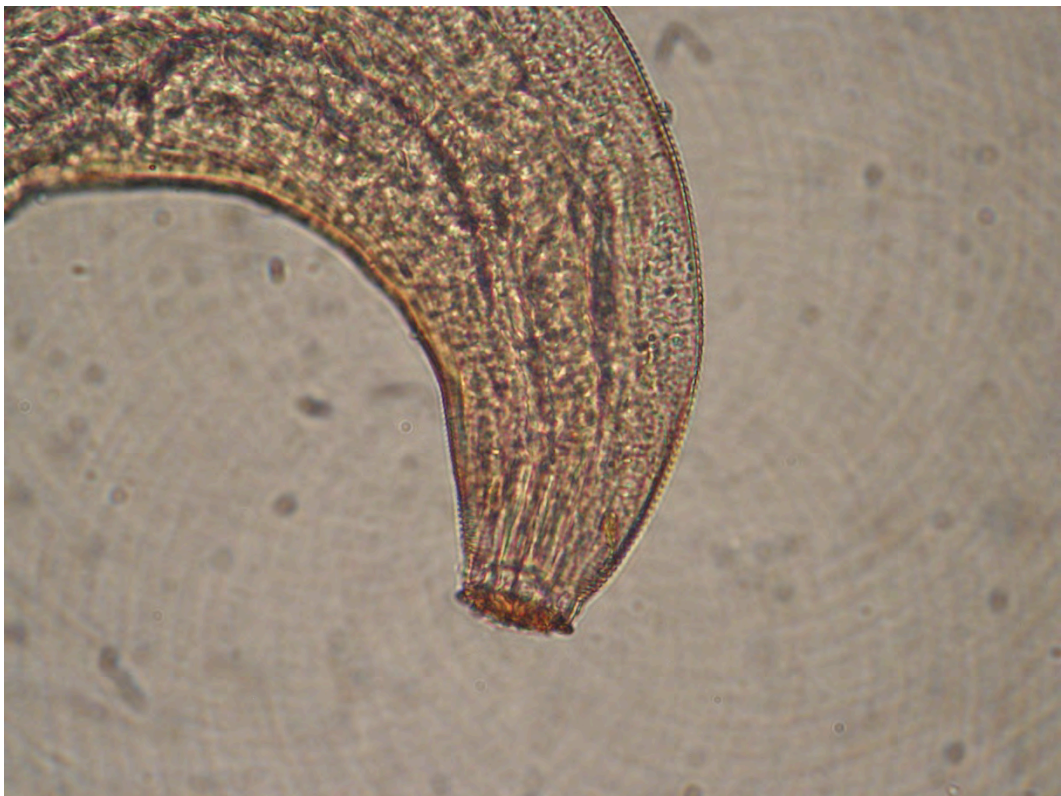


Figure 4.3.9. Type C, anterior, showing simple mouthparts associated with bacterial feeding.

All images above were taken using an Olympus compound microscope with camera attachment, at either 40x/0.65 or 100x/1.25 magnification.

#### 4.3.5 Turbellaria indet. sp.

Turbellaria are free-living flatworms with a simple body and basic nervous system, centred on the head and the mouthparts in the mid ventral surface, they measure 3-5 mm (pers. obs. based on species present, 2012) and typically live less than a year. Turbellaria move easily over the surface of the sediment using a combination of excreted mucus, muscular action and beating cilia, causing a diffusive action on the sediment surface. Turbellaria use a sensory system to select particles (detritus or microorganisms) on which to feed and these are taken into the opening of the digestive tract via an everted muscular pharynx. They cannot see, but have dark/light photoreceptors that are visible as two small 'eyespot' near the head (Missouri Department of Conservation, 2013; Miami University Department of Zoology, 2013; Janssens, 2013). Their prey of choice varies but they are normally grazing scavengers or predators (Jennings 1957). They reproduce through their life (< 1 year) and fecundity levels are estimated at 1-100, depending on species (Jennings, 1957).

#### 4.3.6 Prosobranchia

##### ***Peringea (Hydrobia) ulvae***

*Peringea ulvae* are prosobranch molluscs commonly found grazing on estuarine muddy surfaces, measuring typically 4-6 mm and living 1-2 years. They are grazers and surface deposit feeders, feeding on any particles found on the grazing surface (often eelgrass or macroalgae) including minerals and diatoms. Their feeding is restricted by particle size but they can feed by using radula to scrape microorganisms off sediment particles too large for digestion (Lopez and Korfoed 1980 on ETI Bioinformatics, 2013). Their diet is mostly comprised of diatoms (Herman, 2000). *P. ulvae* re-suspends particles in the water column as it feeds and leaves a furrow and mucous trail in the sediment as it moves, impacting on the upper few mm of the sediment (Fenchel, 1975 and 1988; Orvain et al., 2004). Females lay up to 50 eggs per mass and are sexually mature at less than a year old (de Kluijver, et al., on ETI Bioinformatics, 2013).

#### 4.3.7 Bivalves

##### ***Macoma balthica***

*M. balthica* is a bivalve mollusc of the family *Tellinidae*. Common across Northern Europe, it is a typical estuarine species and can often be very abundant (Green, 1968). Found from the upper mid -shore to sublittoral, it shows a preference for muddy; fine particle, sediment (Wolff, 1973; BIOTIC, 2013). Primarily considered to be a deposit feeder it may utilise its siphons to filter feed if the concentration of particles in the water is sufficient (Bradfield & Newell, 1961; Fish and Fish, 1989). This suspension feeding is most likely to occur where currents are strong or where there is a clean sandy substratum- this is likely to be fairly rare at study sites in the Humber given prevailing turbid, muddy, conditions (Skilleter and Peterson, 1994), so scoring will be weighted towards deposit feeding accordingly. *Macoma* occurs a few cm below sediment surface, and is commonly found together with *Cerastoderma edule*, growing to a size of up to 25 mm. Sexual maturity is related to size but typically occurs between 1<sup>st</sup> and 2<sup>nd</sup> year of life (Chambers and Milne, 1975; Fish and Fish 1989; BIOTIC, 2012). When covered by water *M. balthica* re-suspends surface sediment as its siphon searches for food particles, these particles are then drawn down into the inhalant siphon, along with the water, which also serves to oxygenate the sediment surrounding it (Widdows et al, 1998; Michaud, 2005).

### ***Abra tenuis***

A small bivalve of less than 15 mm, with a life span of 1-2 years, found burrowing in intertidal estuarine mud at salinities of around 30 (Barnes, 1994). *Abra tenuis* prefers soft clay and mud bottoms with abundant organic detritus. It is primarily a surface deposit feeder, but like many bivalves it may use its siphon to filter feed in the appropriate environmental conditions. It exists in the top 0.05cm of the sediment and has limited movement, disturbing the sediment surface in a radius of up to 70 mm. Maturity is at one year, typically in summer months and fecundity is estimated at 1000 eggs per breeding episode (Casagranda and Boudouresque, 2005; Hughes 1975, Widdicombe and Austen 1999; BIOTIC, 2013; de Kluijver et al., on Bioinformatics 2013).

### ***Scrobicularia plana***

Up to 65 mm adult shell length, with a life span of up to 18 years. Can burrow to 200 mm depth in the sediment, leaving a star shaped mark at the surface to mark the position of its inhalant siphon. When covered by the tide, *S.plana* extends its siphon and feeds detritus or particulate matter on the sediment surface. Sexual maturity is at around 2-3 years, or when the shell length exceeds 20 mm (Mouneyrac, 2008; Hughes 1969; Roberson 1979). Aerated mud is found around *Scrobicularia plana* burrows, demonstrating its ability to modify the nature surrounding sediment. It competes directly with *Macoma balthica* when population densities are high (Green, 1968). It is mature at 2-3 years and reproduces annually; fecundity is estimated at 100-1000 (Ruiz et al., 1994). Salinity range is broad, found down to salinities of 10 and up to full marine conditions (Green, 1968)

### **Tellinoidea**

Some bivalves in this study could not be accurately identified to species level due to damage to the animal or instances of juveniles where identifying features were not developed. Where this was the case they have been placed in the broader category of the super family Tellinoidea, based on basic features observable. Generalised family traits have been scored for these animals (See Table 4.3.1-4.3.3.) based on information in the BIOTIC (2013) database.

### ***Cerastoderma edule***

The Common Cockle, *Cerastoderma* are burrowing bivalves, widely distributed across Europe in sandy or muddy sediments, around 20 mm in length with a life span of up to 10 years. They are able to tolerate a wide range of salinities (From 6 to 35). They are primarily suspension feeders living in the top few centimetres of the sediment, feeding on suspended plankton and detritus (Iglesias et al., 1992). They have a number of avian predators and are also fished commercially in some areas (Fish and Fish, 1989). *Cerastoderma* disturbs the sediment by its vertical and horizontal movements, burrowing up to 60 mm deep, and re-suspends sediment in the water column as it feeds (Ciutat et al., 2006). Maturity is at 1-2 years and reproduction is annual, with fecundity estimated at 30,000 (Boyden, 1971; BIOTIC, 2013).

Only a few adults were found in this study, but it is likely that specimens listed as Cardiidae are very young examples of *Cerastoderma edule* that lack adult features required to confirm identification. Traits scoring for Cardiidae reflect this, particularly in the absence of any other Cardiidae species at these sites.

#### 4.3.8. Copepoda

Copepods sampled at these sites have the appearance of free-living Harpacticoid copepods. This study does not identify them to species level but examination by IECS laboratory staff (Chris Baulcombe and Oliver Dawes – Benthic Taxonomists, IECS 2013) indicated the genus *Tachidius*, a free-living harpacticoid copepod well known in the type of muddy estuarine environments found at the study sites under consideration here (Reed, 1990). These animals are highly mobile and are capable of particle selection as they graze on diatoms and microalgae, across a wide salinity range, disturbing the sediment surface as they feed (Giere, 2009; Buffan-Dubau et al., 1996). Species sampled here were up to 2 mm (pers. obs. 2012).

#### 4.3.9 Ostracoda

A Crustacean, identified to Class level for the purposes of this study, Ostracoda sp. are given generalised traits based on the information below.

Ostracods are found in a range of aquatic environments and a number of species inhabit estuarine habitats. Benthic ostracods are commonly detritivores or filter feeders; they either burrow into the substratum, in which case their carapaces tend to be smooth, small, robust and sometimes elongated or epifaunal types which more likely exhibit carapaces with keels or frills. Those found on coarser substrata in higher energy environments tend to have more robust heavily ribbed or reticulated carapaces (MIRACLE, 2013). There are a variety of complex reproductive strategies across the class Ostracoda including brooding eggs within carapace, which has been noted in samples gathered for this study.

Ostracoda for Humber sites in this project have relatively smooth elongate carapaces with slight speckling/indentation effect but no projections or distinct patterning beyond this. This suggests that they are likely to be benthic, burrowing Ostracoda, probably detritivorous. Ostracoda that swim freely typically have long setae on their antenna, which are not present in bottom dwelling species, or in the animals sampled here. Bottom dwellers tend to be generalist scavengers, feeding on algae and detritus. Mature at 4-5 weeks with a life span of around 3 months (Green, 1968; Marine Education Society of Australasia, 2013). Specimens sampled here had a body length of 1 mm-2 mm, and eggs were observed in brooding pouches (pers. obs. 2011).

#### 4.3.10 Opisthobranchia

##### ***Retusa obtusa***

A carnivorous, opisthobranch mollusc, up to 15 mm total body length, *Retusa obtusa* feeds on *Peringea (Hydrobia) ulvae* and foraminiferans. It has no jaw or radula, but instead has an alimentary opening with internal gizzard plates (Thompson, 1976). It is found buried in mud and sandy mud, at salinities down to 20, burrowing shallowly and disturbing the upper layers of the sediment (Fish and Fish, 1989). *Retusa obtusa* breeds between March and December, breeding once in its life span of less than a year. Egg masses are found on the parental shell, at 112-305 eggs per individual recorded. Development is direct. (Thompson, 1976; Berry 1989; Berry and Thompson, 1990)



#### 4.3.11 Isopoda

##### ***Cyathura carinata***

*Cyathura carinata* is an isopod inhabiting vertical tubes in stable estuarine sediments. Occasionally found in great numbers it is more usual to find them, as they are in this study, at a rate of only a few individuals per sample (Fish and Fish, 1989). *Cyathura carinata* is an ambush predator (Ferreira, 2007), waiting in its tube for passing prey, usually *Hediste diversicolor* (Wegele et al., 1981). It grows up to around 14 mm in length (Kroyer, 1847; de Kluijver and Ingalsuo, 2013) and has a lifespan of around 19 months (Cruz et al, 2003). Its movement is limited aside from short, dynamic predatory burst and it is not capable of swimming, but it ventilates the sediment via burrow/tube building and conveys matter downwards. (Burbanck and Burbanck, 1974; Legrand and Juchault, 1963; Marques et al., 1994)

Fecundity is estimated at 18-63 eggs per female and females die once juveniles are released from brood pouch (Ólafsson, 1985). Reproduction is at around two years old, although this is a lesser age in warmer climates (Cruz et al, 2003). *Cyathura carinata* has been found in the stomachs of Flounder and they may be a source of food source for fish in Humber. Salinity range for this species is reported at between 7 and 35 (Ólafsson, 1985; Cruz et al., 2003) suggesting this species is euryhaline and well adapted to the rigors of estuarine existence.

#### 4.3.12 Amphipoda

##### ***Corophium volutator***

The amphipod *Corophium volutator* was found just once across the whole survey. It is often abundant at both Paull and Welwick (Barnett, 1984) but is occasionally almost entirely absent for short periods, as in this instance (Dr. Krysia Mazik, IECS – pers. comm.2012). It has been included here despite its single occurrence as it is typical of these study sites.

*Corophium volutator* is a euryhaline species commonly found inter tidally on mudflats, often at great density (Meadows & Reid 1966; McLusky, 1967). It constructs a U-shaped burrow (Hart, 1930; McLusky, 1967) and creates a current through the burrow via movement of its pleopods. This oxygenates the burrow and also draws in food particles (particulate organic matter), which are captured by fine, filtering fringes on the gnathopods (Green, 1968). It grows to 10-20 mm in length, with a lifespan of less than a year. Reproduction is episodic throughout its life, with fecundity estimated at around 50 eggs per breeding event (Green, 1968; Ólafsson & Persson, 1986; Marine Ecological Surveys Limited, 2008; BIOTIC, 2013).

#### 4.3.13 Collembola

##### ***Isotomurus palustris***

This collembolan species is commonly known as the marsh springtail, inhabiting the upper shore of an estuarine saltmarsh (Hopkin, 2013). Here it was found primarily inside the realignment area, occasionally in great numbers. Some species burrow when the upper shore is inundated by the tide (Barnes, 1994) and are able to hide in cracks and crevices until the water retreats. Collembola species living in similar habitat have been observed to trap air in the fine hairs on their bodies and survive comfortably for hours, or even days, submerged (BIOTIC, 2013). This observation has not been made for *Isotomurus palustris*, but could explain their distribution at mid shore levels in 2010. *Isotomurus palustris* was identified as main species sampled here, but a further species identified to genera *Sminthurides* was present at Welwick. As it is a true freshwater species and represented by only one individual, its traits have not been included here.

Life processes of Collembola occur at different rates based on available food sources (Van Amelsvoort and Usher, 1989). This plasticity, even within species, enables springtails to occupy a wide variety of habitats. They are primarily deposit feeder, selecting decaying organic matter as a food source, grazing mainly on the sediment surface. Juveniles are born as mini adults and continue to moult throughout their lifespan once mature. Up to 50 instars have been observed in some species. They are highly mobile, using a 'spring' – like mechanism on the underside of their lower abdomen to propel themselves over some distance (Dunn, 1996; Commonwealth Scientific and Industrial Research Organisation, 2013). They are typically found in large groups at high densities, preferring lower salinity environments (Earthlife Web, 2013, Santorufo et al., 2014). Species sampled here were approximately 2-4 mm (pers. obs. 2012).

#### 4.3.14 Diptera

##### ***Dolichopodidae***

The larval stage of the Diptera fly found primarily inside the realignment areas in this study, but is common in estuaries through a wide range of salinities (Fish and Fish, 89). Traits included here are those that pertain to the benthic larval life stage. A full discussion of this is given in detail in BTA methods (3.6).

These larvae are maggot-like in appearance, with short un-jointed legs, free living in and on aquatic sediment, measuring up to 20 mm. They are often detritivores but some are also carnivorous, consuming nematodes, oligochaetes and some polychaete species (LaSalle and Bishop, 1990). Some are capable of limited swimming, but most are restricted to crawling on the sediment surface, where they cause some diffusive mixing. They are highly euryhaline (Fitter and Manuel, 1995).

#### 4.3.15 Alkborough Specific Species

At the Alkborough site a number of species included various fly larvae as well as some species that are regarded as being close to freshwater (Mazik et al., 2012). Although many of the estuarine species detailed above were also found there, the following species were found at Alkborough alone and are some reflection on its marked difference in salinity compared to Welwick and Paull.

#### 4.3.16 Diptera Larvae

##### **Chironomidae**

The larval stage of Chironomidae, or Plumed Gnat, has a worm-like form and is up to 30 mm long, with a life span of less than 6 months. They are often found in muddy aquatic sediment where they form an important part of the diet of fish and birds. Many species burrow in the mud and build a delicate tube of silk and debris (Fitter and Manuel, 1995). Most species feed on detritus or microalgae (Milton -Ward and Cummins, 1979), although they are sometimes predatory, attacking other Chironomidae species (Malloch, 1917; University of Michigan Museum of Zoology, 2013).

##### **Ceratopogonidae**

The larvae of small, biting midges, between 5mm and 12mm long depending on species, some are able to swim weakly but most are confined to the sediment surface, where they are free-living and deposit feed on detritus. Longevity is estimated at 6 months (Malloch, 1917; Fitter and Manuel, 1995).

##### **Tipulidae**

Tipulidae, commonly known as Crane flies, have a larval form of robust, fleshy, grubs that grow up to 50 mm in length, with a short life span of less than six months. They are often found

under stones or in the sediment and are exclusively carnivorous, preying upon other invertebrates with well-developed anterior armature (Malloch, 1917; Fitter and Manuel, 1995). They are free-living, causing some surficial biodiffusing as they move and are typically found at low salinities in fresh to brackish water.

#### **Trichoptera**

The larvae of the Caddis fly (family Trichoptera) vary in size from 3mm to 40mm and are often found living in tubular cases. They are broadly free living, but some species are associated with loose tubes or netting made of silk and debris, which are used to capture food items (microorganisms or invertebrates). They are largely omnivores but some are entirely carnivorous. Life span is less than six months and they are typically found at very low salinities (Malloch, 1917; Fitter and Manuel 1995).

#### 4.3.17 Freshwater and Brackish Water Gastropod Species

##### ***Planorbis* Species**

*Planorbis* sp. is a common family of gastropods, known as Ramshorn snails, measuring 8mm across. They are epifaunal, grazing on detritus using radula, but some species have been shown to specifically make use of bacteria (Calow, 1975). Life span is variable across species but is generally around two years. They are mature at less than six months and produce clutches of 10-15 eggs (Barlow and Muench, 1951)

##### ***Gyraulus* sp.**

*Gyraulus* is a second genus of Ramshorn snail, in the same family as *Planorbis*, above. They are smaller than *Planorbis*, rarely exceeding 7 mm in total shell length (Buckle, 2012). *Gyraulus* graze on the sediment surface using radula to consume algae and detritus, causing diffusion of the sediment surface as they move (ARKIVE, 2013). Age at maturity is less than six months and fecundity is estimated at 10-20 eggs per clutch (Brown, 2001; Bouchet, 2013).

##### ***Assiminea grayana***

Known as the 'Dun Sentinel', *Assiminea* is a small brackish to fresh water prosobranch gastropod, measuring around 3 mm in length. Typically found in the upper reaches of salt marshes in fresh to brackish water (de Kluijver et al, 2013) it grazes primarily on detritus and decaying animal matter using radula. Eggs are laid singly in gelatinous jackets at between 1 and 10 per clutch (Abbott, 1958). Clear information on life span could not be found for this species but similar species within the genus have been observed to live around 3 years in the field (Kurata and Kikuchi, 2000).

#### 4.3.18 Alkborough Oligochaeta

##### ***Limnodrilus hoffmeisteri***

A small, elongate, worm, roughly 20-35 mm long, *Limnodrilus hoffmeisteri* is found commonly in freshwater but is also present in estuarine environments, up to a salinity of around 5. They are free living and burrow through the sediment, consuming detritus and microorganisms. Lifespan varies according to local conditions but it is thought that they may live up to two years and are sexually mature at around one year. In some populations *L.hoffmeisteri* die after breeding, while others go on to reproduce for a second season. Fecundity levels are low at approximately 1-10 per breeding event (Kennedy, 1966; Budd, 2003).

#### 4.3.19 Mysidae

##### ***Schistomysis kervillei/ornata***

A mysid shrimp, similar to *S.spiritus* below, *S.kervillei/ornata* are small at up to 20 mm and are found in shallow, brackish waters where they graze on particulate organic matter (Barnes 1994; de Kruijver and Ingalsuo, on ETI Bioinformatics, 2013). They are free living, epifaunal animals, with a lifespan of less than a year. Mature at less than six months, reproduction is constant, with fecundity at approximately 10-50 eggs per breeding event (Mauchline, 1971; Barnes, 1994). *S.kervillei* and *S.ornata* are very similar in appearance and are challenging to identify with certainty. Since they are so similar it is likely that they also express similar traits and they have not been separated to specific species here.

##### ***Schistomysis spiritus***

A small Mysid shrimp of around 18 mm, *S.spiritus* is short lived at less than a year. Found amongst plant growth in shallow waters and estuaries it feeds primarily on suspended organic particles, just above the sediment surface, causing some surficial biodiffusing as it moves. It is mature at less than six months, reproduces seasonally and has a fecundity level of around 10-100 eggs per breeding event (Mauchline, 1971; Williams and Collins 1984; Vicente and Sorbe, 1995; Van Couwelaar on Bioinformatics, 2013).

#### 4.3.20 Alkborough Amphipoda

##### ***Gammarus salinus***

A gammarid amphipod with wide ranging salinity tolerance, *G.salinus* can be found from salinities of 35 to as low as 1 or 2, although they are often only found in a specific salinity band in given area as they avoid populations of other *Gammarus* species (Barnes, 1994). They grow up to around 33 mm in length and are found in all types of brackish water, on the sediment surface or amongst stones and algal growths, at the upper limit of tidal inundation, where they graze on surface deposits and particulate organic matter (Skadsheim, 1990; Barnes, 1994; Budd, 2003).

##### ***Gammarus sp.***

Generalised traits for the genus *Gammarus* have been used where the small size or condition of the animal has made accurate identification impossible. These animals are similar across the genus but given that they show a preference for isolation from other similar *Gammarus* species (Barnes, 1994), weight has been given to the traits expressed by *Gammarus salinus*, as it is the only other gammarid sampled in this survey (see above and Table 2.1-2.3).

Table 4.3.1 SPECIES/ TRAITS SCORES: FEEDING METHOD, FEEDING APPARATUS, FOOD TYPE AND MOBILITY																			
Species	Feeding Method					Feeding Apparatus					Food Type					Adult Mobility			
	FM/D	FM/SS	FM/FS	FM/OS	FM/P	FA/J	FA/T	FA/R	FA/S	FA/M	FT/M	FT/D	FT/S	FT/I	FT/B	AM/S	AM/L	AM/M	AM/H
Hediste diversicolor	0.3	0	0.1	0.3	0.3	1	0	0	0	0	0.3	0.3	0.1	0.3	0	0	0	1	0
Nereidae sp.	0.33	0	0	0.33	0.33	1	0	0	0	0	0.33	0.33	0	0.33	0	0	0	1	0
Nephtys sp.	0	0	0	0.2	0.8	1	0	0	0	0	0	0.2	0	0.8	0	0	0	1	0
Nephtys hombergii	0	0	0	0.2	0.8	1	0	0	0	0	0	0	0	1	0	0	0	0	1
Nais elingeris	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Paranais littoralis	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0
Streblospio shrubsoli	0.5	0	0.5	0	0	0	1	0	0	0	0	0.5	0.5	0	0	1	0	0	0
Eteone longa/flava	0	0	0	0.5	0.5	1	0	0	0	0	0	0.2	0	0.8	0	0	0	0	1
Pygospio elegans	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0
Heterochaete costata	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0
Cirratulidae sp.	0.5	0.5	0	0	0	0.5	0.5	0	0	0	0	1	0	0	0	0	1	0	0
Manayunkia aestuarina	0.5	0	0.5	0	0	0	1	0	0		0	0.5	0.5	0	0	1	0	0	0
Echytraeidae sp.	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0
Tubificoides benedii	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0
Nematode sp. A	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0
Nematode sp. B	0	0	0	0.5	0.5	0	0	0	0	1	0	0	0	1	0	0	0	1	0
Nematode sp. C	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0.5	0.5	0
Cyathura carinata	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0.5	0.5	0	0
Copepoda Tachidius	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
Ostracoda sp.	1	0	0	0	0	1	0	0	0	0	0.5	0.5	0	0	0	0	0	1	0
Corophium volutator	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0.5	0.5	0
Hydrobia ulvae	0	1	0	0	0	0	0	1	0	0	0.5	0.5	0	0	0	0	0	1	0
Macoma balthica	0.5	0	0.5	0	0	0	0	0	1	0	0	0.5	0.5	0	0	0	0.5	0.5	0
Scrobicularia plana	1	0	0	0	0	0	0	0	1	0	0	0.5	0.5	0	0	0	0.5	0.5	0
Cerastoderma edule	0	0	1	0	0	0	0	0	1	0	0.5	0	0.5	0	0	0	1	0	0
Abra tenuis	0	0.5	0.5	0	0	0	0	0	1	0	0	0.5	0.5	0	0	0	0	1	0
Cardiidae sp.	0	0	1	0	0	0	0	0	1	0	0.5	0	0.5	0	0	0	1	0	0
Tellinoidae sp.	0.5	0	0.5	0	0	0	0	0	1	0	0.5	0	0.5	0	0	0	1	0	0
Retusa obtusa	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	0
Isotomurus palustris	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0.5	0.5
Diptera dolichopodidae	0	0	0	0.5	0.5	1	0	0	0	0	0	0.5	0	0.5	0	0	0	1	0

<b>Table 4.3.1 cont. SPECIES/ TRAITS SCORES: FEEDING METHOD, FEEDING APPARATUS, FOOD TYPE AND MOBILITY</b>																			
Species	Feeding Method					Feeding Apparatus					Food Type					Adult Movement			
	FM/D	FM/SS	FM/FS	FM/OS	FM/P	FA/J	FA/T	FA/R	FA/S	FA/M	FT/M	FT/D	FT/S	FT/I	FT/B	AM/S	AM/L	AM/M	AM/H
Turbellaria Sp.	0.3	0	0	0	0.7	0	0	0	0	1	0.25	0.25	0	0.5	0	0	0	0	1
Gammarus salinus	1	0	0	0	0	1	0	0	0	0	0.5	0.5	0	0	0	0	0	0.5	0.5
Schistomysis kervillei/ornata	0.5	0	0.5	0	0	1	0	0	0	0	5	0.5	0	0	0	0	0	1	0
Schistomysis spiritus	0.5	0	0.5	0	0	1	0	0	0	0	0	0.5	0.5	0	0	0	0	1	0
Assiminea grayana	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
Limnodrilus hoffmeisteri	0	1	0	0	0	0	0	0	0	1	0.5	0.5	0	0	0	0	0	1	0
Chironomidae Larvae	0.5	0	0	0	0.5	1	0	0	0	0	0	0.5	0	0	0.5	0	1	0	0
Ceratopogonidae Larvae	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0
Tipulidae Larvae	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0
Planorbis sp.	1	0	0	0	0	0	0	1	0	0	0	0.5	0	0	0.5	0	0	1	0
Trichoptera Larvae	0	0	0.5	0	0.5	1	0	0	0	0	0.5	0	0	0.5	0	0	0.5	0.5	0
Gyraulus sp.	1	0	0	0	0	0	0	1	0	0	0.5	0.5	0	0	0	0	0	1	0
Gammarus Sp.	1	0	0	0	0	1	0	0	0	0	0.5	0.5	0	0	0	0	0	0.5	0.5
Tubificidae	0	1	0	0	0	0	0	0	0	1	0	0.5	0	0	0.5	0	0	1	0
Collembola sp.	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0.5	0.5

**TRAITS CODING**

<p><b>FEEDING METHODS (FM)</b>  D - DEPOSIT FEEDER (SURFACE)  SS - SUBSURFACE DEPOSIT FEEDER  FS - FILTER/PARTICLE SELECTION  OS - OPPORTUNISTIC SCAVENGER  P - PREDATOR</p>	<p><b>FOOD TYPE (FT)</b>  M - MICROORGANISMS/DIATOMS  D - DETRITUS  S - SUSPENDED PARTICLES  I - INVERTEBRATES  B - BACTERIA</p>
<p><b>FEEDING APPARATUS (FA)</b>  J - JAWS/MANDIBLES  T - TENTACULAR  R - RADULA  S - SIPHON  M - SIMPLE MOUTH</p>	<p><b>ADULT MOVEMENT (AM)</b>  S - SESSILE  L - LOW  M - MEDIUM  H - HIGH</p>

Species	Position		Living Habitat					Bioturbatory Mode						Adult Body Length					
	P/I	P/E	LH/T	LH/PB	LH/SP	LH/F	LH/I	B/U	B/D	B/SB	B/BB	B/GB	B/BV	B/OV	<2mm	2-5mm	5mm-1cm	1-2cm	2 - >5cm
Hediste diversicolor	1	0	0	0	1	0	0	0	0	0	0	0.5	0	0.5	0	0	0	0	0
Nereidae sp.	1	0	0	0	1	0	0	0	0	0	0	0.5	0	0.5	0	0	0	0.5	0.5
Nephtys sp.	1	0	0	0	0.5	0.5	0	0	0	0	0	1	0	0	0	0	0	0	1
Nephtys hombergii	1	0	0	0	0.5	0.5	0	0	0	0	0	1	0	0	0	0	0	0	1
Nais elingeris	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0.5	0.5	0	0
Paranais littoralis	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0.5	0.5	0
Streblospio shrubsoli	1	0	1	0	0	0		0	0.5	0.5	0	0	0	0	0	0	1	0	0
Eteone longa/flava	1	0			0.2	0.8		0	0	0	0	1	0	0	0	0	0	0	1
Pygospio elegans	1	0	1	0	0	0		0	0.5	0.5	0	0	0	0	0	0	0	1	0
Heterochaete costata	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0
Cirratulidae sp.	0.8	0.2	0.2		0.4	0.4	0	0	0	0	1	0	0	0	0	0	0	0	1
Manayunkia aestuarina	1	0	1	0	0	0		0	0.5	0.5	0	0	0	0	0	0.5	0.5	0	0
Enchytraeidae	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0
Tubificoides benedii	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
Nematode sp. A	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0
Nematode sp. B	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0
Nematode sp. C	1	0	0	0	0	0.5	0.5	0	0	0	1	0	0	0	1	0	0	0	0
Cyathura carinata	1	0	1	0	0	0	1	0	0.5	0	0	0	0.5	0	0	0	0	1	0
Copepoda Tachidius	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Ostracoda sp.	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0
Corophium volutator	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Hydrobia ulvae	0	1	0	0	0	1		0	0	1	0	0	0	0	0	0.5	0.5	0	0
Macoma balthica	1	0	0	0	1	0		0	0.5	0	0	0	0.5	0	0	0	0	1	0
Scrobicularia plana	1	0	0	0	1	0	0	0	0.5	0	0	0	0.5	0	0	0	0	0	1
Cerastoderma edule			0	0	1	0		0	0.4	0.2	0	0	0.4	0	0	0	0	0	1
Abra tenuis			0	0	1	0		0	0.33	0.33	0	0	0.33	0	0	0	0.8	0.2	0
Cardiidae sp.	1	0	0	0	1	0	0	0	0.4	0.2	0	0	0.4	0	0	0	0	0	1
Tellinoidae sp.	1	0	0	0	1	0	0	0	0.33	0.33	0	0	0.33	0	0	0	0	0.5	0.5
Retusa obtusa	1	0		0	0	0		0	0	0	1	0	0	0	0	0	0.8	0.2	0
Isotomurus palustris			0	0	0	1		0	0	1	0	0	0	0	0	1	0	0	0
Diptera dolichopodidae	0.5	0.5	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0

Table 4.3.2 cont. SPECIES/ TRAITS SCORES: POSITION, LIVING HABITAT, BIOTURBATORY MODE AND BODY LENGTH																			
Species	Position		Living Habitat					Bioturbatory Mode						Adult Body Length					
	P/I	P/E	LH/T	LH/PB	LH/SP	LH/F	LH/I	B/U	B/D	B/SB	B/BB	B/GB	B/BV	B/OV	<2mm	2-5mm	5mm-1cm	1-2cm	2->5cm
Turbellaria Sp.	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0
Gammarus salinus	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1
Schistomysis kervillei/ornata	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0
Schistomysis spiritus	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0
Assiminea grayana	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0.5	0.5	0	0
Limnodrilus hoffmeisteri	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0
Chironomidae Larvae	1	0	0.5	0	0	0.5	0	0	0	0	0.5	0	0.5	0	0	0	0	0	1
Ceratopogonidae Larvae	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0
Tipulidae Larvae	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1
Planorbis sp.	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0
Trichoptera Larvae	1	0	0.5	0	0	0.5	0	0	0	0	0.5	0	0.5	0	0	0	0	0	1
Gyraulus sp.	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0
Gammarus Sp.	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1
Tubificidae	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0.5	0.5
Collembola sp.	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0

#### TRAITS CODING

<b>POSITION</b> I - INFAUNAL E - EPIFAUNAL	<b>BIOTURBATORY MODE</b> U - UPWARD CONVEYER D - DOWNWARD CONVEYER GB- GALLERY BIODIFFUSER SB - SURFICIAL BIODIFFUSER BB - BURROWING BIODIFFUSER OV - OPEN BURROW VENTILATOR BV - BLIND BURROW VENTILATOR
<b>LIVING HABITAT</b> T- TUBE DWELLING PB- PERMANENT BURROW SP - SEMI PERMANENT BURROW F - FREE LIVING I - INTERSTICIAL E – EPIBENTHIC	<b>ADULT BODY LENGTH</b> <2MM 2-5MM 5MM-1CM 1-2CM 2->5 CM



Species	Longevity					Salinity Preference					Fecundity (Number of Eggs)					Reprod. Freq.		Maturity			
	<6mths	6-18mths	18mth-2yrs	2-5yrs	>5yrs	S/5	S/10	S/15	S/20	S/25	F/10	F/100	F/1K	F/10K	F/>10K	RF/S	RF/I	<6mths	≥6mths	6mth - 1yr	1-2yr
Hediste diversicolor	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0.8	0.2
Nereidae	0	0	1	0	0	0	0	0	0.5	0.5	0	0	0	1	0	1	0	0	0	0.8	0.2
Nephtys sp.	0	0	0	1	0	0	0	0	0.5	0.5	0	0	0	0	1	0	1	0	0	0	1
Nephtys hombergii	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1
Nais elingeris	0	1	0	0	0	0.33	0.33	0.33	0	0	1	0	0	0	0	0	1	1	0	0	0
Paranais littoralis	0	1	0	0	0	0	0.25	0.25	0.25	0.25	1	0	0	0	0	0	1	1	0	0	0
Streblospio shrubsoli	0	1	0	0	0	0	0.25	0.25	0.25	0.25	0	0.5	0.5	0	0	0	1	1	0	0	0
Eteone longa/flava	0	0	1	0	0	0	0	0	0.5	0.5	0	0	0.5	0.5	0	0	1	0	0	1	0
Pygospio elegans	0	1	0	0	0	0	0.25	0.25	0.25	0.25	0	0.5	0.5	0	0	0	1	1	0	0	0
Heterochaete costata	0	0	1	0	0	0	0.33	0.33	0.33	0	0	0	1	0	0	1	0	0	0	0	1
Cirratulidae	0	0	0.5	0.5	0	0.2	0.2	0.2	0.2	0.2	0	0.25	0.25	0.25	0.25	0	1	0	0	1	0
Manayunkia aestuarina	0	0	1	0	0	0	0	0.5	0.5	0	0	0	0	0	1	0	1	0	1	0	0
Enchytraeidae	0	0	1	0	0	0.2	0.2	0.2	0.2	0.2	1	0	0	0	0	0	1	1	0	0	0
Tubificoides benedii	0	0	0	1	0	0	0	0.33	0.33	0.33	0	0	1	0	0	0	1	0	0	1	0
Nematode sp. A	0	1		0	0	0	0.25	0.25	0.25	0.25	1	0	0	0	0	0	1	1	0	0	0
Nematode sp.B	0	1	0	0	0	0	0.25	0.25	0.25	0.25	1	0	0	0	0	0	1	1	0	0	0
Nematode sp. C	0	1	0	0	0	0	0.25	0.25	0.25	0.25	1	0	0	0	0	0	1	1	0	0	0
Cyathura carinata	0	0	0	1	0	0	0.25	0.25	0.25	0.25	1	0	0	0	0	1	0	0	0	0	1
Copepoda Tachidius	0	1	0	0	0	0.2	0.2	0.2	0.2	0.2	0.33	0.33	0.33	0	0	0	1	1	0	0	0
Ostracoda sp.	1	0	0	0	0	0	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0	0	1	1	0	0	0
Corophium volutator	0	1	0	0	0	0	0.25	0.25	0.25	0.25	0.5	0.5	0	0	0	0	1	0	1	0	0
Hydrobia ulvae	0	0	1	0	0	0	0	0	0.5	0.5	1	0	0	0	0	0	1	0	0	1	0
Macoma balthica	0	0	0	0	1	0	0	0.5	0.5	0	0	0	0	1	0	0	1	0	0	0	1
Scrobicularia plana	0	0	0	0	1	0	0.25	0.25	0.25	0.25	0	0	1	0	0	0	1	0	0	0	1
Cerastoderma edule	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	1	0	0	1	0	0	0	1
Abra tenuis	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0
Cardiidae sp.	0	0	0	0	1	0	0	0	0.5	0.5	0	0	0	1	0	0	1	0	0	1	0
Tellinoidae sp.	0	0	0	0.5	0.5	0	0.25	0.25	0.25	0.25	0	0	1	0	0	0	1	0	0	0	1
Retusa obtusa	0	1	0	0	0	0	0	0	0.5	0.5	0	0	1	0	0	1	0	0	0	1	0

**TRAITS CODING**

**Table 4.3.3 cont. SPECIES/ TRAITS SCORES: LONGEVITY, SALINITY PREFERENCE, FECUNDITY, REPRODUCTIVE FREQUENCY AND AGE AT MATURITY**

Species	Longevity					Salinity Preference					Fecundity (Number of Eggs)					Reproductive Frequency		Maturity			
	<6mths	6-18mths	18mth-2Yrs	2-5yrs	>5yrs	S/5	S/10	S/15	S/20	S/25	F/10	F/100	F/1K	F/10K	F/>10K	RF/S	RF/I	<6mths	≥6mths	6mth - 1yr	1-2yr
Isotomurus palustris	1	0	0	0	0	0.5	0.5	0	0	0	0	1	0	0	0	0	1	1	0	0	0
Diptera dolichopodidae	1	0	0	0	0	0.25	0.25	0.25	0.25	0	0	0	0	0	0	0	0	0	0	0	0
Turbellaria Sp.	0	1	0	0	0	0	0	0.33	0.33	0.33	0.5	0.5	0	0	0	0	1	1	0	0	0
Gammarus salinus	0	1	0	0	0	0.2	0.2	0.2	0.2	0.2	0	1	0	0	0	0	1	1	0	0	0
Schistomysis kervillei/ornata	0	1	0	0	0	0.5	0.5	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Schistomysis spiritus	0	1	0	0	0	0.33	0.33	0.33	0	0	0	1	0	0	0	0	1	1	0	0	0
Assimineia grayana	0	0	0	1	0	0.5	0.5	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Limnodrilus hoffmeisteri	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0.5	0.5	0	0	1	0
Chironomidae Larvae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratopogonidae Larvae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tipulidae Larvae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Planorbis sp.	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Trichoptera Larvae	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gyraulus sp.	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0
Gammarus Sp.	0	1	0	0	0	0.2	0.2	0.2	0.2	0.2	1	0	0	0	0	0	1	0	0	1	0
Tubificidae	0	0	1	0	0	0.2	0.2	0.2	0.2	0.2	0	0	1	0	0	0	1	0	0.5	0.5	0
Collembola sp.	1	0	0	0	0	0.5	0.5	0	0	0	0	1	0	0	0	0	1	1	0	0	0

<b>LONGEVITY</b> < 6 Months 6-18 months 18 months -2 years 2-5 years > 5 years	<b>SALINITY PREFERENCE</b> 5 - PSU 1-5 10-PSU 5-10 15 - PSU 10-15 20 - PSU 15-20 25 - PSU 20-25+	<b>FECUNDITY (NUMBER OF EGGS)</b> 10 -10-50 100 - 50-100 1K - 100- 1000 10K - 1000-10,000 >10K - 10,000 AND ABOVE
<b>REPRODUCTIVE FREQUENCY</b> S - SEMALPAROUS I - ITEROPAROUS	<b>AGE ATMATURITY</b> < 6 Months ≥ 6 months 6 months - 1 year 1-2 years	M - 1,000,000 OR MORE.

## 4.4 Biological Traits Analysis Results

All data were square root transformed prior to analysis and Bray-Curtis similarity was used in the construction of resemblance matrices. Traits/Modalities coding used here is that given in Methods, Table 3.1.

### 4.4.1 Multivariate Analysis

#### *Multivariate Analysis: Salinity and Elevation*

##### **Traits x Abundance**

PERMANOVA results indicated significant change between sites for all trait categories, weighted by abundance, with  $F=$  of 28.941 and  $p<0.01$ . Elevation gradient also returned significant values with  $p<0.01$  and  $F=$  3.6392. Tests between sites, within elevation bands, indicated Alkborough was significantly different to both Paull and Welwick in both bands ( $p<0.01$ ). Paull and Welwick were not significantly different in either band. In tests within sites, between elevations (<2.4 m and >2.4 m), Alkborough and Welwick showed a significant difference between upper and lower shore with  $p<0.01$ , but Paull did not. The lack of distinction between the <2.4 m and >2.4 m elevation bands at Paull is emphasised Fig 4.4.53 below, also displaying the clear separation of Alkborough from the two higher salinity sites.

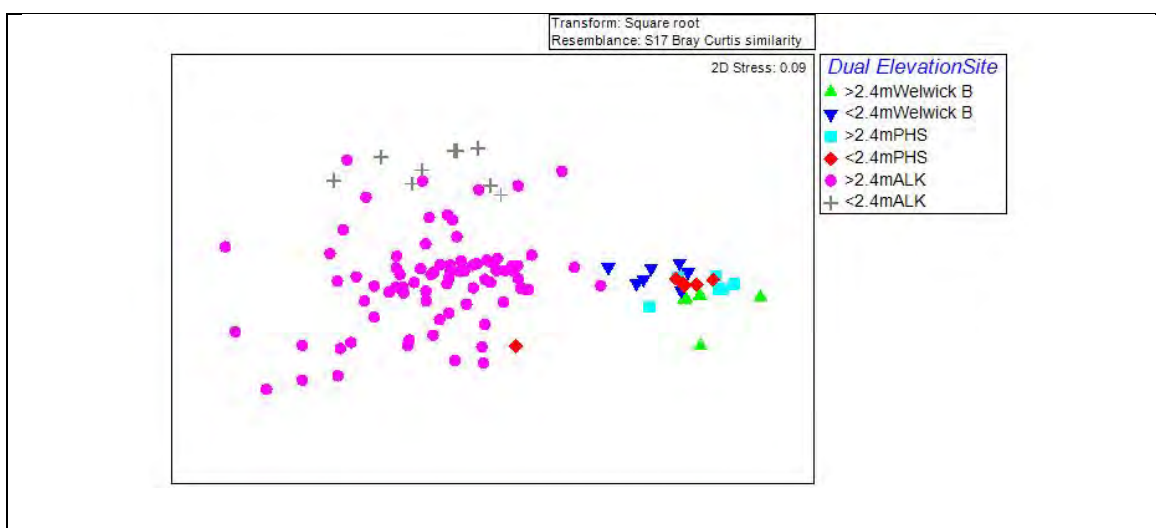


Fig 4.4.1. MDS for all variables weighted by abundance.

SIMPER analysis was also performed for this traits data set (weighted by abundance) and supported the MDS and PERMANOVA results (Table 4.3.1). SIMPER results showed a high % average similarity within each elevation band for all groups, apart from Alkborough >2.4 m, which was significantly lower at 50.28%. This indicated a low variability in trait composition within elevation bands, suggesting homogeneity between replicates and sampling stations.

Across all bands at Paull and Welwick the trait RF (Reproductive Frequency) was a major contributor to trait composition in both bands. Distinctions between bands were also caused by traits with lower % contributions, such as the differences in expression of the trait S (Salinity Preference) in the upper and lower shore bands at Welwick. Here, the upper shore expressed S/10 (Salinity Preference/5-10) while the lower shore expressed both S/15 and S/20 (Table 4.4.1).

At Paull there was little separating the two elevation bands, with only a few difference in percentage contribution of key traits. At Alkborough the traits composition was quite different between elevation bands. A major contributing trait was RF (Reproductive Frequency) for both bands, but was expressed by the modality RF/S (Reproductive Frequency/Semelparous) on the lower shore and by RF/I (Reproductive Frequency/Iteroparus) on the upper shore.

When bands were compared for average dissimilarity, both within sites and along the elevation gradient the results indicated Alkborough was different when compared to both Paull and Welwick. Alkborough upper shore was 83.70% dissimilar to the upper shore at Welwick, and 77.54% compared to the upper shore at Paull. The same was true of the <2.4m band at Alkborough, which was 80.77% dissimilar to <2.4m at Welwick and 83.17% dissimilar to the same band at Paull. There was less distinction between Welwick and Paull (Table 4.4.2).

Table 4.4.1.

Average Similarity - % Trait Contribution (Abundance Weighted) by Elevation Band						
Elevation	Welwick 2011	% Contribution	Paull 2011	% Contribution	Alkborough 2011	% Contribution
<2.4 m Elevation	RF/I	5.18	RF/I	5.10	P/I	7.18
	P/I	5.08	LH/F	4.47	AM/M	7.18
	B/BB	4.80	F/10	4.22	L/18mth-2yrs	7.18
	FA/M	4.77	AM/M	4.21	BL/1-2cm	7.12
	LH/F	4.77	BL/2-5mm	4.18	RF/S	7.12
	M/<6mth	4.75	P/I	3.95	FT/D	6.94
	L/6- 18mth	4.73	M/<6mth	3.89	M/1-2yr	6.91
	F/10	4.71	L/6- 18mth	3.66	FM/SS	6.91
	AM/M	4.68	FA/M	3.41	FA/M	6.91
	BL/2-5mm	4.40	B/BB	3.40		
	FT/I	4.14	S/20	2.91		
	FM/P	3.48	FT/I	2.84		
	S/20	2.71	B/SB	2.55		
	S/15	2.66	FM/SS	2.51		
			S/25	2.50		
			FM/P	2.37		
			L/18mth-2yrs	2.37		
		S/15	2.31			
	Average Similarity%	77.97	Average Similarity %	64.26	Average Similarity %	68.61
>2.4 m Elevation	RF/I	5.83	RF/I	4.78	LH/F	6.95
	M/<6mth	5.58	P/I	4.61	AM/M	6.38
	LH/F	5.30	BL/2-5mm	3.91	RF/I	5.66
	BL/2-5mm	5.22	LH/F	3.27	L/<6mth	4.99
	AM/M	5.10	F/10	3.26	P/I	4.96
	P/I	4.32	M/<6mth	3.23	B/BB	4.94
	F/10	4.18	L/6- 18mth	3.22	FA/M	4.38
	L/6- 18mth	4.15	AM/M	3.15	F/10	4.20
	FA/M	4.13	L/18m-2yrs	3.13	FM/D	3.73
	B/BB	4.13	B/BB	3.04	S/10	3.62
	FT/I	3.78	FA/M	3.03	BL/5mm-1cm	3.62
	FM/P	3.07	S/20	2.94	P/E	3.43
	S/10	2.92	LH/T	2.93		
	B/SB	2.39	AM/S	2.93		
			M/≥6mth	2.93		
			FA/T	2.92		
			F/>10K	2.92		
		S/15	2.82			
		FT/I	2.76			
	Average Similarity %	72.70	Average Similarity %	78.88	Average Similarity %	50.28

Table 4.4.2 SIMPER Average Dissimilarity for all site and elevations 2011 (Abundance)

% Dissimilarity Between Elevation Band/Sites Along the Salinity Gradient (Abundance Weighted)						
Site/Elevation	Welwick <2.4 m	Paull <2.4 m	Alkborough <2.4 m	Welwick >2.4 m	Paull >2.4 m	Alkborough >2.4 m
Welwick <2.4 m						
Paull <2.4 m	32.01					
Alkborough <2.4 m	80.77	83.17				
Welwick >2.4 m	34.52	33.88	88.72			
Paull >2.4 m	32.49	31.46	86.79	29.05		
Alkborough >2.4 m	76.05	77.54	60.18	83.70	83.22	

## Traits x Biomass

PERMANOVA results for all trait categories, weighted by biomass, indicated a significant change in trait composition along the salinity ( $p < 0.01$  and  $F = 19.2$ ) and elevation gradients ( $p < 0.01$  and  $F = 2.1262$ ).

When the abundance-weighted multivariate traits data was tested between elevation bands, along the salinity gradient, Alkborough was significantly different to both Paull and Welwick, a  $p < 0.01$ . Paull and Welwick were different in the  $< 2.4$  m band, but not in the  $> 2.4$  m band. When elevation bands were compared within sites there was a difference at Welwick and Alkborough, at  $p < 0.05$ , but not at Paull.

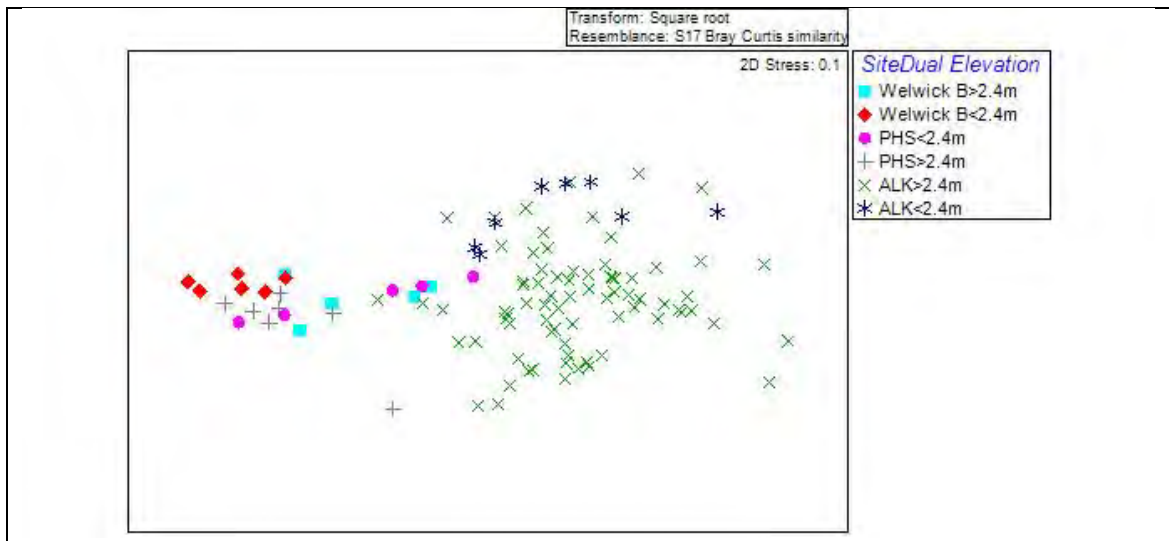


Fig 4.4.2 MDS of all variables weighted by biomass.

The MDS plot for all traits combined (Fig 4.4.2) confirmed Alkborough as distinctly different to both Paull and Welwick. Paull and Welwick showed some distinction between stations in the  $> 2.4$  m elevation band but overlapped in terms of upper shore traits composition.

SIMPER analysis also showed Alkborough as different to Paull and Welwick, as well as highlighting the distinction between the two elevation bands at Alkborough. Average similarity was low in both bands at Alkborough, particularly in the lower shore band, suggesting heterogeneity between samples.

RF (Reproductive Frequency) was a significant contributor to trait composition, as it was with abundance-weighted data. Both bands showed it as a major contributor to trait composition but on the lower shore RF/S (Reproductive Frequency/Semelparous) was expressed, while on the upper shore the modality RF/I (Iteroparous) was expressed instead. The trait L (longevity) also showed a variation in expression between elevation bands, with the modality L/ $< 6$  mth being expressed on the upper shore, while L/18mth-2yrs was a major contributor on the lower shore. At Welwick the trait FM (Feeding Method) changed in expression between  $< 2.4$  m and  $> 2.4$  m. FM/FS (Filter or Particle Selection) was a contributor at 4.16% on the lower shore, while at  $> 2.4$  m FM/D (Deposit) was the only FM modality expressed, at a contribution to total trait composition of 2.97% (Table 4.3.109). There was no notable pattern at Paull.

Average dissimilarity, across both gradients, indicated Alkborough was significantly different to Paull and Welwick, in both elevation bands. The highest dissimilarity was between Welwick  $< 2.4$  m and Alkborough  $< 2.4$  m with an average dissimilarity of 92.03% (Table 4.4.4). Full similarity and dissimilarity output is given in Appendices 7.2).

Table 4.4.3 SIMPER Average similarity for all sites and elevations 2011 (Biomass).

Average Similarity - % Trait Contribution (Biomass Weighted) by Elevation Band						
Elevation	Welwick 2011	% Contribution	Paull 2011	% Contribution	Alkborough 2011	% Contribution
<2.4 m Elevation	RF/I	5.64	P/I	4.73	P/I	7.78
	LH/SP	5.63	AM/M	4.35	AM/M	7.61
	F/10K	5.56	RF/I	3.78	L/18m-2yrs	6.76
	M/1-2yr	5.55	BL/1-2cm	3.67	LH/F	6.72
	FA/S	5.52	LH/SP	3.65	B/BB	6.71
	L/>5yrs	5.48	F/10K	3.64	BL/1-2cm	6.55
	P/I	4.89	S/20	3.60	FA/M	6.39
	BL/1-2cm	4.77	FT/I	3.09	FT/D	6.32
	FM/FS	4.16	FM/P	2.85	RF/S	5.60
	AM/L	4.12	LH/F	2.85		
	S/20	4.11	BL/18m-2yrs	2.72		
	FT/S	3.92	M/1-2yr	2.69		
	B/D	3.84	F/10	2.68		
			FA/J	2.52		
			BL/2-5mm	2.51		
			M/6mth - 1yr	2.51		
			FT/D	2.50		
			FM/D	2.34		
		FM/FS	2.08			
		FT/S	2.07			
	Average Similarity%	74.92	Average Similarity %	51.86	Average Similarity %	49.09
>2.4 m Elevation	P/I	5.51	AM/M	5.13	LH/F	7.41
	AM/M	5.39	S/20	4.65	P/I	6.90
	BL/1-2cm	4.95	P/I	4.46	AM/M	6.82
	LH/SP	4.95	LH/SP	4.33	RF/I	4.62
	S/20	4.29	F/10K	4.32	FA/J	4.41
	FA/J	4.15	BL/1-2cm	4.31	B/BB	4.17
	F/10K	4.10	L/18mth-2yrs	4.24	BL/5mm-1cm	3.93
	L/18m-2yrs	3.78	M/6mth - 1yr	3.94	L/<6m	3.73
	RF/S	3.68	RF/I	3.88	F/10	3.58
	M/6mth - 1yr	3.35	FT/D	3.61	FA/M	3.47
	FT/D	2.97	M/1-2yr	2.89	S/10	3.47
	FT/I	2.95	FA/J	2.79	S/5	3.45
	FM/D	2.89	FM/D	2.74	FT/D	3.42
	B/GB	2.86	RF/S	2.70	M/<6mth	3.17
	B/OV	2.86	FT/M	2.46		
FM/P	2.83	FA/S	2.20			
		FM/FS	2.11			
	Average Similarity %	57.47	Average Similarity %	62.21	Average Similarity %	43.27



Table 4.4.4 SIMPER Average dissimilarity for all 2011 sites and elevations (Biomass).

% Dissimilarity Between Elevation Band/Sites (Biomass Weighted)						
Site/Elevation	Welwick <2.4 m	Paull <2.4 m	Alkborough <2.4 m	Welwick >2.4 m	Paull >2.4 m	Alkborough >2.4 m
Welwick <2.4 m						
Paull <2.4 m	57.61					
Alkborough <2.4 m	92.03	77.82				
Welwick >2.4 m	54.38	43.17	79.36			
Paull >2.4 m	40.37	48.61	89.60	47.32		
Alkborough >2.4 m	90.87	76.88	62.39	77.70	87.46	

### Traits x Abundance

PERMANOVA results indicated a significant difference between elevation bands at Alkborough for all variables combined ( $p < 0.01$ ) and  $F = 3.4488$ .

Tests showed thirteen significantly different pairs of elevation bands: 3.3 m/0 m; 3.3 m/2.6 m; 3.35 m/2.6 m; 3.35 m/0 m; 3.35 m/-2 m; 3.1 m/0 m; 3.3 m/-2 m; 3.2 m/2.6 m; 3.2 m/0 m; 3.2 m/-2m; 2.7 m/2.6 m; 2.7 m/0 m and 2.7 m/-2 m, all at  $p < 0.05$ . This indicated that the main distinction along the elevation gradient was between stations over 3.3 m and those much lower, at 2.6 m and less. MDS analysis also showed lower shore elevations bands as separate from upper shore groups (Fig 4.4.57).

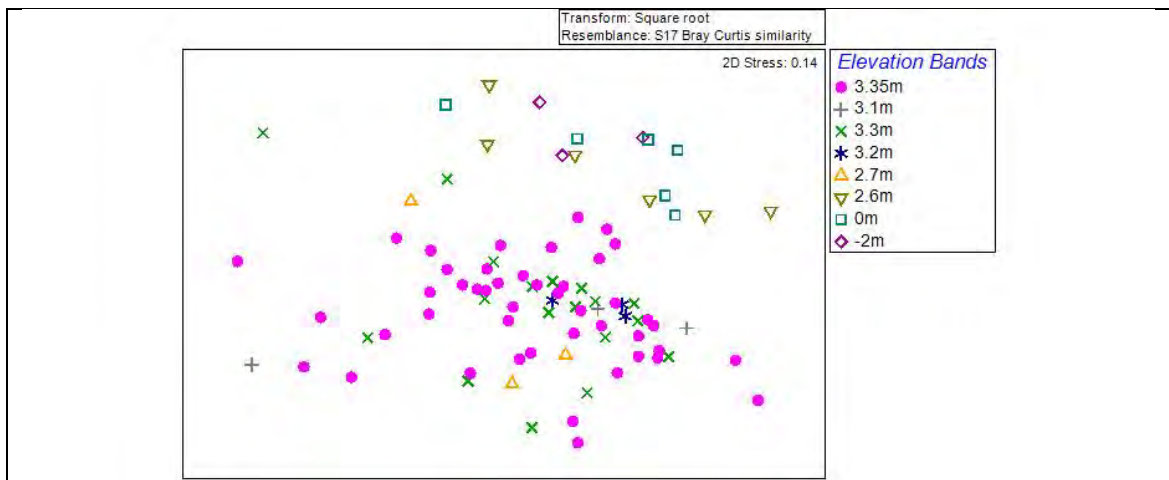


Fig 4.4.3 MDS for all traits at Alkborough weighted by abundance.

SIMPER analysis was also performed for this data set and indicated changes along the elevation gradient. Within- site % average similarity was particularly high in the -2m and 3.2m elevation bands at 77.89% and 78.97% respectively, indicating a strong similarity between replicates and within-band samples.

Between elevation bands the % Average Dissimilarity was high when upper and lower shore bands were compared, with 3.35m/-2m being 62.23% dissimilar. When geographically closer bands were compared dissimilarity was lower, such as 0m/-2m at 31.50%. The bands where the highest levels of dissimilarity were found between them when compared, were 3.1m/-2m and 3.1m/2.6m (Table 4.3.10. See Appendix 9.1 and 9.2 for full SIMPER tables).

Table 4.4.5 SIMPER Average Similarity for Alkborough 2011.

%Average Similarity: Alkborough 2011 (Abundance-Weighted)	
Elevation	Average Similarity%
-2 m	77.89
0 m	66.88
2.6 m	54.03
2.7 m	50.72
3.1 m	31.76
3.2 m	78.97
3.3 m	53.91
3.35 m	51.66

Table 4.4.6 Average dissimilarity at Alkborough x N

% Average Dissimilarity: Alkborough 2011 (Abundance Weighted)								
Elevation	-2m	0m	2.6m	2.7m	3.1m	3.2m	3.3m	3.35m
-2m								
0m	31.50							
2.6m	36.32	39.47						
2.7m	62.27	63.35	63.38					
3.1m	70.84	67.18	68.86	58.98				
3.2m	57.33	55.13	56.70	51.62	48.99			
3.3m	60.81	60.88	60.78	58.81	54.69	38.02		
3.35m	62.23	62.37	62.09	50.23	55.07	41.99	46.45	

### Traits x Biomass

PERMANOVA results for all traits, weighted by biomass, indicated a significant change in trait expression between elevation bands ( $p < 0.01$  and  $F = 2.838$ ). Tests between pairs of elevation bands showed 16 with a significant ( $p < 0.05$ ) change in trait composition: these were mainly pairs of bands at different ends of the gradient, but exceptions to this were 3.1m/3.2m and 2.7m/2.6m, which showed changes in trait profile over a short change in elevation.

MDS analysis showed separation of the highest and lowest shore elevation bands, with a particular distinction between 3.1m, 3.2m and 3.3m in comparison to all bands below them (Fig 4.3.58).

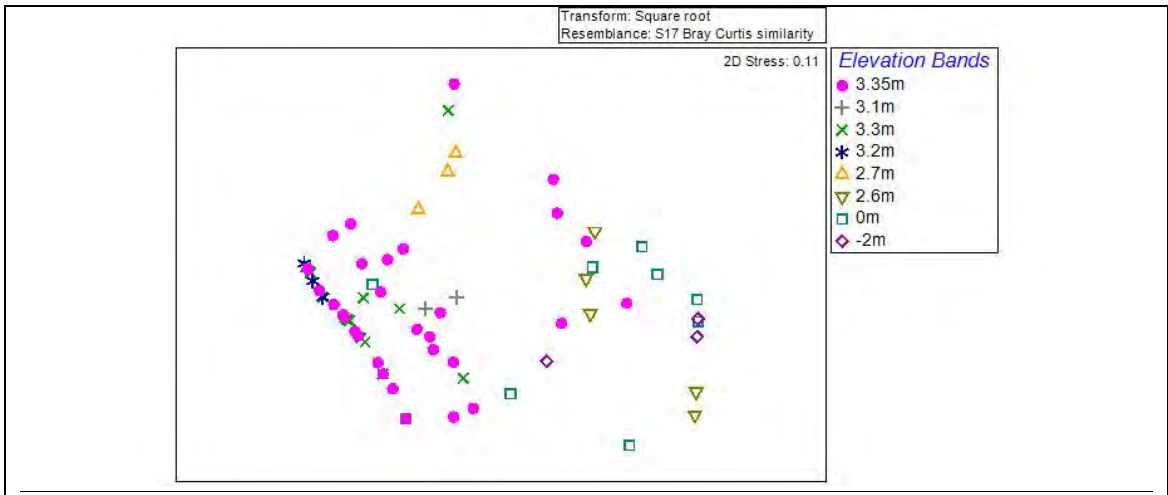


Fig 4.4.4 MDS for all variables weighted by biomass. With outlier 102B removed.

SIMPER analysis was applied to the same data set and the results emphasised the distinction between bands shown in the MDS (Fig 4.3.58). Within-band similarity was high for a number of the bands (See Table 4.2.118), while comparisons between elevation bands supported the MDS output and showed particularly high dissimilarity between 2.7m and -2m at 74.53%, 2.6m, and 2.7m at 69.87% and 3.35m and 2.6m at 67.16% (Table 4.2.119).

Table 4.4.7 SIMPER Average Similarity for Alkborough 2011.

%Average Similarity: Alkborough 2011 Biomass-Weighted)	
Elevation	Average Similarity%
-2m	83.46
0m	44.25
2.6m	45.05
2.7m	70.39
3.1m	70.86
3.2m	77.04
3.3m	48.93
3.35m	42.51

Table 4.4.8 SIMPER Average Dissimilarity for Alkborough 2011.

% Average Dissimilarity: Alkborough 2011 (Biomass Weighted)								
Elevation	-2m	0m	2.6m	2.7m	3.1m	3.2m	3.3m	3.35m
-2m								
0m	48.27							
2.6m	45.92	56.17						
2.7m	74.53	66.01	69.87					
3.1m	56.95	56.31	65.73	59.77				
3.2m	59.55	58.79	57.81	52.90	52.22			
3.3m	63.63	62.56	64.71	58.81	49.70	42.65		
3.35m	65.01	62.93	67.16	61.68	52.85	51.58	55.07	

## 4.4.2 Univariate Analysis

### Feeding Method (FM)

Figure 4.4.5 A1-C2 below shows mean trait expression per station with the trait scores weighted first by abundance and then by biomass. At Welwick 2011, for the trait FM (Feeding Method), weighted by abundance, there was a clear distinction between upper and lower shore elevation bands, primarily due to the much higher levels of the modality FM/D (Deposit feeders) in the upper shore elevation band. For the biomass-weighted traits data at Welwick 2011 there were no obvious patterns, due to differences in biomass between the upper and lower shore, with substantially higher levels at <2.4m (Fig.4.4.5 A2). However, there was a discernibly higher proportion of FM/FS (Filter or Particle Selection) being expressed on the lower shore. At Paull 2011, for both data sets there was no visible pattern along the elevation gradient (Fig.4.4.5 B1 and B2). At Alkborough in 2011, traits data weighted by both abundance and biomass showed a change in modalities expressed between upper and lower shore bands. In both data sets the lower band (<2.4m) was dominated by FM/SS (Subsurface Deposit). In the upper elevation band (>2.4m) for abundance weighted data the main trend was for FM/D (Deposit Feeder-Surface). For biomass weighted data the upper shore showed no clear visual trends.

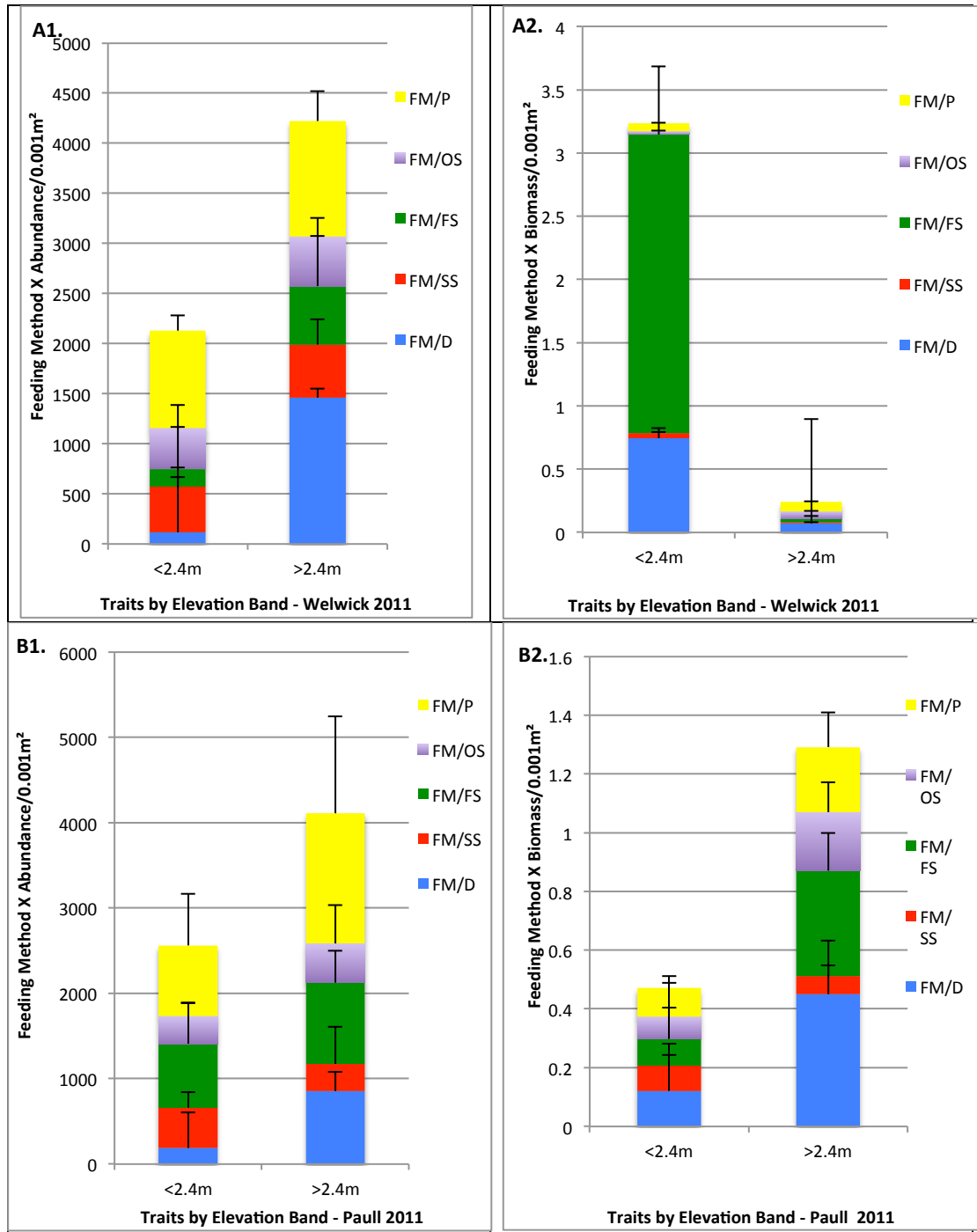
### **Feeding Method x Abundance**

PERMANOVA results were all significant for FM in terms of abundance, indicating a change in trait expression with gradient.  $P < 0.01$  for both between sites and elevation bands. F values were 21.158 for salinity and 3.5589 for elevation. Tests to compare sites within each elevation band (<2.4m or >2.4m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of FM expression ( $p < 0.01$ ). No significant difference was found between Paull and Welwick. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.01$ ) and Welwick ( $p < 0.05$ ), but not at Paull.

### **Feeding Method x Biomass**

PERMANOVA analysis for the trait FM in terms of biomass showed significant changes in trait expression for between sites ( $p < 0.01$  and  $F = 12.75$ ), but not for elevation. Tests to compare

sites within each elevation band (<2.4m or >2.4m), between sites, indicated that, for both elevation bands, Alkborough was significantly different to Paull and Welwick in terms of FM expression ( $p < 0.01$ ). In the upper elevation band (>2.4m) no significant difference was found between Paull and Welwick, while in the <2.4m band there was a significant difference between Paull and Welwick ( $p < 0.05$ ). Within each site only Welwick showed a significant difference between upper and lower shore ( $p < 0.01$ ).



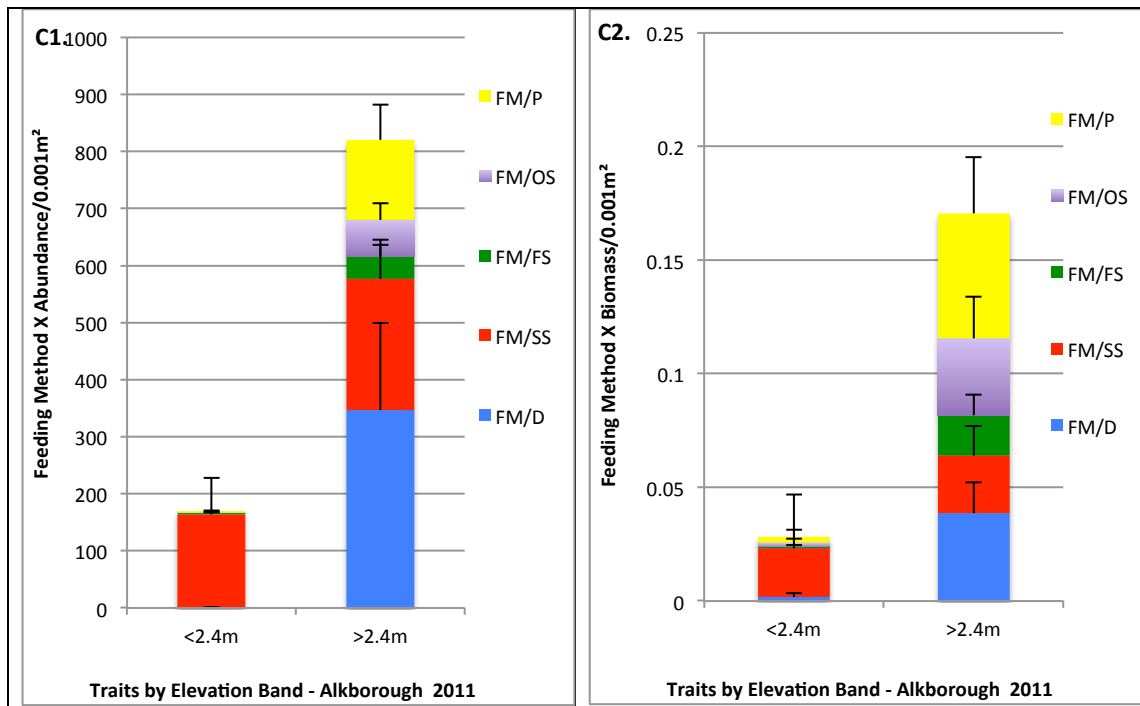


Fig. 4.4.5. A.1-C2. A1, FM (feeding Method) weighted by abundance at Welwick 2011. A2, FM weighted by biomass at Welwick 2011. B1, FM weighted by abundance at Paull 2011. B2, FM weighted by biomass at Paull 2011. C1, FM weighted by abundance at Alkborough 2011. C2, FM weighted by biomass at Alkborough 2011. See Table 3.1 for full coding.

### ***Feeding Apparatus (FA)***

At Welwick the most notable change was the increasing dominance of FA/M (Simple Mouth) in the lower shore bands. This modality was also expressed in the upper shore band, but was expressed alongside FA/J (Jaws or Mandibles) and FA/T (Tentaculated) in similar proportions. At Welwick, in terms of biomass, there was a clear distinction between the upper and lower shore elevation bands with FA/S (Siphon) strongly represented at <2.4 m and absent in the >2.4 m upper band. At Paull, for traits weighted by abundance and biomass, there was no clear pattern between elevation bands. At Alkborough both sets of trait data were dominated by FA/M (Simple Mouth) and FA/J (Jaws or Mandibles) along the whole gradient. In the abundance-weighted data there was a clear change between elevation bands from a mix of these two modalities in the >2.4 m band to FA/M (Simple Mouth) only in the >2.4 m band. Between sites there was a notable difference between Alkborough and the other two sites in terms in range of traits expressed; only two traits (FA/Simple Mouth and FA/Jaws Mandibles) were expressed at Alkborough, across both elevation bands, in contrast to at least four at Paull and Welwick (Fig 4.4.6 A1-C2).

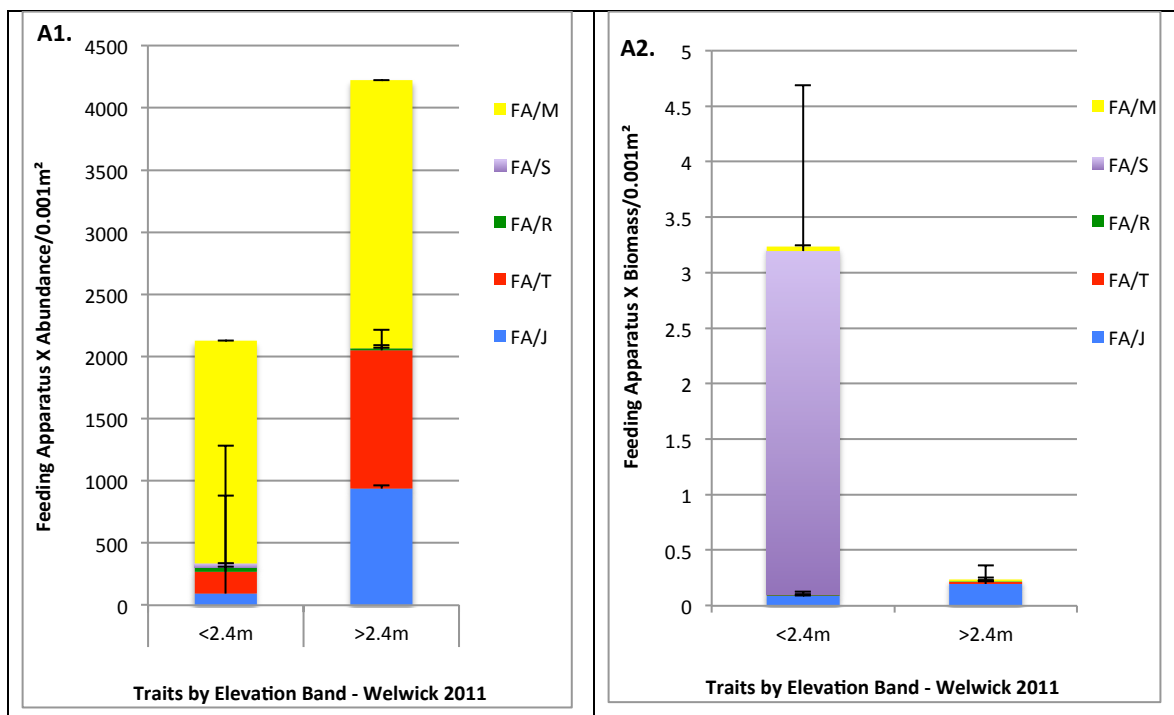
### **Feeding Apparatus x Abundance**

PERMANOVA analysis for the trait FA in terms of abundance showed significant changes in trait expression between sites ( $p < 0.01$  and  $F = 31.307$ ), but not for elevation band. Tests to compare sites within each elevation band (<2.4 m or >2.4 m), between sites, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of FA (Feeding Method) expression, with  $p < 0.01$ . There was no significant difference between

Paul and Welwick in either the <2.4 m or >2.4 m elevation band. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.01$ ) and Welwick ( $p < 0.05$ ), but not at Paul.

### Feeding Apparatus x Biomass

PERMANOVA analysis of the trait FA (Feeding Apparatus), in terms of biomass, indicated significant change in trait expression between sites and elevation bands. Between sites  $p < 0.01$  and  $F = 31.307$  and for elevation  $p < 0.05$  and  $F = 3.423$ . Tests to compare sites within each elevation band (<2.4 m or >2.4 m), between sites, indicated that, for both elevation bands, Alkborough was significantly different from Paul and Welwick in terms of FA (Feeding Method) expression,  $p < 0.01$ . There was a significant difference between Welwick and Paul in the lower shore band ( $p < 0.01$ ), but not in the upper shore band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ), but not at Paul or Alkborough.





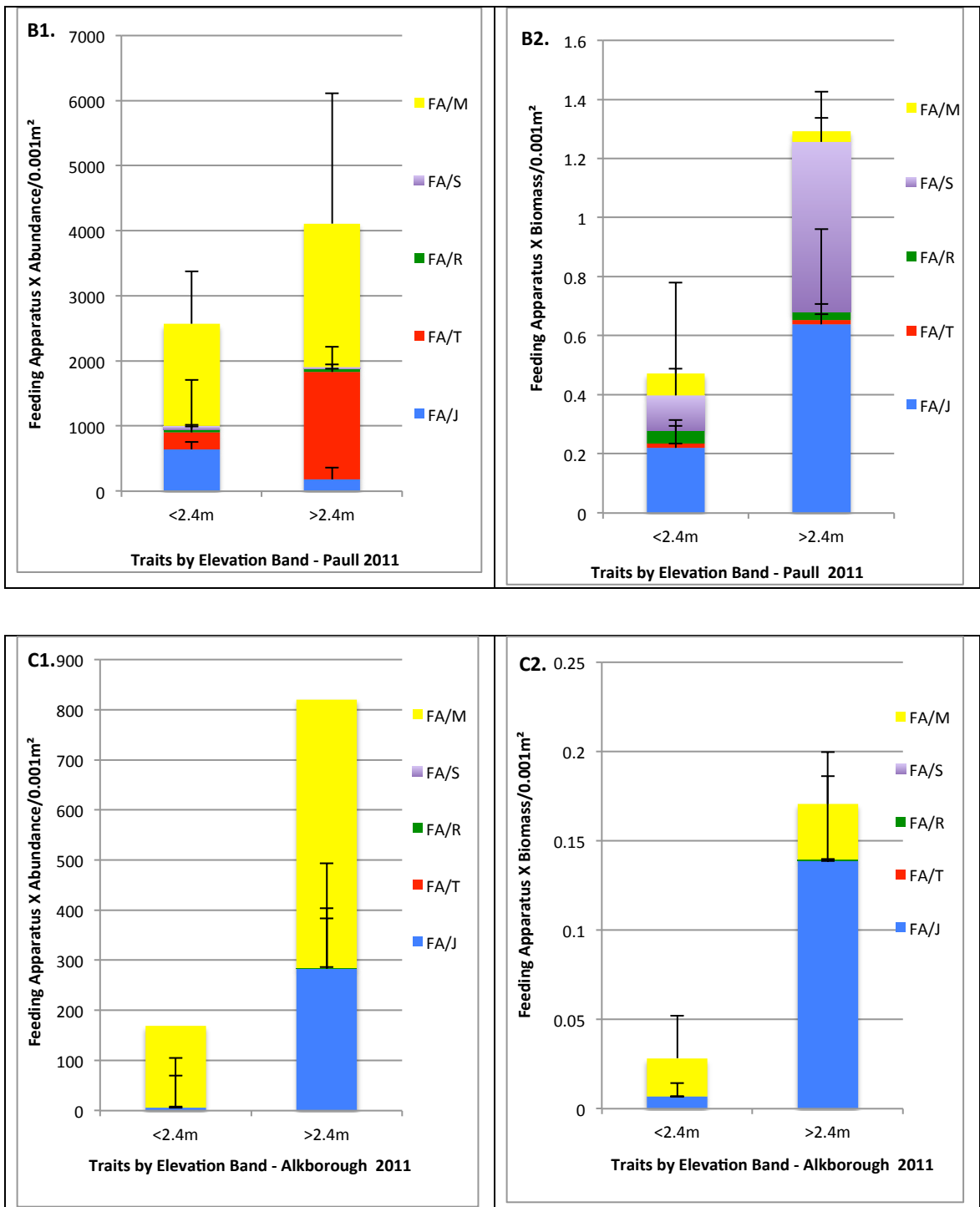


Fig. 4.4.6. A.1-C2. A1, FA (Feeding Apparatus), by abundance at Welwick 2011. A2, FA by biomass at Welwick 2011. B1, FA by abundance at Paull 2011. B2, FA by biomass at Paull 2011. C1, FA, by abundance, at Alkborough 2011. C2, FA by biomass at Alkborough 2011. See Table 3.1 for traits coding.

### **Food Type (FT)**

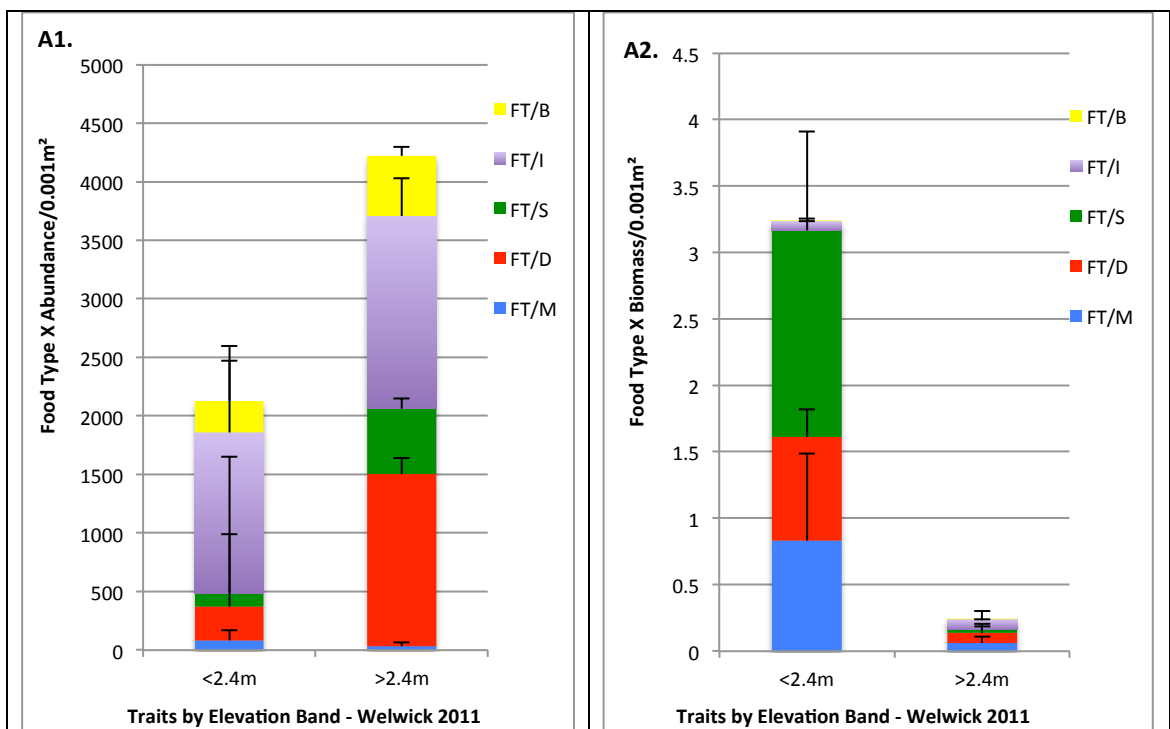
For the trait Food Type (FT) the main pattern for both abundance and biomass weighted data sets was a higher proportion of the expression of the trait FT/D (Food Type/Detritus) in the <2.4 m elevation band compared to the >2.4 m band. This was the case at both Welwick and Alkborough where it caused the main distinction between upper and lower shore. At Paull there was no visual trend discernable.

## Food Type x Abundance

PERMANOVA analysis for the trait FT in terms of abundance showed significant changes in trait expression between sites and elevation bands. Between sites  $p < 0.01$  and  $F = 31.30$ , and for elevation band  $p < 0.05$  and  $F = 2.86$ . Tests to compare sites within each elevation band (<2.4 m or >2.4 m), indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of FA (Feeding Method) expression, with  $p < 0.01$ . There was a significant difference between Paull and Welwick in the <2.4 m band ( $p < 0.05$ ), but not in the >2.4 m band. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.01$ ) and Welwick ( $p < 0.05$ ), but not at Paull.

## Food Type x Biomass

PERMANOVA analysis for the trait FT in terms of biomass showed significant changes in trait expression between sites ( $p < 0.01$  and  $F = 15.45$ ) but not between elevation band. Tests to compare sites within each elevation band (<2.4 m or >2.4 m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of FT (Food Type) expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the <2.4 m band ( $p < 0.05$ ), but not in the >2.4 m band. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.05$ ) and Welwick ( $p < 0.01$ ), but not at Paull, which was the likely cause of the non-significant PERMANOVA result for elevation.



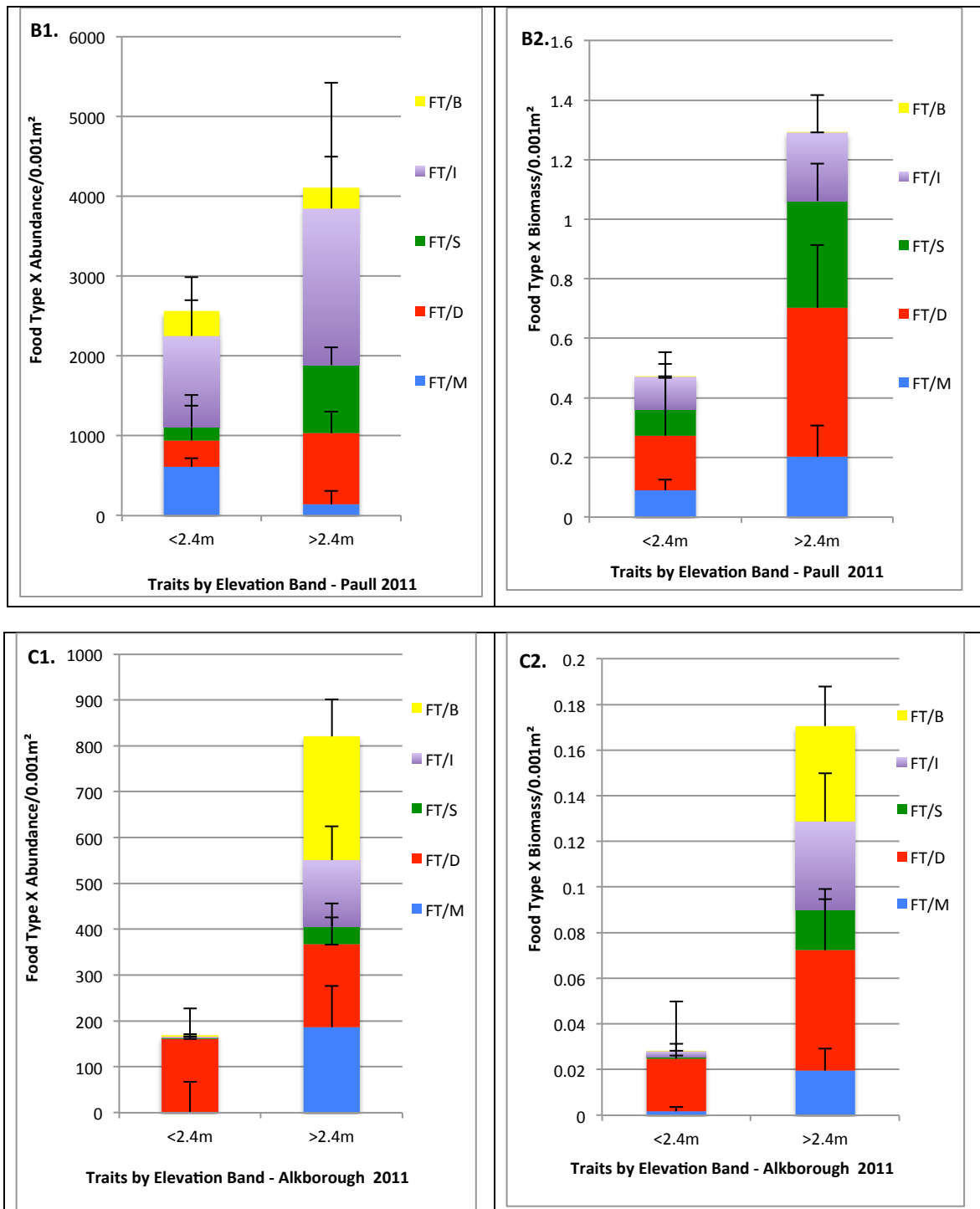


Fig. 4.4.7. A.1-C2. A1, FT weighted by abundance at Welwick 2011. A2, FT by biomass at Welwick 2011. B1, FT by abundance at Paull 2011. B2, FT by biomass at Paull 2011. C1, FT by abundance at Alkborough 2011. C2, FT by biomass at Alkborough 2011. See Table 3.1 for traits coding.

**Adult Mobility (AM)**

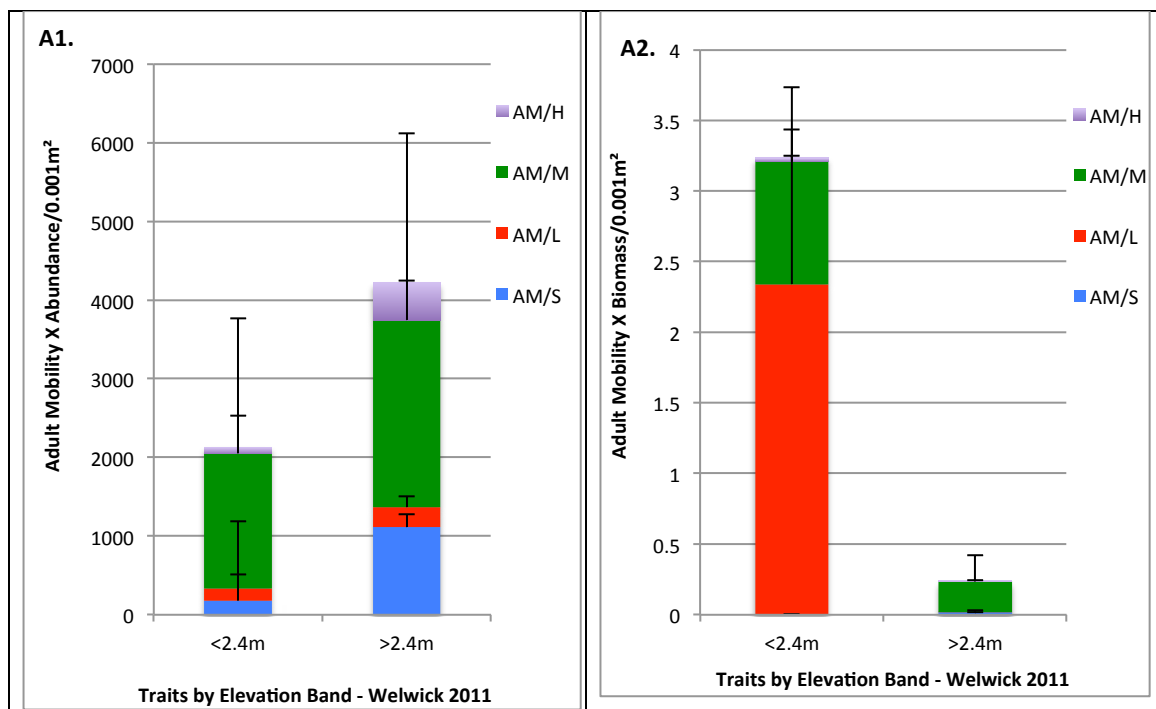
For abundance weighted data for the trait Adult Mobility (AM) there was some distinction between bands at Welwick and Alkborough. At both sites there was a dominance of the modality AM/M (Adult Mobility/Medium) in the <2.4m bands. For biomass weighted data there was a strong delineation between bands at Welwick (Fig 4.4.8 A2) with AM/L (Adult Mobility/Low) dominating the lower shore band and being absent in the >2.4 m band. Paull showed no clear distinction between elevation bands.

### Adult Mobility x Abundance

PERMANOVA results were significant for AM in terms of abundance, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 35.24$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m), indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of AM (Adult Mobility) expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the >2.4m band ( $p < 0.05$ ), but not in the <2.4m band. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.05$ ) and Welwick ( $p < 0.01$ ), but not at Paull.

### Adult Mobility x Biomass

PERMANOVA results were significant for AM, in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 35.24$ ). Elevation was not a significant factor in trait expression at any site. Tests to compare sites within each elevation band (<2.4m or >2.4m), indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of AM (Adult Mobility) expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the <2.4 m band ( $p < 0.05$ ), but not in the >2.4 m band.



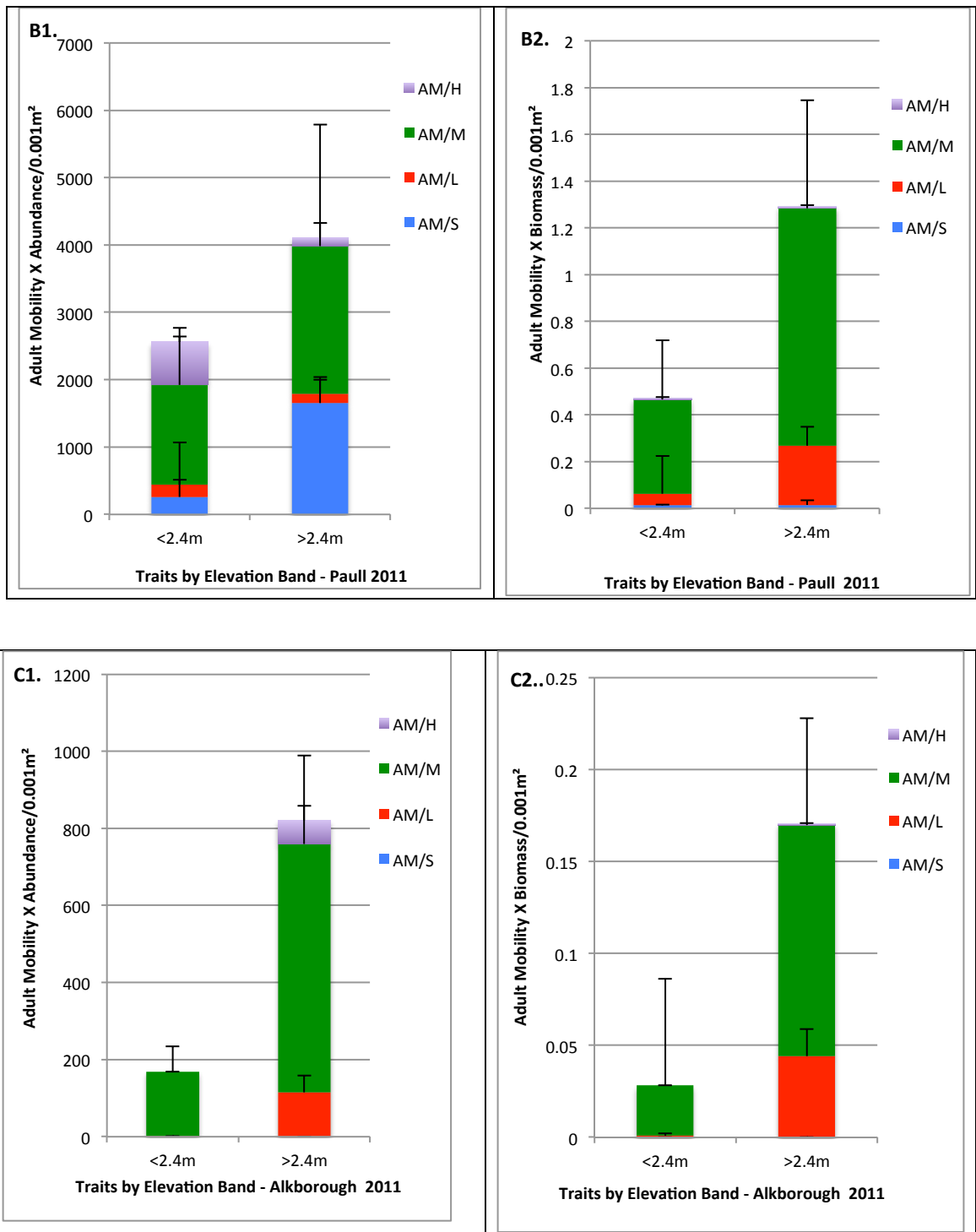


Fig. 4.4.8. A.1-C2. A1, AM (Adult Mobility) weighted by abundance at Welwick 2011. A2, AM by biomass at Welwick 2011. B1, AM by abundance at Paull 2011. B2, AM by biomass at Paull 2011. C1, AM by abundance at Alkborough 2011. C2, AM by biomass at Alkborough 2011. See Table 3.1 for traits coding.

**Position (P)**

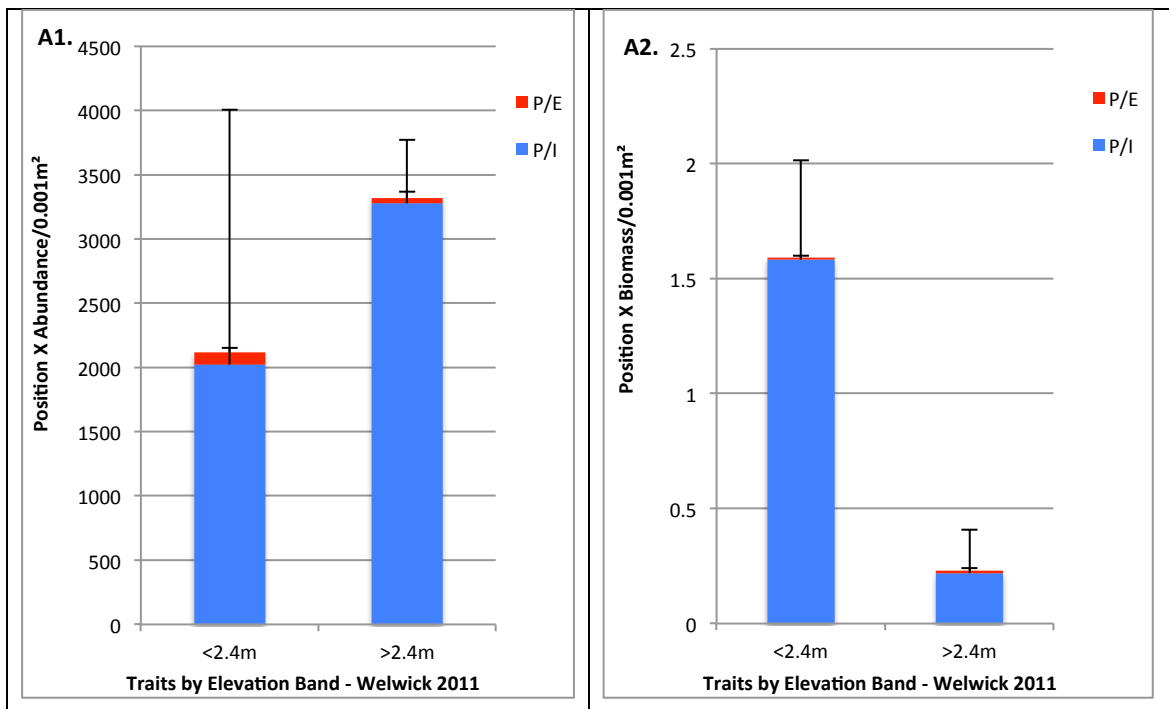
For the trait P (Living Position) there was not clear distinction between elevations at Welwick and Paull for either abundance or biomass-weighted data. At Alkborough there was a clear difference between upper and lower shore elevation bands for both data sets. In the >2.4 m band P/I (Position/Infaunal) dominated but P/E (Position/Epifaunal) was also present. In the <2.4 m band P/E was absent completely.

### Position x Abundance

PERMANOVA results were significant for P (Position), in terms of abundance, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 33.64$ ). Elevation band was significant at Alkborough ( $p < 0.01$ ) but not at Paull or Welwick. Tests to compare sites within each elevation band (<2.4 m or >2.4 m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of P (Position) expression, with ( $p < 0.01$ ). No significant difference was found between Paull and Welwick in either elevation band.

### Position x Biomass

PERMANOVA results were significant for P, in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 24.96$ ). Tests to compare sites within each elevation band (<2.4m or >2.4m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of P (Position) expression ( $p < 0.01$ ). There was no significant difference between Paull and Welwick in either elevation band. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.01$ ) and Welwick ( $p < 0.01$ ), but not at Paull.



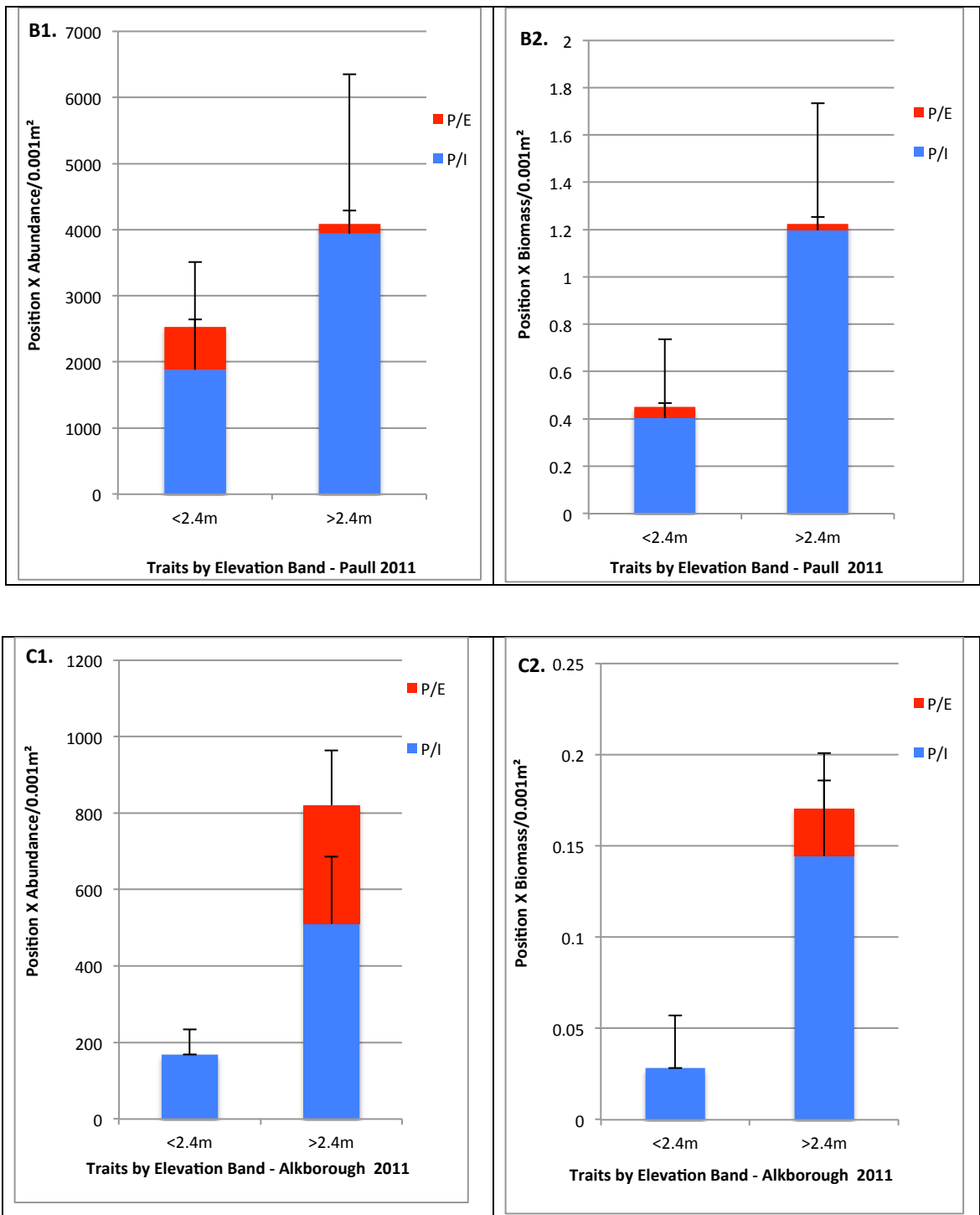


Fig. 4.4.9. A.1-C2. A1, P (Position) by abundance at Welwick 2011. A2, P by biomass at Welwick 2011. B1, P by abundance at Paull 2011. B2, P by biomass at Paull 2011. C1, P by abundance at Alkborough 2011. C2, P by biomass at Alkborough 2011. See Table 3.1 for traits coding.

### **Living Habitat (LH)**

For LH (Living Habitat), weighted by abundance and biomass at Welwick there was no strong pattern visible between the two elevation bands in terms of trait composition, but for abundance-weighted data there was a higher proportion of LH/T (Living Habitat/Tube Dwelling) in the >2.4 m band. At Alkborough, for abundance-weighted data, the lower shore was dominated by LH/F (Free Living). The upper shore also showed a high proportion of LH/F, but included contributions from the modalities LH/SP (Semi-Permanent Burrow) and LH/T (Tube Dwelling). For traits in terms of biomass at Alkborough the modality that caused

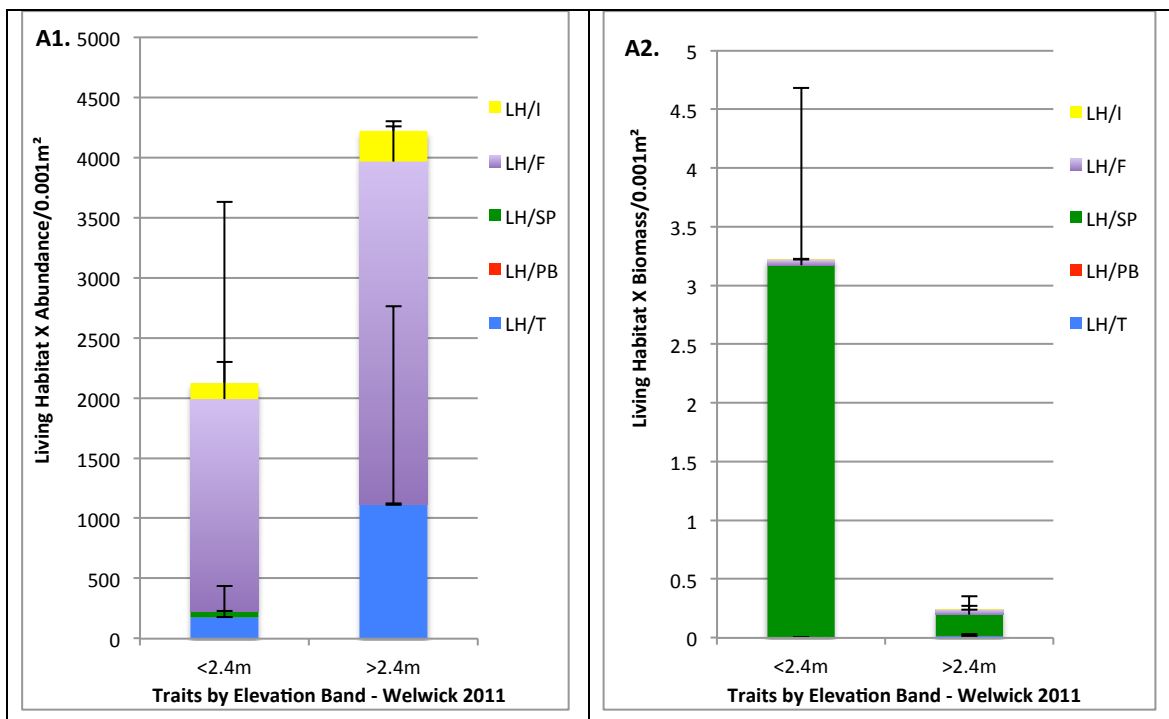
distinction between elevation bands was LH/T (Tube Dwelling), which was present on the upper shore but absent at <2.4m. No clear pattern was discernable at Paull.

### Living Habitat x Abundance

PERMANOVA results were significant for LH (Living Habitat) in terms of abundance, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 35.81$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of LH (Living Habitat) expression, ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the >2.4 m band ( $p < 0.05$ ), but not in the <2.4 m band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ), but not at Paull or Alkborough.

### Living Habitat x Biomass

PERMANOVA results were significant for LH, in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 21.89$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m), indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of P (Position) expression ( $< 0.01$ ). There was a significant difference in trait expression between Paull and Welwick in the <2.4 m band ( $p < 0.01$ ), but not in the >2.4 m elevation band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ), but not at Paull or Alkborough.





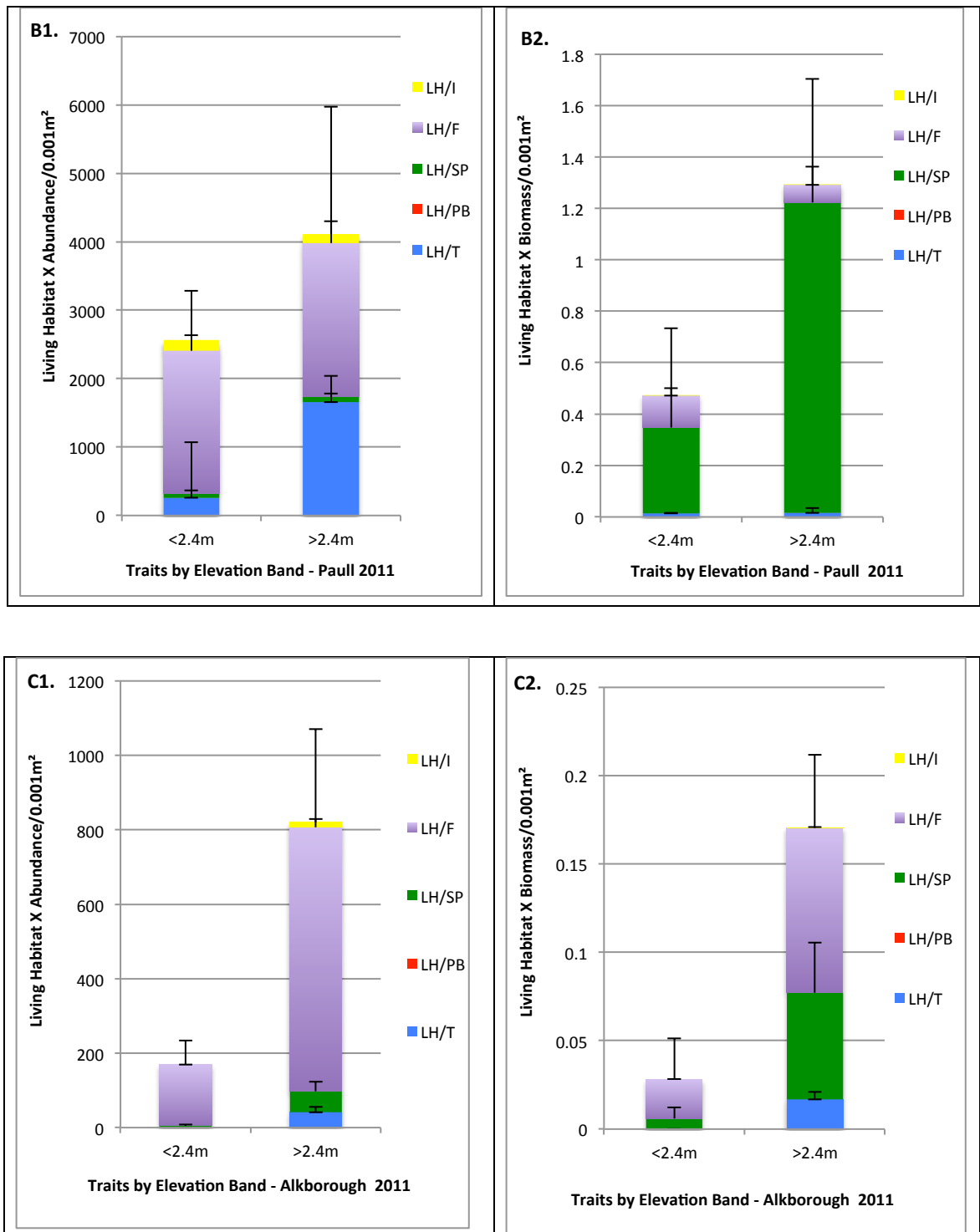


Fig. 4.4.10. A.1-C2. A1, LH weighted by abundance at Welwick 2011. A2, LH weighted by biomass at Welwick 2011. B1, LH weighted by abundance at Paull 2011. B2, LH weighted by biomass at Paull 2011. C1, LH weighted by abundance at Alkborough 2011. C2, LH weighted by biomass at Alkborough 2011. See Table 3.1 for traits coding.

### **Bioturbation**

At Welwick for abundance-weighted data the main change with elevation was the higher proportion of B/BB (Bioturbation/Burrowing Biodiffuser) on the lower shore, with a corresponding decrease in expression of B/SB (Bioturbation/Surficial Biodiffuser) which was more prominent in the >2.4 m band. For biomass-weighted data at Welwick there was a clear distinction between bands. B/D (Downward Conveyer) and B/BV (Blind Burrow Ventilator)

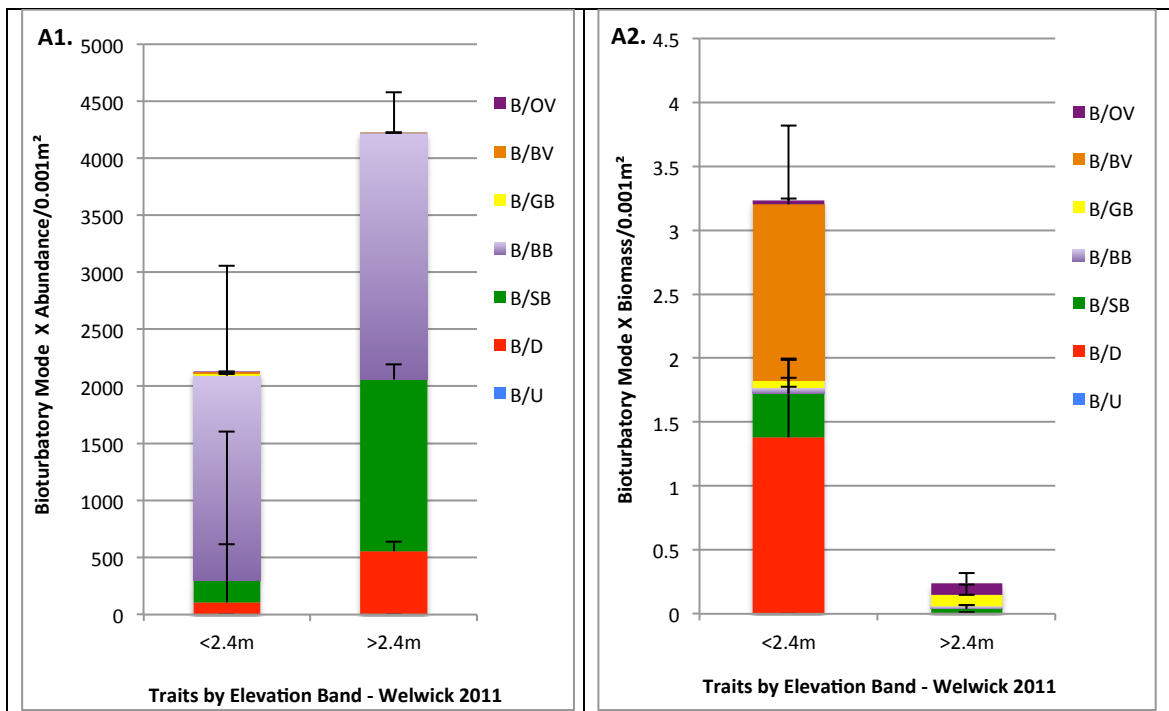
were expressed strongly in the >2.4 m and were completely absent in the >2.4 m band. At Alkborough, for both biomass and abundance weighted data, the modality B/BB (Burrowing Biodiffuser) dominated the lower shore band, while the >2.4m band showed traits B/SB (surficial Biodiffuser) and B/BV (Blind Burrow Ventilator) that were absent in the lower shore elevation band. There was no clear pattern in either data set at Paull (Fig 4.4.11 A1-C2).

### Bioturbation x Abundance

PERMANOVA results for B (Bioturbation), in terms of abundance, indicated a change in trait expression between sites ( $p < 0.01$  and  $F = 25.55$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m), indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of B ( $p < 0.01$ ). There was a significant difference in trait expression between Paull and Welwick in the <2.4 m band ( $p < 0.01$ ), but not in the >2.4 m band. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.01$ ) and Welwick ( $p < 0.01$ ), but not at Paull.

### Bioturbation x Biomass

PERMANOVA results were significant for B, in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 15.39$ ) and elevation band ( $p < 0.05$  and  $F = 2.87$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m) indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of B ( $p < 0.01$ ). There was a significant difference in trait expression between Paull and Welwick in the <2.4 m band ( $p < 0.01$ ), but not in the >2.4 m band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ) and Alkborough ( $p < 0.01$ ), but not at Paull.



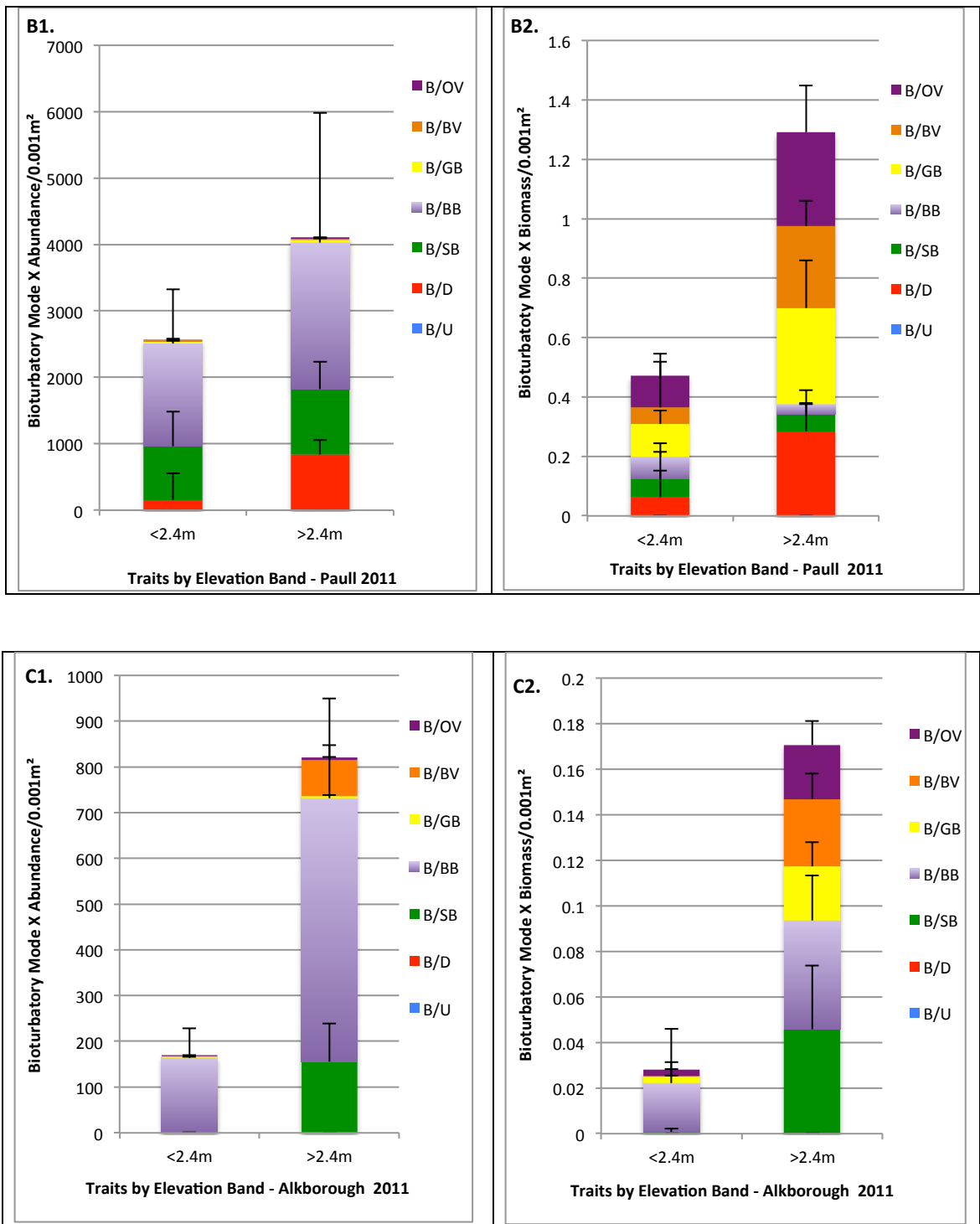


Fig. 4.4.11. A.1-C2. A1, B weighted by abundance at Welwick 2011. A2. B weighted by biomass at Welwick 2011. B1, B weighted by abundance at Paull 2011. B2, B weighted by biomass at Paull 2011. C1. B weighted by abundance at Alkborough 2011. C2, B weighted by biomass at Alkborough 2011. See Table 3.1 for traits coding.

**Adult Body Length (BL)**

For abundance-weighted data, for the trait Body Length (BL), there was a difference between bands at Welwick. The lower shore expressed BL/2->5cm more than the upper shore and also showed expression of the trait BL/1-2cm, which was absent on the upper shore. For the biomass-weighted Welwick data the lower shore was characterised by a much higher proportion of BL/2->5cm compared to the upper shore band (Fig 4.4.12 A1 and A2). At Paull no

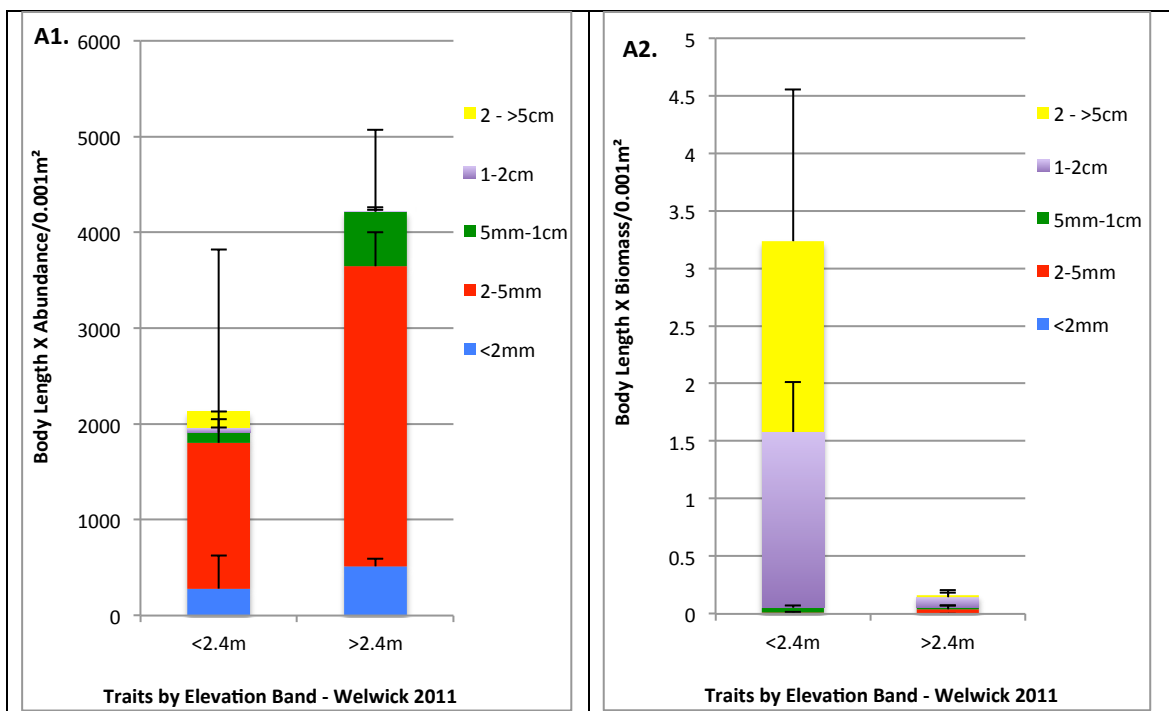
clear pattern was discernable across the gradient. Alkborough showed a distinction between elevations for both data sets, with BL/1-2cm dominating the <2.4 m elevation band, compared to a range of modalities on the upper shore.

### Body Length x Abundance

PERMANOVA results were significant for BL in terms of abundance, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 22.31$ ) and elevation bands ( $p < 0.01$  and  $F = 3.86$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m), indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of BL expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the >2.4 m band ( $p < 0.05$ ), but not in the <2.4 m band. Within each site a significant difference was found between the upper and lower shore at Welwick and Alkborough ( $p < 0.01$ ), but not at Paull.

### Body Length x Biomass

PERMANOVA results were also significant for BL in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 14.577$ ) and elevation band ( $p < 0.05$  and  $F = 2.879$ ). Tests to compare sites within each elevation band (<2.4m or >2.4m) indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of BL expression, with  $p < 0.01$ . There was a significant difference between Paull and Welwick in the <2.4m band ( $p < 0.05$ ), but not in the >2.4m band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.05$ ) and Alkborough ( $p < 0.01$ ), but not at Paull.



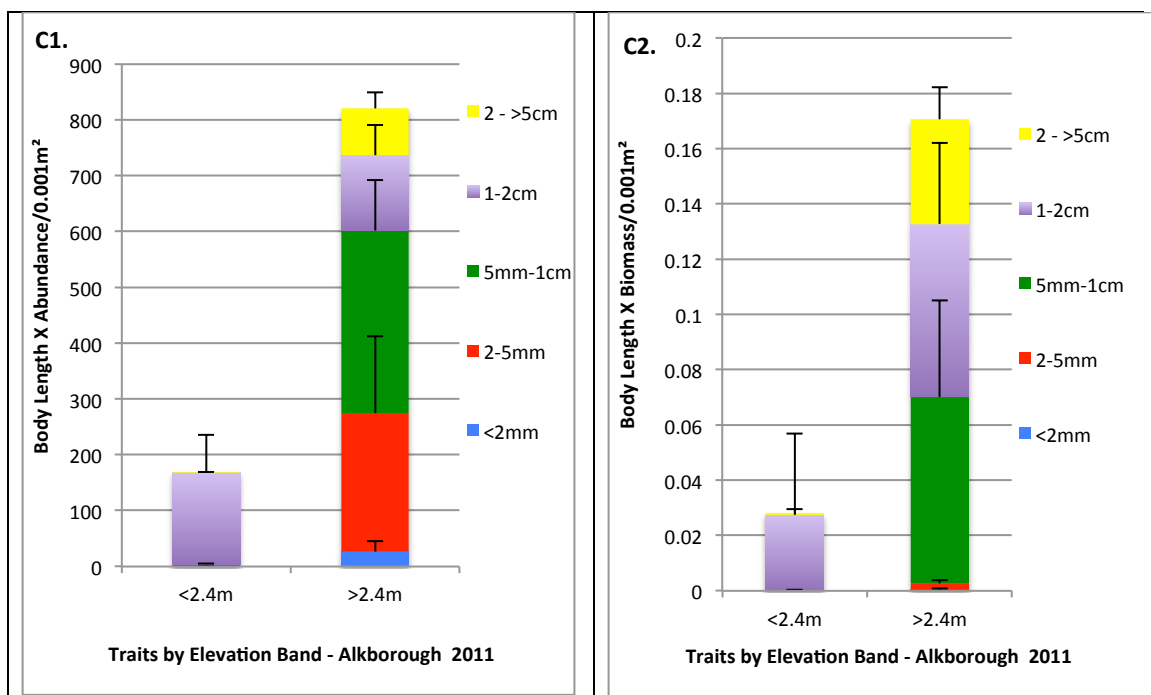
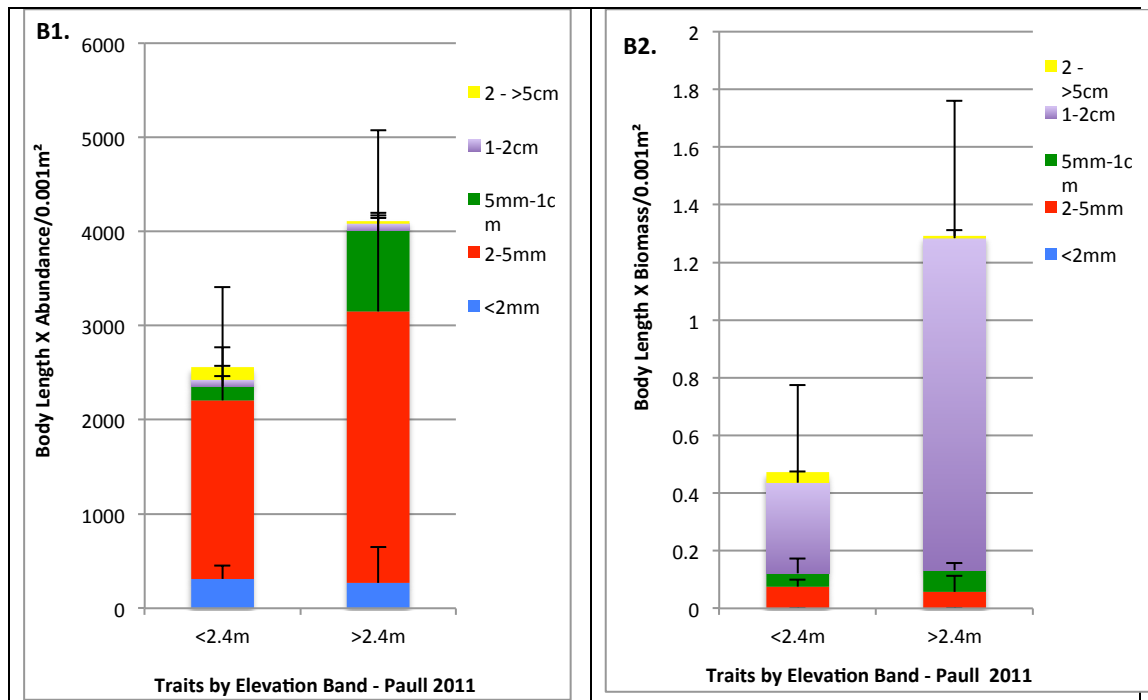


Fig. 4.4.12. A.1-C2. A1, BL weighted by abundance at Welwick 2011. A2, BL weighted by biomass at Welwick 2011. B1, BL weighted by abundance at Paull 2011. B2, BL weighted by biomass at Paull 2011. C1, BL weighted by abundance at Alkborough 2011. C2, BL weighted by biomass at Alkborough 2011. See Table 3.1 for traits coding.

### Longevity (L)

At Welwick, for the trait Longevity (L) there was a change in trait composition across the elevation gradient for both data sets. For abundance-weighted data the main difference between bands was the modality L/<6mth, which was represented on the upper shore but not at <2.4 m elevation. For biomass-weighted data the change between elevation bands was distinct with the <2.4 m band being dominated by L/>5yrs, which was expressed in much

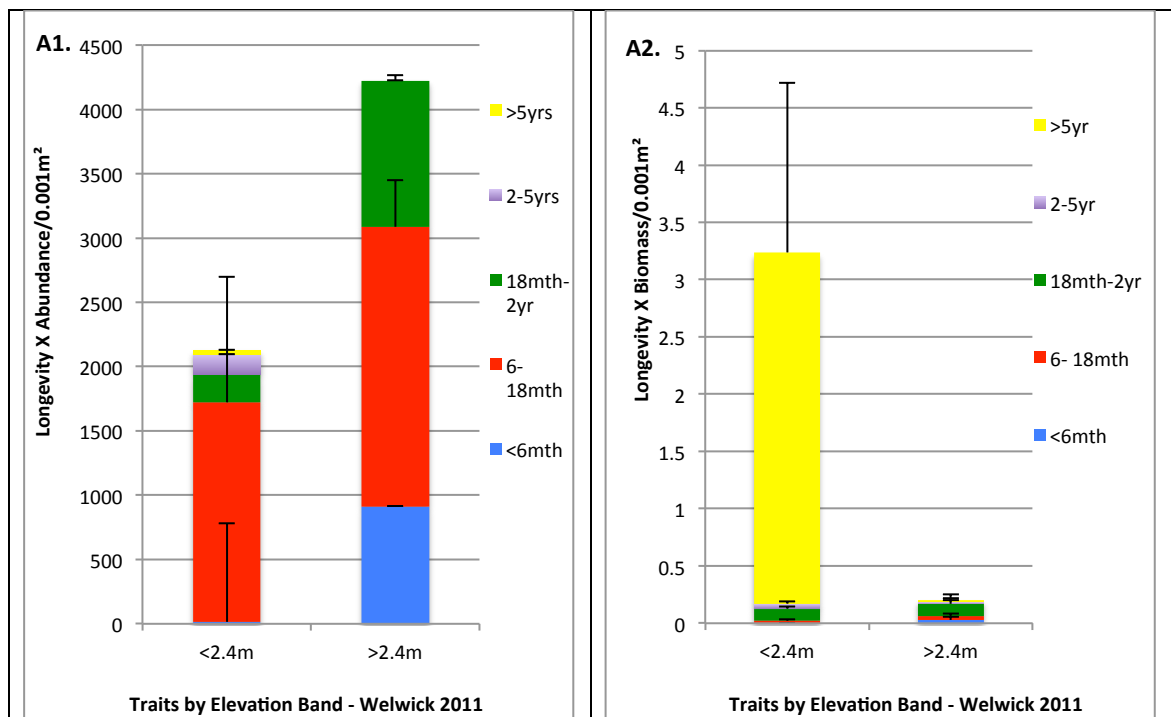
smaller amounts on the upper shore. At Alkborough both data sets show a clear distinction between elevation bands. The <2.4 m band was dominated almost entirely by L/18mth-2yrs, compared to a range of modalities on the upper shore. There was no distinct pattern at Paull.

### Longevity x Abundance

PERMANOVA results for L, in terms of abundance, indicated a change in trait expression along the salinity gradient ( $p < 0.01$  and  $F = 20.66$ ) and elevation gradient ( $p < 0.01$  and  $F = 4.42$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of L expression ( $p < 0.01$ ). There was a significant difference in trait expression between Paull and Welwick in the >2.4 m band ( $p < 0.01$ ), but not in the <2.4 m band. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.01$ ) and Welwick ( $p < 0.01$ ), and also at Paull ( $p < 0.05$ ).

### Longevity x Biomass

PERMANOVA results were also significant for L, in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 15.56$ ) and elevation bands ( $p < 0.05$  and  $F = 3.4$ ). Tests to compare sites within each elevation band (<2.4m or >2.4m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of L expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the <2.4m band ( $p < 0.05$ ), but not in the >2.4m band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ) and Alkborough ( $p < 0.01$ ), but not at Paull.



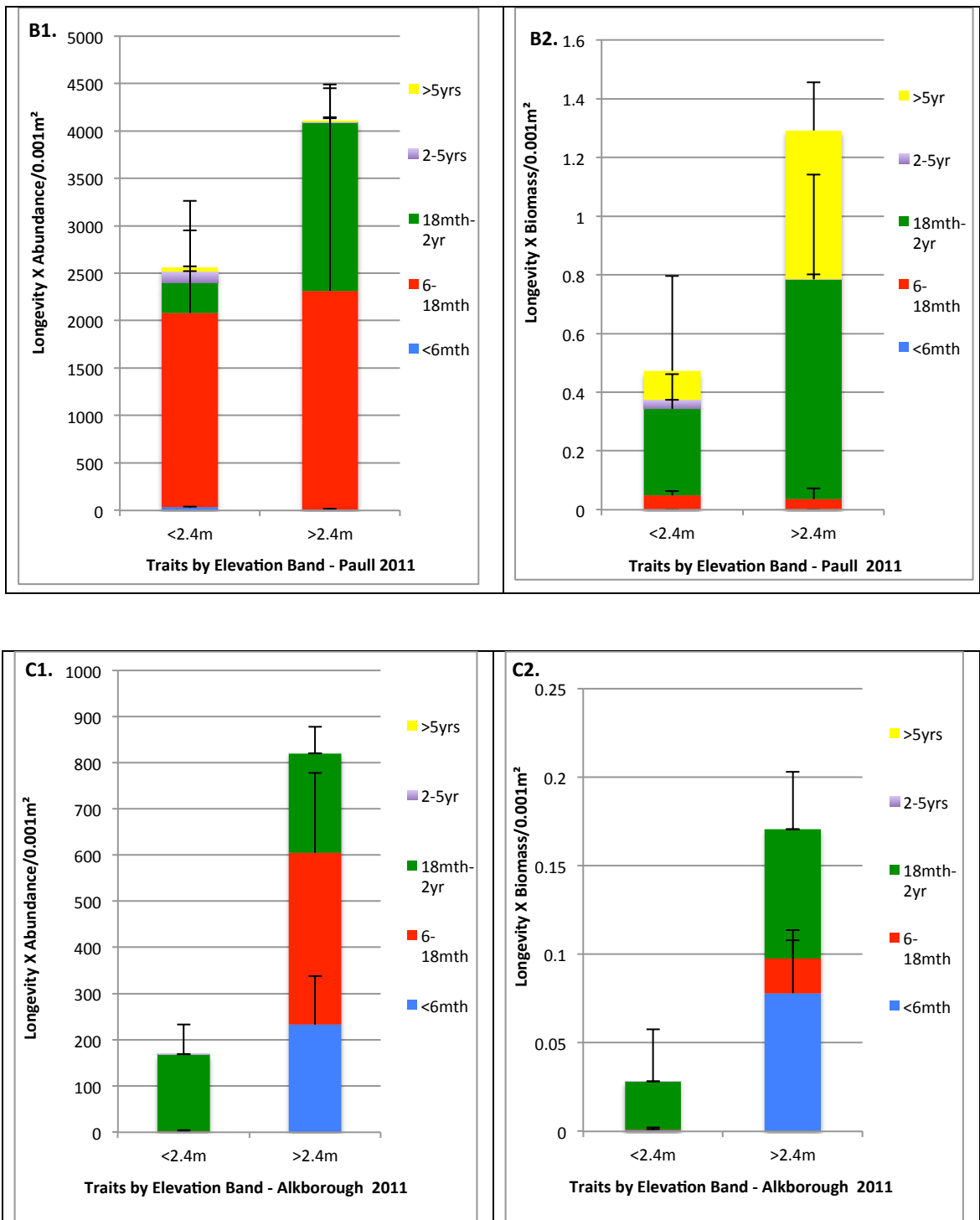


Fig. 4.4.13. A.1-C2. A1, L weighted by abundance at Welwick 2011. A2, L weighted by biomass at Welwick 2011. B1, L weighted by abundance at Paull 2011. B2, L weighted by biomass at Paull 2011. C1, L weighted by abundance at Alkborough 2011. C2, L weighted by biomass at Alkborough 2011. See Table 3.1 for traits coding.

### ***Salinity Preference (S)***

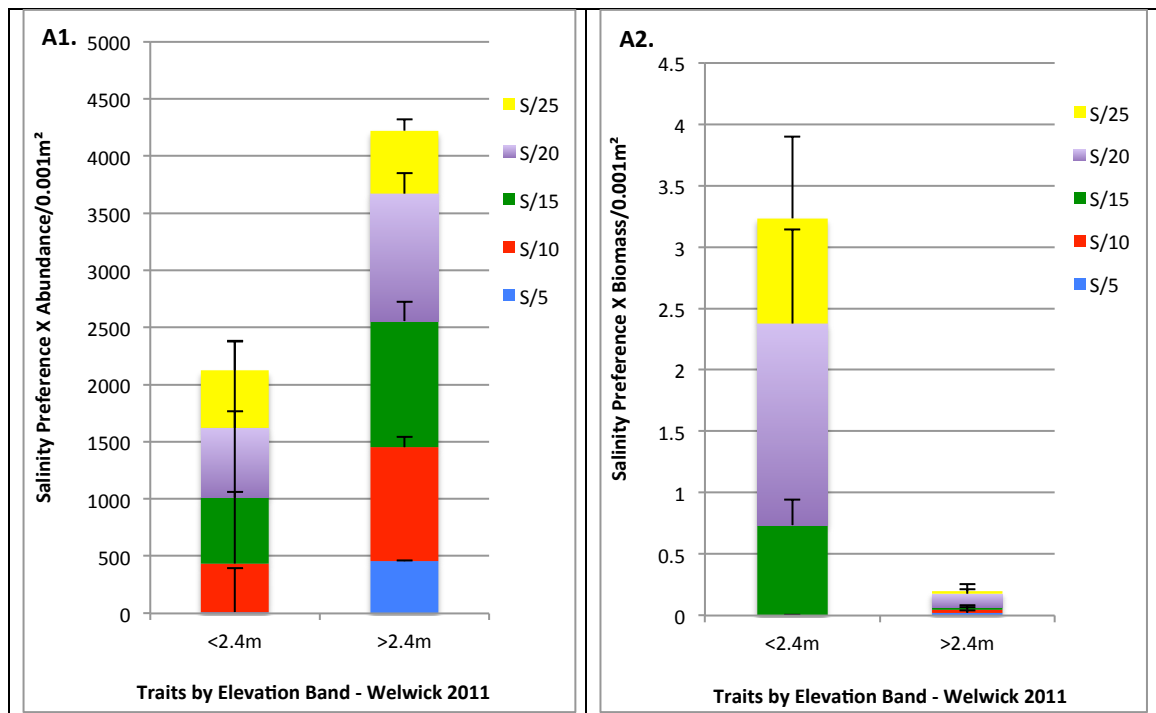
At Welwick the strongest distinction between elevation bands was in the biomass-weighted data, showing much higher expression of S/25 (S/20-25) and S/20 (S/15-20) on the lower shore compared to the >2.4m elevation band. At Paull no pattern in trait composition was visually apparent. At Alkborough both data sets showed a clear difference between elevation bands with S/5 (S/1-5) strongly expressed on the upper shore and absent on the lower shore.

### Salinity Preference x Abundance

PERMANOVA results for the trait S, in terms of abundance, indicated a change in trait expression between sites ( $p < 0.01$  and  $F = 40.35$ ) and elevation bands ( $p < 0.05$  and  $F = 3$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m), indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of S expression ( $p < 0.01$ ). There was no significant difference in trait expression between Paull and Welwick in either elevation band. Within each site a significant difference was found between the upper and lower shore at Alkborough ( $p < 0.01$ ) and Welwick ( $p < 0.05$ ), but not at Paull.

### Salinity Preference x Biomass

PERMANOVA results were also significant for S, in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 15.56$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m) indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of S expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the <2.4 m band ( $p < 0.01$ ), but not in the >2.4 m band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ) and Alkborough ( $p < 0.01$ ), but not at Paull.





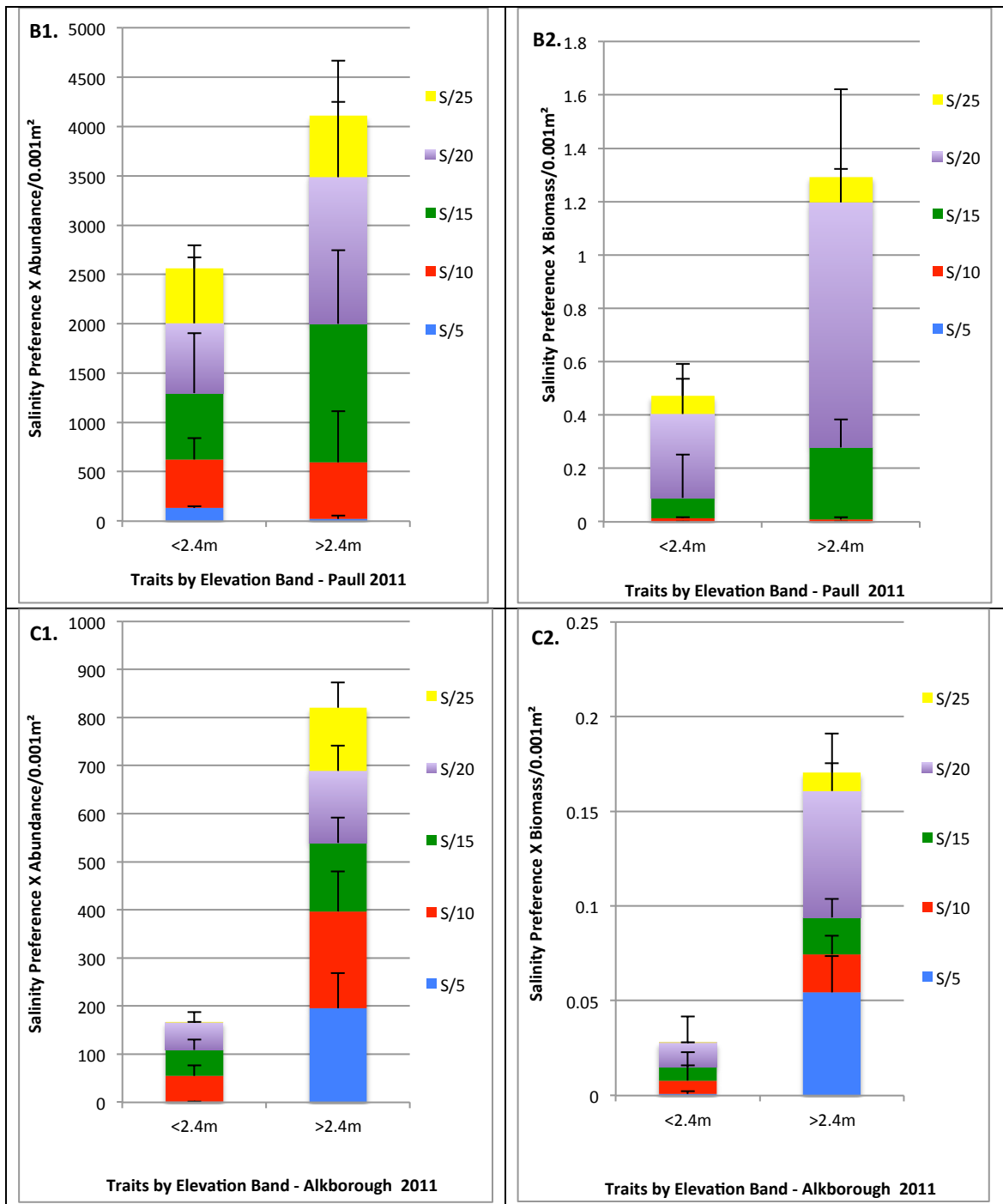


Fig. 4.4.14. A.1-C2. A1, S weighted by abundance at Welwick 2011. A2, S weighted by biomass at Welwick 2011. B1, S weighted by abundance at Paull 2011. B2, S weighted by biomass at Paull 2011. C1, S weighted by abundance at Alkborough 2011. C2, S weighted by biomass at Alkborough 2011. See Table 3.1 for traits coding.

### **Fecundity (F)**

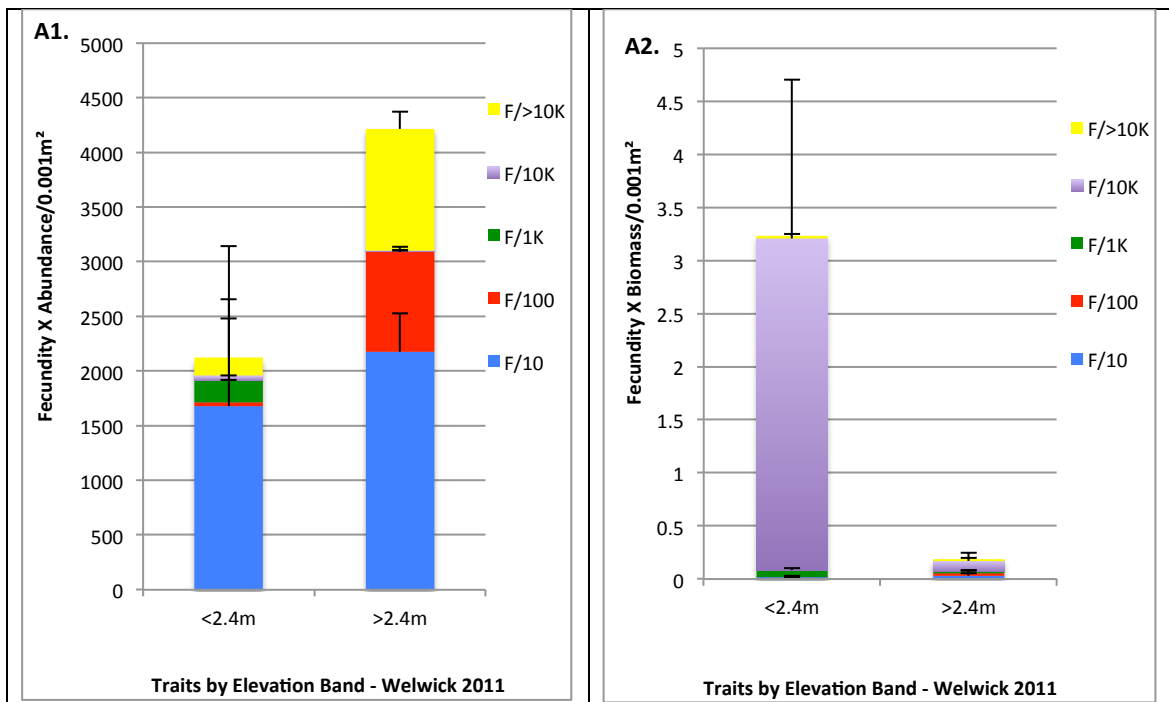
For the trait Fecundity (F) Welwick showed change between upper and lower shore with the modality F/>10K (Number of Eggs >10k) being expressed at much higher proportions on the upper shore than the lower shore for abundance-weighted data (Fig 4.3.11 A1). This was also the case at Paull (Fig 4.3.11 B2). At Alkborough both biomass and abundance-weighted data indicated a change in trait composition between elevation bands with the differentiating trait F/1k (Number of Eggs 1000), dominating on the lower shore but absent at >2.4 m elevation.

### Fecundity x Abundance

PERMANOVA results were significant for F in terms of abundance, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 17.667$ ) and elevation bands ( $p < 0.01$  and  $F = 6.2318$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m) indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of F (Fecundity) expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the >2.4 m band ( $p < 0.05$ ), but not in the <2.4 m band. Within each site a significant difference was found between the upper and lower shore at Welwick and Alkborough ( $p < 0.01$ ), and also at Paull ( $p < 0.05$ ).

### Fecundity x Biomass

PERMANOVA results were also significant for F in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 14.59$ ) and elevation bands ( $p < 0.05$  and  $F = 3.16$ ). Tests to compare sites within each elevation band (<2.4 m or >2.4 m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of F (Fecundity) expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the <2.4m band ( $p < 0.01$ ), but not in the >2.4 m band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ) and Alkborough ( $p < 0.01$ ), but not at Paull.



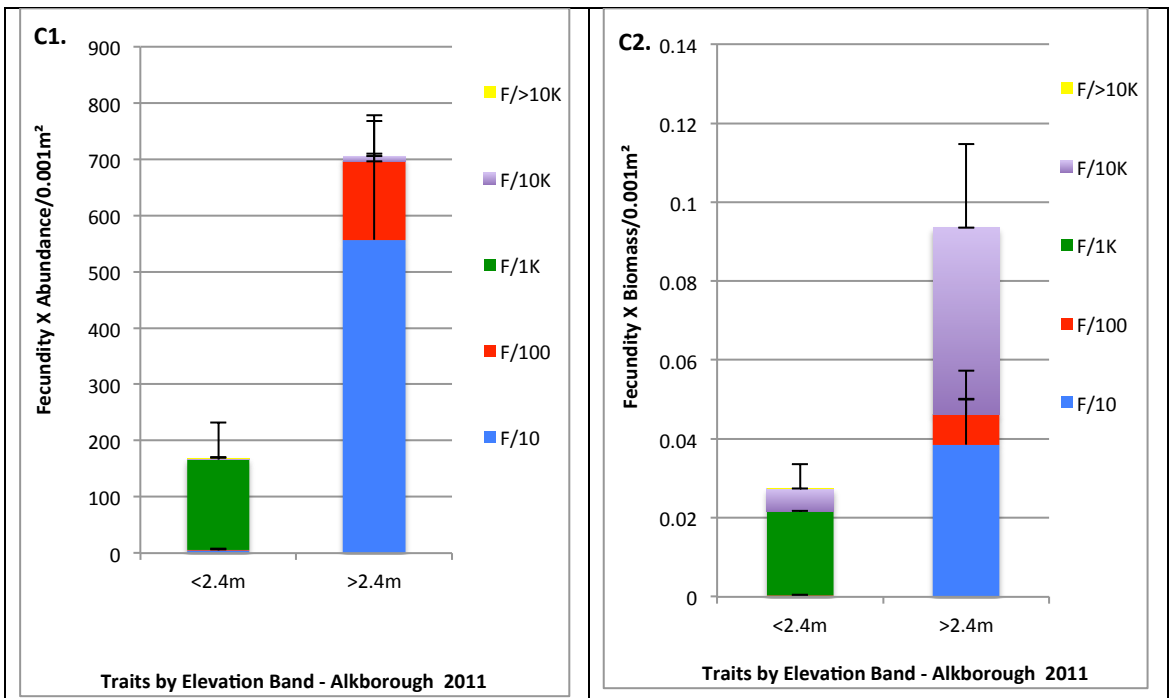
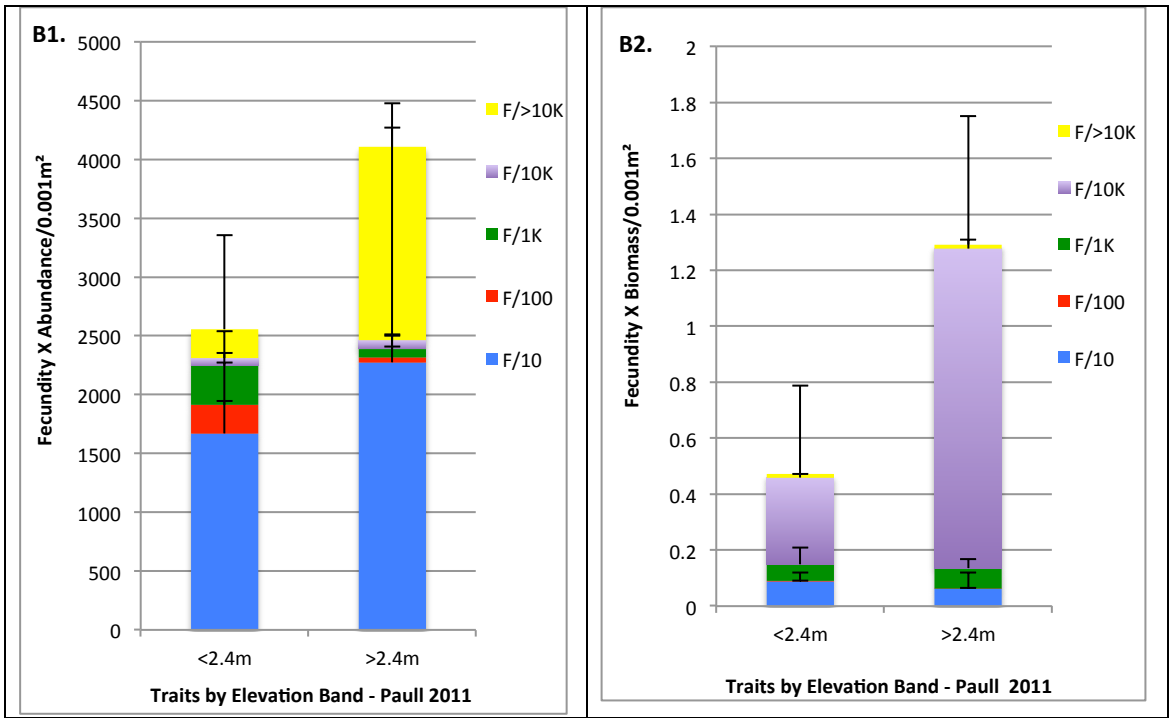


Fig. 4.4.15. A.1-C2. A1, F by abundance at Welwick 2011. A2, F by biomass at Welwick 2011. B1, F by abundance at Paull 2011. B2, F by biomass at Paull 2011. C1, F by abundance at Alkborough 2011. C2, F by biomass at Alkborough 2011. See Table 3.1 for traits coding.

### Reproductive Frequency (RF)

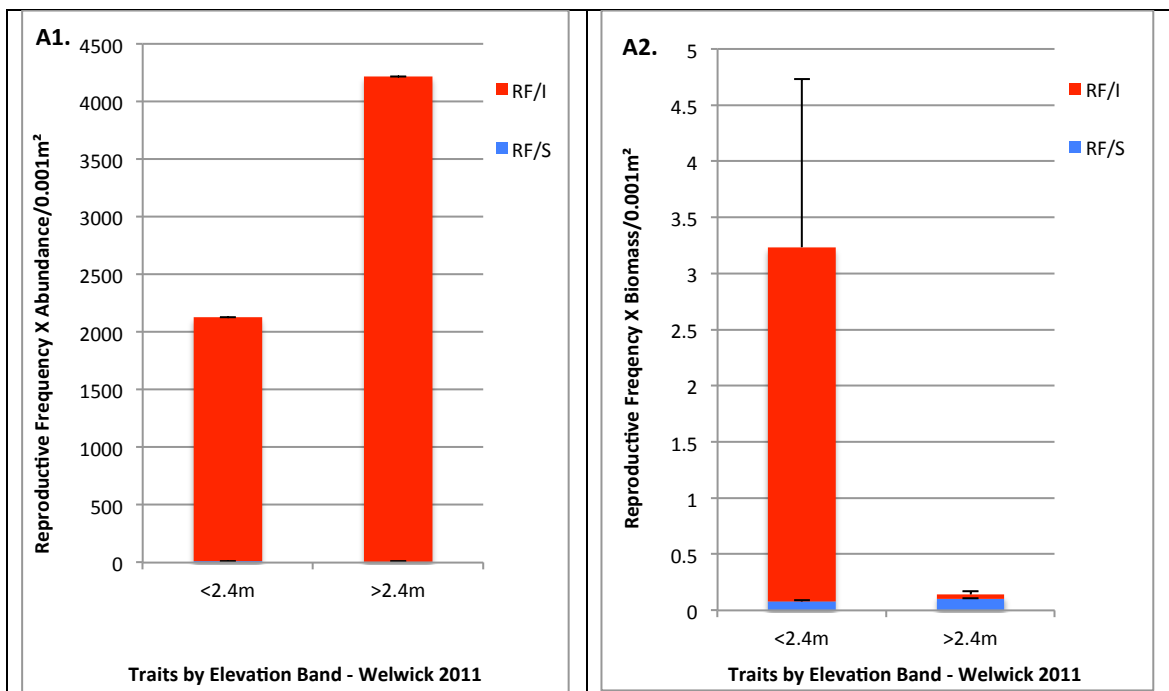
For the trait RF there was no clear visual pattern in either biomass or abundance-weighted data sets at both Paull and Welwick (Fig 4.4.12 A1-B2). At Alkborough a clear pattern was discernable, as the <2.4m elevation band was almost completely dominated by the modality RF/S (RF/Semelparous) and the >2.4m band largely dominated by the modality RF/I (RF/Iteroparous).

### **Reproductive Frequency x Abundance**

PERMANOVA results were significant for RF in terms of abundance, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 30.11$ ) and elevation bands ( $p < 0.01$  and  $F = 6.2$ ). Tests to compare sites within each elevation band (<2.4m or >2.4m) indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of RF (Reproductive Frequency) expression ( $p < 0.01$ ). There was no significant difference between Paull and Welwick in either band. Within each site a significant difference was found between the upper and lower shore at Welwick and Alkborough ( $p < 0.01$ ), but not at Paull.

### **Reproductive Frequency x Biomass**

PERMANOVA results were also significant for RF in terms of biomass, indicating a change in trait between sites ( $p < 0.01$  and  $F = 18.725$ ) and elevation bands ( $p < 0.05$  and  $F = 4.1236$ ). Tests to compare sites within each elevation band (<2.4m or >2.4m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of RF (Reproductive Frequency) expression ( $p < 0.01$ ). There was also a significant difference between Paull and Welwick in both the <2.4m and >2.4m elevation band ( $p < 0.05$ ). Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ) and Alkborough ( $p < 0.01$ ), but not at Paull.



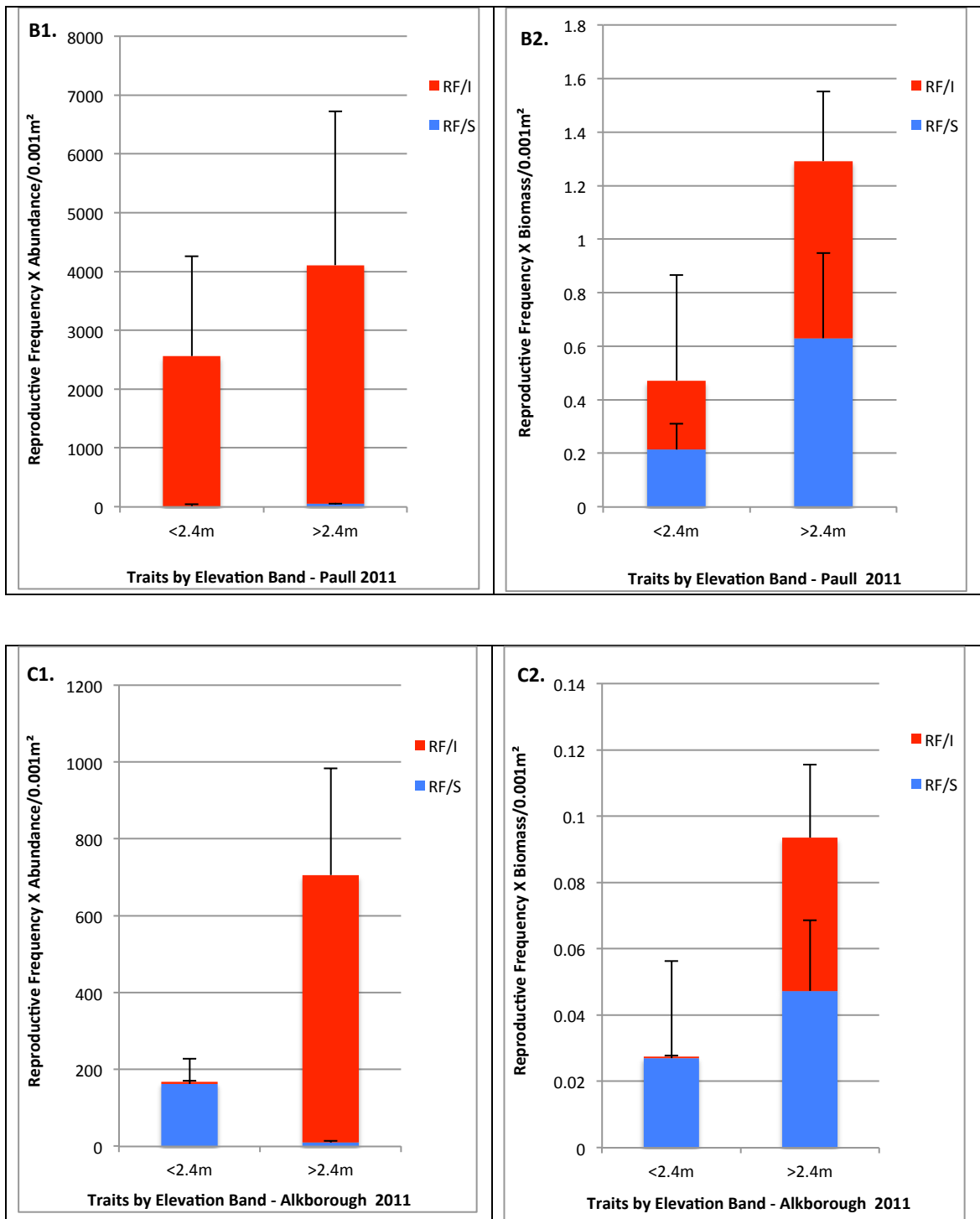


Fig. 4.4.16. A.1-C2. A1, RF weighted by abundance at Welwick 2011. A2, RF weighted by biomass at Welwick 2011. B1, RF weighted by abundance at Paull 2011. B2, RF weighted by biomass at Paull 2011. C1, RF weighted by abundance at Alkborough 2011. C2, RF weighted by biomass at Alkborough 2011. See Table 3.1 for traits coding.

**Age at Maturity (M)**

For the trait Age at Maturity (M) Welwick showed a distinction between upper and lower shore for both abundance and biomass-weighted data sets. In the abundance-weighted data modality causing the distinction was  $M/\geq 6\text{mth}$ , which was expressed in much higher proportions at >2.4 m compared to <2.4 m. In the biomass-weighted data at Welwick  $M/1\text{-}2\text{yrs}$  was expressed strongly at <2.4 m and minimally at >2.4 m. There was no obvious trend in either data set at Paull, but at Alkborough there was a clear separation between <2.4 m and >2.4m for both data sets. For abundance weighted data >2.4 m was dominated by  $M/<6\text{mths}$

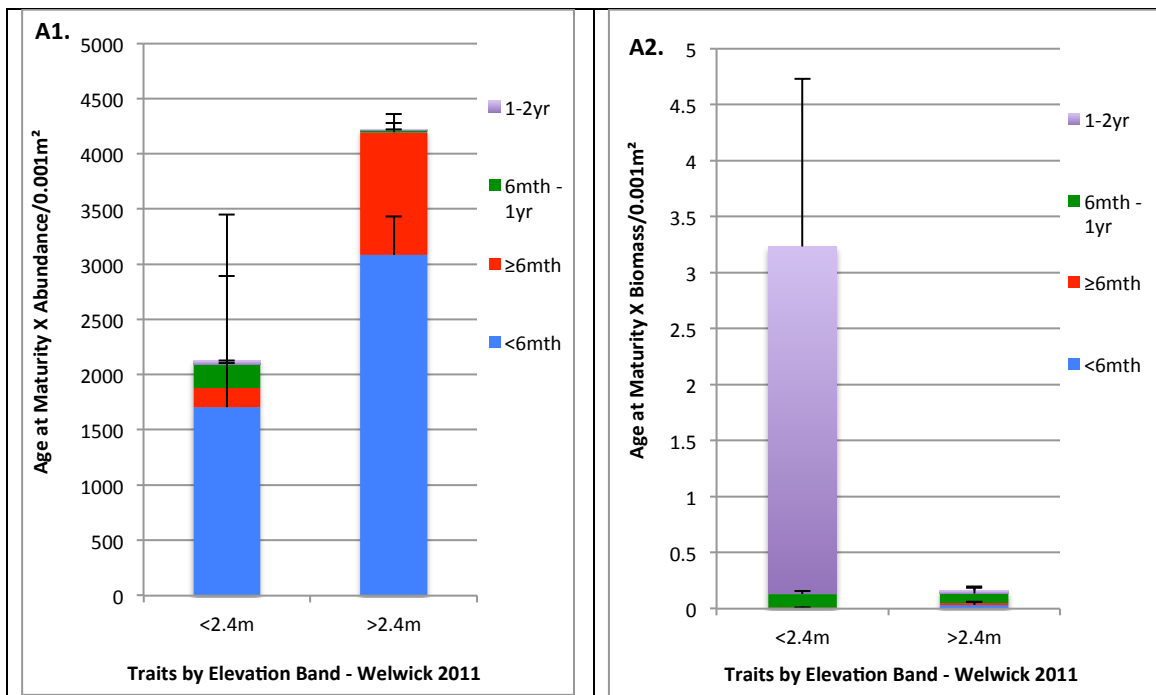
while at <2.4m M/1-2yrs dominated trait expression. For biomass-weighted data at Alkborough the pattern was similar but the dominant modalities (M/<6mths on the upper shore and M/1-2yrs on the lower shore) were present alongside a wider range of other modalities (Fig 4.4.17 C1 and C2).

### Age at Maturity x Abundance

PERMANOVA results were significant for M in terms of abundance, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 21.2$ ) and elevation bands ( $p < 0.01$  and  $F = 7.91$ ). Tests to compare sites within each elevation band (<2.4m or >2.4m), indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of M expression ( $p < 0.01$ ). There was a significant difference between Paull and Welwick in the >2.4m band ( $p < 0.05$ ), but not in the <2.4m band. Within each site a significant difference was found between the upper and lower shore at Welwick and Alkborough ( $p < 0.01$ ), but not at Paull.

### Age at Maturity x Biomass

PERMANOVA results were also significant for M in terms of biomass, indicating a change in trait expression between sites ( $p < 0.01$  and  $F = 13.99$ ) and elevation band ( $p < 0.05$  and  $F = 3.02$ ). Tests to compare sites within each elevation band (<2.4m or >2.4m), along the salinity gradient, indicated that, for both elevation bands, Alkborough was significantly different from Paull and Welwick in terms of M expression ( $p < 0.01$ ). There was also a significant difference between Paull and Welwick in the <2.4m band ( $p < 0.01$ ) but not in the >2.4m elevation band. Within each site a significant difference was found between the upper and lower shore at Welwick ( $p < 0.01$ ) and Alkborough ( $p < 0.01$ ), but not at Paull.



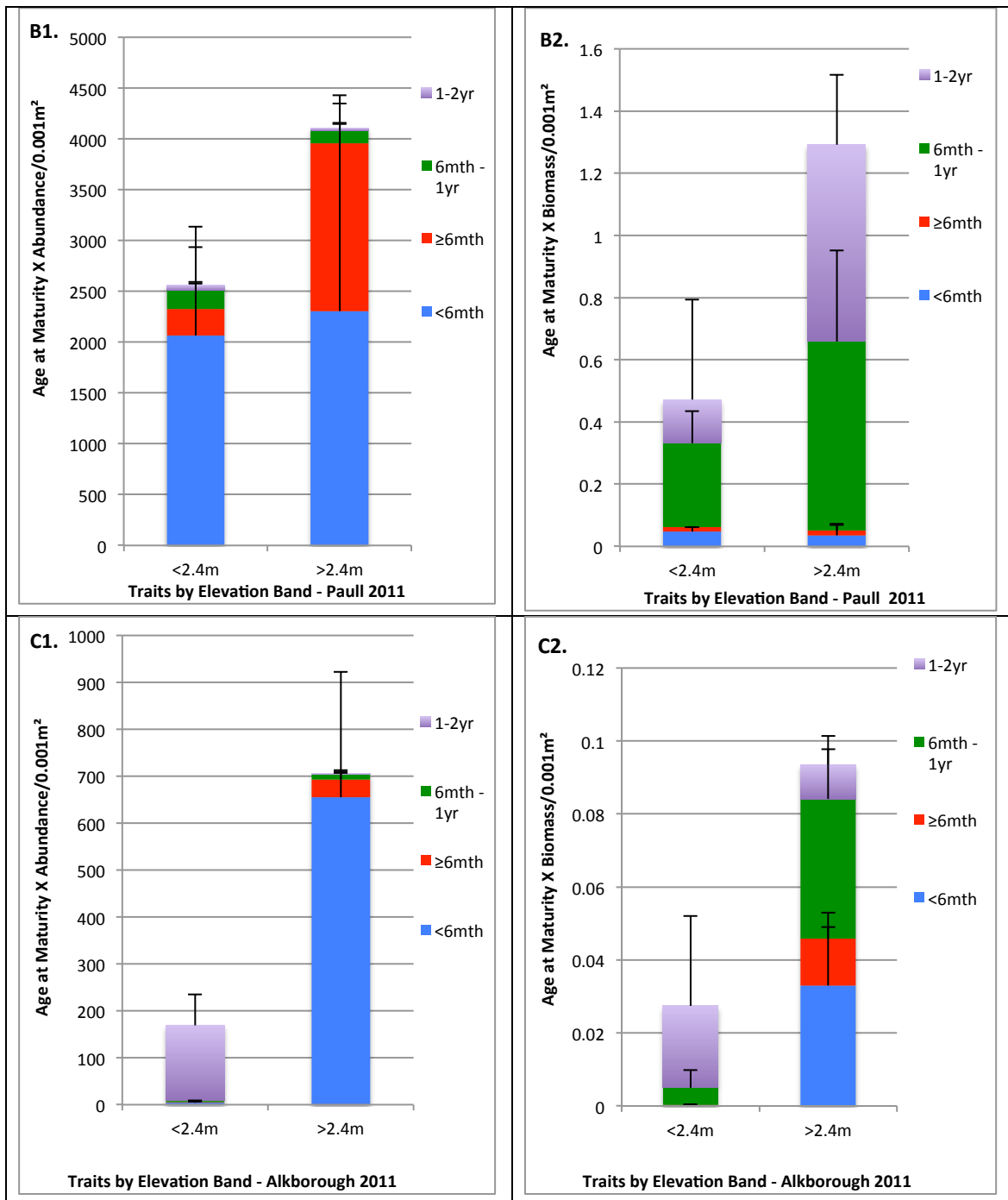


Fig. 4.4.17. A.1-C2. A1, M by abundance at Welwick 2011. A2, M by biomass at Welwick 2011. B1, M by abundance at Paull 2011. B2, M by biomass at Paull 2011. C1, M by abundance at Alkborough 2011. C2, M by biomass at Alkborough 2011. See Table 3.1 for traits coding.

## Alkborough Elevation Detail: Univariate

### Feeding Method (FM)

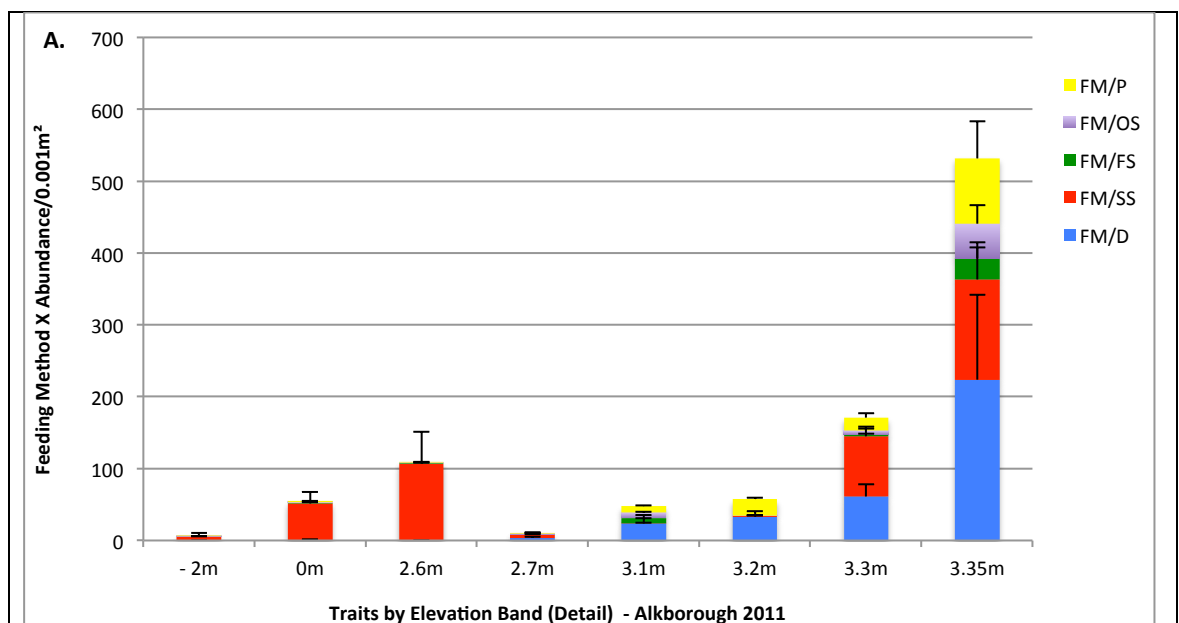
Traits expression along the elevation gradient showed changes for both biomass and abundance weighted data, particularly between stations above and below the 3 m elevation band. In the bands below 3 m there was a tendency in both data sets towards FM/SS (Feeding Method/Subsurface Deposit) being expressed and a marked decline in expression of FM/D (FM/Deposit Feeder -Surface). The higher shore bands also showed a wider array of FM modalities, with less variation below 3m.

### Feeding Method x Abundance

PERMANOVA results were significant for FM in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 3.95$ ). Tests indicated that a significant difference in trait expression existed between 14 pairs of bands. These were mainly bands that were at quite different elevations such as 3.35 m/2.6 m; 3.35 m/-2 m; 3.35 m/0 m, and 3.3 m/0 m, but some were in close proximity and still significantly difference, such as bands 3.1 m/ -2 m; 3.2 m/2.6 m; 2.7 m /2.6 m; 2.7 m ( $p < 0.05$ ).

### Analysis of Variance – Weighted by Biomass

PERMANOVA results were significant for FM in terms of biomass, indicated a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 2.54$ ). Tests indicated that a significant difference in trait expression existed between 14 pairs of bands: 0 m/2.7 m; 0 m/-2 m; 3.35 m/2.7 m; 3.35 m/2.6 m; 3.35 m/-2 m; 3.1 m/3.2 m; 3.1 m/2.7 m; 3.1 m/2.6 m; 3.1 m/-2 m; 3.3 m/2.7 m; 3.2 m/2.7 m; 3.2 m/-2 m; 2.7 m/2.6 m; and 2.7 m/-2 m, all at  $p < 0.05$ .





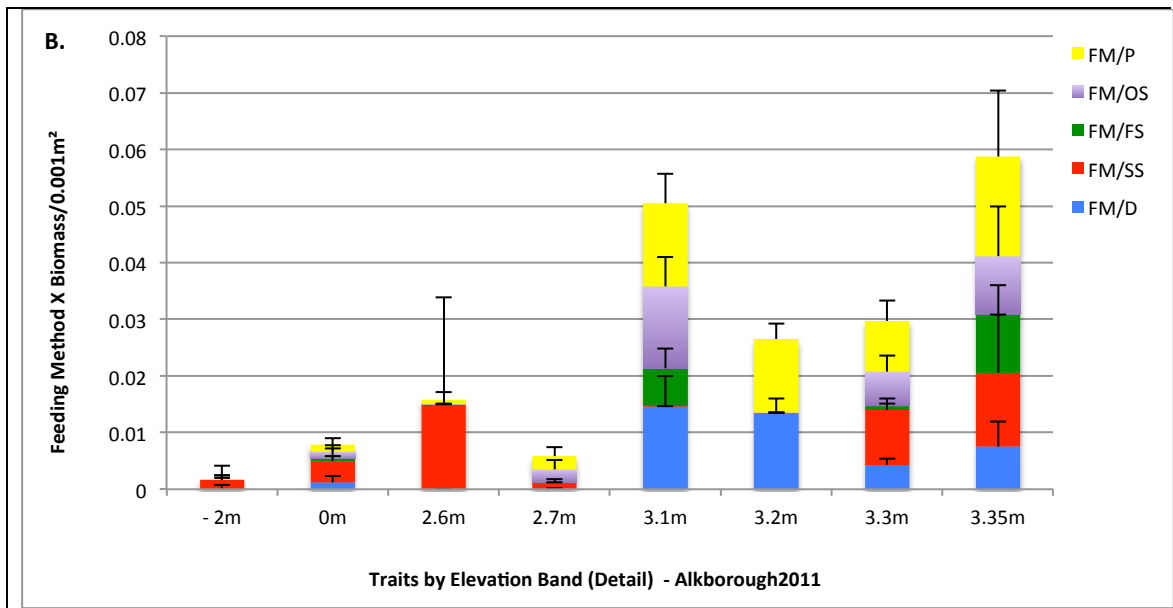
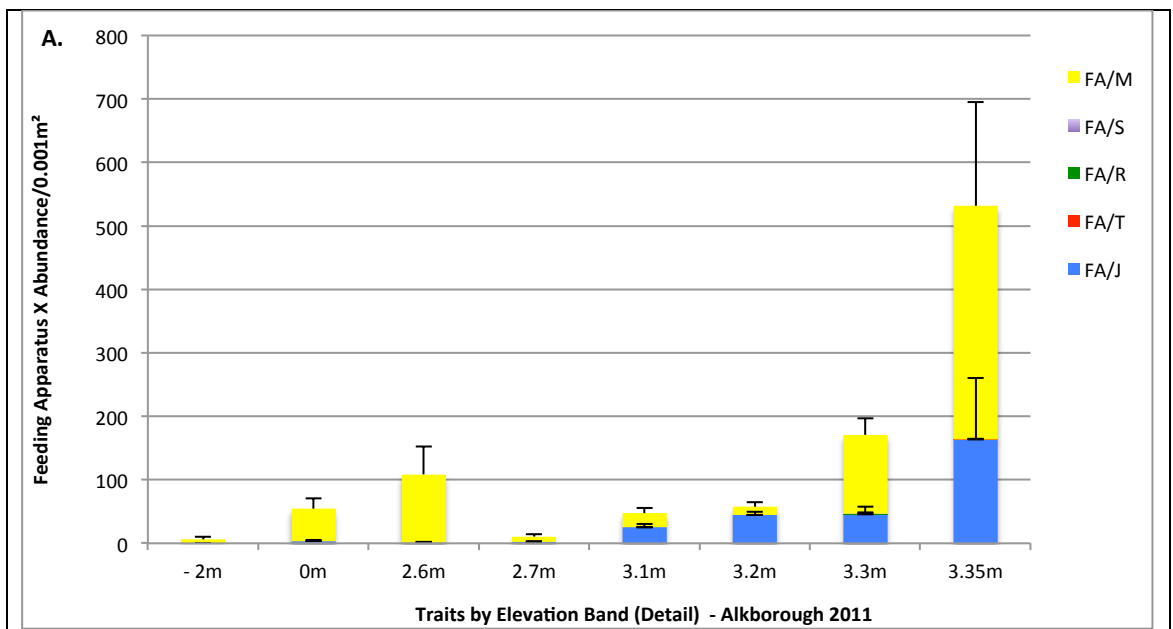


Fig 4.4.18 A-B. A, FM by abundance at Alkborough 2011 across eight elevation bands. B, FM by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Feeding Apparatus (FA)

Trait expression changed along the elevation gradient for both abundance and biomass weighted data. Abundance-weighted data showed a more distinct separation between elevation bands below 3m, where a clear change is seen from expression of FA/M (FA/Simple Mouth) and FA/J (FA/Jaws or Mandibles), to dominance by FA/M (FA/Simple Mouth) only.



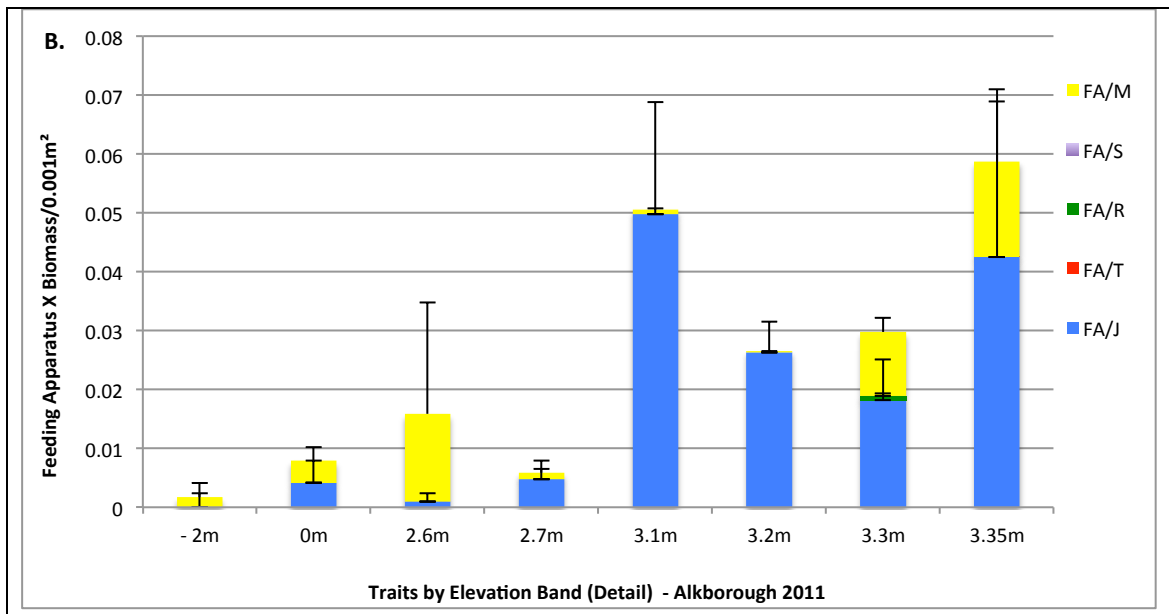


Fig 4.4.19 A-B. A, FA weighted by abundance at Alkborough 2011 across eight elevation bands. B, FA weighted by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Feeding Apparatus x Abundance

PERMANOVA results were significant for FA in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 3.4488$ ). Tests indicated that a significant difference in trait expression existed between 13 pairs of bands: 3.35 m /2.6 m; 3.35/0 m; 3.3 m/2.6 m; 3.3 m/0 m; 3.35 m/-2 m; 3.3 m/-2 m; 3.2 m/0 m; 3.2 m/-2 m and 2.7 m/0 m at  $p = 0.01$ . The pairs 3.1 m/0 m; 3.2 m/2.6 m; 2.7 m/2.6 m and 2.7 m/-2 m all returned  $p < 0.05$ .

### Feeding Apparatus x Biomass

PERMANOVA results were significant for FA in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 2.0484$ ). Tests indicated that a significant difference in trait expression existed between 8 pairs of bands: 3.35 m/2.6 m; 3.35 m/-2 m; 3.1 m/2.7 m; 3.3 m/-2 m; 3.2 m/2.7 m; 3.2 m/-2 m; 2.7 m/2.6 m and 2.7 m/-2 m all at  $p < 0.05$

### Food Type (FT)

Both sets of data indicated a change in trait expression along the elevation gradient, particularly between stations above and below 2.7 m. The most noticeable trend was the dominance of the modality FT/D (Food Type/Detritus) at the lower end of the elevation gradient (-2 m, 0 m and 2.6 m), when compared to the rest of the gradient. The middle shore around 3.2 m-3.3 m showed a distinct rise in the expression of FT/B (FT/Bacteria) compared to other bands in the gradient, for both data sets.

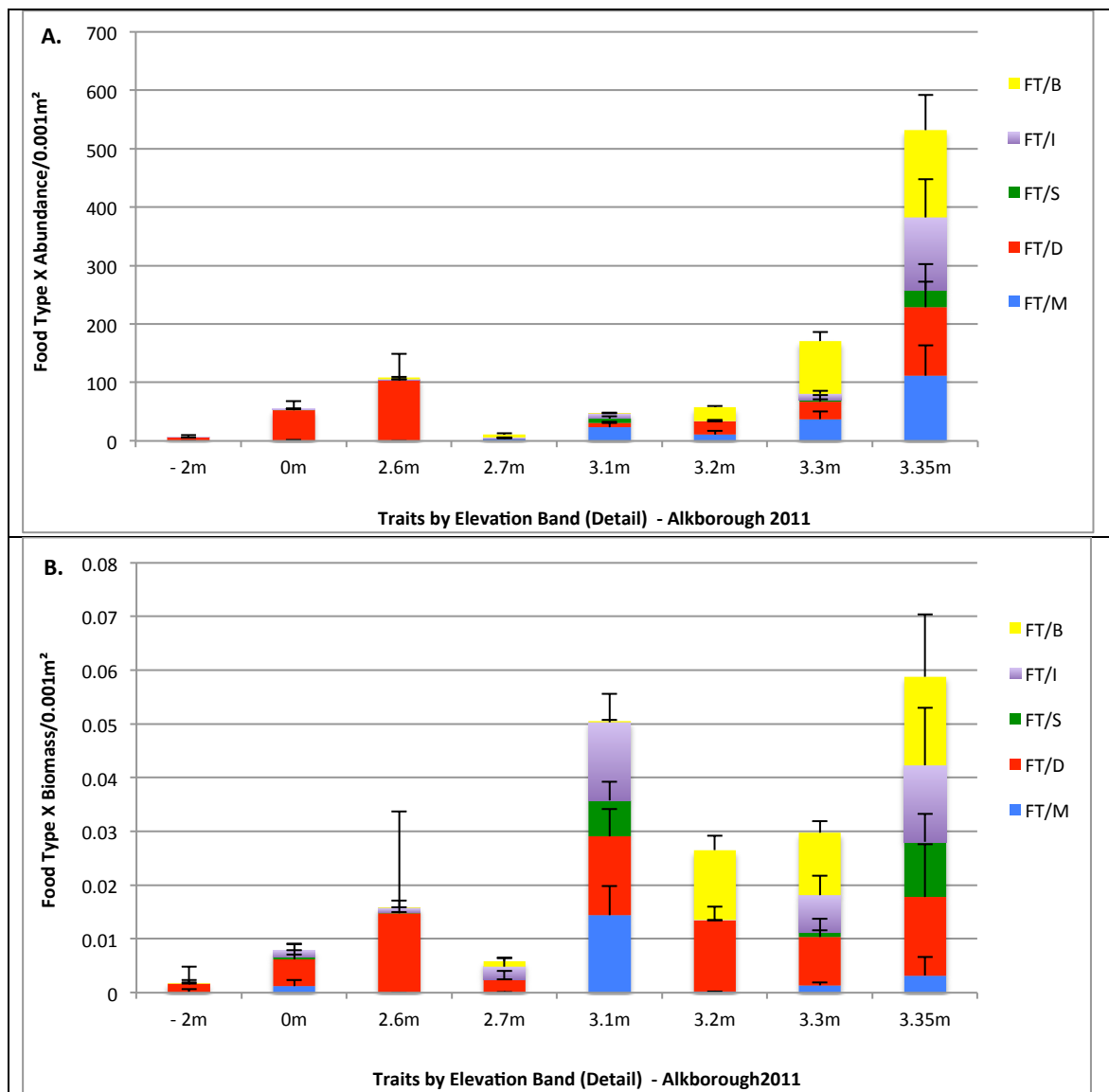


Fig 4.4.20 A-B. A, FT by abundance at Alkborough 2011 across eight elevation bands. B, FT by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Food Type x Abundance

PERMANOVA results were significant for FT in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 3.0534$ ). Tests indicated that a significant difference in trait expression existed between 11 pairs of bands: 3.35 m/0 m; 3.3 m/0 m; 3.35 m/2.6 m; 3.35 m/-2 m and 3.3 m/2.6 m at  $p = < 0.01$ . The pairs 3.1 m/0 m; 3.3 m/-2 m; 3.2 m/2.6 m; 3.2 m/-2 m; 2.7 m/2.6 m and 2.7 m/-2 m all returned  $p$ -values of  $< 0.05$ .

### Food Type x Biomass

PERMANOVA results were significant for FT in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 2.452$ ). Tests indicated that a significant difference in trait expression existed between 15 pairs of bands: 3.35 m/2.7 m; 3.1 m/-2 m; 3.3 m/2.7 m; 3.3 m/-2 m; 3.2 m/2.6 m; 3.2 m/-2 m and 2.7 m/-2 m at  $p < 0.01$ . The pairs 0 m/2.7 m; 3.35 m/-2 m; 3.1 m/3.2 m; 3.1 m/2.7 m; 3.3 m/2.6 m, 3.3 m/2.6 m; 3.2 m/2.7 m and 2.7 m/2.6 m all returned  $p < 0.05$ .

### Adult Mobility (AM)

There was no clear pattern discernable across the eight elevation bands for either biomass or abundance-weighted traits data for AM. Only the elevation band 3.2m (biomass and abundance weighted) stood out as having a higher proportion expression of the modality AM/L (AM/Low) compared to all other elevation bands (Fig 4.3.30).

### Adult Mobility x Abundance

PERMANOVA results were not significant for AM in terms of abundance. Tests indicated no significant difference in trait expression between elevation bands.

### Adult Mobility x Biomass

PERMANOVA results were also not significant for AM in terms of biomass. Tests indicated no significant difference in trait expression between elevation bands.

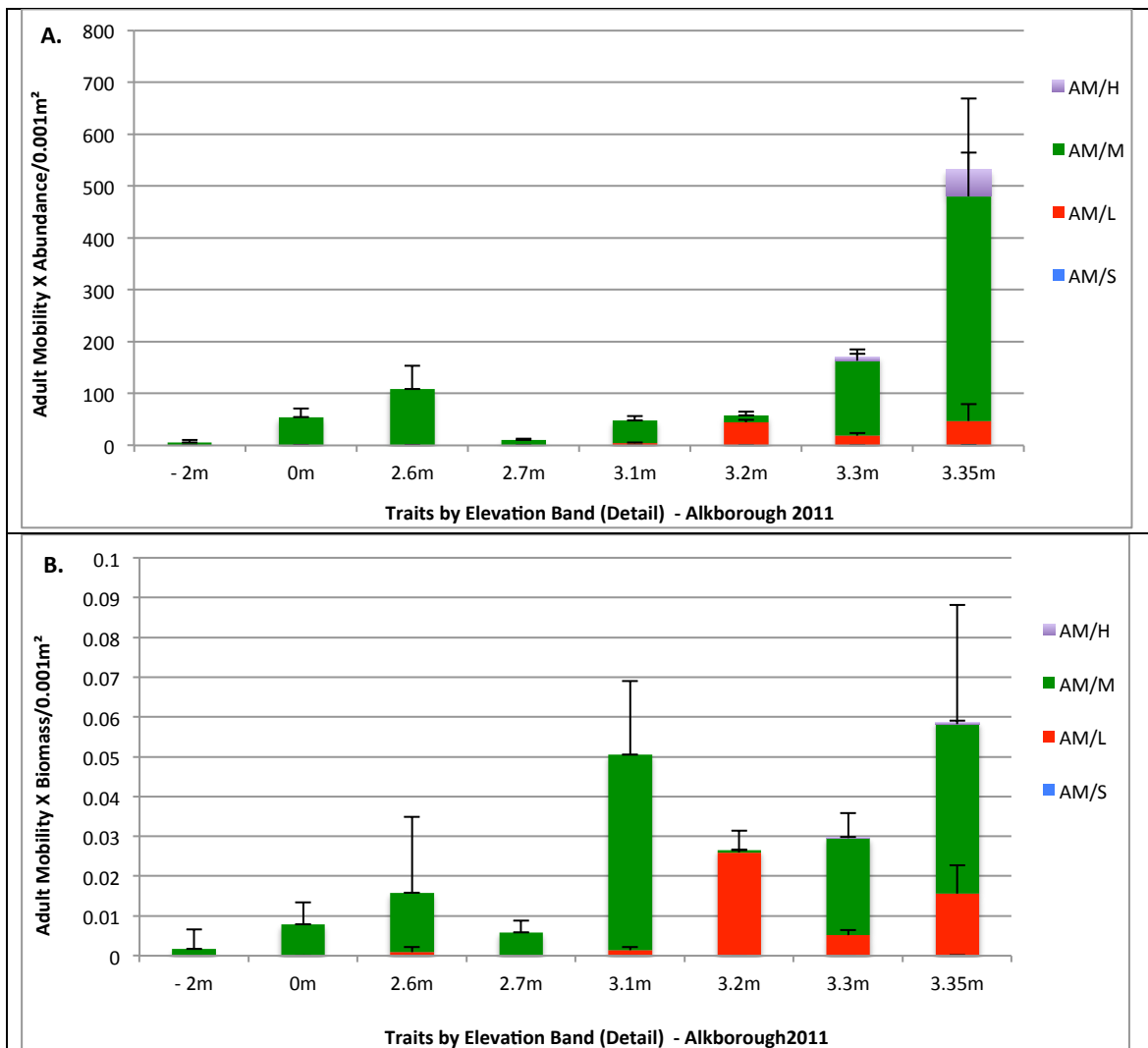


Fig 4.4.21 A-B. A, AM by abundance at Alkborough 2011 across eight elevation bands. B, AM by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Position (Infaunal/Epifaunal)

There were changes in trait expression visible along the elevation gradient for both biomass and abundance-weighted data for Position (P). The most noticeable difference was between bands below 2.7 m and those including and above 2.7 m. In the lower set of band the modality P/E (P/Epifaunal) was absent, while in the higher elevation set of bands there was a mix of P/E and P/I (P/Infaunal).

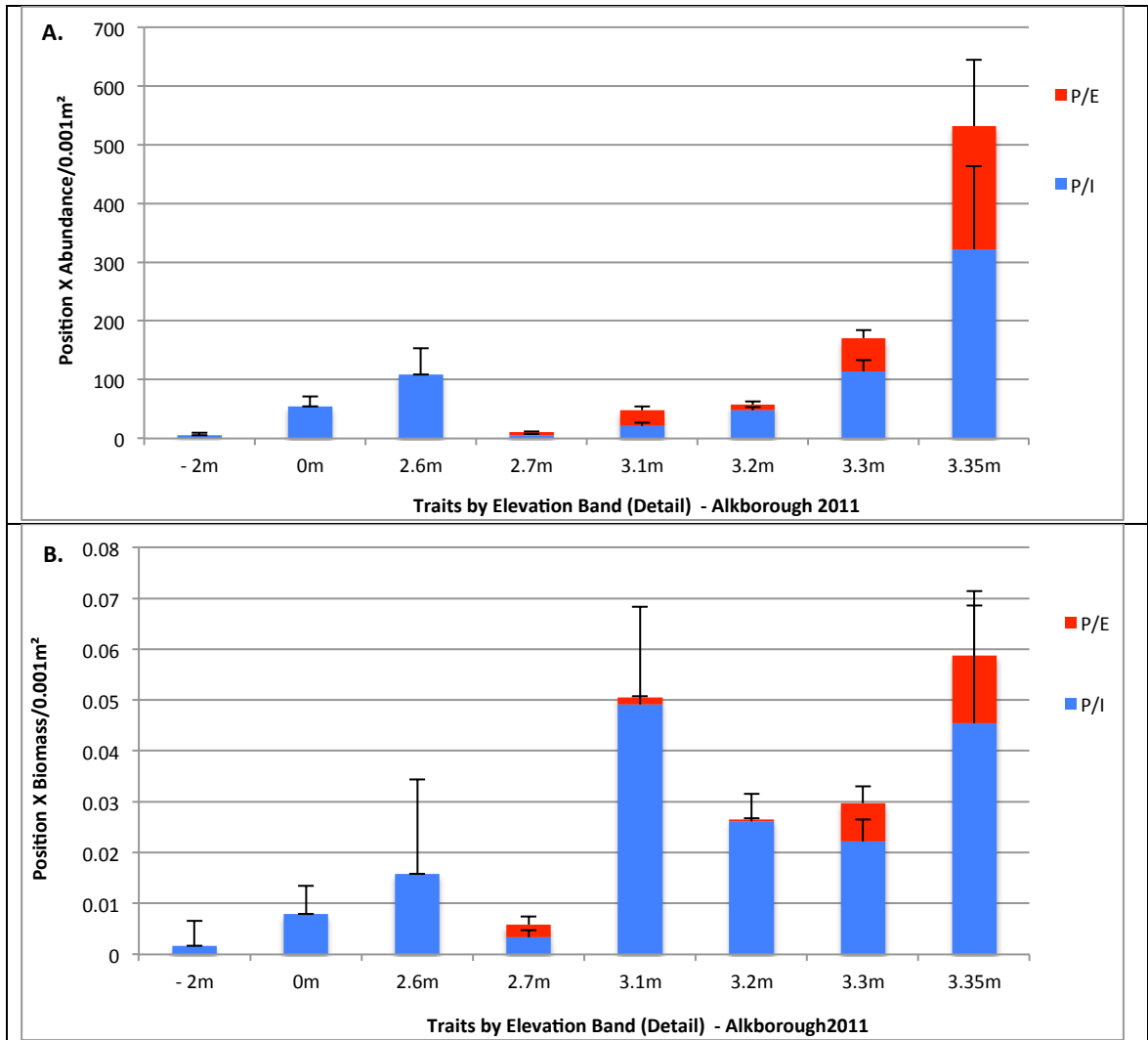


Fig 4.4.22 A-B. A, P by abundance at Alkborough 2011 across eight elevation bands. B, P by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Position x Abundance

PERMANOVA results were significant for P in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 3.5681$ ). Tests indicated that a significant difference in trait expression existed between 11 pairs of bands: 3.35 m/2.6 m; 3.35/0m; 3.3 m/0 m; 3.3 m/2.6 m; 3.35 m/-2 m; 3.1 m/2.6 m; 3.1 m/0 m; 3.3 m/-2 m; 3.3 m/2.6 m; 3.3 m/0 m and 3.2 m/0 m all returned  $p < 0.05$ .

### Position x Biomass

PERMANOVA results were also significant for P in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 2.1071$ ). Tests indicated that a significant difference in trait expression existed between 8 pairs of bands: 3.35 m/2.6 m; 3.35 m/-2 m; 3.1 m/3.2 m; 3.1 m/2.7 m; 3.1 m/2.6 m; 3.1 m/-2 m; 3.3 m/-2 m and 2.7 m/-2 m, all at  $p < 0.05$ .

### Living Habitat (LH)

Abundance-weighted trait data for Living Habitat (LH) showed the modality LH/F (LH/Free Living) dominating the length of the gradient across all eight bands, with no pattern or change apparent. For biomass-weighted data LH/F was still strongly expressed but other modalities dominated some elevation bands, particularly LH/SP (Semi-Permanent Burrow) at 3.1 m, indicating a clear difference between some bands for this trait.

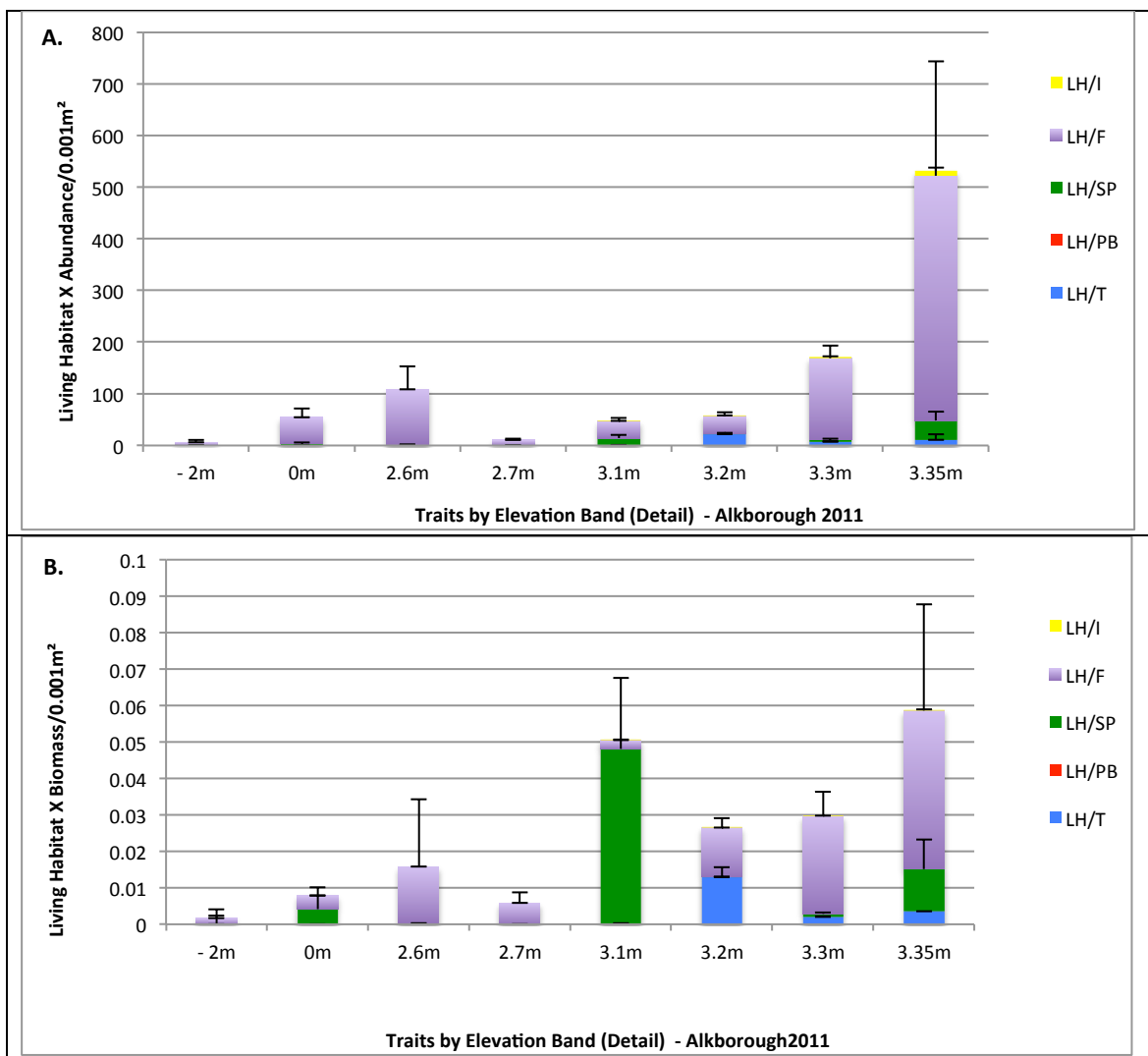


Fig 4.4.23 A-B. A, LH by abundance at Alkborough 2011 across eight elevation bands. B, LH by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Living Habitat - Abundance

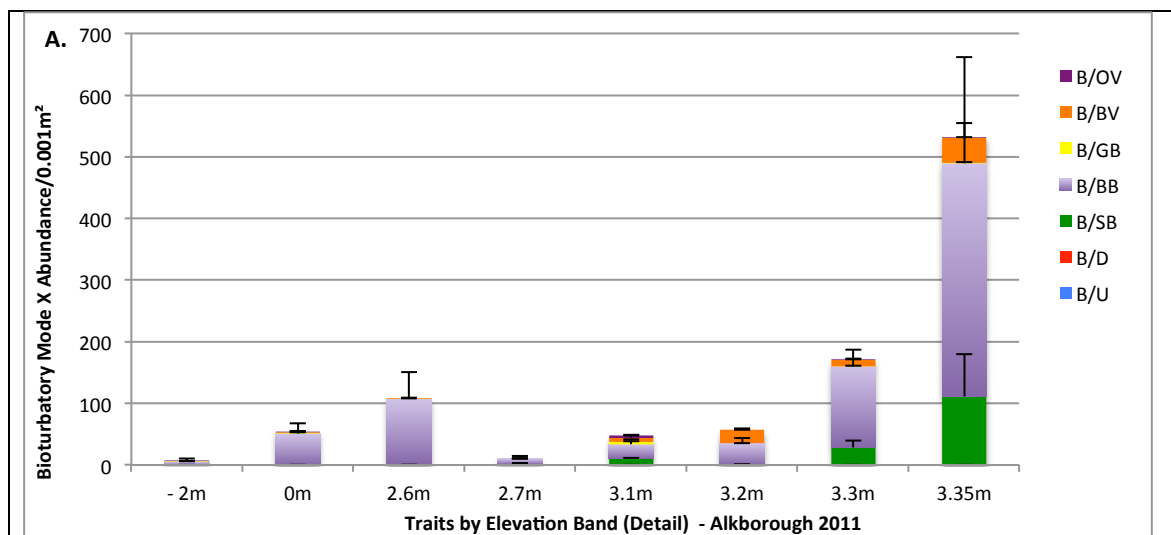
PERMANOVA results were not significant for LH in terms of abundance. Tests indicated no significant difference in trait expression between elevation bands.

### Living Habitat - Biomass

PERMANOVA results were significant for LH in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 2.0052$ ). Tests indicated that a significant difference in trait expression existed between 10 pairs of bands: 3.35m/2.7m; 3.1m/3.2m; 3.1m/2.7m; 3.3m/2.7m; 2.7m/-2m; 0m/3.3m; 3.1m/-2m; 3.2m/2.7m; 3.2m/-2m and 2.7m/2.6m all returned  $p < 0.05$ . At 3.1 m there was dominance by the trait LH/SP. This peak is likely due to the presence of 21 *Hediste diversicolor* at this station, outnumbering those collected at all other stations. This is unlikely to be due to elevation as the species is found at both higher and lower elevations at other sites and is more likely due to random sampling and the naturally patchy distribution of the benthos.

### Bioturbation (B)

For both abundance and biomass –weighted data the trait Bioturbation (B) changed in expression across the elevation gradient at Alkborough. B/BB (B/Burrowing Biodiffuser) dominated almost exclusively at 2.7m and below, for abundance-weighted data, while the upper shore expressed the same modality strongly, but alongside significant contributions from B/SB (B/Surficial Biodiffuser) and B/BV (B/Blind Burrow Ventilator). Biomass-weighted data was more varied across the gradient, with a large number of bands expressing trait composition distinctively.



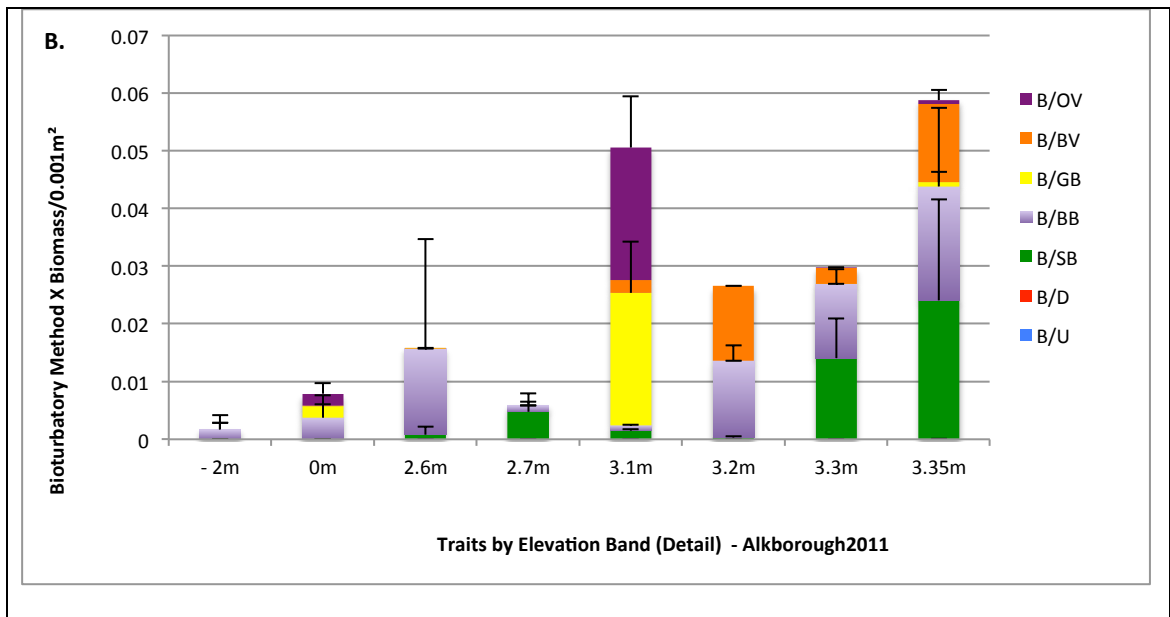


Fig 4.4.24 A-B. A, 'B' by abundance at Alkborough 2011 across eight elevation bands. B, 'B' by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Bioturbation x Abundance

PERMANOVA results were significant for B in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.05$  and  $F = 1.9341$ ). Tests indicated that a significant difference in trait expression existed between 8 pairs of bands: 3.35 m/2.6 m; 3.35 m/0 m; 3.35 m/-2 m; 3.3 m/0 m; 3.2 m/2.7 m; 3.2 m/0 m; 3.2 m/-2 m and 2.7 m/0 m all at  $p < 0.05$ .

### Bioturbation x Biomass

PERMANOVA results were also significant for B in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 2.3772$ ). Tests indicated that a significant difference in trait expression existed between 12 pairs of bands: 0m/3.35 m; 0 m/3.3 m; 0 m/2.7 m; 3.2 m/-2 m; 2.7 m/-2 m; 3.3 m/2.7 m; 3.2 m/2.7 m; 2.7 m/2.6 m; 0 m/3.3 m; 3.35 m/2.7 m; 3.35 m/-2 m and 3.1 m/2.7 m, all at  $p < 0.05$ .

### Body Length (BL)

There was a difference between elevation bands for both biomass-weighted and abundance-weighted traits data for Body Length (BL). There was a variation in modalities expressed across the whole gradient but the main trend was the dominance of BL/1-2cm in all bands below 2.7 m and a wider range of modalities in the bands above.



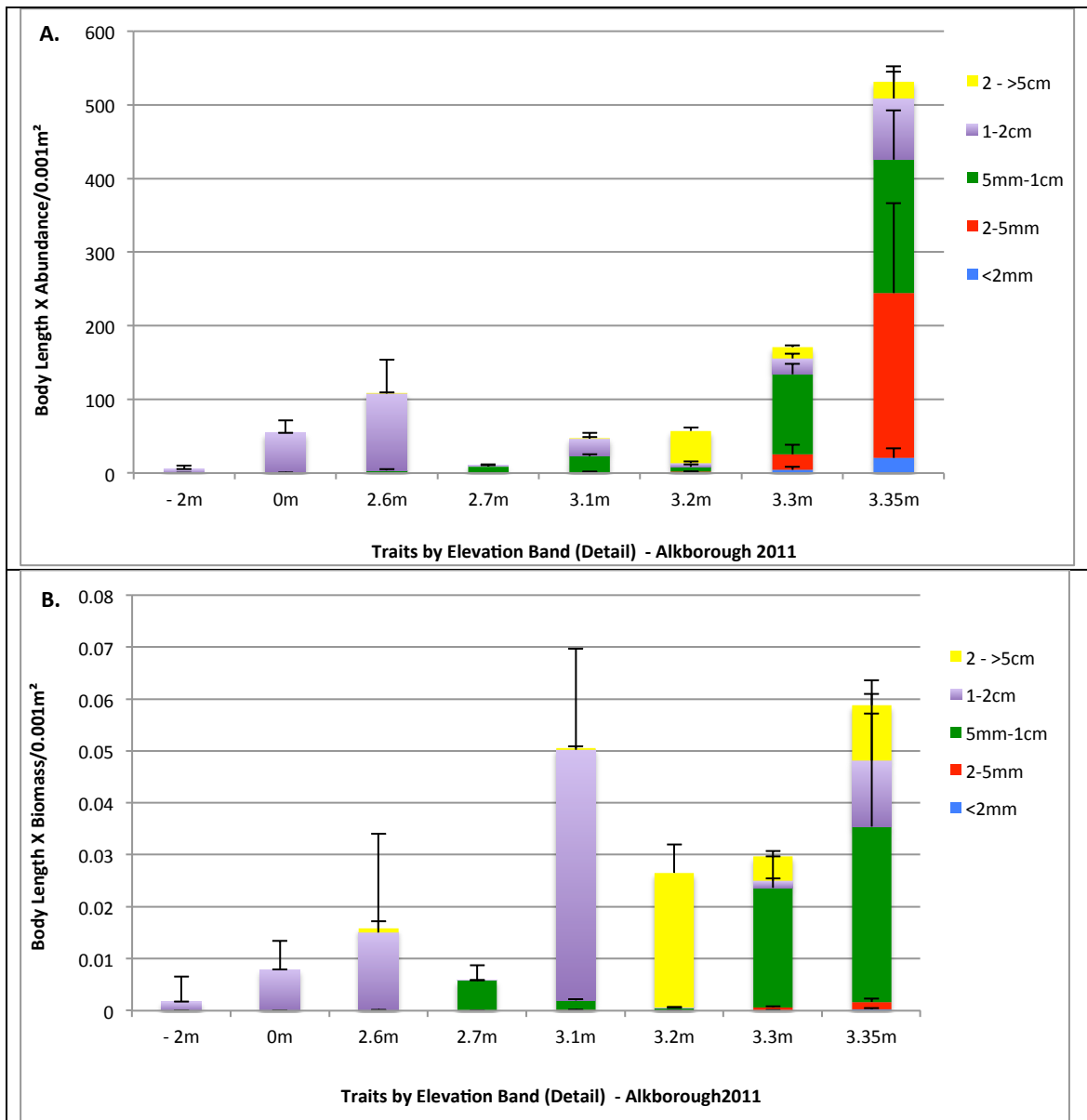


Fig 4.4.25 A-B. A, BL weighted by abundance at Alkborough 2011 across eight elevation bands. B, BL weighted by biomass at Alkborough 2011 across eight elevation bands. Error bars removed for clarity. See Table 3.1 for traits coding.

### Bioturbation x Abundance

PERMANOVA results were significant for BL in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 3.8666$ ). Tests indicated that a significant difference in trait expression existed between 11 pairs of bands: 3.35 m/2.6 m, 3.35 m/0 m and 3.3 m/0 m; 3.35 m/-2 m; 3.1 m/2.6 m; 3.1 m/0 m; 3.3 m/2.6 m; 3.3 m/-2 m; 3.2 m/2.6 m; 3.2 m/0 m and 3.2 m/-2 m, all at  $p < 0.05$ .

### Body Length x Biomass

PERMANOVA results were also significant for BL in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 3.6952$ ). Tests indicated that a significant difference in trait expression existed between 17 pairs of bands: 0 m/3.35 m; 0 m/3.3 m; 0 m/3.2 m; 3.35 m/2.6 m; 3.35 m/-2 m; 3.1 m/3.2 m; 3.1 m/-2 m; 3.3

m/2.6 m; 3.3 m/-2 m; 3.2 m/2.6 m; 3.2 m/-2 m; 3.35 m/2.7 m; 3.1 m/2.7 m; 3.1 m/2.6 m; 3.3 m/2/7 m; 3.2 m/2.7 m and 2.7 m/-2 m all returned  $p < 0.05$ .

### Longevity

There were clear changes visible along the eight-band elevation gradient for both biomass and abundance weighted data for the trait L. Difference in trait composition was most noticeable between bands below 2.7 m meters, which were strongly dominated by the modality L/18mth-2yrs, compared to a mixture of modalities in the bands above them. The same trend was apparent for both abundance and biomass-weighted data sets.

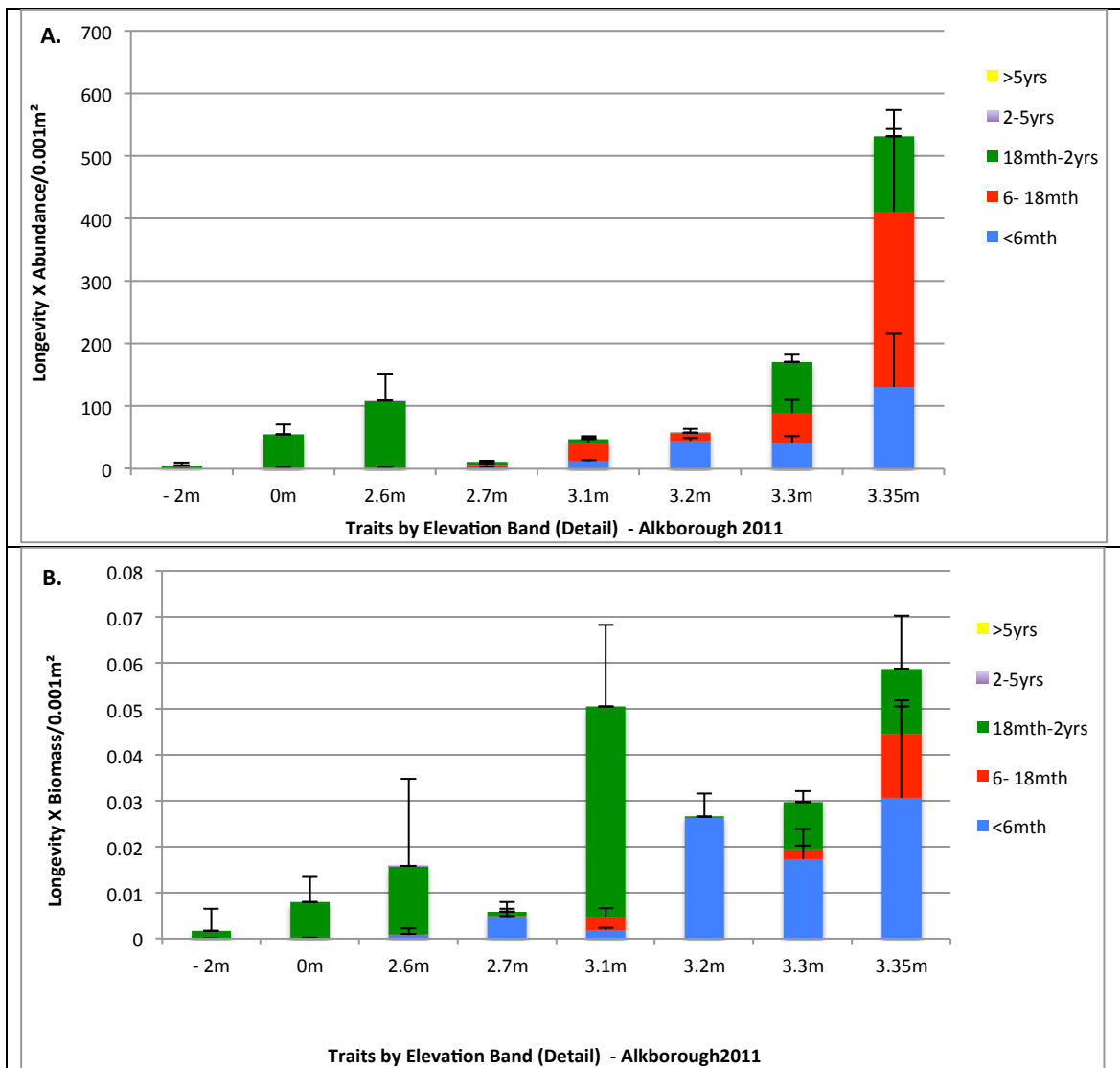


Fig 4.4.26 A-B. A, L weighted by abundance at Alkborough 2011 across eight elevation bands. B, L weighted by biomass at Alkborough 2011 across eight elevation bands.. See Table 3.1 for traits coding.

### Longevity x Abundance

PERMANOVA results were significant for L in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 4.1581$ ). Tests indicated that a significant difference in trait expression existed between 11 pairs of bands: 3.35 m /2.6 m; 3.35 m/0 m; 3.3 m/0 m; 3.3 m/2.6 m; 3.3 m/-2 m; 3.3 m/-2 m; 3.1 m/2.6 m; 3.1 m/0 m; 3.2 m/0 m, 3.2 m/-2 m and 2.7 m/0 m all at  $p < 0.05$ .

## Longevity x Biomass

PERMANOVA results were also significant for L in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 3.6462$ ). Tests indicated that a significant difference in trait expression existed between 20 pairs of bands: 0 m/3.35 m; 0 m/3.3 m; 0 m/2.7 m; 3.35 m/2.7 m; 3.35 m/-2 m; 3.1 m/-2 m; 3.3 m/2.7 m; 3.3 m/2.6 m; 3 m/-2 m; 3.2 m/-2 m; 2.7 m/2.6 m and 2.7 m/-2 m all at  $p < 0.01$ . The remaining eight pairs all returned significant p-values of  $< 0.05$ .

## Salinity (S)

Abundance and Biomass-weighted data for Salinity Preference (S) both indicated a change in trait expression across the elevation gradient. There was a difference between many of the bands, but the broad trend was a strong presence of S/5 (S/1-5psu) above 3.1 m, and a clear change to dominance by S/20 (S/15-20psu) in the bands 3.1m and below

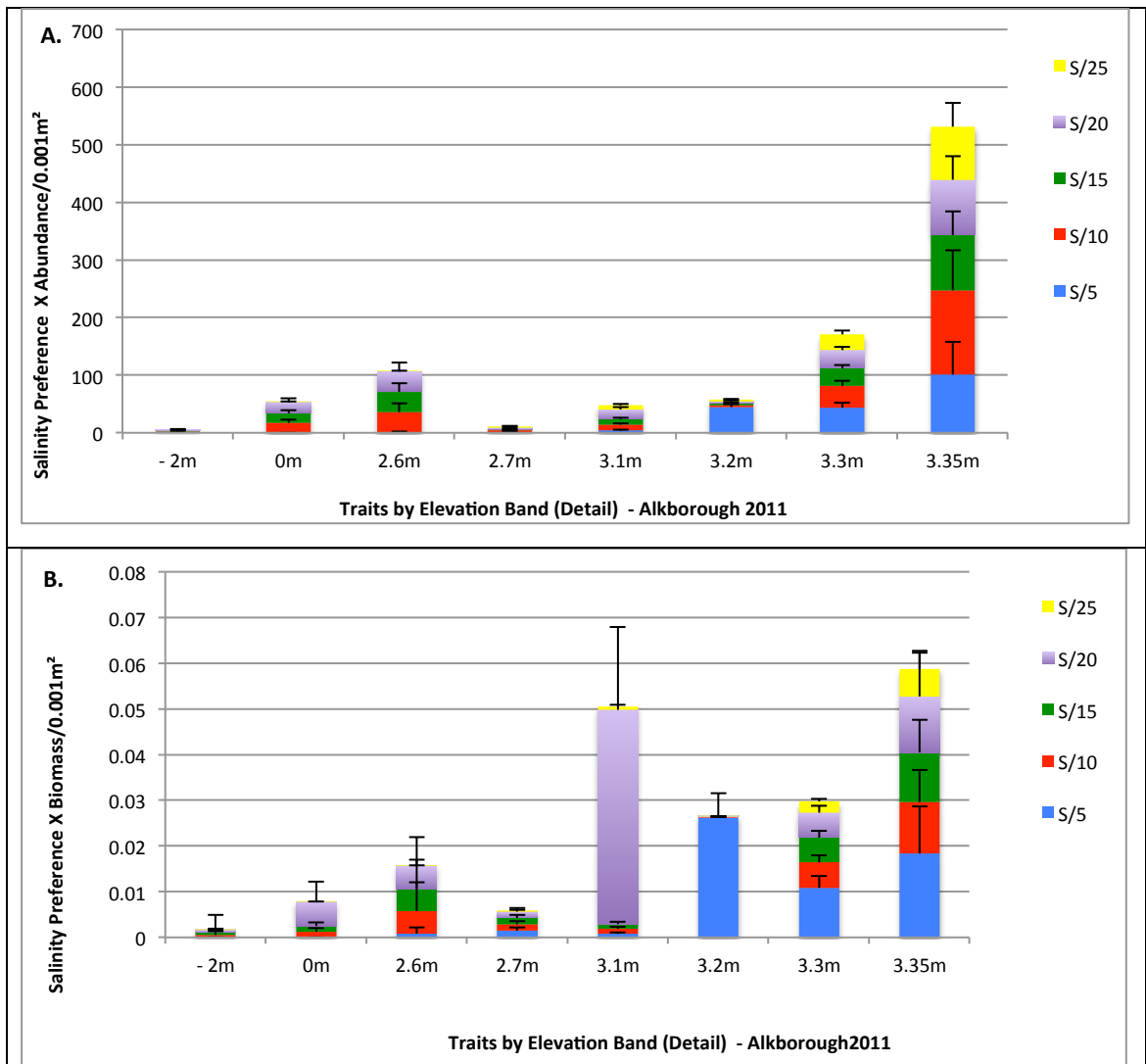


Fig 4.4.27 A-B. A, S weighted by abundance at Alkborough 2011 across eight elevation bands. B, S weighted by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Salinity Preference x Abundance

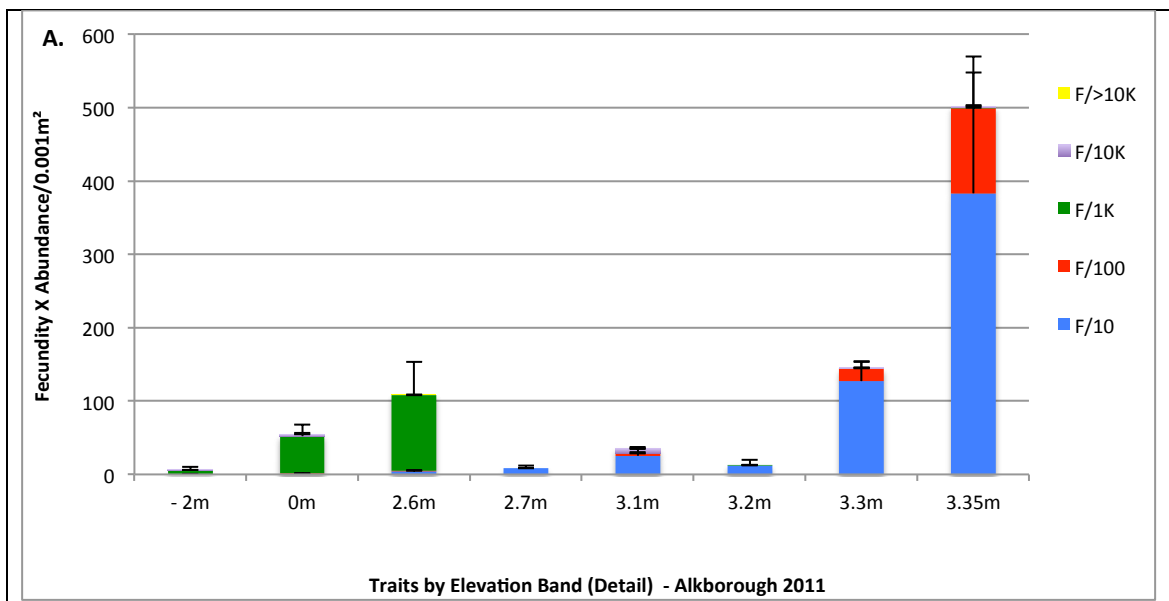
PERMANOVA results were significant for S in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 2.1407$ ). Tests indicated that a significant difference in trait expression existed between 7 pairs of bands: 3.2m/-2m; 3.2m/0m; 3.3m/-2m; 3.3m/0m; 3.35m/-2m; 3.35m/0m and 3.35/2.6m, all at  $p < 0.05$ .

### Salinity Preference x Biomass

PERMANOVA results were also significant for S in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 2.0346$ ). Tests indicated that a significant difference in trait expression existed between 10 pairs of bands: 0m/3.35 m; 0 m/3.3 m; 3.35 m/2.7 m; 3.35 m/-2 m; 3.1 m/3.2 m; 3.1 m/2.7 m; 3.1 m/-2 m; 3.3 m/-2 m; 3.2 m/-2 m and 2.7 m/-2 m, all at  $p < 0.05$ .

### Fecundity (F)

There was a clear change in trait expression between elevation bands for Fecundity (F) for both data sets. The broad trend was F/10 (F/10-50 eggs) dominating at 2.7 m and above, while below this elevation F/1K (F/100-1000 eggs) was expressed strongly. The elevation band 3.1 m stood out as particularly distinct in the biomass-weighted data with a high proportion of F/10K (F/1000-10,000 eggs) being expressed there but absent from all other bands.



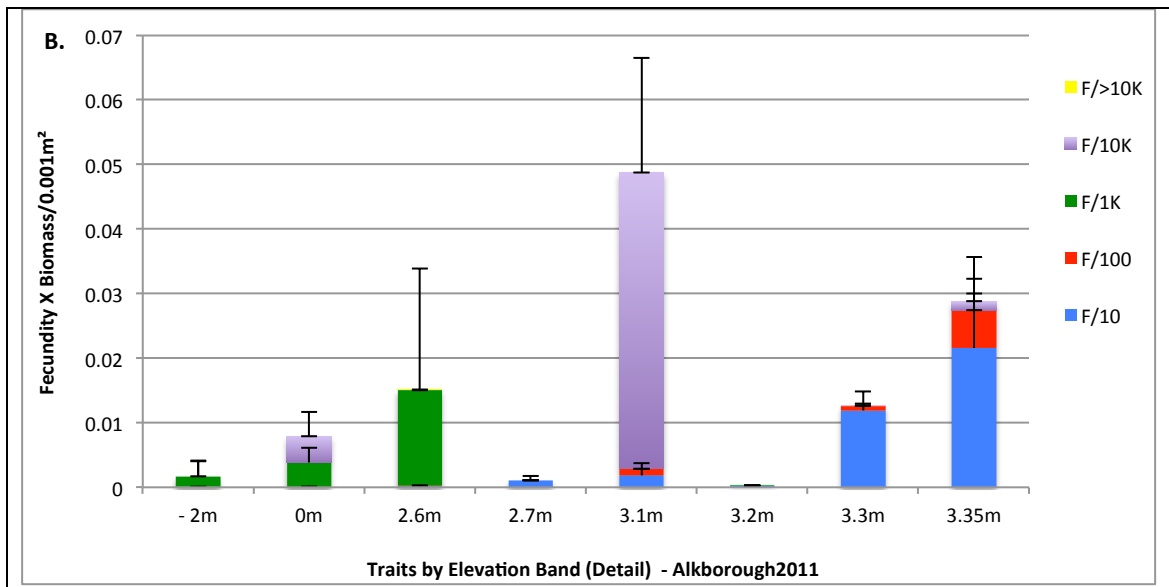


Fig 4.4.28 A-B. A. F by abundance at Alkborough 2011 across eight elevation bands. B, F by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Fecundity x Abundance

PERMANOVA results were significant for F in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 7.492$ ). Tests indicated that a significant difference in trait expression existed between 8 pairs of bands: 2.7 m/0 m; 3.2 m/0 m; 3.3 m/-2 m; 3.3 m/0 m; 3.3 m/2.6 m; 3.35 m/0 m; 3.35 m/-2 m and 3.35 m/2.6 m all at  $p < 0.05$

### Fecundity x Biomass

PERMANOVA results were also significant for F in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 6.2078$ ). Tests indicated that a significant difference in trait expression existed between 20 pairs of bands: 0 m/3.35 m; 0 m/3.3 m; 3.35 m/2.6 m; 3.35 m/-2 m; 3.1 m/-2 m; 3.3 m/2.6 m; 3.3 m/-2 m; 3.2 m/2.6 m; 3.2 m/-2 m; 2.7 m/-2 m; 0 m/3.2 m; 0 m/2.7 m; 3.35 m/3.3 m; 3.35 m/2.7 m; 3.1 m/3.2 m; 3.1 m/2.7 m; 3.1 m/2.6 m; 3.3 m/3.2 m; 3.3 m/2.7 m; 3.2 m/2.7 m and 2.7 m/2.6 m, all at  $p < 0.05$ .

### Reproductive Frequency (RF)

Fig 4.4.29, below, shows a clear change in the expression of Reproductive Frequency (RF) along the gradient for both biomass and abundance-weighted data sets. For abundance-weighted data there was a clear distinction between bands 2.6m and below and all of those above. The lower set of bands was dominated by RF/S (RF/Semelparous), while those above primarily expressed the modality RF/I (RF/Iteroparous). For biomass weighted data there was the same split between the two modalities between higher and lower bands but the lower shore dominance of RF/S began at 3.1 m.

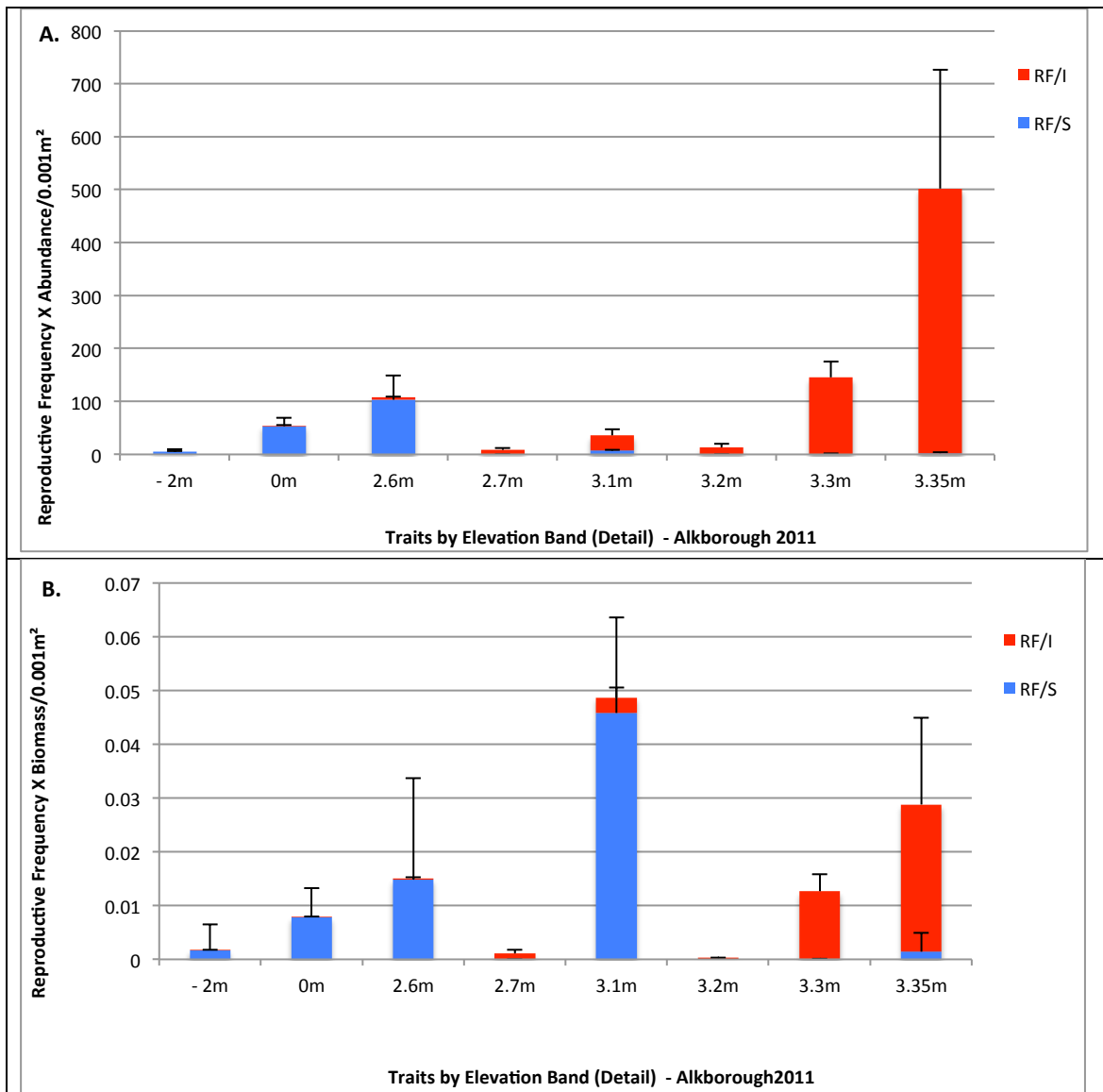


Fig 4.4.29 A-B. A, RF weighted by abundance at Alkborough 2011 across eight elevation bands. B, RF weighted by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Reproductive Frequency x Abundance

PERMANOVA results were significant for RF in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 11.906$ ). Tests indicated that a significant difference in trait expression existed between 15 pairs of bands: 3.35 m/2.6 m; 3.35 m/0 m; 3.35 m/-2 m; 3.3 m/2.6 m; 3.3 m/0 m; 3.3 m/-2 m; 3.2 m/0 m and 2.7 m/0 m all at  $p < 0.01$ . A further eight pairs returned  $p < 0.05$ .

### Reproductive Frequency x Biomass

PERMANOVA results were also significant for RF in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 8.1396$ ). Tests indicated that a significant difference in trait expression existed between 15 pairs of bands: 3.35 m/0 m; 3.3 m/0 m; 3.35 m/2.6 m; 3.35 m/-2 m; 3.3 m/2.6 m; 3.3 m/-2 m; 3.2 m/-2 m and 2.7 m/-2 m returned  $p < 0.01$ . A further seven pairs showed significant change with gradient at  $p < 0.05$ .

### Age at Maturity (M)

Abundance-weighted data for the trait Age at Maturity (M) showed a clear change along the eight-band elevation gradient, particularly between high and low shore bands. At 2.6 m and below (0 m and -2 m) trait expression was dominated by the modality M/1-2yr, while the bands above primarily expressed M/<6mth, with some contribution along the upper shore from other modalities. For biomass-weighted traits data the pattern was similar with M/1-2yrs being expressed below 3.1m and not above, but with the addition of the modality M/6mth-1yr to the composition of lower shore bands.

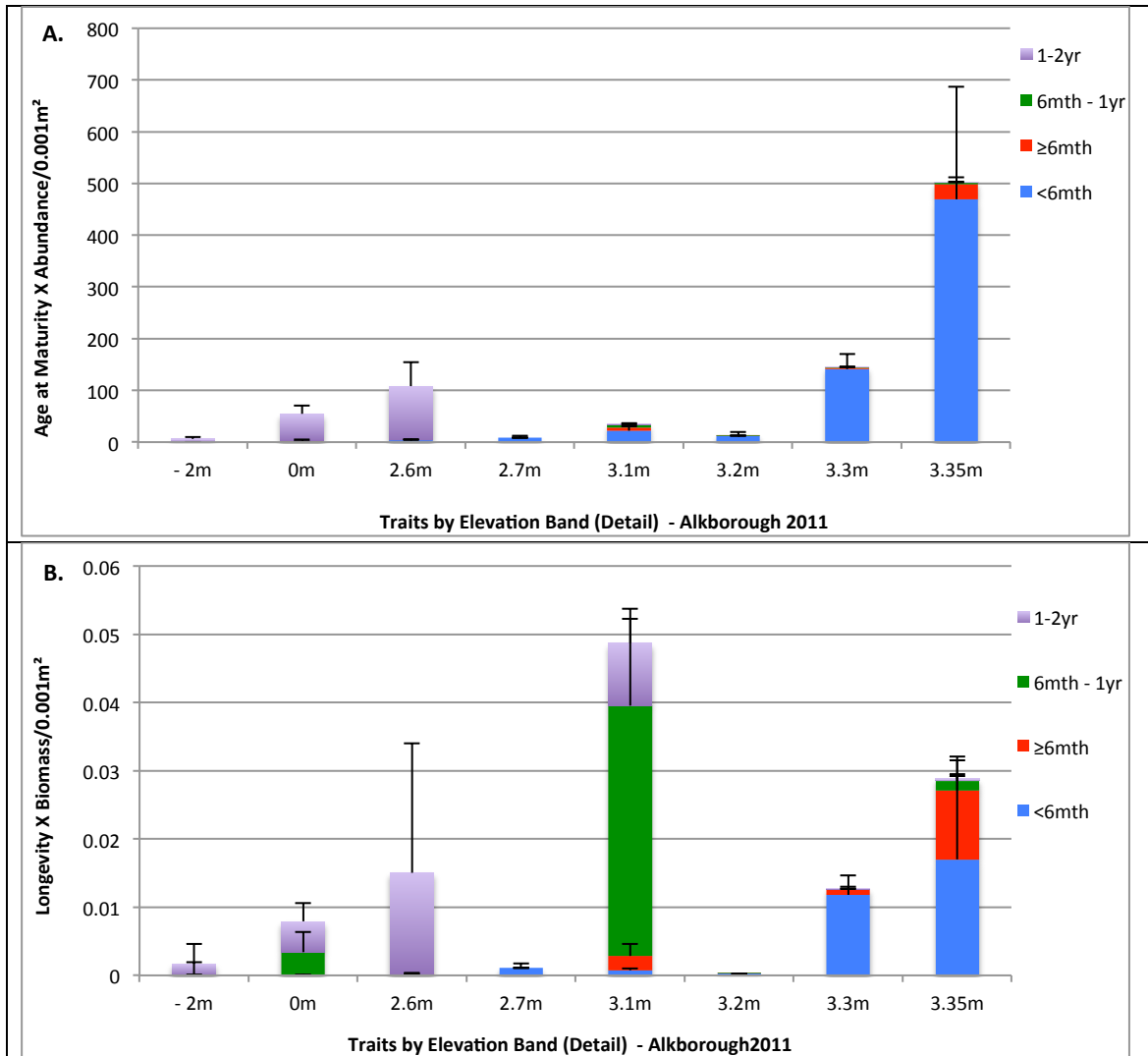


Fig 4.4.30 A-B. A, M weighted by abundance at Alkborough 2011 across eight elevation bands. B, M weighted by biomass at Alkborough 2011 across eight elevation bands. See Table 3.1 for traits coding.

### Age at Maturity x Abundance

PERMANOVA results were significant for M in terms of abundance, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 9.2639$ ). Tests indicated that a significant difference in trait expression existed between 16 pairs of bands: 3.35 m/2.6 m; 3.35 m/0 m; 3.35 m/-2 m; 3.3 m/2.6 m; 3.3 m/0 m; 3.3 m/-2 m; 3.2 m/0 m; 3.2 m/-2 m; 2.7 m/0 m; 2.7 m/-2 m, 2.7 m/2.6 m; 3.2 m/2.6 m; 3.2 m/2.7 m; 3.1 m/-2 m; 3.1 m/0 m and 3.1 m/2.6 m, all at  $p < 0.05$ .

### **Age at Maturity x Biomass**

PERMANOVA results were also significant for M in terms of biomass, indicating a change in trait expression along the elevation gradient at Alkborough ( $p < 0.01$  and  $F = 6.5454$ ). Tests indicated that a significant difference in trait expression existed between 20 pairs of bands: 0 m/3.35 m; 0 m/3.3 m; 3.35 m/2.6 m; 3.35 m/-2 m; 3.3 m/2.7 m; 3.3 m/2.6 m; 3.3 m/-2 m; 3.2 m/2.7 m; 3.2 m/-2 m and 2.7 m/-2 m, all at  $p < 0.01$ . Ten other pairs: 0 m/3.2 m; 0 m/2.7 m; 3.35 m/3.2 m; 3.35 m/2.7 m; 3.1 m/3.2 m; 3.1 m/2. m; 3.1 m/2.6 m; 3.1 m/2.6 m; 3.1 m/-2 m; 3.2 m/2.6 m and 2.7 m/2.6 m returned  $p < 0.05$ .



## Chapter 5

### Discussion

This study examined changes in the functional characteristics of estuarine benthos in relation to changes in salinity (as given by the distance between sites along the estuarine gradient) and two elevation bands (upper and lower shore). Differences were found in both, using a traditional taxonomic approach together with biological traits analysis. The study sites were a combination of estuarine mudflat in the <2.4m elevation band and salt marsh habitat in the >2.4 m band. Species found at Paull and Welwick tended to be characteristic of temperate estuarine environments (Green, 1968; Little, 2000; Mazik et al 2010) and included polychaetes and bivalves in the lower shore bands, such as *Macoma balthica* and *Eteone longa/flava*, salt marsh species such as *Isotomerus palustris* in the upper band, and a high abundance of Nematoda across both elevations. Alkborough had lower diversity and abundance compared to Paull and Welwick and was characterised by oligochaetes such as *Baltidrilus costatus* (*Heterochaete costata*) at <2.4 m and species with low salinity tolerance at >2.4, such as *Gyraulus* sp. Along the salinity gradient, species varied from *Nephtys hombergii* at Welwick with a 20-25 salinity range, to fresh water species such as *Planorbis* at Alkborough, tolerant of salinities of <5 (Fuji, 2003; Mazik et al., 2010; Mazik et al., 2011).

There was a change in community structure and traits expression along between sites and elevation band. For structure, this was in terms of species composition, species richness, biomass and abundance, all of which had higher values at Paull and Welwick compared to Alkborough, as well as some difference between Paull and Welwick in the >2.4 m band. Differences between <2.4 m and >2.4 m were found consistently at Welwick and Alkborough, but not at Paull. Benthic structural change along abiotic gradients is well established in the literature (Moreira et al, 1993; Ysebaert et al, 2003; Hampel et al, 2009; Barros et al, 2012). In terms of traits, lower species richness at Alkborough (no more than 4 species per sample station at <2.4 m) meant a reduced trait profile, with fewer modalities expressed. Traits showed a difference between <2.4 m and >2.4 m consistently at Welwick and Alkborough, but not at Paull. Sediment composition also showed a difference between elevation bands at Welwick and Alkborough, but not at Paull.

While most benthic variables showed a significant change along the gradients for community structure and community function, Paull was an exception to this. The elevation gradient at Paull showed no significant change in any of the community structure variables, no significant variation in any biomass-weighted traits, and only a few abundance-weighted traits (Mobility and Fecundity) showed a change in expression. These results contradict findings for elevation at Welwick and Alkborough. The most likely explanation for the lack of variability between elevation bands at Paull is that the gradient sampled there was less steep than at the other two sites, meaning there was not a sufficient difference in environmental regime to cause a change in benthic structure and composition. The topography at Paull made it difficult to safely sample the true lower shore on foot and hovercraft access was not an option for this project. In addition to this, elevation data for this project were taken from that measured in other studies (Mazik et al. 2007), which focussed on the high shore region, but not the mid or lower shore. This left an area that was known to be <2.4 m, but could not be divided further due to a lack of information. This meant that stations P5 and P6, both in the <2.4 m band, were

quite different in taxonomic composition and trait expression, but could not accurately be separated. These two factors could be responsible for a lack of significant changes in structure and trait expression in the results for Paull. This is supported by aspects of the detailed elevation band study in which some significant results were produced between the lowest (<2.4 m) and highest (2.61 m and 2.8 m) elevation bands in terms of expression of the traits for Feeding Method, Feeding Apparatus, Mobility, Bioturbation, Living Habitat, Longevity, Fecundity and Age at Maturity.

#### *Between Site Differences (Salinity Gradient)*

Differences in community structure variables and traits expression were consistent between sites when Alkborough was compared to Paull and Welwick, typically at both <2.4 m and >2.4 m. Exceptions to this were 'J and H'. Evenness did not change significantly between Alkborough and the other two sites, but it was a lower value at Welwick compared to Paull (see table 4.2.1), suggesting a higher variability in species numbers at Welwick. H' only showed a change in the <2.4 m band between Alkborough and Paull/Welwick. Species diversity at Alkborough was much lower in the <2.4 m band than at the other two sites. This was almost certainly due to the low levels of salinity there, combined with the increased impact of immersion experienced on the lower shore compared to the >2.4 m elevation band.

Every trait showed changes in modality profile when Welwick/Alkborough and Paull/Alkborough were compared, for both biomass-weighted and abundance-weighted data.

At <2.4 m, for biomass and abundance-weighted traits, Living Habitat (LH) was a particularly distinctive trait separating these sites, with LH/Semi-Permanent Burrow making a major contribution to trait composition at Welwick and Paull, while at Alkborough LH/Free Living had a high percentage contribution. This is likely to be due to the absence of bivalves at Alkborough and the dominance, particularly in terms of abundance, of free-living oligochaete species such as *Baltidrilus costatus* (*Heterochaete costata*) at Alkborough <2.4 m

Adult Mobility (AM), Living Habitat, Bioturbation (B) and Longevity (L) also showed significant change in modality expression along the salinity gradient when Alkborough/Welwick and Alkborough/Paull were compared. Some of these changes were in terms of different modalities being expressed, but in some cases at Alkborough modalities were absent or minimally represented. L/>5yrs, and B/Downward Conveyer were not expressed at Alkborough at all, while LH/Semi-Permanent Burrow and FA/Tentaculated were only expressed once, in the same replicate, at low abundances (<10 individuals). This indicates a potential loss of functioning. Longer-lived species are associated with established, stable communities (Frank, 1968), while downward conveying/particle capture and burrow construction are important bioturbatory activities that mix sediment and increase surface area for solute exchange (Wenzhöfer and Glud, 2004; Jones and Frid, 2009)

Comparisons between Paull and Welwick indicated only some traits were sensitive to change, but this depended on how the data had been weighted. For biomass-weighted traits data there was a very clear pattern. When Paull >2.4m and Welwick >2.4m were compared there was significant difference in trait composition for every category except Reproductive Frequency (RF). When the <2.4 m band was compared between the two sites, trait composition was very similar, with only Position (P) showing a difference in expression – a slight increase in the modality 'Epifaunal' in the >2.4 m band at Paull. Welwick and Paull both experience broadly similar environmental conditions at >2.4 m, with a relatively small salinity

gradient between them, compared to Alkborough and this may explain the lack of change in trait expression in this elevation band. Even the difference in terms of the presence of a higher expression of P/Epifaunal at Paull should be treated with caution as epifaunal species are mobile and may be sampled by chance outside of their typical habitat.

For abundance-weighted data there was a less clear trend, with the upper shore results indicating seven traits that showed a variation between sites: Feeding Method, Feeding Apparatus, Food Type, Position, Body Length, Bioturbation and Reproductive Frequency. The lower shore abundance-weighted data highlighted Food Type, Bioturbation and Longevity as significantly different in expression between sites along the salinity gradient. Overall, biomass-weighted data seemed to give more consistent results, not just for the consideration of the salinity gradient between sites but also when elevation was considered within each site. For example, at Paull all biomass-weighted traits showed no significant difference in modality profile along the elevation gradient, while the abundance weighted data indicated difference in Longevity and Fecundity. When a trait varied in expression between elevation bands the biomass-weighted data tended to be easier to interpret than abundance-weighted data, emphasising dominant modalities, the trade-off being less detail for less well represented traits. Some studies have concluded that biomass weighting is the most effective for traits analysis as it is thought biomass is better linked to function (Cesar and Frid, 2009; Bolam and Eggleton, 2014). However, biomass is not necessarily the answer to the traits weighting issue, as there is still risk of skewing the data; one large bivalve could increase the biomass of a sample, but only be sparsely distributed and hence make a limited contribution to overall community function. The same skewing could also occur with abundance-weighted trait data when high densities occur together with low biomass (Bolam et al., 2010). For example Nematoda in this study at Welwick dominate the trait Feeding Apparatus with the modality 'Simple Mouth' due to very high abundance levels. The majority of these animals are in the 2mm-5mm Body Length modality so it is likely that, despite high densities, they are not having as large an impact on, for instance, sediment reworking as a smaller number of animals in modalities at 1cm and above.

### *Elevation*

At Paull, changes in elevation band did not show changes community structure or trait expression (likely for the reasons outlined regarding limited gradient), but was a strong influence at Welwick and Alkborough. This agrees with the literature, in terms of community structure, where elevation is known to cause changes in aspects such as taxonomic composition and abundance (Zedler, 1977; Crain et al., 2004; Mazik et al., 2010).

Welwick 2011 did not show a significant change in sediment composition between elevation bands. Changes in sediment composition can influence species presence or absence (Little 2000; Mazik et al., 2010; Gray and Elliott, 2009) and some difference was seen in the samples taken at Welwick 2010, but in other structural respects, including taxonomic composition, both years showed distinct difference between <2.4 m and >2.4 bands so it is possible that the changes in mud/sand content were not sufficient to account for community composition differences. Variables that did not alter significantly with elevation, were 'J and H', indices indicating that the relative range (H') and spread (J) of species was unchanged with elevation. The variables abundance, taxonomic composition and biomass were affected by changes in

elevation. There was also a difference in these structural variables between Welwick 2010/2011 on the upper shore. A significant part of this difference could have been linked to the change in sampling design between years, with a change in station location, (see Methods 3.1), but physical and biological aspect, such as accretion and colonisation by new species could also have been factors. Although change in community structure and function over time is not of direct interest to this study, the significant change in the >2.4 m band between years is notable. It is possibly attributable to high levels of accretion taking place there, increasing elevation and decreasing inundation, observed at other MR sites in the Humber (Mazik et al., 2010).

In the BTA analysis Welwick showed changes in trait expression between the <2.4 m band and >2.4 m bands for all biomass-weighted traits and most abundance-weighted traits, except Food Type and Position, suggesting that elevation was a significant factor in trait composition. Modalities that dominated trait composition in a band are summarised below for both data sets (Table 5.1 and 5.2). Traits given are those that showed difference in modalities expressed, rather than those with a similar traits profile but differences in terms of proportions. For example, for Bioturbation/Blind Burrow Ventilator only occurred at <2.4 m in both years and contrasted with traits found on the upper shore, where B/Surficial Biodiffusers accounted for over half of the trait expression. This is significant in terms of links to functioning, as burrow building and ventilation are important in sediment mixing and solute exchange. The traits BL and L also showed a change between bands and indicated that the <2.4 m band was characterised by longer lived and longer bodied species. Longevity is indicative of long-term community stability and the size of a species is linked to its bioturbation potential, in combination with Adult Mobility (See Table 5.1, Biomass Weighted). Traits expressed at >2.4 m were linked to the presence of epifaunal species, such as Collembola, and generally indicated smaller body size and less burrow building activity, which has similar implications to those discussed above for bioturbation, in terms of reduced sediment mixing and solute exchange. Some of the variability between bands could be attributed to semi-terrestrial species, such as *Isotomerus palustris*, which was responsible for a strong expression of Adult Mobility/High in the >2.4 m band. However, at Welwick 2011 tube building species (*Manayunkia aestuarina*) were recorded in high numbers at >2.4 m, having been absent in 2010 and this indicates potential functional change in terms of sediment modification.

Table 5.1 Dominating Modalities by elevation band- Biomass-Weighted.

Dominating Modalities at <2.4m/>2.4m at 2011 – Biomass Weighted		
Biomass -Weighted	Welwick 2011 <2.4m	Welwick 2011 >2.4m
Bioturbation	Blind Burrow Ventilator and Downward Conveyer	Surficial Biodiffuser and Gallery Biodiffuser
Longevity	>5 Years	18mth -2yrs and <6mths
Mobility	Low and Medium	Medium and High
Reproductive Frequency	Iteroparous	Iteroparous and Semalparous
Body Length	1-2cm /2->5cm	1-2cm/2-5mm/2->5cm
Position	Infaunal	Epifaunal/Infaunal
Fecundity	10K	1-10/100/10K
Feeding Apparatus	Siphon	Jaws/Mandibles
Living Habitat	Semi-Permanent Burrow	Semi-Permanent Burrow and Free Living and Tube-dwelling.

Abundance-weighted data also showed changes in expression, but high densities of Nematoda (particularly in 2011) meant that different traits were emphasised, compared to biomass-weighted data, which emphasised the traits of heavier species, such as *Macoma balthica* (Table 5.2). This meant that the Bioturbation/Burrowing Biodiffuser modality dominated trait composition at <2.4m in both year groups, as well as shorter Body Length and Longevity modalities, implying reduced bioturbation potential in comparison to the biomass-weighted data set. Apart from this, there were similar trends in both data sets, particularly in terms of a wider range of modalities being expressed on the upper shore in 2011. The presence of tube dwelling species is notable again, and the abundance weighted data emphasises the associated modalities Feeding Apparatus/Tentaculated and Mobility/Sessile, which are likely attributable to high densities of *Manayunkia aestuarina* in 2011. The implication of this is a potential increase in function in terms of sediment stabilisation and downward conveying of material suspended in the water column. This relates to work by Jones and Frid (2009) who found a change in the presence/absence of tube dwelling species (*Pygospio elegans*) with changes in environmental conditions and linked their presence to sediment reworking and microbial community habitat in terms of oxygenated tubes.

Table 5.2 Dominating Modalities by elevation band- Abundance-Weighted

Dominating Modalities at <2.4m/>2.4m at Welwick 2011 –Abundance Weighted		
Abundance-Weighted	Welwick 2011 <2.4m	Welwick 2011 >2.4m
Bioturbation	Burrowing Biodiffuser	Surficial Biodiffuser and Burrowing Biodiffuser
Longevity	6-18mths	6-18mths and <6mth
Mobility	Medium	Medium, Sessile, High
Reproductive Frequency	Iteroparous	Iteroparous
Body Length	2-5mm/<2mm/2->5mm	2-5mm/<2mm and 5mm-1cm
Position	Infaunal/Epifaunal	Infaunal/Epifaunal
Fecundity	10	10/100/>10k
Feeding Apparatus	Simple Mouth	Simple Mouth and Jaws/Mandibles and Tentaculated
Living Habitat	Free-Living	Free-Living and Tube dwelling.

Alkborough showed a large difference between <2.4 m and >2.4 m, but the separation of Alkborough data in to the eight elevation bands only showed limited additional information. There were significant differences between these eight bands, when high and low bands were compared, as shown by MDS ordination of the distance between upper and lower shore trait expression. The detailed banding was valuable for indicating the point at which these changes occurred (around 2.7 m and 3.1 m) but generally the <2.4 m and >2.4 m bands were enough to show the main changes in gradient and were also directly comparable with the other sites.

There was a delineation between upper and lower shore for almost all traits, except Living Habitat and Mobility, which showed no significant difference between <2.4 m and >2.4 m in PERMANOVA analysis.

For biomass-weighted data, traits that showed a significant change across the elevation gradient included Position and Reproductive Frequency, both of which made significant contributions to trait composition in each band (Table 5.3). The differences in Position were related to changes in habitat, with no epifaunal animals at <2.4 m but a high proportion at >2.4m where tidal inundation was limited. The functional implications of this are a reduction in bioturbatory modes that cause sediment mixing and oxygenation below the sediment surface. This was reflected in the Bioturbation modalities, in which Surficial Biodiffuser accounted almost half of trait expression in the >2.4 m band. The lower band was characterised by longer lived and longer bodies species compared to the upper shore, broadly indicative of a stable benthic community, but a limited range of modalities were expressed due to low species richness; in some categories only one or two modalities were expressed, compared to a wider range at >2.4 m (e.g. Body Length, Age at Maturity and Longevity). Although this reduced trait profile suggests a potential loss of functioning, studies acknowledge that ecological function can be largely unchanged when species composition changes (Bremner et al., 2003; Sigala et al., 2012) and in this case, although the number and abundance of species was very low at Alkborough in the <2.4 m elevation band (5 species and a total abundance of 205) a surprising number of modalities were represented. For instance, at station S13, where only two species were sampled, 36 out of a possible 60 modalities were present. The species richness aspect of

this is comparable with the findings of Törnroos et al. (2014), who showed that reduced taxonomic richness was associated with a reduction in overall function, but that the reduction in number of taxon was not reflective of the degree of reduction in functioning.

Table 5.3 Dominating modalities by elevation band at Alkborough. Biomass-Weighted.

Dominating Modalities at <2.4m/>2.4m at Alkborough 2011 –Biomass Weighted		
Biomass-Weighted	Alkborough 2011 <2.4m	Alkborough 2011 >2.4m
Bioturbation	Burrowing Biodiffusers	Surficial Biodiffuser and Burrowing Biodiffuser
Longevity	18mths-2yrs	<6mths
Feeding Method	Subsurface Deposit	Surface Deposit and Predator and Opportunistic Scavenger
Reproductive Frequency	Semelparous	Iteroparous
Body Length	1-2cm	5mm-1cm
Position	Infaunal	Infaunal and Epifaunal
Fecundity	1K	10 and 100
Feeding Apparatus	Simple Mouth	Jaws/Mandibles and Simple Mouth
Maturity	1-2yrs	<6mths
Food Type	Detritus	Detritus, Bacteria and Invertebrates

In terms of traits expression for abundance-weighted data, the distinction between bands was emphasised by Reproductive Frequency, Iteroparous on the upper shore and Semelparous on the lower shore, Body Length, 5mm-1cm on the upper shore and 1-2cm on the lower shore, and Age at Maturity, <6mth on the upper shore and 1-2yrs on the lower shore (Table 5.4). Functional implications were similar to the biomass-weighted data set, with the >2.4m band showing a reduction in infaunal species and an absence of burrow builders. This indicates with a potential loss of sediment mixing at depth, as epifaunal species (e.g. *Assimineia grayana*) are almost always surficial biodiffusers, only causing diffusive mixing in the upper few mm of the sediment.

Table 5.4 Dominating modalities by elevation band at Alkborough. Abundance-Weighted.

Dominating Modalities at <2.4m/>2.4m at Alkborough 2011 –Abundance Weighted		
Abundance-Weighted	Alkborough 2011 <2.4m	Alkborough 2011 >2.4m
Bioturbation	Burrowing Biodiffuser	Burrowing Biodiffuser and Surficial Biodiffuser
Longevity	18mths-2yrs	<6mth and 6-18mth
Feeding Method	Sub-Surface Deposit	Surface Deposit
Reproductive Frequency	Semelparous	Iteroparous
Body Length	1-2cm	5mm-1cm and 2-5mm
Position	Infaunal	Infaunal/Epifaunal
Fecundity	1K	10 and 100
Feeding Apparatus	Simple Mouth	Simple Mouth and Jaws/Mandibles
Age at Maturity	1-2 yrs.	<6mths
Food Type	Detritus	Bacteria, Microorganisms and Detritus

It is not certain why traits such as Living Habitat and Mobility, in both data sets, were not subject to change with elevation band at Alkborough, in contrast to the Welwick in both years. It may be due to variable distribution at Alkborough, (SIMPER results indicated high heterogeneity within bands), or due to a much lower species richness at the site compared to the other two sites, leading to limitations in the range of traits present. Within Alkborough species richness and diversity were both low in the <2.4 m elevation band, but increased at >2.4 m. This can be attributed to the presence of terrestrial and freshwater species in the >2.4 m that would not be found on an estuarine foreshore, as well as to the effects of sampling effort. The higher number of samples taken at >2.4 m compared to the lower shore area at Alkborough is likely a confounding factor in the data. It may have been more appropriate to have removed some of the >2.4 m samples at Alkborough from the analysis in order to make them comparable with data collected from Paull and Welwick. A further confounding factor at Alkborough was the very high levels of flora at >2.4 m elevation. While some vegetative encroachment of mudflat was visible at both Paull and Welwick, at Alkborough this growth was dense and appeared well established (See Methods Fig. 3.4-3.10). It may have been helpful to build some of these physical aspects in to PERMANOVA as additional factors for a more meaningful analysis.

Generally, the traits that consistently showed a change between sites and elevation bands were Bioturbation, Reproductive Frequency, Fecundity, Living Habitat, Body Length, Longevity, Age at Maturity, Feeding Apparatus, Salinity Preference and Mobility, with the food-based traits to a lesser extent (FA, FM, FT). A number of other studies, using a similar selection of traits, have concluded that traits show changes in composition along a range of gradients, natural and man-made (Oug et al.2012; Verissimo et al., 2012; Van der Linden et al., 2012; Sigala et al., 2012).



The way in which feeding-based traits were expressed in this study is consistent with the finding of Bremner et al. (2003), which concluded that feeding traits were most useful when considered together with a range of other traits. Traits relating to feeding have strong links to bioturbation but presenting them with other traits gave them wider ecological and biological context and showed the links; for instance, expression of FA/Siphon is linked to a similar proportion of B/Blind Burrow Ventilator in this study. Bioturbation consistently showed a clear change in modality expression between sites and elevation bands along both gradients and appeared sensitive to changes in both gradients. Jones and Frid (2009) used bioturbation as one of four categories in trait analysis between differing topographies and found that it was lower when sediment surface roughness was manipulated. However, they concluded that the use of a wider range of traits would have given more detail and showed wider links to functioning, although it was not specified which additional traits may have been more informative. The addition of bioturbation, together with eleven other traits (including feeding method, habitat and mobility) in the study by Paganelli et al. (2012) along the Emilia-Romagna coast also showed that these traits were sensitive to changes in spatial gradients, in an area of variable environmental conditions. That study also emphasised the link between burrowing bioturbatory activity and increased functioning, in terms of extension of the redox potential discontinuity, increased nitrification processes and associated presence of a wider range of species that would not be able to live in anoxic sediment.

Studies along pollution gradients in aquatic and terrestrial ecosystems have also shown changes in functional trait expression (Oug et al, Braga et al 2000; Santorufo et al, 2014), while others have used BTA to demonstrate the impact of anthropogenic activities. For example, Tillin et al. (2006) showed bottom trawling can lead to a temporary reduction in the range of functional traits in the benthos, a finding supported by Bolam et al. (2014). Larger scale studies have examined changes in functioning between regions, such as the work by Bremner et al (2006b) and Paganelli et al (2012), which suggested trait composition was influenced by a number of environmental factors. Natural gradient studies include riverine sediment gradients (Descloux et al, 2014), which also saw changes in trait composition, as well as studies of coastal lagoons and estuaries (Marchini et al, 2008; van der Linden, 2012), which described changes in trait profiles between sampling sites. While these studies agreed with the general trends in this study, not all identified the same trait categories as dominant or significant in terms of causing distinction between samples. For example, the study by Van der Linden et al. (2012) found that the trait Salinity Preference was highly significant in determining species distribution in the Mondego, hence showing the effect of salinity on species presence or absence (JNCC, 2004). However, in this study, although salinity preference did show variation in proportion of modalities present, and was a useful trait in separating samples, it was not a particularly dominant category in any of the sampled areas. This is best illustrated in the >2.4 m band at Alkborough (lowest point on the salinity gradient and limited tidal inundation) where all 5 salinity modalities were well represented, ranging from salinity preferences of 1-30. Oug et al (2012) indicated that mobility, feeding method and body size were responsible for differentiating between assemblages, together with sediment dwelling depth and larval mode. Traits analysis by Bremner (2003) identified mobility, attachment to substratum, and body form as important trait categories. The present study also found mobility and body length were dominant traits, but other categories (e.g. attachment and body form) were not analysed here (as discussed in Methods), and this links to some of the issues regarding trait selection and standardisation for comparison, discussed below.

In summary, this project rejected the null hypotheses and indicated that community structure and functioning both changed along the salinity and elevation gradients. Differing taxonomic assemblages showed differences in trait expression, suggesting that benthic activity that relates to ecosystem function, particularly bioturbation and closely linked traits such as feeding, mobility and body size, will alter with community composition. Traits that were particularly important in differentiating sites and elevation bands in the Humber were Living habitat, Body length, Position, Reproductive Frequency, as well as Bioturbation and the three feeding categories. Each of the thirteen traits analysed showed some variance in expression for at least one of the gradients considered here. Changes in trait expression did not correlate to a loss of overall function, except in cases of highly reduced species richness.

### *Implications*

The findings here suggested that although benthic community trait profiles changed between sites along the salinity gradient this was not necessarily matched by an overall loss of trait diversity. If a sharp drop in species richness, such as that at Alkborough <2.4 m, is not always matched by an equally sharp drop in trait range, as was the case here, this has implications for other impacts on the benthos (Törnroos et al.2014) For instance, where a pollution gradient or dredging event may have significantly reduced species richness the functional traits loss may not be as severe as the loss implied by taxonomic assessment alone. This suggests that biological traits analysis is a useful addition to traditional taxonomic analysis in terms of understanding benthic ecosystem function. As well as this, the process of assembling trait information for each study increases the information available on species traits, and with continued traits studies there is the potential for the approach to become increasingly easy to add to traditional studies as established databases become available.

In terms of elevation bands there were changes in trait profiles between upper and lower shore elevation bands; this change did not represent an overall loss of functioning, but it does have potential implications in terms of the development of managed realignment sites in the Humber. The sites sampled at Welwick and Paull were both subject to managed realignment with the aim of creating compensatory habitat for that lost to flood defence upgrades, and port extensions on the south bank of the Humber, at Immingham, specifically, estuarine mudflat. The creation of compensatory habitat for that lost to development is a requirement in the Humber (Mazik et al., 2010) due to its multiple protective designations, and the Environment Agency require replacement at a ratio of 1:3 for land lost to defence upgrades (Mazik, 2010. DEFRA 2010). Article 6 of the EU Habitat Directive, also requires 'the re-creation of comparable habitat' to that lost to development (EU Commission, 2000). The >2.4m elevation band in this study indicates that structural variables as well as functional traits within the managed realignment site do not match the established mudflat outside it, and although it is not particularly less functionally diverse than the <2.4 m elevation band, it is different to the trait profiles of mudflat and this implies that reference conditions may not have been met.

### *Critique and Further Work*

Using BTA in this study showed a clear difference in trait profiles with changes in abiotic conditions. However, the approach is not currently without a mix of advantages and disadvantages. As mentioned in earlier chapters there is no clear consensus on how traits

should be selected and which traits are most appropriate for a given study (Bremner 2006a; Paganelli et al., 2012). As outlined above, some studies used trait categories that were not applied in this study, as here traits were selected that were most indicative of function and relevant to conditions at the study sites. For instance, some studies included the trait Body Form (Bremner, 2008; Oug et al., 2012), but this was excluded here as the majority of species are infaunal, in soft sediment, and body form is more pertinent to species subject to physical stresses, such as tidal flow, as those attached on a rocky substratum might be.

Another recurring issue with BTA is the limited data that exists for species (Bremner et al, 2006a; Marchini et al., 2008), and this often becomes an aspect of trait selection (Van der Linden et al 2012), as it was here (Methods 3.3). Local species variability may also be an issue, for example, in the case of body length/size, the literature does not always agree with the physical properties of species sampled. An example from this project is the body length of *Nephtys hombergii*. Reported in the literature as up to 200mm (Hartmann-Schröder, 1996; Hayward and Ryland, 2009), it has not been recorded in the Humber at this length (Professor Mike Elliott, IECS 2014; Will Musk Senior Taxonomist, IECS 2014; Oliver Dawes Senior Taxonomist, IECS 2014, pers. comm.), nor was it observed in any samples taken in this study (pers. obs.). While adjustments can be made in this category using local knowledge and observation the same is not true for less readily observed traits. Characteristics such longevity and age at maturity, could not be discerned in this way but may also differ locally compared to information stated in the literature. This implies that trait scoring may not always accurately reflect actual biological conditions at the study sites.

Once trait categories are selected there is also a current issue with the effort required to assemble traits data (Bolam and Eggleton, 2014). If a substantial number of traits are used, as is advised (Bremner et al, 2006a) then a large amount of detailed data is required to create an accurate traits matrix. Although there are some data resources available (e.g. MarLin BIOTIC and the literature reviews of BTA studies) they are not complete, or exhaustive, and were of use here mainly for well studied species, suggesting more work is needed in this area to make BTA a more attractive approach where time-scale is an issue. In the present study some improvements could have been made in terms of traits selected. Ideally, further effort could have been made to obtain information that would have supported a more detailed reproductive trait category. For example, developmental type could have been achievable, as used Törnroos et al. 2014 with 4 modalities (fragmentation, direct, lecithotrophic and planktotrophic), but exploration of literature at the planning stage in 2011 did not suggest this.

Another issue in this study was the interpretation of BTA results. The aim was to see if benthic community function changed along the two gradients, and the results did answer this, to a degree, in terms of traits selected, but limited analysis made it difficult to discern the ecological implications of these changes. A more detailed statistical analysis of traits within bands and sites may have helped to indicate more clearly the degree to which changes in functional composition equated to a potential reduction or increase in functioning. In addition to this, the fact that BTA is a proxy for function, rather than a measure of it, meant that changes, and their potential significance could not be quantified in the same way as some community structure variables. This is an established aspect of the BTA system and is obviously not an issue per se, rather it is something that should be foremost when selecting traits as it means links to function need to be robust and well-established, as well as meaningful to the

aims of the study. Traits in the benthos such as bioturbation and feeding habits are linked to functions such as sediment mixing, solute exchange and secondary production (Naeem et al., 1994; Jones and Frid, 2009; Benke, 2010; Törnroos and Bonsdorff, 2012; Bolam and Eggleton, 2014), but others do not have such clear associations. For example, salinity preference was selected as a trait in this study based on its successful use in the literature (Van der Linden et al. 2012) but when it was analysed here it appeared to be indicative of adaptation to environmental conditions rather than a strong proxy for functional change. It would be useful for future work to build traits that might be measurable in terms of impact on functioning. The use of Body Volume could be more meaningful than BL, and could be combined with mobility and bioturbation data to produce an approximate bioturbation potential figure, which would have a real link to rate processes in the sediment. Bioturbation traits could also benefit from being re-categorised, with the inclusion of 'stabilisation' to cover some species and it would be useful if a depth modality could be added, rendering the scoring more meaningful in ecosystem terms.

Initially data was assembled to display traits in charts as a proportion of total species present. This was visually clear and showed change in trait composition between sites and elevation bands at a glance, but meant any differences detected were due to purely to changes in trait profile. This did not take in to account effects of difference in abundance and biomass at each site/station, for example the massive drop in abundance and biomass at Alkborough, and could, theoretically, have shown the same trait profile for 6 individuals or 6000. The aim of the project was to look for changes in ecosystem function (as represented by BTA proxy functional traits) and large differences in abundance and biomass seemed relevant to this as they were the only measured aspects of the project that provided a link, however soft, between the proxy traits and genuine levels of functioning. Retrospectively it may be that displaying charts with traits as a proportion would have been a useful addition to the results, illustrating change purely in terms of BTA trait profile. Below, in Fig. 5.1 the differences are illustrated and the proportional chart gives clearer trait detail and would have allowed for a more in-depth discussion of changes in trait profile - in the context of the weighted data. A full set of charts showing proportional changes in trait composition is included in Appendix 10. The standardisation of values prior to analysis was also considered but was ultimately not followed through for similar reasons to those given above. Standardisation of data prior to analysis would have meant results that showed change only in terms of trait profiles, reducing both biomass and abundance weighted data to relative percentages. Proportional trait profiles are useful and certainly have a place in BTA analysis but, as outlined above, can be dangerous without weighting provided by biomass/abundance figures. An example of this from the Humber can be taken from a study by Mazik (2004) in which species sampled at Saltend are the same as those at Alkborough 2011 <2.4 m (Oligochaete sp., *Hediste diversicolor* and Nematode sp.) and are also proportionally similar. In the study by Mazik (2004), oligochaete species comprised between 88-99% of the community (seasonal variation) and *H.diversicolor* 0.2-11% with Nematode sp. at 0.1% throughout. At Alkborough <2.4 m, in this study, oligochaetes comprised 94.4%, *H.diversicolor* 3.9% and Nematode sp. 0.5% which would produce a very similar trait profile. Critically, at Alkborough <2.4 m, this equates to a mean of 21 individual oligochaetes per core (0.001m<sup>2</sup>) while at Saltend the mean number of individual oligochaetes per core was 1238. These individuals at Saltend were also observed to have a much larger than average body size. Saltend was a highly enriched site and very different from the Alkborough lower shore area but a standardised data set would have indicated the two

sites were highly similar. The opposing argument to this is that, in non-standardised data, changes in biomass and abundance figures can cause analysis to suggest differences between sites that have very similar traits profiles and may be very similar functionally, bar a small but statistically significant variance in abundance or biomass. This justifies the inclusion of standardised trait data but not its use as the central point of analysis in this project. In future studies it may be of benefit to run an analysis of the standardised data set and discuss the resulting trait profiles in the context of known physical variations.

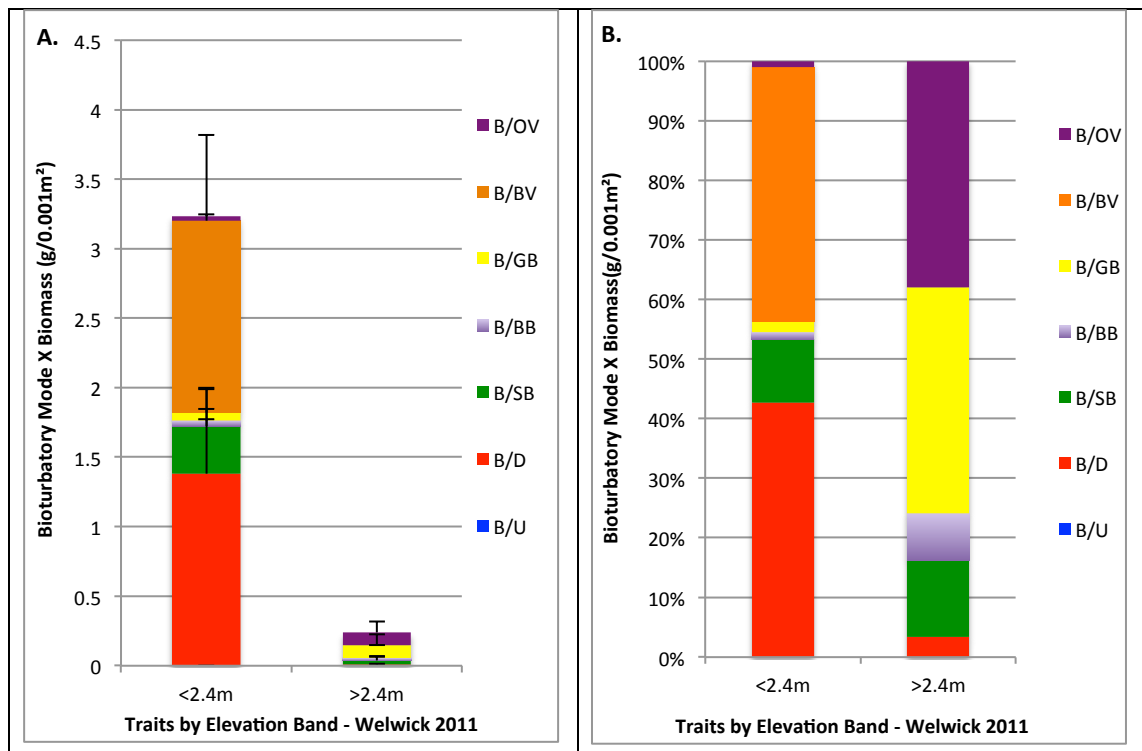


Fig. 5.1 Example of the issue of data presentation. A. Bioturbation trait data at Welwick 2011, weighted by biomass, showing strong contrast between upper and lower shore.. B. The same data presented proportionally, showing changes in trait profile more clearly.

In terms of smaller species sampled in this project (<500 $\mu$ ) there were limited data available and feeding trait classification of the Nematoda was largely based on two studies (Romeyn and Bouwman, 1983; Weiser, 1953), together with selected literature and careful personal examination of sampled animals. A recent study of estuarine nematodes indicated that BTA was no stronger than taxonomy in detecting special patterns, (Alves et al, 2014) but concluded it was useful in deepening functional knowledge of species and was also robust enough to allow for identification errors at species level, an issue in nematode studies, including this one. Copepods presented a similar problem in terms of identification and those in this study could only be identified to genus level. The impact of the inclusion of meiofaunal size range species was noticeable and nematodes in particular had a strong effect on abundance-weighted traits data, due to high densities at Paull and Welwick. Integrating and scoring these species together with macrofaunal species was labour intensive, but it was valuable in terms of increasing knowledge of the functional role of Humber nematode species, which are not well studied.

Another issue encountered in this project is the weighting of data, either by abundance or biomass. High densities of meiofaunal size range species emphasised certain modalities in abundance weighted data, even when transformed (which may also change interpretation), and biomass-weighted traits behaved in a similar way with an emphasis on the traits of much larger animals, such as *Macoma balthica* and *Hediste diversicolor*. Both weighting techniques were used here to determine any difference between the two, with both agreeing that changes took place, but with differing emphasis on which modalities were responsible for the distinction. On the whole, both weighting methods showed meaningful results, but biomass-weighted traits tended to return a more consistent result across all thirteen traits categories. For instance, at Paull, biomass-weighted data showed no significant variance for any traits, while abundance weighted data showed Longevity and Fecundity as differing between elevation bands. This agrees with Bolam and Eggleton (2014) who highlight the difference in BTA results depending on method of weighting used and suggest the use of biomass gives a stronger link to impact on functioning. They also suggest that trait composition has stronger links to secondary production than it does to taxonomic composition; this is important because secondary production is a measurable aspect of functioning and strong links give a robustness to the use of traits as a proxy for functioning. A possible way biomass and abundance could have been combined in this study is to have calculated the biomass ratio per sample (i.e. Biomass/Abundance, Gray and Elliott 2009) and used this to multiply trait scores. Both of these are a possible consideration for further BTA work

In terms of sampling, it might have been of value to extend the salinity gradient further along the estuary, and take measurements specifically for this study rather than relying on those established in the literature. The distance between Paull and Welwick was much less than that between Paull and Alkborough so many of the main changes in community structure and trait composition along the salinity gradient were between Alkborough and the two north bank sites. An additional sampling site much closer to the estuary mouth may have provided a more robust set of results and would be recommended for future studies. The same is true of the elevation gradient at Paull, where an extended gradient would have been preferable and would be recommended for similar studies with suitable resources.

Finally, further work is needed in terms of developing defined trait selection strategy and trait analysis protocol. This study was initially guided by others in the literature and used traits that other studies had reported positively on (See 3.6 BTA Methods). Following other methodology led to the inclusion of traits that overlap and may have over-complicated, or bias, the analysis. An example of this is the three traits relating to feeding (FM, FA and FT), which are closely related and could have been reduced to one or two traits only. A candidate for exclusion would be FA, as apparatus used for feeding is strongly linked to feeding method. FM is a clearer expression of this as it is more useful to know that a species is a predator than that it uses jaws to feed, rendering FA redundant. Fundamentally, more effort is required in the BTA process to build a trait system that focuses on measurable processes and traits whose presence or absence has a genuine ecological consequence – this is key for any further work. Although there are some useful guidelines currently available for approaching BTA trait selection (Bremner et al, 2006a), studies point to a lack of standard methodology, meaning it is sometimes difficult to directly compare results (Verissimo et al.2012; Paganelli et al., 2012). If aspects continue to be developed with this in mind, along with clear links to function, BTA

has potential to be combined to good effect with community structure studies, deepening understanding of benthic assemblages and their role in wider ecosystem function.

## Chapter 6

### Conclusions

In this study, where the gradient was sufficient in extent, changes were observed in both community structure elements and functional traits composition, refuting both null hypotheses. Community structure analysis between sites agreed with established understanding that components such as abundance, species richness and biomass decrease with a reduction in salinity in estuaries. The same components also changed with elevation but at Welwick it was the <2.4m band that showed higher values, while at Alkborough the >2.4m band presented much higher abundance, richness, biomass and diversity values. This is attributed to the presence of semi-terrestrial and freshwater species at >2.4m at Alkborough and a higher sampling effort in the realignment area. Changes in functional trait composition were observed for all traits analysed, but the overall breadth of trait expression was largely unaffected, except in areas of highly reduced species richness at <2.4 m elevation, in low salinity conditions, at Alkborough. Traits that were most useful in showing change were bioturbation and associated traits such as living habitat, mobility, body length, and feeding modes, which all had strong links to function. Reproductive traits (fecundity, age at maturity and reproductive frequency) also showed sensitivity to change and have established links to production. Using the BTA approach gave a deeper understanding of links between benthic activity and ecosystem function, and increased collected knowledge of the characteristics of local biota.

The aim of attempting to integrate smaller species (250 $\mu$  sieve size) in to the study was met, with the inclusion of Nematoda down to <2mm in body length, along with copepods of a similar size identified to genus level. Traits scores were achievable for these animals in all categories and they make a noticeable contribution to trait composition, particularly in the abundance-weighted data set. Overall, the application of BTA was valuable in indicating aspects of fundamental biology in the study area and linking them, via proxy traits, to wider functioning, increasing understanding of the ecosystem and adding depth and context to the traditional taxonomic approach.



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## Appendix 1.

Skewness and kurtosis values for PSA at all sites.

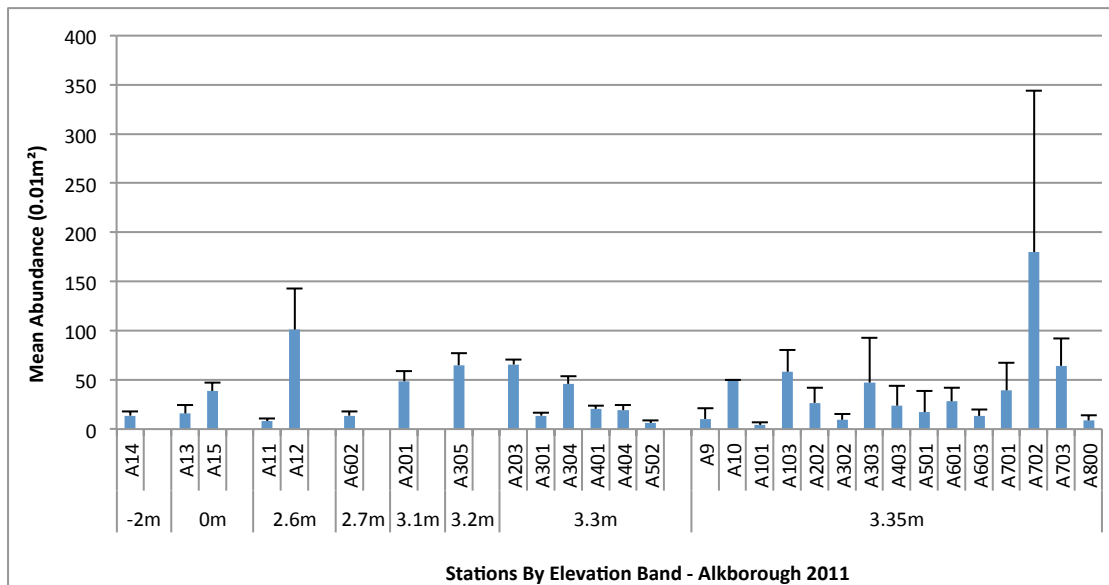
Site/Station	Skewness (Phi)	Kurtosis (Phi)
Welwick 10 S1	0.043	0.890
Welwick 10 S2	0.140	0.851
Welwick 10 S3	0.044	0.850
Welwick 10 S4	0.292	0.908
Welwick 10 S5	0.412	0.885
Welwick 10 S6	0.305	0.789
Welwick 10 S7	0.434	0.844
Welwick 10 S8	0.447	0.840
Welwick 10 S9	0.419	0.820
Welwick 10 S10	0.288	0.756

Site/Station	Skewness (f)	Kurtosis (f)
Welwick 11 S1	0.126	0.833
Welwick 11 S2	-0.004	1.154
Welwick 11 S3	0.088	0.857
Welwick 11 S4	0.377	0.894
Welwick 11 S5	0.195	0.766
Welwick 11 S6	0.016	0.757

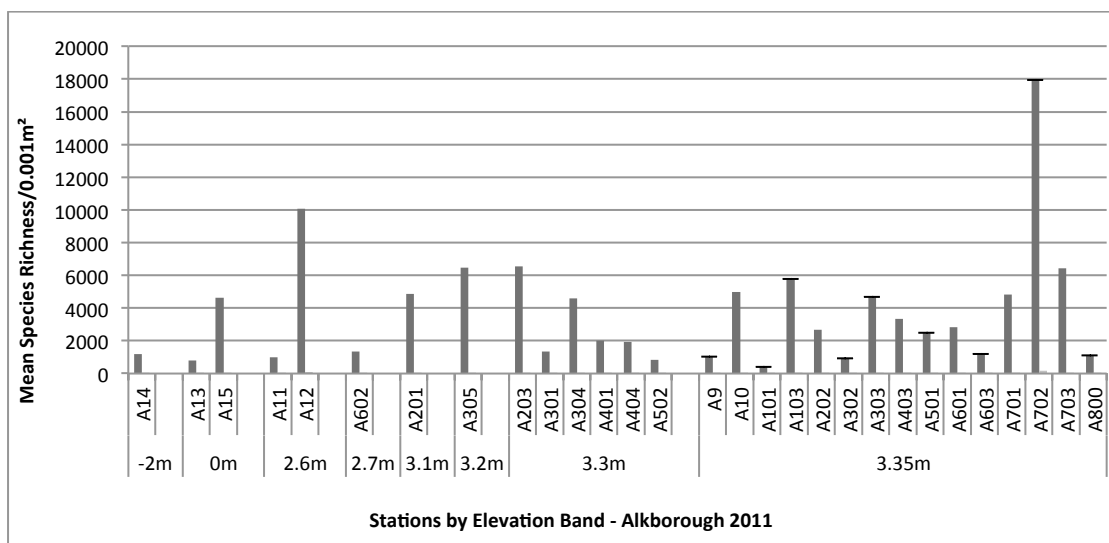
Site/Station	Skewness (f)	Kurtosis (f)
Paull 11 S1	0.314	0.843
Paull 11 S2	0.329	0.887
Paull 11 S3	0.205	0.783
Paull 11 S4	0.449	0.970
Paull 11 S5	0.183	0.806
Paull 11 S6	-0.086	0.942

Site/Station	Skewness (Phi)	Kurtosis (Phi)
ALK 9	-0.084	0.962
ALK 101	-0.128	0.933
ALK 102	-0.157	1.035
ALK 103	-0.066	0.911
ALK 201	-0.140	0.934
ALK 202	-0.145	0.974
ALK 203	-0.153	0.990
ALK 301	-0.089	0.967
ALK 302	0.107	0.802
ALK 303	-0.071	0.947
ALK 304	-0.139	1.030
ALK 305	-0.203	1.136
ALK 401	-0.094	0.996
ALK 403	-0.116	0.972
ALK 404	-0.109	0.978
ALK 501	-0.084	0.951
ALK 502	0.000	0.866
ALK 601	-0.018	0.846
ALK 602	-0.326	1.319
ALK 603	-0.116	0.969
ALK 701	-0.087	0.997
ALK 702	-0.053	0.935
ALK 703	0.284	0.886
ALK 800	-0.096	0.979
ALK 11	0.290	0.850
ALK 12	0.020	0.795
ALK 13	0.137	0.756
ALK 14	0.220	0.835
ALK 15	0.135	0.788

Appendix 2. Detailed elevation band for Alkborough, showing mean abundance and biomass/0.001m<sup>2</sup>



Mean abundance /0.001m<sup>2</sup> across eight elevation bands at Alkborough. No significant change was shown along the gradient

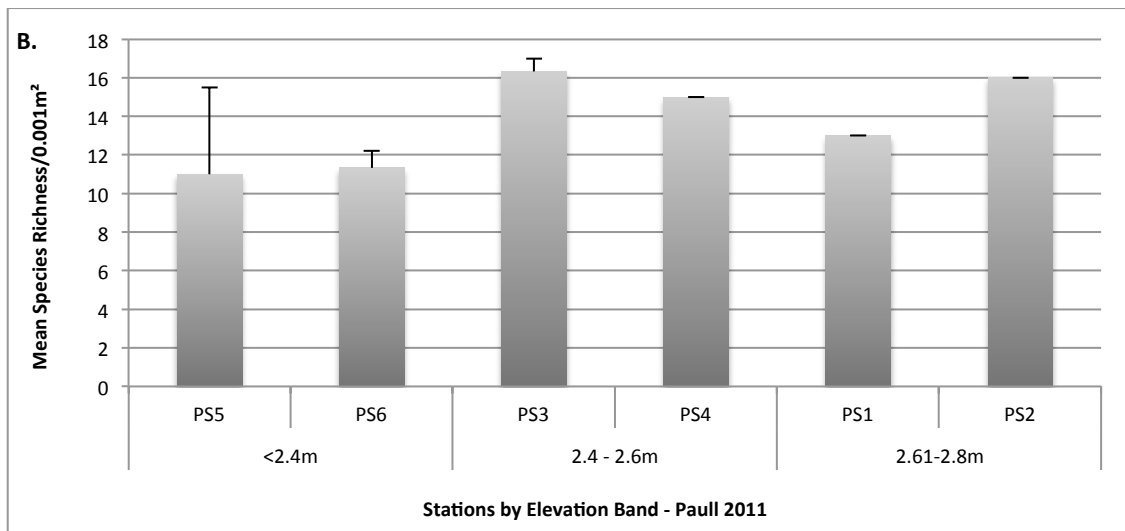
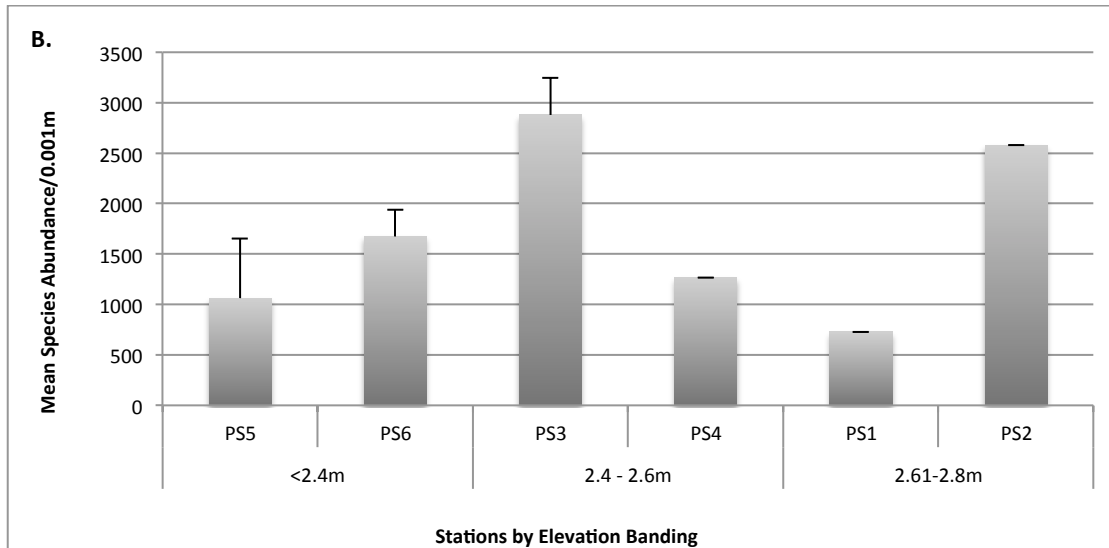


Mean species richness/0.001m<sup>2</sup> across 8 elevation bands at Alkborough.

Appendix 3.

Paull: Elevation Gradient

PERMANOVA results showed no significant difference along the elevation gradient for abundance, 'J', 'H, biomass or species richness.



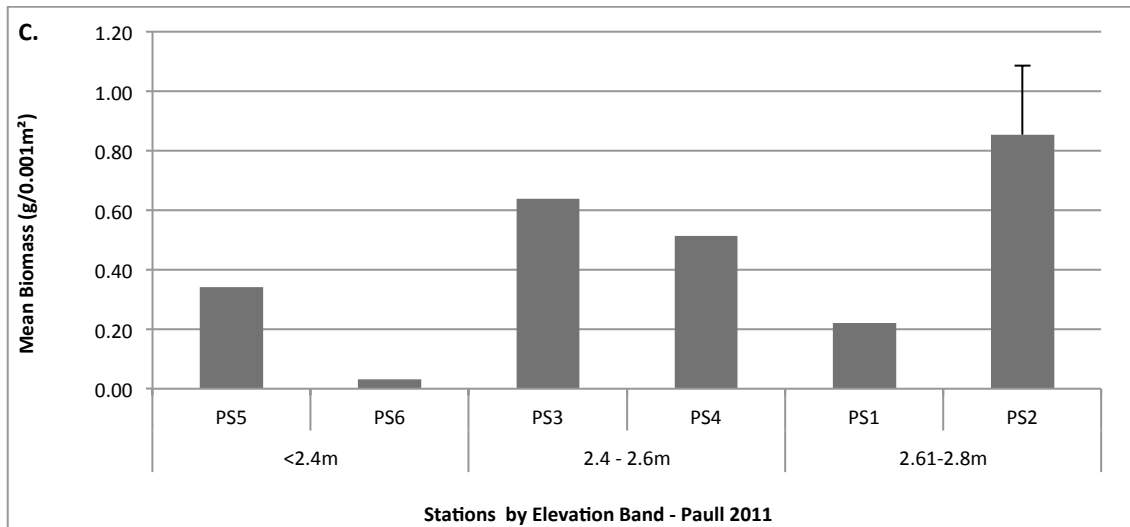


Fig 4.2.4 A-C. A, Mean abundance /0.001m<sup>2</sup> across three elevation bands. B, Mean species richness /0.001m<sup>2</sup> across three elevation bands. C, Mean biomass /0.001m<sup>2</sup> across three elevation bands. Table 4.2.1 for Std.Dev. values.

#### 4.2.4 Paull, Elevation Detail - Multivariate

Figure 4.2.10 shows all variables for Paull in an MDS plot across three elevation bands and gives a visual representation of the lack of statistically significant difference between groups. This is supported by PERMANOVA results, which returned non-significant values across the three-band analysis. PERMANOVA output for all variables at Paull in 2011 across the three band elevation gradient did not indicate any significant difference between elevation bands. A SIMPER analysis was also performed for this data set and also suggested a lack of difference between bands. Within-band similarity was high for the 2.4m-2.6m and 2.61m-2.8m bands, but was notably lower within the <2.4m band, reflecting the separation between samples PS5 and PS6 in the MDS plot below (Fig. 4.2.10.). Between elevation bands, dissimilarity was particularly low between the middle and upper elevation bands at 37.10% (Table 4.2.3).

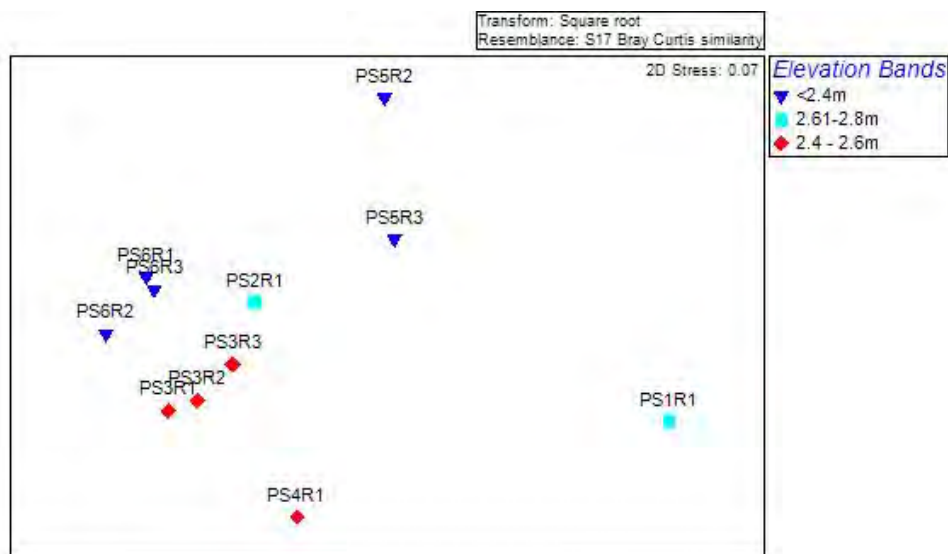


Figure 4.2.10. MDS plot showing the distribution of samples at Paull 2011 across three elevation bands,

Table 4.2.3 Average dissimilarity between bands at Paull 2011.

% Dissimilarity Between Elevation Bands - Paull 2011 Triple Banding			
Elevation	<2.4m	2.4m-2.6m	2.61m-2.8m
<2.4			
2.4-2.6m	42.88		
2.61-2.8m	48.62	37.10	

Table 4.2.4 SIMPER output for Paull 2011 across three elevation bands.

Average Similarity - % Species Contribution by Elevation Band		
Elevation	Paull 2011	% Contribution
<2.4m	Nematode Type B	20.53
	Nematode Type A	16.30
	<i>Manayunkia aestuarina</i>	13.78
	Average Similarity%	48.55
2.4m -2.6m	Nematode Type A	24.06
	<i>Manayunkia aestuarina</i>	20.43
	Nematode Type B	12.01
	Nematode Type C	9.56
	Average Similarity %	75.20
2.61-2.8m	<i>Manayunkia aestuarina</i>	36.79
	Nematode Type B	12.48
	<i>Copepoda Tachidius</i>	11.90
	Average Similarity %	57.24

## Appendix 4

### % Average Dissimilarity for All sites 2011 – Taxonomic Composition

#### Appendix 4. 1

*Groups Welwick B>2.4m & Welwick B<2.4m*

Average dissimilarity = 52.16

Group Welwick B>2.4m

Group Welwick B<2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Collembola (Isotomidae)	17.74	0.20	9.49	1.03	18.19	18.19
Manayunkia aestuarina	18.53	4.41	7.28	1.25	13.96	32.15
Enchytraeidae	16.76	2.29	6.84	1.72	13.11	45.25
Nematode Type C	14.99	10.52	4.33	2.02	8.30	53.55
Nematode Type A	18.36	14.79	4.02	1.42	7.70	61.25

*Groups Welwick B>2.4m & PAULL>2.4m*

Average dissimilarity = 45.27

Group Welwick B>2.4m

Group PAULL>2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Manayunkia aestuarina	18.53	27.61	7.92	2.40	17.49	17.49
Collembola (Isotomidae)	17.74	0.78	7.66	1.00	16.91	34.40
Nematode Type B	23.78	18.22	4.36	1.18	9.63	44.03
Nematode Type A	18.36	21.00	4.34	1.25	9.60	53.62
Enchytraeidae	16.76	10.01	4.09	1.29	9.05	62.67

*Groups Welwick B<2.4m & PAULL>2.4m*

Average dissimilarity = 44.20

Group Welwick B<2.4m

Group PAULL>2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Manayunkia aestuarina	4.41	27.61	11.19	2.52	25.32	25.32
Nematode Type A	14.79	21.00	5.10	1.75	11.54	36.86
Nematode Type B	17.87	18.22	4.80	1.58	10.85	47.72
Enchytraeidae	2.29	10.01	3.62	1.90	8.19	55.91
Tubificoides benedii	6.63	1.35	2.71	1.19	6.13	62.03

Groups Welwick B>2.4m & PAULL<2.4m  
Average dissimilarity = 50.79

Species	Group Welwick B>2.4m			Group PAULL<2.4m		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Collembola (Isotomidae)	17.74	2.60	8.28	0.83	16.31	16.31
Enchytraeidae	16.76	7.64	6.00	1.33	11.81	28.12
Manayunkia aestuarina	18.53	11.00	5.44	0.88	10.72	38.84
Nematode Type A	18.36	14.03	5.14	0.95	10.11	48.95
Nematode Type B	23.78	16.29	4.84	0.74	9.53	58.48
Nematode Type C	14.99	11.15	4.82	1.16	9.48	67.96

Groups Welwick B<2.4m & PAULL<2.4m  
Average dissimilarity = 46.79

Species	Group Welwick B<2.4m			Group PAULL<2.4m		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Manayunkia aestuarina	4.41	11.00	5.38	1.80	11.50	11.50
Nematode Type B	17.87	16.29	5.14	0.80	10.99	22.49
Nematode Type A	14.79	14.03	4.72	0.89	10.10	32.59
Copepoda Tachidius	4.45	10.41	3.99	1.10	8.52	41.11
Tubificoides benedii	6.63	4.38	3.71	1.18	7.93	49.04
Enchytraeidae	2.29	7.64	3.38	1.20	7.23	56.27
Nematode Type C	10.52	11.15	3.38	0.87	7.22	63.49

Groups PAULL>2.4m & PAULL<2.4m  
Average dissimilarity = 44.79

Species	Group PAULL>2.4m			Group PAULL<2.4m		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Manayunkia aestuarina	27.61	11.00	8.24	1.26	18.40	18.40
Nematode Type A	21.00	14.03	5.93	1.10	13.25	31.65
Nematode Type B	18.22	16.29	5.35	1.12	11.95	43.60
Enchytraeidae	10.01	7.64	3.44	1.32	7.69	51.29
Copepoda Tachidius	6.68	10.41	3.07	0.97	6.86	58.15
Nematode Type C	10.78	11.15	2.96	1.02	6.60	64.75

Groups Welwick B>2.4m & ALK>2.4m  
Average dissimilarity = 95.00

Species	Group Welwick B>2.4m			Group ALK>2.4m		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	23.78	0.51	18.40	6.36	19.37	19.37
Collembola (Isotomidae)	17.74	0.00	16.34	1.02	17.20	36.57
Nematode Type A	18.36	0.41	14.36	2.16	15.11	51.68
Manayunkia aestuarina	18.53	0.00	12.22	1.61	12.86	64.54



Groups Welwick B<2.4m & ALK>2.4m  
Average dissimilarity = 94.84

Group Welwick B<2.4m                      Group ALK>2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	17.87	0.51	18.32	5.23	19.32	19.32
Nematode Type A	14.79	0.41	15.37	4.32	16.20	35.52
Nematode Type C	10.52	0.40	10.86	4.94	11.46	46.97
Tubificoides benedii	6.63	0.00	7.11	1.50	7.49	54.47
Tellinacea sp.	4.74	0.00	5.08	3.88	5.35	59.82
Copepoda	4.45	0.01	4.64	2.09	4.89	64.71
Tachidius						

Groups PAULL>2.4m & ALK>2.4m  
Average dissimilarity = 94.77

Group PAULL>2.4m                      Group ALK>2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Manayunkia aestuarina	27.61	0.00	20.87	4.18	22.02	22.02
Nematode Type A	21.00	0.41	15.03	2.28	15.86	37.88
Nematode Type B	18.22	0.51	12.31	2.22	12.99	50.87
Nematode Type C	10.78	0.40	7.59	3.30	8.01	58.88
Enchytraeidae	10.01	1.78	6.07	2.28	6.41	65.28

Groups PAULL<2.4m & ALK>2.4m  
Average dissimilarity = 96.29

Group PAULL<2.4m                      Group ALK>2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	16.29	0.51	13.08	1.98	13.59	13.59
Nematode Type A	14.03	0.41	11.23	1.94	11.67	25.26
Hydrobia ulvae	3.62	0.00	9.02	0.55	9.37	34.62
Manayunkia aestuarina	11.00	0.00	8.84	1.93	9.18	43.80
Nematode Type C	11.15	0.40	8.81	2.05	9.15	52.95
Copepoda	10.41	0.01	7.78	1.35	8.08	61.03
Tachidius						

Groups Welwick B>2.4m & ALK<2.4m  
Average dissimilarity = 98.91

Group Welwick B>2.4m                      Group ALK<2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	23.78	0.00	19.27	8.51	19.49	19.49
Collembola (Isotomidae)	17.74	0.00	16.83	1.01	17.02	36.50
Nematode Type A	18.36	0.11	14.97	2.21	15.13	51.64
Manayunkia aestuarina	18.53	0.00	12.50	1.61	12.64	64.28

Groups Welwick B<2.4m & ALK<2.4m  
Average dissimilarity = 98.60

Group Welwick B<2.4m                      Group ALK<2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	17.87	0.00	19.45	7.77	19.73	19.73
Nematode Type A	14.79	0.11	16.21	4.96	16.45	36.17
Nematode Type C	10.52	0.00	11.66	6.63	11.83	48.00
Tubificoides benedii	6.63	0.00	7.37	1.50	7.47	55.47
Tellinacea sp.	4.74	0.00	5.26	3.97	5.33	60.81

Groups PAULL>2.4m & ALK<2.4m  
Average dissimilarity = 98.16

Group PAULL>2.4m                      Group ALK<2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Manayunkia aestuarina	27.61	0.00	21.43	4.17	21.83	21.83
Nematode Type A	21.00	0.11	15.62	2.34	15.91	37.74
Nematode Type B	18.22	0.00	12.88	2.31	13.12	50.86
Nematode Type C	10.78	0.00	8.08	3.84	8.23	59.09
Enchytraeidae	10.01	0.11	7.33	3.15	7.47	66.56

Groups PAULL<2.4m & ALK<2.4m  
Average dissimilarity = 99.11

Group PAULL<2.4m                      Group ALK<2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	16.29	0.00	13.47	1.91	13.59	13.59
Nematode Type A	14.03	0.11	11.54	1.89	11.64	25.23
Hydrobia ulvae	3.62	0.00	10.11	0.55	10.20	35.44
Manayunkia aestuarina	11.00	0.00	9.07	1.91	9.15	44.59
Nematode Type C	11.15	0.00	9.04	1.94	9.12	53.71
Copepoda Tachidius	10.41	0.00	7.98	1.34	8.05	61.76

Groups ALK>2.4m & ALK<2.4m  
Average dissimilarity = 93.14

Group ALK>2.4m                      Group ALK<2.4m

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.45	4.31	34.10	2.08	36.61	36.61
Enchytraeidae	1.78	0.11	11.80	0.90	12.67	49.28
Paranis littoralis	1.80	0.00	11.67	1.05	12.53	61.81

## Appendix 4.2

### % Average Dissimilarity Paul 2011: Three Elevation Bands. Taxonomic Composition

*Groups 2.61-2.8m & 2.4 - 2.6m*

Average dissimilarity = 37.10

Species	Group 2.61-2.8m			Group 2.4 - 2.6m		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type A	8.65	27.18	8.10	2.54	21.82	21.82
Nematode Type B	13.34	20.65	5.51	1.68	14.85	36.67
Manayunkia aestuarina	29.90	26.46	4.28	1.64	11.53	48.20
Enchytraeidae	8.98	10.52	2.65	1.85	7.15	55.35
Nematode Type C	9.54	11.40	2.54	1.60	6.84	62.19

*Groups 2.61-2.8m & <2.4m*

Average dissimilarity = 48.62

Species	Group 2.61-2.8m			Group <2.4m		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Manayunkia aestuarina	29.90	11.00	10.40	1.29	21.38	21.38
Nematode Type B	13.34	16.29	5.08	1.23	10.45	31.83
Nematode Type A	8.65	14.03	4.59	1.52	9.45	41.28
Enchytraeidae	8.98	7.64	4.01	1.40	8.25	49.53
Nematode Type C	9.54	11.15	3.97	1.37	8.17	57.70
Copepoda Tachidius	7.95	10.41	3.32	0.90	6.83	64.53

*Groups 2.4 - 2.6m & <2.4m*

Average dissimilarity = 42.88

Species	Group 2.4 - 2.6m			Group <2.4m		
	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Manayunkia aestuarina	26.46	11.00	7.17	1.31	16.71	16.71
Nematode Type A	27.18	14.03	6.60	1.06	15.40	32.11
Nematode Type B	20.65	16.29	5.49	1.07	12.80	44.92
Enchytraeidae	10.52	7.64	3.16	1.28	7.37	52.29
Copepoda Tachidius	6.05	10.41	2.95	1.01	6.88	59.17
Nematode Type C	11.40	11.15	2.45	0.87	5.71	64.88

## Appendix 4.3

### Alkborough % Average Dissimilarity Species Composition

#### *Groups 3.35m & 3.1m*

Average dissimilarity = 77.17

	Group 3.35m	Group 3.1m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Paranais littoralis	1.75	4.34	14.71	1.50	19.06	19.06
Diptera dolichopodidae	0.42	3.31	13.64	2.65	17.67	36.73
Hediste diversicolor	0.10	2.57	11.44	2.74	14.83	51.56
Corophium volutator	0.61	2.25	9.01	1.69	11.67	63.23

#### *Groups 3.35m & 3.3m*

Average dissimilarity = 71.78

	Group 3.35m	Group 3.3m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Enchytraeidae	1.84	2.42	15.35	1.19	21.38	21.38
Paranais littoralis	1.75	1.98	12.59	1.16	17.53	38.92
Collembola sp.	1.44	1.03	9.74	1.00	13.56	52.48
Chironomidae Larvae	0.37	0.73	6.75	0.58	9.40	61.88

#### *Groups 3.1m & 3.3m*

Average dissimilarity = 69.09

	Group 3.1m	Group 3.3m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Paranais littoralis	4.34	1.98	11.54	1.45	16.71	16.71
Diptera dolichopodidae	3.31	0.99	10.68	1.92	15.46	32.17
Hediste diversicolor	2.57	0.13	10.59	3.16	15.32	47.49
Enchytraeidae	0.00	2.42	9.20	0.96	13.32	60.81

#### *Groups 3.35m & 3.2m*

Average dissimilarity = 82.10

	Group 3.35m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironomidae Larvae	0.37	6.61	34.33	2.58	41.81	41.81
Paranais littoralis	1.75	2.71	11.01	1.56	13.41	55.22
Enchytraeidae	1.84	0.33	7.97	0.99	9.71	64.93

*Groups 3.1m & 3.2m*

Average dissimilarity = 71.74

	Group 3.1m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironomidae Larvae	0.58	6.61	22.79	5.82	31.76	31.76
Diptera dolichopodidae	3.31	0.47	11.16	2.63	15.56	47.32
Hediste diversicolor	2.57	0.00	9.71	3.95	13.53	60.85

*Groups 3.3m & 3.2m*

Average dissimilarity = 73.88

	Group 3.3m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironomidae Larvae	0.73	6.61	29.69	2.83	40.18	40.18
Enchytraeidae	2.42	0.33	9.92	0.97	13.43	53.61
Paranais littoralis	1.98	2.71	8.70	1.39	11.78	65.39

*Groups 3.35m & 2.7m*

Average dissimilarity = 68.78

	Group 3.35m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Enchytraeidae	1.84	2.14	16.61	1.42	24.15	24.15
Paranais littoralis	1.75	1.56	14.31	1.29	20.80	44.95
Collembola sp.	1.44	0.00	10.81	0.84	15.72	60.67

*Groups 3.1m & 2.7m*

Average dissimilarity = 72.25

	Group 3.1m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Paranais littoralis	4.34	1.56	14.33	1.43	19.84	19.84
Hediste diversicolor	2.57	0.00	13.20	4.39	18.26	38.10
Diptera dolichopodidae	3.31	1.15	11.27	2.28	15.59	53.69
Enchytraeidae	0.00	2.14	11.03	3.06	15.27	68.96

*Groups 3.3m & 2.7m*

Average dissimilarity = 61.91

	Group 3.3m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Enchytraeidae	2.42	2.14	16.72	1.98	27.01	27.01
Paranais littoralis	1.98	1.56	11.65	1.07	18.81	45.82
Diptera dolichopodidae	0.99	1.15	7.99	1.09	12.91	58.73
Collembola sp.	1.03	0.00	6.25	0.86	10.09	68.82

*Groups 3.2m & 2.7m*

Average dissimilarity = 79.20

	Group 3.2m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironomidae Larvae	6.61	0.00	40.48	5.16	51.11	51.11
Enchytraeidae	0.33	2.14	11.06	1.88	13.97	65.08

*Groups 3.35m & 2.6m*

Average dissimilarity = 93.52

	Group 3.35m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	5.94	38.47	2.16	41.13	41.13
Enchytraeidae	1.84	0.91	11.85	0.94	12.67	53.80
Paranais littoralis	1.75	0.00	10.21	0.96	10.92	64.72

*Groups 3.1m & 2.6m*

Average dissimilarity = 95.88

	Group 3.1m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	5.94	24.27	2.04	25.31	25.31
Paranais littoralis	4.34	0.00	20.18	2.76	21.05	46.36
Diptera dolichopodidae	3.31	0.00	15.84	3.50	16.52	62.88

*Groups 3.3m & 2.6m*

Average dissimilarity = 93.59

	Group 3.3m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	5.94	34.18	2.31	36.52	36.52
Enchytraeidae	2.42	0.91	13.83	1.09	14.78	51.30
Paranais littoralis	1.98	0.00	13.07	1.16	13.96	65.26

*Groups 3.2m & 2.6m*

Average dissimilarity = 98.61

	Group 3.2m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironomidae Larvae	6.61	0.00	36.64	3.21	37.16	37.16
Heterochaete costata	0.00	5.94	27.74	2.12	28.13	65.29

*Groups 2.7m & 2.6m*

Average dissimilarity = 89.88

	Group 2.7m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	5.94	42.92	3.14	47.75	47.75
Enchytraeidae	2.14	0.91	15.69	1.23	17.46	65.21

*Groups 3.35m & 0m*

Average dissimilarity = 97.60

	Group 3.35m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	4.70	37.19	2.10	38.11	38.11
Enchytraeidae	1.84	0.00	11.59	0.88	11.88	49.98
Paranais littoralis	1.75	0.00	10.60	1.00	10.86	60.84

*Groups 3.1m & 0m*

Average dissimilarity = 88.17

	Group 3.1m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	4.70	22.15	2.91	25.12	25.12
Paranais littoralis	4.34	0.00	20.98	3.17	23.80	48.92
Diptera dolichopodidae	3.31	0.00	16.48	4.49	18.69	67.61

*Groups 3.3m & 0m*

Average dissimilarity = 97.20

	Group 3.3m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	4.70	32.57	2.53	33.51	33.51
Enchytraeidae	2.42	0.00	14.12	0.99	14.52	48.03
Paranais littoralis	1.98	0.00	13.58	1.24	13.97	62.00

*Groups 3.2m & 0m*

Average dissimilarity = 100.00

	Group 3.2m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironomidae Larvae	6.61	0.00	38.14	4.31	38.14	38.14
Heterochaete costata	0.00	4.70	25.75	2.74	25.75	63.89

*Groups 2.7m & 0m*

Average dissimilarity = 100.00

	Group 2.7m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	4.70	41.89	3.30	41.89	41.89
Enchytraeidae	2.14	0.00	20.53	2.68	20.53	62.42

*Groups 2.6m & 0m*

Average dissimilarity = 46.66

	Group 2.6m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	5.94	4.70	25.95	1.69	55.62	55.62
Hediste diversicolor	0.00	0.90	7.32	1.12	15.69	71.31

*Groups 3.35m & -2m*

Average dissimilarity = 96.84

	Group 3.35m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	3.55	36.59	2.03	37.79	37.79
Enchytraeidae	1.84	0.33	13.52	0.98	13.97	51.75
Paranis littoralis	1.75	0.00	12.15	1.03	12.55	64.30

*Groups 3.1m & -2m*

Average dissimilarity = 100.00

	Group 3.1m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Paranis littoralis	4.34	0.00	23.22	3.39	23.22	23.22
Heterochaete costata	0.00	3.55	19.31	3.93	19.31	42.53
Diptera dolichopodidae	3.31	0.00	18.28	5.15	18.28	60.81

*Groups 3.3m & -2m*

Average dissimilarity = 96.57

	Group 3.3m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	3.55	30.61	2.68	31.70	31.70
Paranis littoralis	1.98	0.00	15.65	1.27	16.21	47.91
Enchytraeidae	2.42	0.33	15.36	1.04	15.90	63.81

*Groups 3.2m & -2m*

Average dissimilarity = 98.67

	Group 3.2m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Chironomidae Larvae	6.61	0.00	43.00	5.16	43.58	43.58
Heterochaete costata	0.00	3.55	23.03	3.29	23.34	66.92

*Groups 2.7m & -2m*

Average dissimilarity = 92.58

	Group 2.7m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	0.00	3.55	41.14	4.28	44.43	44.43
Enchytraeidae	2.14	0.33	20.87	2.12	22.54	66.97

*Groups 2.6m & -2m*

Average dissimilarity = 40.10

	Group 2.6m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	5.94	3.55	25.44	1.61	63.44	63.44



Groups 0m & -2m

Average dissimilarity = 36.88

	Group 0m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Heterochaete costata	4.70	3.55	20.44	1.71	55.42	55.42
Hediste diversicolor	0.90	0.00	8.96	1.28	24.29	79.72

#### Appendix 4.4 Welwick 2010 and 2011 Average Dissimilarity

Groups 2010>2.4m & 2010<2.4m

Average dissimilarity = 66.09

	Group 2010>2.4m	Group 2010<2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Tubificoides benedii	1.13	7.55	8.81	2.42	13.33	13.33
Collembola (Isotomidae)	7.15	1.38	8.76	1.73	13.26	26.59
Nematode Type B	3.10	8.70	8.05	1.94	12.18	38.77
Nematode Type A	2.80	7.36	6.49	1.70	9.82	48.59
Macoma balthica	0.00	3.47	4.90	4.02	7.41	56.01
Nematode Type C	1.67	4.67	4.86	1.46	7.35	63.35

Groups 2010>2.4m & 2011>2.4m

Average dissimilarity = 72.33

	Group 2010>2.4m	Group 2011>2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	3.10	23.78	14.65	5.03	20.26	20.26
Nematode Type A	2.80	18.36	11.17	1.83	15.44	35.70
Manayunkia aestuarina	0.69	18.53	10.66	1.42	14.74	50.43
Enchytraeidae	0.38	16.76	10.54	1.92	14.58	65.01

Groups 2010<2.4m & 2011>2.4m

Average dissimilarity = 67.42

	Group 2010<2.4m	Group 2011>2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Collembola (Isotomidae)	1.38	17.74	11.02	0.97	16.34	16.34
Manayunkia aestuarina	0.54	18.53	9.17	1.36	13.60	29.94
Nematode Type B	8.70	23.78	8.85	3.20	13.12	43.06
Enchytraeidae	1.08	16.76	8.60	1.84	12.76	55.82
Nematode Type A	7.36	18.36	6.90	1.48	10.23	66.05

Groups 2010>2.4m & 2011<2.4m  
Average dissimilarity = 76.06

	Group 2010>2.4m	Group 2011<2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	3.10	17.87	13.50	3.42	17.75	17.75
Nematode Type A	2.80	14.79	11.08	3.19	14.57	32.32
Nematode Type C	1.67	10.52	8.25	3.52	10.85	43.17
Collembola (Isotomidae)	7.15	0.20	6.66	1.89	8.76	51.93
Tubificoides benedii	1.13	6.63	5.17	1.27	6.80	58.72
Tellinacea sp.	0.22	4.74	4.20	3.42	5.52	64.24

Groups 2010<2.4m & 2011<2.4m  
Average dissimilarity = 41.77

	Group 2010<2.4m	Group 2011<2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Nematode Type B	8.70	17.87	6.69	1.80	16.03	16.03
Nematode Type A	7.36	14.79	5.51	1.79	13.18	29.21
Nematode Type C	4.67	10.52	4.46	1.79	10.69	39.89
Tubificoides benedii	7.55	6.63	3.45	1.61	8.26	48.16
Manayunkia aestuarina	0.54	4.41	2.73	0.59	6.53	54.68
Copepoda Tachidius	3.01	4.45	2.49	1.55	5.95	60.64

Groups 2011>2.4m & 2011<2.4m  
Average dissimilarity = 52.16

	Group 2011>2.4m	Group 2011<2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Collembola (Isotomidae)	17.74	0.20	9.49	1.03	18.19	18.19
Manayunkia aestuarina	18.53	4.41	7.28	1.25	13.96	32.15
Enchytraeidae	16.76	2.29	6.84	1.72	13.11	45.25
Nematode Type C	14.99	10.52	4.33	2.02	8.30	53.55
Nematode Type A	18.36	14.79	4.02	1.42	7.70	61.25

## Appendix 5

### Traits

#### 5.1 % Average Similarity 2011 weighted by Abundance. Full Tables.

*Group >2.4mWelwick B*

Average similarity: 72.70

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	48.61	4.24	6.80	5.83	5.83
<6m	42.61	4.06	6.74	5.58	11.42
LH/F	40.85	3.85	6.54	5.30	16.72
2-5mm	42.39	3.80	6.18	5.22	21.94
AM/M	37.60	3.71	6.24	5.10	27.04
P/I	40.95	3.14	3.08	4.32	31.36
F/10	35.00	3.04	3.15	4.18	35.54
6- 18m	34.93	3.01	3.04	4.15	39.69
FA/M	34.76	3.00	3.03	4.13	43.82
B/BB	34.76	3.00	3.03	4.13	47.96
FT/I	30.67	2.75	3.51	3.78	51.74
FM/P	25.48	2.23	3.00	3.07	54.81
S/10	23.74	2.12	6.63	2.92	57.72
B/SB	26.30	1.74	3.00	2.39	60.11

*Group <2.4mWelwick B*

Average similarity: 77.97

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	29.27	4.04	8.01	5.18	5.18
P/I	28.60	3.96	8.55	5.08	10.26
B/BB	26.85	3.74	7.01	4.80	15.06
FA/M	26.81	3.72	6.92	4.77	19.83
LH/F	26.64	3.72	7.16	4.77	24.60
<6m	26.25	3.70	7.04	4.75	29.35
6- 18m	26.26	3.69	6.93	4.73	34.08
F/10	26.08	3.68	7.50	4.71	38.80
AM/M	26.26	3.65	7.21	4.68	43.47
2-5mm	24.75	3.43	6.95	4.40	47.87
FT/I	23.42	3.23	5.88	4.14	52.01
FM/P	19.69	2.71	5.80	3.48	55.49
S/20	15.59	2.12	7.48	2.71	58.20
S/15	15.21	2.07	7.53	2.66	60.86

*Group >2.4mPHS*

Average similarity: 78.88

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	43.80	3.77	7.51	4.78	4.78
P/I	42.97	3.63	6.24	4.61	9.39
2-5mm	36.69	3.08	6.53	3.91	13.30
LH/F	31.96	2.58	4.12	3.27	16.57
F/10	32.13	2.57	3.65	3.26	19.83
<6m	32.22	2.55	3.29	3.23	23.06
6- 18m	32.19	2.54	3.23	3.22	26.27
AM/M	31.42	2.48	3.51	3.15	29.42
18m-2yrs	28.86	2.47	5.29	3.13	32.55
B/BB	31.22	2.40	2.74	3.04	35.59
FA/M	31.19	2.39	2.70	3.03	38.61
S/20	26.56	2.32	7.82	2.94	41.55
LH/T	27.69	2.31	4.56	2.93	44.48
AM/S	27.68	2.31	4.55	2.93	47.41
≥6m	27.68	2.31	4.54	2.93	50.33
FA/T	27.68	2.31	4.54	2.92	53.26
F/>10K	27.61	2.30	4.52	2.92	56.17
S/15	25.76	2.23	6.80	2.82	59.00
FT/I	29.22	2.17	2.63	2.76	61.75

Group <2.4mPHS

Average similarity: 64.26

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	32.78	3.28	2.59	5.10	5.10
LH/F	29.03	2.87	2.86	4.47	9.57
F/10	27.12	2.71	2.82	4.22	13.79
AM/M	26.08	2.70	3.03	4.21	18.00
2-5mm	27.66	2.69	2.30	4.18	22.19
P/I	28.42	2.54	1.35	3.95	26.13
<6m	28.14	2.50	1.61	3.89	30.02
6- 18m	27.78	2.35	1.33	3.66	33.68
FA/M	25.55	2.19	1.33	3.41	37.09
B/BB	25.38	2.18	1.33	3.40	40.49
S/20	17.81	1.87	3.12	2.91	43.40
FT/I	21.77	1.82	1.28	2.84	46.23
B/SB	16.14	1.64	10.37	2.55	48.78
FM/SS	14.84	1.62	7.58	2.51	51.30
S/25	15.45	1.61	3.79	2.50	53.80
FM/P	18.46	1.52	1.28	2.37	56.17
18m-2yrs	13.31	1.52	7.17	2.37	58.53
S/15	16.53	1.49	1.36	2.31	60.85

Group >2.4mALK

Average similarity: 50.28

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
LH/F	4.66	3.50	2.70	6.95	6.95
AM/M	4.42	3.21	2.63	6.38	13.33
RF/I	4.14	2.84	1.95	5.66	18.99
<6m	3.89	2.51	1.58	4.99	23.98
P/I	3.86	2.49	1.78	4.96	28.93
B/BB	4.04	2.48	1.51	4.94	33.87
FA/M	3.80	2.20	1.37	4.38	38.25
F/10	3.58	2.11	1.34	4.20	42.44
FM/D	2.91	1.88	1.26	3.73	46.18
S/10	2.46	1.82	2.59	3.62	49.79
5mm-1cm	2.87	1.82	1.30	3.62	53.41
P/E	2.70	1.72	1.22	3.43	56.84
FA/J	2.55	1.69	1.22	3.37	60.21

Group <2.4mALK

Average similarity: 68.61

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	4.47	4.92	4.13	7.18	7.18
AM/M	4.45	4.92	4.13	7.18	14.35
18m-2yrs	4.43	4.92	4.13	7.18	21.53
1-2cm	4.44	4.89	4.14	7.12	28.65
RF/S	4.42	4.89	4.14	7.12	35.77
FT/D	4.35	4.76	3.72	6.94	42.71
1-2yr	4.34	4.74	3.66	6.91	49.63
FM/SS	4.33	4.74	3.52	6.91	56.54
FA/M	4.34	4.74	3.52	6.91	63.45

## Appendix

### 5.2 Average Dissimilarity for 2011, Abundance Weighted.

Groups >2.4mWelwick B & <2.4mWelwick B

Average dissimilarity = 34.52

	Group >2.4mWelwick B	Group <2.4mWelwick B				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FM/D	25.83	5.43	1.30	1.39	3.76	3.76
B/SB	26.30	7.28	1.24	1.34	3.59	7.35
RF/I	48.61	29.27	1.21	1.56	3.51	10.86
2-5mm	42.39	24.75	1.15	1.70	3.32	14.19
<6m	42.61	26.25	1.09	1.78	3.15	17.33
<6m	17.88	2.13	1.07	1.02	3.11	20.44
FT/D	25.94	9.91	1.04	1.09	3.00	23.45
F/100	18.06	3.46	1.00	0.96	2.90	26.35
P/I	40.95	28.60	0.98	1.33	2.83	29.18
LH/F	40.85	26.64	0.98	1.55	2.83	32.01
F/>10K	18.53	4.76	0.93	1.24	2.70	34.71
≥6m	18.54	5.42	0.89	1.16	2.59	37.30
FA/T	18.54	5.41	0.89	1.16	2.59	39.89
AM/S	18.54	5.52	0.89	1.15	2.57	42.45
LH/T	18.54	5.59	0.88	1.15	2.55	45.00
18m-2yrs	19.16	6.56	0.88	1.17	2.54	47.54
FA/J	18.82	5.99	0.88	0.86	2.54	50.08
AM/M	37.60	26.26	0.79	1.64	2.29	52.37
6- 18m	34.93	26.26	0.78	1.69	2.26	54.63
F/10	35.00	26.08	0.77	1.66	2.24	56.87
FA/M	34.76	26.81	0.76	1.62	2.20	59.06
B/BB	34.76	26.85	0.75	1.62	2.19	61.25

Groups >2.4mWelwick B & >2.4mPHS

Average dissimilarity = 29.05

	Group >2.4mWelwick B	Group >2.4mPHS				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
18m-2yrs	19.16	28.86	1.01	2.76	3.49	3.49
LH/T	18.54	27.69	1.00	2.48	3.45	6.94
AM/S	18.54	27.68	1.00	2.48	3.44	10.38
≥6m	18.54	27.68	1.00	2.48	3.44	13.83
FA/T	18.54	27.68	1.00	2.48	3.44	17.27
F/>10K	18.53	27.61	1.00	2.48	3.44	20.71
<6m	17.88	1.60	0.90	1.04	3.09	23.79
P/I	40.95	42.97	0.87	1.73	2.98	26.77
F/100	18.06	4.44	0.76	0.89	2.60	29.37
FM/FS	13.61	21.12	0.75	2.70	2.58	31.95
FT/S	13.13	19.89	0.72	2.55	2.47	34.42
RF/I	48.61	43.80	0.71	1.45	2.46	36.88
B/D	13.11	19.75	0.71	2.54	2.46	39.34
<6m	42.61	32.22	0.71	1.08	2.44	41.78
5mm-1cm	13.72	20.06	0.70	2.67	2.40	44.17
FM/D	25.83	19.92	0.69	1.24	2.37	46.54
FT/D	25.94	20.47	0.69	1.27	2.36	48.91
B/SB	26.30	21.63	0.68	1.34	2.35	51.26
LH/F	40.85	31.96	0.66	1.12	2.27	53.53
FA/M	34.76	31.19	0.65	1.17	2.24	55.77
B/BB	34.76	31.22	0.65	1.17	2.23	58.00
6- 18m	34.93	32.19	0.63	1.21	2.16	60.16

Groups <2.4mWelwick B & >2.4mPHS

Average dissimilarity = 32.49

	Group <2.4mWelwick B	Group >2.4mPHS				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/>10K	4.76	27.61	1.49	2.56	4.57	4.57
18m-2yrs	6.56	28.86	1.46	2.51	4.49	9.06
≥6m	5.42	27.68	1.45	2.47	4.46	13.52
FA/T	5.41	27.68	1.45	2.47	4.46	17.98
AM/S	5.52	27.68	1.44	2.49	4.44	22.42
LH/T	5.59	27.69	1.44	2.50	4.42	26.85
P/I	28.60	42.97	1.04	1.66	3.19	30.03
RF/I	29.27	43.80	1.03	1.63	3.17	33.20
5mm-1cm	4.53	20.06	1.02	2.48	3.13	36.33
B/SB	7.28	21.63	0.95	2.16	2.92	39.25
FM/D	5.43	19.92	0.94	2.39	2.91	42.16
B/D	5.25	19.75	0.94	2.41	2.90	45.06
FT/S	5.57	19.89	0.93	2.34	2.87	47.93
FM/FS	7.43	21.12	0.89	2.19	2.75	50.68
2-5mm	24.75	36.69	0.88	1.60	2.70	53.38
FA/M	26.81	31.19	0.78	1.51	2.40	55.78
FT/I	23.42	29.22	0.78	1.57	2.39	58.17
B/BB	26.85	31.22	0.78	1.50	2.39	60.56

Groups >2.4mWelwick B & <2.4mPHS

Average dissimilarity = 33.88

	Group >2.4mWelwick B	Group <2.4mPHS				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P/I	40.95	28.42	1.16	0.89	3.44	3.44
RF/I	48.61	32.78	1.14	0.89	3.37	6.80
<6m	42.61	28.14	1.09	0.82	3.22	10.02
2-5mm	42.39	27.66	1.07	0.92	3.17	13.19
FM/D	25.83	9.36	1.01	0.99	2.99	16.17
<6m	17.88	2.60	1.01	0.95	2.98	19.16
B/BB	34.76	25.38	0.97	0.86	2.85	22.01
FA/M	34.76	25.55	0.96	0.85	2.85	24.85
FT/D	25.94	11.97	0.95	1.01	2.80	27.65
LH/F	40.85	29.03	0.94	0.85	2.78	30.43
6- 18m	34.93	27.78	0.93	0.80	2.76	33.19
FT/I	30.67	21.77	0.85	0.84	2.51	35.70
B/SB	26.30	16.14	0.84	0.90	2.48	38.18
F/10	35.00	27.12	0.84	0.93	2.48	40.66
AM/M	37.60	26.08	0.84	0.88	2.47	43.13
F/100	18.06	7.76	0.83	0.80	2.45	45.59
FA/J	18.82	11.62	0.82	0.81	2.43	48.01
FM/P	25.48	18.46	0.75	0.88	2.21	50.23
FM/FS	13.61	14.33	0.72	1.49	2.11	52.34
FA/T	18.54	11.37	0.70	0.92	2.07	54.41
AM/S	18.54	11.37	0.70	0.92	2.07	56.48
LH/T	18.54	11.37	0.70	0.92	2.07	58.55
≥6m	18.54	11.37	0.70	0.92	2.07	60.62

Groups <2.4mWelwick B & <2.4mPHS

Average dissimilarity = 32.01

	Group <2.4mWelwick B	Group <2.4mPHS				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
6- 18m	26.26	27.78	1.14	0.94	3.58	3.58
P/I	28.60	28.42	1.14	0.86	3.56	7.14
<6m	26.25	28.14	1.09	0.99	3.42	10.56
RF/I	29.27	32.78	1.09	1.12	3.39	13.95
FA/M	26.81	25.55	1.07	0.85	3.36	17.30
B/BB	26.85	25.38	1.06	0.84	3.32	20.62
2-5mm	24.75	27.66	0.97	1.13	3.02	23.64
LH/F	26.64	29.03	0.96	1.12	3.01	26.65
FT/I	23.42	21.77	0.95	0.87	2.98	29.63
F/10	26.08	27.12	0.89	1.03	2.78	32.41
AM/M	26.26	26.08	0.86	1.00	2.68	35.09
FM/P	19.69	18.46	0.82	0.89	2.56	37.65
FM/FS	7.43	14.33	0.77	1.65	2.40	40.05
B/SB	7.28	16.14	0.76	1.54	2.39	42.44
18m-2yrs	6.56	13.31	0.74	2.45	2.33	44.77
F/>10K	4.76	11.00	0.74	1.96	2.32	47.09
≥6m	5.42	11.37	0.74	1.92	2.31	49.40
FA/T	5.41	11.37	0.74	1.92	2.31	51.70
AM/S	5.52	11.37	0.74	1.96	2.30	54.00
LH/T	5.59	11.37	0.73	1.99	2.29	56.29
S/15	15.21	16.53	0.66	0.96	2.07	58.36
AM/H	5.33	11.71	0.57	1.16	1.79	60.15

Groups >2.4mPHS & <2.4mPHS

Average dissimilarity = 31.46

	Group >2.4mPHS	Group <2.4mPHS				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P/I	42.97	28.42	1.23	0.97	3.90	3.90
F/>10K	27.61	11.00	1.07	1.37	3.40	7.30
RF/I	43.80	32.78	1.06	1.01	3.38	10.68
LH/T	27.69	11.37	1.06	1.34	3.35	14.04
AM/S	27.68	11.37	1.06	1.34	3.35	17.39
≥6m	27.68	11.37	1.06	1.34	3.35	20.74
FA/T	27.68	11.37	1.05	1.34	3.35	24.10
18m-2yrs	28.86	13.31	0.97	1.62	3.10	27.19
6- 18m	32.19	27.78	0.96	0.94	3.05	30.24
FA/M	31.19	25.55	0.94	0.95	2.99	33.23
B/BB	31.22	25.38	0.94	0.95	2.98	36.21
FT/I	29.22	21.77	0.93	1.03	2.96	39.17
<6m	32.22	28.14	0.92	0.97	2.94	42.11
2-5mm	36.69	27.66	0.92	0.98	2.91	45.02
FM/P	25.66	18.46	0.85	1.05	2.69	47.71
F/10	32.13	27.12	0.81	1.02	2.58	50.28
LH/F	31.96	29.03	0.81	1.04	2.56	52.85
AM/M	31.42	26.08	0.78	1.01	2.48	55.33
B/D	19.75	8.55	0.73	1.28	2.32	57.65
S/15	25.76	16.53	0.73	0.95	2.32	59.97
FT/S	19.89	8.81	0.73	1.26	2.31	62.28

Groups >2.4mWelwick B & >2.4mALK  
Average dissimilarity = 83.70

	Group >2.4mWelwick B	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	48.61	4.14	4.21	6.88	5.02	5.02
2-5mm	42.39	1.72	3.93	5.08	4.69	9.72
<6m	42.61	3.89	3.81	4.51	4.55	14.27
LH/F	40.85	4.66	3.58	3.91	4.28	18.55
P/I	40.95	3.86	3.44	3.35	4.11	22.66
AM/M	37.60	4.42	3.27	4.94	3.90	26.56
6- 18m	34.93	2.59	3.14	3.35	3.75	30.32
F/10	35.00	3.58	3.05	3.31	3.65	33.96
FA/M	34.76	3.80	3.01	3.16	3.60	37.56
B/BB	34.76	4.04	2.99	3.15	3.57	41.13
FT/I	30.67	1.19	2.90	3.53	3.46	44.59
FM/P	25.48	1.46	2.37	2.91	2.84	47.43
B/SB	26.30	1.65	2.29	1.75	2.74	50.16
FT/D	25.94	2.34	2.19	1.65	2.62	52.78
FM/D	25.83	2.91	2.12	1.60	2.54	55.32
S/10	23.74	2.46	2.11	2.94	2.52	57.84
S/20	23.12	2.13	1.90	3.11	2.27	60.11

Groups <2.4mWelwick B & >2.4mALK  
Average dissimilarity = 76.05

	Group <2.4mWelwick B	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	29.27	4.14	3.61	4.81	4.75	4.75
P/I	28.60	3.86	3.56	4.79	4.69	9.43
6- 18m	26.26	2.59	3.44	4.40	4.52	13.96
FA/M	26.81	3.80	3.35	3.77	4.40	18.36
2-5mm	24.75	1.72	3.32	5.18	4.37	22.73
B/BB	26.85	4.04	3.32	3.78	4.37	27.10
F/10	26.08	3.58	3.27	4.20	4.30	31.39
<6m	26.25	3.89	3.25	4.00	4.28	35.67
FT/I	23.42	1.19	3.24	4.55	4.25	39.92
LH/F	26.64	4.66	3.19	3.82	4.19	44.11
AM/M	26.26	4.42	3.17	3.76	4.17	48.28
FM/P	19.69	1.46	2.66	4.22	3.49	51.78
S/20	15.59	2.13	1.92	4.77	2.53	54.30
S/15	15.21	2.08	1.88	4.79	2.47	56.77
S/25	14.31	1.74	1.82	4.46	2.39	59.16
FM/OS	12.75	0.85	1.72	4.47	2.27	61.43



Groups >2.4mPHS & >2.4mALK  
Average dissimilarity = 83.22

	Group >2.4mPHS	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	43.80	4.14	3.74	7.22	4.49	4.49
P/I	42.97	3.86	3.67	6.64	4.41	8.90
2-5mm	36.69	1.72	3.29	6.76	3.95	12.85
6- 18m	32.19	2.59	2.74	3.59	3.29	16.15
F/10	32.13	3.58	2.66	3.60	3.19	19.34
AM/S	27.68	0.01	2.63	4.79	3.17	22.50
FA/T	27.68	0.01	2.63	4.78	3.17	25.67
F/>10K	27.61	0.01	2.63	4.75	3.16	28.83
<6m	32.22	3.89	2.62	3.35	3.15	31.97
LH/T	27.69	0.47	2.59	4.59	3.11	35.09
FT/I	29.22	1.19	2.58	3.20	3.10	38.19
≥6m	27.68	0.56	2.58	4.55	3.10	41.29
LH/F	31.96	4.66	2.54	3.54	3.06	44.35
18m-2yrs	28.86	2.40	2.53	4.10	3.04	47.39
FA/M	31.19	3.80	2.52	2.89	3.02	50.41
AM/M	31.42	4.42	2.50	3.23	3.01	53.42
B/BB	31.22	4.04	2.50	2.88	3.00	56.42
S/20	26.56	2.13	2.31	7.68	2.78	59.20
FM/P	25.66	1.46	2.24	2.73	2.69	61.89

Groups <2.4mPHS & >2.4mALK  
Average dissimilarity = 77.54

	Group <2.4mPHS	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	32.78	4.14	3.39	3.65	4.38	4.38
2-5mm	27.66	1.72	3.10	4.33	4.00	8.38
P/I	28.42	3.86	3.03	3.20	3.91	12.29
6- 18m	27.78	2.59	2.95	2.72	3.80	16.09
LH/F	29.03	4.66	2.91	3.39	3.75	19.84
F/10	27.12	3.58	2.87	3.12	3.70	23.54
<6m	28.14	3.89	2.81	2.64	3.63	27.17
FA/M	25.55	3.80	2.72	2.94	3.51	30.67
B/BB	25.38	4.04	2.70	3.07	3.48	34.15
AM/M	26.08	4.42	2.65	3.17	3.41	37.57
FT/I	21.77	1.19	2.36	2.15	3.05	40.61
FM/P	18.46	1.46	2.00	2.26	2.57	43.19
S/20	17.81	2.13	1.93	4.16	2.48	45.67
B/SB	16.14	1.65	1.92	2.16	2.48	48.15
S/15	16.53	2.08	1.75	3.52	2.26	50.41
S/25	15.45	1.74	1.73	3.76	2.23	52.64
FM/SS	14.84	2.40	1.70	2.06	2.19	54.84
18m-2yrs	13.31	2.40	1.55	1.81	2.00	56.84
FM/FS	14.33	0.60	1.49	1.99	1.93	58.76
P/E	12.78	2.70	1.36	1.36	1.76	60.52

Groups >2.4mWelwick B & <2.4mALK  
Average dissimilarity = 88.72

	Group >2.4mWelwick B	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	48.61	0.41	4.65	11.42	5.25	5.25
<6m	42.61	0.22	4.25	5.42	4.79	10.03
2-5mm	42.39	0.11	4.16	5.87	4.69	14.72
LH/F	40.85	4.34	3.67	4.29	4.14	18.86
P/I	40.95	4.47	3.44	3.48	3.87	22.73
F/10	35.00	0.35	3.43	3.88	3.87	26.60
6- 18m	34.93	0.30	3.43	3.78	3.86	30.46
AM/M	37.60	4.45	3.32	5.89	3.74	34.21
FT/I	30.67	0.38	3.03	3.76	3.41	37.62
B/BB	34.76	4.34	3.00	3.35	3.39	41.01
FA/M	34.76	4.34	3.00	3.35	3.39	44.39
FM/P	25.48	0.38	2.53	3.09	2.85	47.24
B/SB	26.30	0.00	2.50	1.90	2.82	50.06
FM/D	25.83	0.33	2.42	1.83	2.73	52.79
S/10	23.74	2.50	2.14	3.04	2.41	55.20
FT/D	25.94	4.35	2.03	1.49	2.28	57.49
FA/J	18.82	0.69	1.89	1.21	2.13	59.62
<6m	17.88	0.00	1.89	1.17	2.13	61.75

Groups <2.4mWelwick B & <2.4mALK  
Average dissimilarity = 80.77

	Group <2.4mWelwick B	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	29.27	0.41	4.26	12.18	5.28	5.28
<6m	26.25	0.22	3.88	7.33	4.81	10.09
6- 18m	26.26	0.30	3.88	6.85	4.80	14.89
F/10	26.08	0.35	3.84	7.66	4.75	19.64
2-5mm	24.75	0.11	3.65	9.36	4.52	24.16
P/I	28.60	4.47	3.55	6.61	4.39	28.55
FT/I	23.42	0.38	3.44	5.80	4.26	32.81
B/BB	26.85	4.34	3.34	4.80	4.14	36.95
FA/M	26.81	4.34	3.33	4.71	4.13	41.07
LH/F	26.64	4.34	3.30	5.02	4.09	45.16
AM/M	26.26	4.45	3.23	4.78	4.00	49.16
FM/P	19.69	0.38	2.89	5.47	3.58	52.73
S/25	14.31	0.20	2.10	7.66	2.60	55.33
S/20	15.59	2.66	1.88	6.08	2.33	57.66
S/15	15.21	2.50	1.85	6.26	2.29	59.96
FM/OS	12.75	0.33	1.84	6.09	2.28	62.24

Groups >2.4mPHS & <2.4mALK

Average dissimilarity = 86.79

	Group >2.4mPHS	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	43.80	0.41	4.18	20.64	4.82	4.82
P/I	42.97	4.47	3.67	8.69	4.22	9.04
2-5mm	36.69	0.11	3.51	11.14	4.04	13.09
<6m	32.22	0.22	3.03	4.72	3.49	16.57
F/10	32.13	0.35	3.02	4.99	3.48	20.06
6- 18m	32.19	0.30	3.02	4.57	3.47	23.53
FT/I	29.22	0.38	2.70	3.48	3.12	26.65
LH/T	27.69	0.00	2.69	4.86	3.10	29.75
AM/S	27.68	0.00	2.69	4.86	3.10	32.84
FA/T	27.68	0.00	2.69	4.85	3.10	35.94
F/>10K	27.61	0.00	2.68	4.83	3.09	39.03
≥6m	27.68	0.27	2.66	4.73	3.07	42.10
LH/F	31.96	4.34	2.61	4.03	3.01	45.11
AM/M	31.42	4.45	2.53	3.48	2.92	48.03
B/BB	31.22	4.34	2.49	2.96	2.87	50.90
FA/M	31.19	4.34	2.49	2.92	2.87	53.77
FM/P	25.66	0.38	2.39	2.98	2.75	56.52
18m-2yrs	28.86	4.43	2.37	4.17	2.73	59.25
S/20	26.56	2.66	2.30	10.41	2.65	61.90

Groups <2.4mPHS & <2.4mALK

Average dissimilarity = 83.17

	Group <2.4mPHS	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	32.78	0.41	4.07	9.65	4.90	4.90
F/10	27.12	0.35	3.46	5.59	4.16	9.06
2-5mm	27.66	0.11	3.42	7.70	4.11	13.17
<6m	28.14	0.22	3.21	3.02	3.86	17.03
P/I	28.42	4.47	3.13	4.53	3.77	20.80
6- 18m	27.78	0.30	3.05	2.18	3.66	24.46
LH/F	29.03	4.34	2.95	3.74	3.55	28.01
FA/M	25.55	4.34	2.81	4.12	3.38	31.40
B/BB	25.38	4.34	2.79	4.17	3.36	34.76
AM/M	26.08	4.45	2.63	3.42	3.17	37.92
FT/I	21.77	0.38	2.43	2.04	2.92	40.84
B/SB	16.14	0.00	2.27	2.30	2.73	43.57
FM/P	18.46	0.38	2.06	2.03	2.48	46.05
S/25	15.45	0.20	2.03	5.30	2.44	48.49
P/E	12.78	0.00	1.86	1.64	2.24	50.72
S/20	17.81	2.66	1.86	4.69	2.23	52.95
S/15	16.53	2.50	1.81	5.45	2.17	55.13
FT/M	11.78	0.33	1.54	1.86	1.85	56.98
FM/FS	14.33	0.37	1.53	1.97	1.84	58.82
FM/SS	14.84	4.33	1.37	2.38	1.65	60.47

Groups >2.4mALK & <2.4mALK

Average dissimilarity = 60.18

	Group >2.4mALK	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/1K	0.48	4.31	2.86	2.36	4.75	4.75
1-2yr	0.54	4.34	2.84	2.33	4.71	9.46
RF/S	0.66	4.42	2.82	2.25	4.69	14.15
RF/I	4.14	0.41	2.26	1.82	3.76	17.91
<6m	3.89	0.22	2.19	1.74	3.64	21.54
FM/SS	2.40	4.33	2.17	1.50	3.60	25.14
18m-2yrs	2.40	4.43	2.16	1.50	3.58	28.73
1-2cm	2.10	4.44	2.14	1.43	3.55	32.28
FT/D	2.34	4.35	1.97	1.58	3.27	35.55
F/10	3.58	0.35	1.95	1.59	3.24	38.78
FA/M	3.80	4.34	1.90	1.32	3.16	41.94
B/BB	4.04	4.34	1.84	1.28	3.06	45.01
P/I	3.86	4.47	1.81	1.33	3.01	48.02
AM/M	4.42	4.45	1.70	1.42	2.82	50.83
5mm-1cm	2.87	0.11	1.68	1.62	2.80	53.63
LH/F	4.66	4.34	1.66	1.41	2.76	56.39
P/E	2.70	0.00	1.65	1.62	2.75	59.14
FM/D	2.91	0.33	1.65	1.65	2.74	61.88

### Appendix 5.3

#### % Average similarity for 2011: Biomass-weighted

Group >2.4mWelwick B

Average similarity: 57.47

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	0.42	3.16	2.90	5.51	5.51
AM/M	0.38	3.10	3.12	5.39	10.90
1-2cm	0.40	2.85	2.64	4.95	15.85
LH/SP	0.40	2.84	2.64	4.95	20.80
S/20	0.30	2.47	2.77	4.29	25.09
FA/J	0.31	2.38	2.72	4.15	29.24
F/10K	0.33	2.36	2.66	4.10	33.35
18m-2yrs	0.24	2.17	3.37	3.78	37.13
RF/S	0.24	2.12	3.46	3.68	40.81
6m - 1yr	0.21	1.92	3.46	3.35	44.15
FT/D	0.25	1.71	2.70	2.97	47.12
FT/I	0.20	1.69	2.95	2.95	50.07
FM/D	0.25	1.66	2.72	2.89	52.96
B/GB	0.21	1.64	2.61	2.86	55.82
B/OV	0.21	1.64	2.60	2.86	58.68
FM/P	0.19	1.63	2.95	2.83	61.51

Group <2.4mWelwick B  
Average similarity: 74.92

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	1.16	4.23	6.68	5.64	5.64
LH/SP	1.16	4.22	6.42	5.63	11.27
F/10K	1.15	4.17	6.31	5.56	16.84
1-2yr	1.15	4.16	6.52	5.55	22.39
FA/S	1.15	4.14	6.46	5.52	27.91
>5yrs	1.14	4.11	6.41	5.48	33.40
P/I	0.84	3.66	6.21	4.89	38.28
1-2cm	0.82	3.57	6.14	4.77	43.05
FM/FS	0.97	3.12	4.27	4.16	47.22
AM/L	0.96	3.09	4.21	4.12	51.33
S/20	0.84	3.08	6.59	4.11	55.45
FT/S	0.81	2.94	6.45	3.92	59.37
B/D	0.77	2.88	6.98	3.84	63.21

Group <2.4mPHS  
Average similarity: 51.86

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	0.40	2.45	2.64	4.73	4.73
AM/M	0.39	2.26	2.42	4.35	9.08
RF/I	0.29	1.96	2.36	3.78	12.86
1-2cm	0.34	1.90	2.21	3.67	16.53
LH/SP	0.35	1.90	2.15	3.65	20.18
F/10K	0.34	1.89	2.21	3.64	23.83
S/20	0.34	1.87	2.13	3.60	27.43
FT/I	0.22	1.60	2.43	3.09	30.52
FM/P	0.21	1.48	2.56	2.85	33.36
LH/F	0.20	1.48	2.15	2.85	36.21
18m-2yrs	0.32	1.41	1.37	2.72	38.94
1-2yr	0.22	1.40	2.71	2.69	41.63
F/10	0.17	1.39	2.08	2.68	44.31
FA/J	0.29	1.31	1.37	2.52	46.84
2-5mm	0.16	1.30	1.99	2.51	49.35
6m - 1yr	0.30	1.30	1.36	2.51	51.85
FT/D	0.25	1.30	2.28	2.50	54.35
FM/D	0.21	1.21	2.48	2.34	56.69
FM/FS	0.18	1.08	2.71	2.08	58.77
FT/S	0.17	1.07	2.70	2.07	60.84

Group >2.4mPHS  
Average similarity: 62.21

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
AM/M	0.66	3.19	3.87	5.13	5.13
S/20	0.62	2.89	2.75	4.65	9.78
P/I	0.68	2.77	1.35	4.46	14.24
LH/SP	0.68	2.69	1.35	4.33	18.57
F/10K	0.66	2.69	1.35	4.32	22.89
1-2cm	0.67	2.68	1.35	4.31	27.20
18m-2yrs	0.55	2.64	3.20	4.24	31.44
6m - 1yr	0.50	2.45	3.60	3.94	35.38
RF/I	0.53	2.42	4.01	3.88	39.26
FT/D	0.46	2.25	4.13	3.61	42.87
1-2yr	0.49	1.80	1.28	2.89	45.76
FA/J	0.47	1.74	1.21	2.79	48.55
FM/D	0.42	1.71	1.43	2.74	51.29
RF/S	0.47	1.68	1.15	2.70	53.99
FT/M	0.29	1.53	4.36	2.46	56.45
FA/S	0.44	1.37	1.08	2.20	58.65
FM/FS	0.36	1.31	1.29	2.11	60.76

Group <2.4mALK  
Average similarity: 49.09

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	0.05	3.82	2.43	7.78	7.78
AM/M	0.05	3.74	2.43	7.61	15.39
18m-2yrs	0.05	3.32	1.67	6.76	22.15
LH/F	0.04	3.30	1.99	6.72	28.87
B/BB	0.04	3.30	1.99	6.71	35.59
1-2cm	0.05	3.22	1.82	6.55	42.14
FA/M	0.04	3.14	1.86	6.39	48.53
FT/D	0.04	3.10	1.87	6.32	54.85
RF/S	0.04	2.75	1.22	5.60	60.45

Group >2.4mALK  
Average similarity: 43.27

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
LH/F	0.05	3.21	1.92	7.41	7.41
P/I	0.06	2.98	1.72	6.90	14.31
AM/M	0.06	2.95	1.91	6.82	21.13
RF/I	0.03	2.00	1.40	4.62	25.75
FA/J	0.05	1.91	1.09	4.41	30.16
B/BB	0.04	1.80	1.20	4.17	34.33
5mm-1cm	0.04	1.70	1.00	3.93	38.25
<6m	0.03	1.61	1.18	3.73	41.99
F/10	0.03	1.55	1.08	3.58	45.57
FA/M	0.03	1.50	1.08	3.47	49.04
S/10	0.03	1.50	1.89	3.47	52.51
S/5	0.03	1.49	1.22	3.45	55.96
FT/D	0.04	1.48	1.17	3.42	59.38
<6m	0.04	1.37	0.83	3.17	62.55

## Appendix 5.4

### Average dissimilarity 2011- Biomass-weighted

Groups >2.4mWelwick B & <2.4mWelwick B  
Average dissimilarity = 54.38

	Group >2.4mWelwick B	Group <2.4mWelwick B				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FA/S	0.13	1.15	3.43	2.59	6.31	6.31
>5yrs	0.17	1.14	3.27	2.36	6.02	12.33
RF/I	0.23	1.16	3.11	2.53	5.72	18.05
1-2yr	0.24	1.15	3.06	2.39	5.63	23.67
AM/L	0.10	0.96	2.83	2.28	5.21	28.88
F/10K	0.33	1.15	2.73	2.19	5.03	33.91
LH/SP	0.40	1.16	2.57	1.90	4.72	38.63
FM/FS	0.19	0.97	2.55	2.03	4.69	43.32
B/BV	0.09	0.77	2.31	2.59	4.25	47.57
B/D	0.14	0.77	2.16	2.43	3.98	51.55
FT/S	0.19	0.81	2.10	2.27	3.86	55.41
2 - >5cm	0.06	0.69	1.96	1.25	3.61	59.02
S/20	0.30	0.84	1.77	1.96	3.26	62.28

Groups >2.4mWelwick B & <2.4mPHS

Average dissimilarity = 43.17

Species	Group >2.4mWelwick B		Group <2.4mPHS		Contrib%	Cum.%
	Av.Abund	Av.Abund	Av.Diss	Diss/SD		
LH/SP	0.40	0.35	1.62	1.44	3.76	3.76
1-2cm	0.40	0.34	1.60	1.42	3.71	7.47
P/I	0.42	0.40	1.59	1.46	3.68	11.15
AM/M	0.38	0.39	1.51	1.51	3.49	14.64
FA/J	0.31	0.29	1.47	1.53	3.42	18.06
F/10K	0.33	0.34	1.47	1.37	3.41	21.47
18m-2yrs	0.24	0.32	1.45	1.79	3.35	24.82
RF/S	0.24	0.28	1.40	1.70	3.23	28.06
S/20	0.30	0.34	1.37	1.50	3.18	31.24
6m - 1yr	0.21	0.30	1.34	1.81	3.11	34.35
FA/S	0.13	0.18	1.28	1.30	2.95	37.30
>5yrs	0.17	0.16	1.24	1.28	2.87	40.18
RF/I	0.23	0.29	1.12	1.17	2.59	42.77
FT/D	0.25	0.25	1.08	1.42	2.51	45.28
B/OV	0.21	0.20	1.07	1.52	2.48	47.76
1-2yr	0.24	0.22	1.06	1.08	2.45	50.21
B/GB	0.21	0.21	1.01	1.50	2.35	52.56
FM/D	0.25	0.21	0.98	1.34	2.28	54.83
B/BV	0.09	0.12	0.90	1.32	2.09	56.92
FT/M	0.17	0.17	0.87	1.59	2.02	58.95
AM/L	0.10	0.12	0.83	1.18	1.92	60.87

Groups <2.4mWelwick B & <2.4mPHS

Average dissimilarity = 57.61

Species	Group <2.4mWelwick B	Group <2.4mPHS	Av.Diss	Diss/SD	Contrib%	Cum.%
	Av.Abund	Av.Abund				
>5yrs	1.14	0.16	3.32	2.76	5.76	5.76
FA/S	1.15	0.18	3.29	2.64	5.72	11.48
1-2yr	1.15	0.22	3.16	2.48	5.49	16.97
RF/I	1.16	0.29	2.99	2.24	5.20	22.16
LH/SP	1.16	0.35	2.83	1.86	4.92	27.08
F/10K	1.15	0.34	2.82	1.89	4.90	31.98
AM/L	0.96	0.12	2.79	2.33	4.84	36.82
FM/FS	0.97	0.18	2.63	2.06	4.56	41.38
B/BV	0.77	0.12	2.22	2.74	3.86	45.24
FT/S	0.81	0.17	2.18	2.33	3.78	49.02
B/D	0.77	0.14	2.18	2.66	3.78	52.80
2 - >5cm	0.69	0.10	1.88	1.17	3.26	56.07
1-2cm	0.82	0.34	1.88	1.46	3.26	59.33
S/20	0.84	0.34	1.84	1.61	3.19	62.52

Groups >2.4mWelwick B & >2.4mPHS  
Average dissimilarity = 47.32

	Group >2.4mWelwick B	Group >2.4mPHS				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/10K	0.33	0.66	2.02	1.83	4.27	4.27
LH/SP	0.40	0.68	1.96	1.58	4.14	8.42
P/I	0.42	0.68	1.93	1.52	4.07	12.49
1-2cm	0.40	0.67	1.91	1.56	4.05	16.54
FA/S	0.13	0.44	1.68	1.39	3.54	20.08
1-2yr	0.24	0.49	1.62	1.70	3.42	23.50
RF/I	0.23	0.53	1.57	1.72	3.31	26.81
>5yrs	0.17	0.42	1.54	1.34	3.26	30.07
S/20	0.30	0.62	1.53	1.65	3.24	33.31
RF/S	0.24	0.47	1.49	1.71	3.14	36.45
AM/M	0.38	0.66	1.48	1.55	3.13	39.58
FA/J	0.31	0.47	1.43	1.46	3.03	42.61
18m-2yrs	0.24	0.55	1.40	1.72	2.97	45.58
6m - 1yr	0.21	0.50	1.30	1.85	2.75	48.33
FM/D	0.25	0.42	1.21	1.57	2.55	50.88
B/BV	0.09	0.31	1.17	1.38	2.47	53.35
FT/S	0.19	0.36	1.16	1.61	2.45	55.80
FM/FS	0.19	0.36	1.16	1.61	2.45	58.26
FT/D	0.25	0.46	1.14	1.56	2.40	60.66

Groups <2.4mWelwick B & >2.4mPHS  
Average dissimilarity = 40.37

	Group <2.4mWelwick B	Group >2.4mPHS				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
>5yrs	1.14	0.42	2.10	1.47	5.19	5.19
FA/S	1.15	0.44	2.08	1.46	5.16	10.35
1-2yr	1.15	0.49	1.94	1.34	4.81	15.17
AM/L	0.96	0.30	1.87	1.45	4.62	19.79
RF/I	1.16	0.53	1.84	1.55	4.55	24.33
FM/FS	0.97	0.36	1.73	1.33	4.29	28.63
LH/SP	1.16	0.68	1.63	1.05	4.03	32.66
F/10K	1.15	0.66	1.61	1.05	3.99	36.64
2 - >5cm	0.69	0.05	1.61	1.13	3.98	40.62
B/BV	0.77	0.31	1.38	1.45	3.43	44.05
B/D	0.77	0.31	1.37	1.43	3.39	47.44
FT/S	0.81	0.36	1.35	1.31	3.35	50.79
18m-2yrs	0.18	0.55	1.05	1.64	2.59	53.38
RF/S	0.16	0.47	1.02	1.73	2.52	55.90
FT/M	0.49	0.29	1.02	1.53	2.52	58.41
S/25	0.51	0.19	1.01	1.21	2.49	60.90



Groups <2.4mPHS & >2.4mPHS

Average dissimilarity = 48.61

	Group <2.4mPHS	Group >2.4mPHS				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
LH/SP	0.35	0.68	2.12	1.65	4.36	4.36
P/I	0.40	0.68	2.09	1.73	4.31	8.67
1-2cm	0.34	0.67	2.08	1.68	4.28	12.95
F/10K	0.34	0.66	2.08	1.68	4.27	17.22
AM/M	0.39	0.66	1.72	1.51	3.54	20.76
S/20	0.34	0.62	1.68	1.46	3.45	24.21
18m-2yrs	0.32	0.55	1.65	1.49	3.40	27.61
1-2yr	0.22	0.49	1.59	1.83	3.27	30.88
RF/S	0.28	0.47	1.54	1.33	3.17	34.05
FA/J	0.29	0.47	1.52	1.36	3.13	37.19
6m - 1yr	0.30	0.50	1.51	1.49	3.11	40.30
FA/S	0.18	0.44	1.51	1.54	3.11	43.41
>5yrs	0.16	0.42	1.44	1.55	2.97	46.39
RF/I	0.29	0.53	1.41	1.50	2.89	49.28
FM/D	0.21	0.42	1.30	1.74	2.67	51.95
FT/D	0.25	0.46	1.30	1.61	2.67	54.62
FM/FS	0.18	0.36	1.17	1.75	2.41	57.02
FT/S	0.17	0.36	1.17	1.74	2.40	59.42
B/GB	0.21	0.34	1.09	1.39	2.25	61.67

Groups >2.4mWelwick B & <2.4mALK

Average dissimilarity = 79.36

	Group >2.4mWelwick B	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
LH/SP	0.40	0.02	3.73	3.63	4.70	4.70
P/I	0.42	0.05	3.68	3.63	4.64	9.34
1-2cm	0.40	0.05	3.41	3.01	4.30	13.64
AM/M	0.38	0.05	3.40	4.01	4.29	17.93
F/10K	0.33	0.02	3.26	2.32	4.11	22.04
FA/J	0.31	0.03	3.04	2.51	3.83	25.87
S/20	0.30	0.04	2.91	2.55	3.66	29.53
6m - 1yr	0.21	0.02	2.33	1.98	2.94	32.47
18m-2yrs	0.24	0.05	2.28	1.82	2.87	35.34
FM/D	0.25	0.02	2.27	3.09	2.86	38.20
RF/S	0.24	0.04	2.25	1.78	2.83	41.04
RF/I	0.23	0.01	2.23	1.67	2.81	43.85
B/GB	0.21	0.02	2.14	2.46	2.69	46.54
B/OV	0.21	0.02	2.14	2.45	2.69	49.23
FT/I	0.20	0.01	2.08	2.89	2.62	51.85
FT/D	0.25	0.04	2.00	2.28	2.52	54.37
FM/P	0.19	0.01	1.97	2.86	2.48	56.85
1-2yr	0.24	0.04	1.79	1.17	2.25	59.10
FM/OS	0.17	0.01	1.76	2.49	2.21	61.31

Groups <2.4mWelwick B & <2.4mALK

Average dissimilarity = 92.03

	Group <2.4mWelwick B	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	1.16	0.01	5.16	12.99	5.61	5.61
FA/S	1.15	0.00	5.13	12.22	5.57	11.18
>5yrs	1.14	0.00	5.10	11.55	5.54	16.72
LH/SP	1.16	0.02	5.09	10.85	5.54	22.25
F/10K	1.15	0.02	5.05	10.33	5.49	27.74
1-2yr	1.15	0.04	4.96	9.99	5.39	33.14
FM/FS	0.97	0.01	4.17	4.87	4.53	37.67
AM/L	0.96	0.01	4.15	4.77	4.51	42.17
P/I	0.84	0.05	3.80	3.97	4.13	46.30
1-2cm	0.82	0.05	3.73	3.92	4.06	50.36
FT/S	0.81	0.01	3.60	11.44	3.91	54.26
S/20	0.84	0.04	3.59	10.71	3.90	58.16
B/D	0.77	0.00	3.48	17.24	3.78	61.95

Groups <2.4mPHS & <2.4mALK

Average dissimilarity = 77.82

	Group <2.4mPHS	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P/I	0.40	0.05	3.08	3.13	3.96	3.96
AM/M	0.39	0.05	2.93	2.66	3.76	7.72
LH/SP	0.35	0.02	2.88	2.60	3.70	11.42
F/10K	0.34	0.02	2.84	2.70	3.65	15.07
RF/I	0.29	0.01	2.78	4.01	3.57	18.64
S/20	0.34	0.04	2.62	2.31	3.37	22.01
1-2cm	0.34	0.05	2.50	2.17	3.21	25.22
6m - 1yr	0.30	0.02	2.30	1.81	2.95	28.18
FA/J	0.29	0.03	2.21	1.78	2.84	31.02
18m-2yrs	0.32	0.05	2.14	1.46	2.75	33.77
FT/I	0.22	0.01	2.13	3.63	2.74	36.51
RF/S	0.28	0.04	2.03	1.64	2.61	39.12
FM/P	0.21	0.01	1.95	3.73	2.51	41.62
2-5mm	0.16	0.00	1.81	2.47	2.33	43.95
F/10	0.17	0.01	1.79	2.71	2.30	46.25
FM/D	0.21	0.02	1.74	3.17	2.24	48.49
FA/S	0.18	0.00	1.71	2.15	2.20	50.69
B/GB	0.21	0.02	1.63	1.94	2.10	52.78
FT/D	0.25	0.04	1.63	1.91	2.09	54.87
1-2yr	0.22	0.04	1.61	2.62	2.07	56.94
>5yrs	0.16	0.00	1.61	2.06	2.06	59.00
FM/FS	0.18	0.01	1.57	4.59	2.02	61.02

Groups >2.4mPHS & <2.4mALK

Average dissimilarity = 89.60

	Group >2.4mPHS	Group <2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
AM/M	0.66	0.05	3.87	5.73	4.32	4.32
P/I	0.68	0.05	3.67	3.09	4.09	8.42
LH/SP	0.68	0.02	3.66	2.45	4.08	12.50
F/10K	0.66	0.02	3.59	2.44	4.01	16.51
1-2cm	0.67	0.05	3.58	2.99	4.00	20.51
S/20	0.62	0.04	3.57	5.71	3.99	24.49
RF/I	0.53	0.01	3.49	2.90	3.89	28.39
18m-2yrs	0.55	0.05	3.31	3.09	3.69	32.08
6m - 1yr	0.50	0.02	3.28	2.78	3.66	35.74
FT/D	0.46	0.04	2.67	5.82	2.98	38.73
1-2yr	0.49	0.04	2.62	2.52	2.92	41.65
FA/J	0.47	0.03	2.54	1.95	2.84	44.49
RF/S	0.47	0.04	2.52	2.16	2.81	47.30
FA/S	0.44	0.00	2.37	1.63	2.64	49.94
FM/D	0.42	0.02	2.25	2.51	2.51	52.45
>5yrs	0.42	0.00	2.25	1.60	2.51	54.96
FT/M	0.29	0.01	2.01	2.24	2.24	57.20
FM/FS	0.36	0.01	1.95	2.11	2.18	59.38
FT/S	0.36	0.01	1.95	2.11	2.18	61.56

Groups >2.4mWelwick B & >2.4mALK

Average dissimilarity = 77.70

	Group >2.4mWelwick B	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
LH/SP	0.40	0.02	3.73	3.81	4.80	4.80
1-2cm	0.40	0.03	3.63	3.46	4.67	9.47
P/I	0.42	0.06	3.52	3.02	4.53	14.00
F/10K	0.33	0.01	3.36	2.54	4.33	18.33
AM/M	0.38	0.06	3.28	3.37	4.22	22.55
S/20	0.30	0.03	2.92	2.57	3.76	26.31
FA/J	0.31	0.05	2.71	2.12	3.49	29.80
RF/S	0.24	0.02	2.61	2.05	3.36	33.15
18m-2yrs	0.24	0.03	2.44	1.92	3.15	36.30
6m - 1yr	0.21	0.01	2.42	2.16	3.12	39.41
B/OV	0.21	0.01	2.21	2.71	2.84	42.26
B/GB	0.21	0.01	2.21	2.71	2.84	45.10
FM/D	0.25	0.02	2.14	2.78	2.75	47.85
1-2yr	0.24	0.01	2.12	1.54	2.72	50.57
FT/D	0.25	0.04	2.07	2.42	2.67	53.24
FT/I	0.20	0.02	1.90	2.47	2.45	55.69
RF/I	0.23	0.03	1.86	1.32	2.39	58.08
FM/P	0.19	0.03	1.75	2.24	2.25	60.34

Groups <2.4mWelwick B & >2.4mALK

Average dissimilarity = 90.87

	Group <2.4mWelwick B	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FA/S	1.15	0.00	5.07	11.38	5.58	5.58
LH/SP	1.16	0.02	5.06	9.68	5.57	11.15
F/10K	1.15	0.01	5.06	9.72	5.56	16.72
1-2yr	1.15	0.01	5.04	9.90	5.55	22.26
>5yrs	1.14	0.00	5.04	10.84	5.55	27.81
RF/I	1.16	0.03	4.98	10.45	5.48	33.29
FM/FS	0.97	0.01	4.11	4.71	4.52	37.82
AM/L	0.96	0.02	4.03	4.42	4.44	42.26
1-2cm	0.82	0.03	3.79	3.85	4.17	46.43
P/I	0.84	0.06	3.71	3.81	4.08	50.51
S/20	0.84	0.03	3.57	8.99	3.93	54.44
FT/S	0.81	0.01	3.54	9.84	3.90	58.34
B/D	0.77	0.00	3.44	15.32	3.79	62.13

Groups <2.4mPHS & >2.4mALK

Average dissimilarity = 76.88

	Group <2.4mPHS	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/10K	0.34	0.01	3.00	3.68	3.90	3.90
P/I	0.40	0.06	2.96	2.78	3.85	7.75
LH/SP	0.35	0.02	2.93	3.06	3.81	11.56
AM/M	0.39	0.06	2.85	2.50	3.70	15.27
1-2cm	0.34	0.03	2.80	2.88	3.64	18.91
S/20	0.34	0.03	2.68	2.55	3.48	22.40
6m - 1yr	0.30	0.01	2.39	2.04	3.11	25.51
RF/I	0.29	0.03	2.34	2.86	3.05	28.56
18m-2yrs	0.32	0.03	2.33	1.71	3.03	31.59
RF/S	0.28	0.02	2.22	1.70	2.88	34.48
FA/J	0.29	0.05	2.06	1.71	2.68	37.15
1-2yr	0.22	0.01	1.98	4.39	2.58	39.73
FT/I	0.22	0.02	1.95	3.00	2.54	42.27
FT/D	0.25	0.04	1.75	2.26	2.28	44.55
FM/P	0.21	0.03	1.75	2.78	2.27	46.82
B/GB	0.21	0.01	1.72	2.24	2.23	49.06
FA/S	0.18	0.00	1.66	2.13	2.16	51.21
2-5mm	0.16	0.01	1.66	2.41	2.16	53.37
FM/D	0.21	0.02	1.64	3.03	2.13	55.50
B/OV	0.20	0.01	1.58	1.69	2.06	57.56
>5yrs	0.16	0.00	1.56	2.05	2.03	59.58
FM/FS	0.18	0.01	1.51	3.88	1.96	61.54

Groups >2.4mPHS & >2.4mALK

Average dissimilarity = 87.46

	Group >2.4mPHS	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
AM/M	0.66	0.06	3.76	4.85	4.30	4.30
LH/SP	0.68	0.02	3.61	2.34	4.13	8.44
P/I	0.68	0.06	3.60	3.07	4.12	12.55
S/20	0.62	0.03	3.56	5.51	4.08	16.63
F/10K	0.66	0.01	3.55	2.25	4.06	20.69
1-2cm	0.67	0.03	3.55	2.46	4.05	24.74
18m-2yrs	0.55	0.03	3.38	2.99	3.86	28.61
6m - 1yr	0.50	0.01	3.31	2.82	3.78	32.39
RF/I	0.53	0.03	3.21	2.89	3.67	36.05
FT/D	0.46	0.04	2.68	4.58	3.06	39.11
1-2yr	0.49	0.01	2.60	2.05	2.97	42.09
RF/S	0.47	0.02	2.50	1.81	2.86	44.95
FA/J	0.47	0.05	2.46	1.99	2.81	47.76
FA/S	0.44	0.00	2.34	1.63	2.67	50.43
>5yrs	0.42	0.00	2.22	1.60	2.54	52.98
FM/D	0.42	0.02	2.19	2.47	2.50	55.48
FT/M	0.29	0.01	1.97	2.28	2.25	57.73
FM/FS	0.36	0.01	1.92	2.11	2.20	59.93
FT/S	0.36	0.01	1.92	2.11	2.20	62.12

Groups <2.4mALK & >2.4mALK

Average dissimilarity = 62.39

	Group <2.4mALK	Group >2.4mALK				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/S	0.04	0.02	2.48	1.58	3.97	3.97
18m-2yrs	0.05	0.03	2.26	1.56	3.63	7.60
1-2cm	0.05	0.03	2.25	1.50	3.60	11.20
P/I	0.05	0.06	2.22	1.46	3.56	14.76
FA/J	0.03	0.05	2.20	1.35	3.53	18.29
AM/M	0.05	0.06	2.10	1.49	3.36	21.66
1-2yr	0.04	0.01	2.06	1.39	3.30	24.95
LH/F	0.04	0.05	1.90	1.36	3.05	28.01
F/1K	0.03	0.01	1.90	1.23	3.04	31.05
5mm-1cm	0.01	0.04	1.87	1.20	3.00	34.05
FM/SS	0.04	0.02	1.87	1.33	2.99	37.04
FT/D	0.04	0.04	1.82	1.41	2.92	39.97
<6m	0.00	0.04	1.74	1.02	2.79	42.75
B/BB	0.04	0.04	1.73	1.27	2.77	45.52
FA/M	0.04	0.03	1.68	1.26	2.70	48.22
RF/I	0.01	0.03	1.60	1.27	2.56	50.78
S/5	0.01	0.03	1.54	1.16	2.46	53.24
S/20	0.04	0.03	1.52	1.36	2.44	55.68
F/10	0.01	0.03	1.47	1.21	2.35	58.03
B/SB	0.00	0.03	1.44	0.92	2.31	60.35

## Appendix 6.1

### Paull 2011 – Full Average Similarity Tables Abundance-weighted

Group 2.61-2.8m

Average similarity: 69.29 (No SD is given due to lack of replicates)

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	37.26	3.20	#####	4.62	4.62
P/I	35.79	2.92	#####	4.22	8.84
18m-2yrs	31.05	2.83	#####	4.09	12.93
≥6m	29.94	2.64	#####	3.81	16.73
FA/T	29.93	2.64	#####	3.80	20.54
AM/S	29.93	2.64	#####	3.80	24.34
LH/T	29.93	2.64	#####	3.80	28.14
F/>10K	29.90	2.64	#####	3.80	31.94
2-5mm	28.27	2.44	#####	3.53	35.47
B/SB	23.76	2.29	#####	3.30	38.78
S/20	24.42	2.14	#####	3.08	41.86
FM/FS	22.73	2.05	#####	2.96	44.83
FT/D	22.06	2.01	#####	2.91	47.73
S/15	23.53	2.00	#####	2.89	50.62
5mm-1cm	21.76	1.99	#####	2.88	53.50
FM/D	21.44	1.89	#####	2.73	56.23
FT/S	21.26	1.87	#####	2.70	58.92
B/D	21.18	1.86	#####	2.69	61.61

Group 2.4 - 2.6m

Average similarity: 84.01

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	47.08	3.91	10.09	4.66	4.66
P/I	46.57	3.85	9.47	4.58	9.24
2-5mm	40.89	3.40	13.83	4.04	13.28
6- 18m	38.03	3.23	20.00	3.84	17.12
F/10	37.79	3.23	21.71	3.84	20.97
<6m	38.00	3.23	20.02	3.84	24.81
LH/F	37.46	3.18	21.25	3.79	28.60
FA/M	37.43	3.18	19.35	3.78	32.38
B/BB	37.41	3.18	19.51	3.78	36.16
AM/M	37.28	3.17	22.41	3.77	39.93
FT/I	35.76	3.00	20.80	3.57	43.51
FM/P	31.96	2.79	11.36	3.32	46.83
S/20	27.63	2.26	8.48	2.70	49.52
18m-2yrs	27.76	2.19	4.42	2.61	52.13
S/15	26.87	2.19	7.07	2.61	54.74
LH/T	26.57	2.04	3.65	2.43	57.17
AM/S	26.56	2.04	3.64	2.43	59.60
FA/T	26.55	2.04	3.63	2.43	62.03

Group <2.4m

Average similarity: 84.54

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	37.82	4.12	13.06	4.87	4.87
P/I	34.10	3.80	9.32	4.50	9.37
6- 18m	33.33	3.53	6.58	4.17	13.54
LH/F	33.33	3.52	8.56	4.16	17.70
<6m	33.32	3.52	6.23	4.16	21.86
2-5mm	32.08	3.45	7.90	4.08	25.94
F/10	31.10	3.31	6.97	3.92	29.86
FA/M	30.66	3.29	7.09	3.89	33.75
AM/M	29.82	3.28	9.57	3.88	37.63
B/BB	30.46	3.27	7.37	3.87	41.50
FT/I	26.13	2.73	4.52	3.23	44.73
FM/P	22.15	2.28	4.34	2.70	47.43
S/20	20.35	2.27	15.28	2.68	50.11
S/15	19.84	2.23	15.60	2.64	52.75
S/25	17.52	1.88	10.49	2.22	54.97
S/10	16.43	1.74	6.83	2.06	57.03
FM/SS	16.36	1.67	7.68	1.97	59.00
B/SB	17.86	1.66	11.82	1.97	60.97

## Appendix 6.2

### Average Dissimilarity Results Paull 2011: Abundance Weighted- Elevation Detail.

Paull 2011 Elevation Bands 2.61-2.8m and 2.4m - 2.6m

Average dissimilarity = 23.77

Elevation	2.61m-2.8m	2.4m-2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FT/I	16.13	35.76	1.10	1.83	4.63	4.63
FA/M	18.72	37.43	1.06	1.53	4.47	9.10
FM/P	13.06	31.96	1.06	2.16	4.47	13.56
B/BB	18.86	37.41	1.05	1.52	4.43	18.00
L/6- 18mth	20.52	38.03	0.99	1.49	4.18	22.17
AM/M	19.68	37.28	0.99	1.71	4.15	26.33
M/<6mth	20.65	38.00	0.98	1.49	4.13	30.46
F/10	20.82	37.79	0.96	1.60	4.03	34.49
LH/F	20.97	37.46	0.92	1.68	3.88	38.37
P/I	35.79	46.57	0.85	1.32	3.57	41.94
BL/2-5mm	28.27	40.89	0.80	1.44	3.35	45.29
RF/I	37.26	47.08	0.79	1.33	3.33	48.61
FA/T	29.93	26.55	0.55	1.62	2.32	50.94
AM/S	29.93	26.56	0.55	1.62	2.32	53.26
M/≥6mth	29.94	26.55	0.55	1.62	2.32	55.58
LH/T	29.93	26.57	0.55	1.62	2.32	57.90
F/>10K	29.90	26.46	0.55	1.63	2.32	60.22

Paull 2011 Elevation Bands 2.61-2.8m & <2.4m  
Average dissimilarity = 27.42

Elevation	2.61m-2.8m	<2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/>10K	29.90	13.21	0.95	2.47	3.46	3.46
L/18m-2yr	31.05	14.54	0.95	2.49	3.46	6.92
M/≥6mth	29.94	13.65	0.92	2.36	3.37	10.29
FA/T	29.93	13.65	0.92	2.35	3.37	13.66
AM/S	29.93	13.65	0.92	2.35	3.37	17.03
LH/T	29.93	13.65	0.92	2.35	3.37	20.40
L/6- 18mth	20.52	33.33	0.90	1.40	3.29	23.68
<6mth	20.65	33.32	0.90	1.41	3.27	26.95
FA/M	18.72	30.66	0.84	1.21	3.07	30.02
B/BB	18.86	30.46	0.82	1.20	3.01	33.03
LH/F	20.97	33.33	0.82	1.49	2.99	36.02
F/10	20.82	31.10	0.74	1.30	2.70	38.72
FT/I	16.13	26.13	0.73	1.31	2.68	41.40
AM/M	19.68	29.82	0.70	1.28	2.54	43.94
P/I	35.79	34.10	0.69	3.07	2.53	46.46
BL/5mm-1cm	21.76	9.95	0.68	2.61	2.48	48.94
RF/I	37.26	37.82	0.66	2.19	2.39	51.33
FM/P	13.06	22.15	0.64	1.32	2.35	53.68
B/D	21.18	10.26	0.62	2.15	2.26	55.93
FM/D	21.44	10.79	0.60	2.01	2.21	58.14
FT/S	21.26	10.58	0.60	2.05	2.20	60.34

Paull 2011 Elevation Bands 2.4 - 2.6m & <2.4m  
Average dissimilarity = 19.67

Elevation	2.4m-2.6m	<2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P/I	46.57	34.10	0.69	1.77	3.51	3.51
1L/8mth-2yrs	27.76	14.54	0.69	1.95	3.50	7.01
F/>10K	26.46	13.21	0.69	1.93	3.50	10.50
LH/T	26.57	13.65	0.67	1.89	3.42	13.92
AM/S	26.56	13.65	0.67	1.89	3.42	17.34
FA/T	26.55	13.65	0.67	1.88	3.42	20.76
M/≥6m	26.55	13.65	0.67	1.88	3.42	24.18
RF/I	47.08	37.82	0.61	1.73	3.08	27.26
BL/2-5mm	40.89	32.08	0.54	1.53	2.74	30.00
FT/I	35.76	26.13	0.53	1.55	2.69	32.69
FM/P	31.96	22.15	0.51	1.61	2.59	35.28
BL/5mm-1cm	19.21	9.95	0.48	1.97	2.46	37.73
B/D	19.04	10.26	0.46	1.81	2.34	40.07
FT/S	19.21	10.58	0.46	1.85	2.32	42.40
FM/D	19.17	10.79	0.45	1.87	2.30	44.69
B/BB	37.41	30.46	0.44	1.56	2.23	46.92
FA/M	37.43	30.66	0.44	1.57	2.22	49.14
F/10	37.79	31.10	0.43	1.43	2.18	51.32
FM/FS	20.32	17.19	0.42	1.81	2.15	53.46
AM/M	37.28	29.82	0.42	1.40	2.14	55.60
FT/D	19.68	13.25	0.41	1.60	2.10	57.70
S/20	27.63	20.35	0.41	1.69	2.09	59.79
S/15	26.87	19.84	0.41	1.85	2.09	61.88



## Appendix 7.1

### Pauli 2011 Average Similarity- Biomass Weighted

Group 2.61-2.8m

Average similarity: 71.45

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
AM/M	0.67	3.69	4.85	5.17	5.17
S/20	0.65	3.59	4.96	5.02	10.19
P/I	0.69	3.58	4.24	5.01	15.20
18m-2yrs	0.63	3.56	7.80	4.99	20.19
LH/SP	0.67	3.49	4.39	4.89	25.07
F/10K	0.67	3.48	4.49	4.87	29.95
1-2cm	0.67	3.48	4.47	4.87	34.82
FA/J	0.61	3.35	6.37	4.68	39.50
RF/S	0.61	3.33	6.31	4.66	44.16
6m - 1yr	0.56	3.18	8.48	4.45	48.61
B/GB	0.43	2.37	6.39	3.32	51.93
B/OV	0.43	2.36	6.31	3.30	55.23
FT/D	0.41	2.11	5.71	2.96	58.19
FT/M	0.35	1.97	9.77	2.76	60.95

Group 2.4 - 2.6m

Average similarity: 52.18

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
AM/M	0.59	2.75	3.99	5.28	5.28
RF/I	0.57	2.61	4.28	5.00	10.28
S/20	0.54	2.36	2.59	4.52	14.80
18m-2yrs	0.46	2.20	4.19	4.22	19.02
6m - 1yr	0.43	2.11	4.33	4.04	23.06
FT/D	0.45	2.05	3.48	3.92	26.98
P/I	0.60	1.96	0.90	3.75	30.73
LH/SP	0.61	1.90	0.90	3.64	34.37
F/10K	0.59	1.90	0.90	3.63	38.01
1-2cm	0.59	1.89	0.90	3.63	41.63
1-2yr	0.49	1.48	0.90	2.85	44.48
FT/M	0.24	1.40	4.08	2.69	47.16
LH/F	0.20	1.37	2.03	2.63	49.80
FA/S	0.49	1.36	0.89	2.61	52.41
>5yrs	0.46	1.35	0.89	2.58	54.99
FM/D	0.39	1.27	0.98	2.44	57.43
F/10	0.19	1.25	1.81	2.39	59.82
2-5mm	0.17	1.19	2.79	2.28	62.10

Group <2.4m

Average similarity: 50.58

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	0.39	2.26	2.21	4.48	4.48
AM/M	0.38	2.04	2.09	4.03	8.51
RF/I	0.31	1.99	2.15	3.93	12.43
LH/SP	0.34	1.69	1.89	3.35	15.78
1-2cm	0.34	1.69	1.97	3.34	19.12
F/10K	0.33	1.68	1.97	3.32	22.44
S/20	0.33	1.63	1.97	3.22	25.67
FT/I	0.22	1.50	2.08	2.96	28.63
LH/F	0.21	1.42	1.91	2.81	31.45
FA/M	0.18	1.37	1.90	2.72	34.16
FM/P	0.21	1.37	2.18	2.71	36.87
B/BB	0.18	1.37	1.89	2.70	39.57
1-2yr	0.23	1.36	2.21	2.68	42.25
F/10	0.17	1.32	1.82	2.62	44.87
2-5mm	0.17	1.30	1.75	2.57	47.44
FA/S	0.21	1.29	2.20	2.55	49.99
>5yrs	0.19	1.25	2.18	2.47	52.46
6- 18m	0.15	1.21	1.59	2.40	54.86
<6m	0.15	1.19	1.55	2.35	57.22
FT/D	0.25	1.19	1.91	2.34	59.56
S/15	0.17	1.16	2.16	2.29	61.85

## Appendix 7.2

### Paull 2011 Average Dissimilarity- Biomass-Weighted

Groups 2.61-2.8m & 2.4 - 2.6m

Average dissimilarity = 36.18

	Group 2.61-2.8m	Group 2.4 - 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
LH/SP	0.67	0.61	1.60	1.14	4.41	4.41
P/I	0.69	0.60	1.57	1.08	4.33	8.74
1-2cm	0.67	0.59	1.55	1.10	4.27	13.01
F/10K	0.67	0.59	1.53	1.08	4.24	17.25
RF/S	0.61	0.35	1.40	1.09	3.87	21.12
FA/J	0.61	0.35	1.38	1.09	3.82	24.94
FA/S	0.24	0.49	1.36	1.38	3.76	28.70
>5yrs	0.22	0.46	1.29	1.37	3.58	32.27
1-2yr	0.38	0.49	1.25	1.48	3.46	35.74
S/20	0.65	0.54	1.15	1.14	3.19	38.92
AM/M	0.67	0.59	1.14	1.31	3.14	42.06
RF/I	0.35	0.57	1.08	1.48	2.98	45.04
18m-2yrs	0.63	0.46	1.07	1.26	2.95	47.98
B/OV	0.43	0.25	0.99	1.09	2.74	50.72
B/GB	0.43	0.25	0.99	1.07	2.73	53.45
B/BV	0.17	0.34	0.94	1.42	2.61	56.05
FM/D	0.39	0.39	0.94	1.15	2.60	58.66
FM/FS	0.28	0.37	0.94	1.50	2.60	61.26

Groups 2.61-2.8m & <2.4m

Average dissimilarity = 46.15

	Group 2.61-2.8m	Group <2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
LH/SP	0.67	0.34	2.04	1.55	4.43	4.43
18m-2yrs	0.63	0.30	2.04	1.46	4.41	8.84
F/10K	0.67	0.33	2.03	1.56	4.41	13.25
1-2cm	0.67	0.34	2.03	1.55	4.40	17.65
RF/S	0.61	0.26	2.02	1.51	4.37	22.01
S/20	0.65	0.33	1.97	1.52	4.28	26.29
FA/J	0.61	0.27	1.97	1.52	4.27	30.56
P/I	0.69	0.39	1.93	1.53	4.18	34.73
AM/M	0.67	0.38	1.92	1.52	4.16	38.89
6m - 1yr	0.56	0.28	1.81	1.45	3.93	42.82
B/OV	0.43	0.18	1.43	1.51	3.09	45.91
B/GB	0.43	0.19	1.38	1.52	3.00	48.91
FT/D	0.41	0.25	1.24	1.62	2.69	51.60
FM/D	0.39	0.21	1.17	1.59	2.54	54.14
FT/M	0.35	0.16	1.13	1.45	2.46	56.60
1-2yr	0.38	0.23	1.10	1.43	2.38	58.97
FM/OS	0.34	0.17	1.00	1.50	2.17	61.14

Groups 2.4 - 2.6m & <2.4m

Average dissimilarity = 52.27

	Group 2.4 - 2.6m	Group <2.4m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P/I	0.60	0.39	2.18	1.79	4.16	4.16
LH/SP	0.61	0.34	2.17	1.66	4.16	8.32
1-2cm	0.59	0.34	2.12	1.70	4.05	12.37
F/10K	0.59	0.33	2.11	1.71	4.03	16.40
1-2yr	0.49	0.23	1.76	1.89	3.38	19.78
FA/S	0.49	0.21	1.76	1.84	3.36	23.14
AM/M	0.59	0.38	1.73	1.58	3.31	26.45
>5yrs	0.46	0.19	1.68	1.95	3.21	29.66
18m-2yrs	0.46	0.30	1.65	1.71	3.16	32.82
S/20	0.54	0.33	1.61	1.48	3.08	35.90
RF/I	0.57	0.31	1.61	1.54	3.08	38.98
6m - 1yr	0.43	0.28	1.57	1.76	3.00	41.99
FT/D	0.45	0.25	1.41	1.66	2.69	44.68
RF/S	0.35	0.26	1.35	1.35	2.59	47.26
FM/D	0.39	0.21	1.35	1.71	2.58	49.85
FA/J	0.35	0.27	1.34	1.40	2.57	52.42
FM/FS	0.37	0.18	1.31	1.83	2.51	54.93
FT/S	0.37	0.18	1.31	1.81	2.51	57.44
B/D	0.34	0.16	1.23	1.90	2.36	59.80
B/BV	0.34	0.15	1.22	1.88	2.34	62.14

## Appendix 8.1

### Alkborough 2011 Average Similarity – Abundance-weighted

Group 3.35m

Average similarity: 51.66

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
LH/F	4.53	3.52	2.90	6.82	6.82
AM/M	4.27	3.17	2.72	6.14	12.96
RF/I	4.35	3.03	2.27	5.87	18.83
<6m	4.10	2.77	1.89	5.36	24.19
P/I	3.68	2.26	1.62	4.38	28.57
B/BB	3.80	2.20	1.36	4.27	32.83
F/10	3.73	2.16	1.38	4.18	37.02
FM/D	3.02	2.12	1.48	4.10	41.12
P/E	2.84	2.06	1.55	3.98	45.10
5mm-1cm	2.90	1.95	1.43	3.78	48.88
FA/M	3.54	1.92	1.23	3.72	52.60
FA/J	2.66	1.86	1.26	3.60	56.20
S/10	2.38	1.81	2.58	3.50	59.70
S/5	2.25	1.73	1.97	3.36	63.06

Group 3.1m

Average similarity: 31.76

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
FM/D	4.48	2.31	1.42	7.29	7.29
RF/I	5.15	2.29	1.43	7.23	14.51
<6m	5.06	2.23	1.50	7.01	21.52
AM/M	5.02	2.06	1.09	6.48	28.00
P/E	3.96	2.02	1.78	6.37	34.38
LH/F	4.61	2.02	1.78	6.37	40.75
2-5mm	2.80	1.50	5.00	4.72	45.47
6- 18m	4.78	1.38	0.58	4.33	49.80
F/10	4.82	1.38	0.58	4.33	54.13
S/10	2.70	1.37	1.96	4.31	58.44
FT/M	4.10	1.36	0.58	4.29	62.73

Group 3.3m

Average similarity: 53.91

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
LH/F	4.60	3.51	2.35	6.51	6.51
RF/I	4.13	3.13	2.64	5.81	12.33
AM/M	4.08	3.03	2.37	5.62	17.94
B/BB	3.95	2.88	1.73	5.34	23.28
<6m	3.99	2.75	1.77	5.11	28.39
P/I	3.52	2.57	2.38	4.78	33.16
F/10	3.58	2.51	1.72	4.65	37.81
FM/D	3.42	2.39	1.65	4.44	42.25
FA/M	3.53	2.35	1.48	4.37	46.62
5mm-1cm	3.23	2.18	1.63	4.04	50.66
P/E	3.10	2.03	1.46	3.76	54.42
FA/J	2.99	2.01	1.82	3.74	58.15
S/10	2.25	1.68	2.49	3.11	61.27

Group 3.2m

Average similarity: 78.97

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
LH/F	6.41	4.71	7.80	5.97	5.97
RF/I	6.38	4.71	7.80	5.97	11.94
<6m	6.38	4.71	7.80	5.97	17.91
AM/M	5.97	4.21	5.37	5.32	23.23
FA/M	5.44	3.55	3.87	4.49	27.72
B/BB	5.44	3.55	3.87	4.49	32.22
F/10	5.44	3.55	3.87	4.49	36.71
5mm-1cm	5.28	3.48	3.78	4.41	41.12
P/I	5.24	3.42	3.63	4.33	45.45
FM/SS	5.16	3.39	3.82	4.29	49.75
FT/B	5.16	3.39	3.82	4.29	54.04
18m-2yrs	5.11	3.39	3.82	4.29	58.34
P/E	3.57	2.71	5.21	3.43	61.77

Group 2.7m

Average similarity: 50.72

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	3.60	3.59	3.89	7.07	7.07
P/I	3.17	3.48	4.53	6.86	13.93
AM/M	3.09	3.25	6.55	6.40	20.33
F/10	3.05	3.25	6.55	6.40	26.73
LH/F	2.36	2.75	3.55	5.43	32.16
<6m	2.31	2.75	3.55	5.43	37.59
FA/M	2.20	2.37	5.01	4.68	42.26
B/BB	2.20	2.37	5.01	4.68	46.94
5mm-1cm	1.73	1.97	2.59	3.88	50.82
FM/D	1.86	1.75	6.46	3.45	54.27
S/10	1.74	1.51	2.27	2.98	57.25
S/15	1.74	1.51	2.27	2.98	60.23

Group 2.6m

Average similarity: 54.03

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	6.14	3.77	2.86	6.98	6.98
LH/F	6.10	3.74	2.84	6.92	13.90
AM/M	6.09	3.68	2.77	6.81	20.71
FM/SS	6.06	3.66	2.76	6.78	27.49
FA/M	6.06	3.66	2.76	6.78	34.27
B/BB	6.06	3.66	2.76	6.78	41.05
18m-2yrs	6.06	3.66	2.76	6.78	47.83
1-2cm	5.98	3.64	2.83	6.73	54.56
FT/D	5.94	3.61	2.82	6.67	61.24

Group 0m

Average similarity: 66.88

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	4.90	4.60	3.44	6.88	6.88
1-2cm	4.89	4.60	3.44	6.88	13.77
AM/M	4.88	4.60	3.44	6.88	20.65
18m-2yrs	4.85	4.60	3.44	6.88	27.52
RF/S	4.85	4.60	3.44	6.88	34.40
FT/D	4.74	4.42	3.02	6.61	41.01
1-2yr	4.73	4.40	2.96	6.57	47.58
FM/SS	4.70	4.34	2.84	6.49	54.07
FA/M	4.71	4.34	2.84	6.49	60.56

Group -2m

Average similarity: 77.89

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
FM/SS	3.60	5.71	14.50	7.33	7.33
FA/M	3.60	5.71	14.50	7.33	14.66
AM/M	3.60	5.71	14.50	7.33	21.99
P/I	3.60	5.71	14.50	7.33	29.33
LH/F	3.60	5.71	14.50	7.33	36.66
B/BB	3.60	5.71	14.50	7.33	43.99
18m-2yrs	3.60	5.71	14.50	7.33	51.32
FT/D	3.55	5.63	16.07	7.22	58.54
1-2cm	3.55	5.63	16.07	7.22	65.77

## Appendix 8.2 Average Dissimilarity – Abundance- weighted

Groups 3.35m & 3.1m

Average dissimilarity = 55.07

	Group 3.35m	Group 3.1m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/10	3.73	4.82	2.47	1.61	4.48	4.48
B/BB	3.80	4.73	2.44	1.56	4.43	8.91
FA/M	3.54	4.73	2.42	1.58	4.40	13.31
6- 18m	2.85	4.78	2.37	1.63	4.30	17.61
AM/M	4.27	5.02	2.27	1.79	4.12	21.73
RF/I	4.35	5.15	2.22	1.69	4.04	25.77
<6m	4.10	5.06	2.19	1.67	3.97	29.74
LH/F	4.53	4.61	2.02	1.58	3.66	33.41
FT/M	1.90	4.10	1.99	1.56	3.61	37.02
P/I	3.68	3.30	1.94	1.34	3.52	40.54
FM/D	3.02	4.48	1.84	1.76	3.35	43.89
5mm-1cm	2.90	2.91	1.63	1.24	2.96	46.85
P/E	2.84	3.96	1.59	1.74	2.88	49.73
2-5mm	1.99	2.80	1.34	1.55	2.44	52.17
FT/B	2.43	1.05	1.34	1.11	2.43	54.60
1-2cm	1.74	2.64	1.33	1.40	2.42	57.02
S/15	1.96	2.46	1.28	1.77	2.32	59.34
S/20	2.05	2.36	1.26	1.67	2.28	61.63

Groups 3.35m & 3.3m

Average dissimilarity = 46.45

	Group 3.35m	Group 3.3m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
B/BB	3.80	3.95	1.73	1.33	3.73	3.73
<6m	4.10	3.99	1.73	1.42	3.73	7.46
FA/M	3.54	3.53	1.71	1.36	3.68	11.14
F/10	3.73	3.58	1.68	1.37	3.61	14.75
LH/F	4.53	4.60	1.66	1.39	3.58	18.33
RF/I	4.35	4.13	1.65	1.43	3.56	21.89
AM/M	4.27	4.08	1.61	1.47	3.46	25.34
P/I	3.68	3.52	1.58	1.37	3.41	28.75
6- 18m	2.85	2.34	1.46	1.32	3.15	31.90
FT/B	2.43	2.73	1.44	1.35	3.11	35.01
FM/D	3.02	3.42	1.42	1.35	3.06	38.07
5mm-1cm	2.90	3.23	1.41	1.35	3.04	41.11
P/E	2.84	3.10	1.36	1.38	2.92	44.03
FM/SS	2.04	2.17	1.34	1.24	2.88	46.91
FA/J	2.66	2.99	1.33	1.24	2.86	49.77
<6m	2.36	2.80	1.32	1.19	2.83	52.60
18m-2yrs	2.01	2.23	1.29	1.23	2.78	55.38
FT/M	1.90	2.17	1.25	1.24	2.70	58.08
S/5	2.25	2.51	1.13	1.11	2.44	60.52

Groups 3.1m & 3.3m

Average dissimilarity = 54.69

	Group 3.1m	Group 3.3m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/10	4.82	3.58	2.37	1.55	4.34	4.34
B/BB	4.73	3.95	2.33	1.41	4.27	8.61
FA/M	4.73	3.53	2.31	1.47	4.23	12.83
6- 18m	4.78	2.34	2.29	1.68	4.18	17.02
AM/M	5.02	4.08	2.15	1.51	3.93	20.95
<6m	5.06	3.99	2.13	1.54	3.89	24.84
RF/I	5.15	4.13	2.07	1.54	3.79	28.62
LH/F	4.61	4.60	2.07	1.47	3.78	32.40
FT/M	4.10	2.17	1.96	1.52	3.58	35.98
P/I	3.30	3.52	1.90	1.30	3.48	39.46
FM/D	4.48	3.42	1.87	1.63	3.41	42.88
5mm-1cm	2.91	3.23	1.68	1.20	3.07	45.94
P/E	3.96	3.10	1.65	1.48	3.01	48.96
FT/B	1.05	2.73	1.53	1.19	2.80	51.75
<6m	0.33	2.80	1.44	1.26	2.63	54.38
1-2cm	2.64	1.70	1.32	1.42	2.42	56.80
FM/SS	1.05	2.17	1.29	1.08	2.36	59.16
2-5mm	2.80	1.35	1.28	1.48	2.34	61.50

Groups 3.35m & 3.2m

Average dissimilarity = 41.99

	Group 3.35m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FM/SS	2.04	5.16	1.93	1.68	4.59	4.59
<6m	4.10	6.38	1.88	1.65	4.48	9.07
18m-2yrs	2.01	5.11	1.87	1.68	4.44	13.51
RF/I	4.35	6.38	1.79	1.56	4.27	17.79
FT/B	2.43	5.16	1.77	1.53	4.21	21.99
FA/M	3.54	5.44	1.74	1.46	4.14	26.13
LH/F	4.53	6.41	1.67	1.56	3.97	30.10
F/10	3.73	5.44	1.66	1.40	3.96	34.07
B/BB	3.80	5.44	1.65	1.38	3.92	37.99
AM/M	4.27	5.97	1.59	1.50	3.79	41.78
5mm-1cm	2.90	5.28	1.59	1.47	3.78	45.56
P/I	3.68	5.24	1.56	1.42	3.73	49.29
2-5mm	1.99	3.15	1.27	1.64	3.02	52.31
F/100	1.50	3.02	1.19	1.58	2.83	55.13
B/SB	1.78	3.15	1.06	1.52	2.53	57.67
P/E	2.84	3.57	0.99	1.60	2.35	60.01

Groups 3.1m & 3.2m

Average dissimilarity = 48.99

	Group 3.1m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FM/SS	1.05	5.16	2.25	1.53	4.60	4.60
FT/B	1.05	5.16	2.25	1.53	4.60	9.20
18m-2yrs	1.05	5.11	2.19	1.64	4.46	13.66
FA/M	4.73	5.44	2.01	1.20	4.10	17.76
B/BB	4.73	5.44	2.01	1.20	4.10	21.87
F/10	4.82	5.44	2.00	1.18	4.08	25.95
LH/F	4.61	6.41	1.88	1.10	3.84	29.79
<6m	5.06	6.38	1.87	1.10	3.82	33.61
RF/I	5.15	6.38	1.86	1.10	3.80	37.41
6- 18m	4.78	1.85	1.86	2.60	3.80	41.21
AM/M	5.02	5.97	1.85	1.13	3.78	44.99
5mm-1cm	2.91	5.28	1.76	1.03	3.58	48.57
P/I	3.30	5.24	1.73	1.00	3.53	52.10
FT/M	4.10	1.55	1.62	3.30	3.30	55.40
<6m	0.33	3.15	1.42	2.35	2.91	58.31
FM/D	4.48	3.52	1.37	2.27	2.80	61.10

Groups 3.3m & 3.2m

Average dissimilarity = 38.02

	Group 3.3m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FM/SS	2.17	5.16	1.78	1.63	4.68	4.68
18m-2yrs	2.23	5.11	1.74	1.62	4.57	9.25
<6m	3.99	6.38	1.66	1.32	4.38	13.62
RF/I	4.13	6.38	1.59	1.39	4.17	17.79
FT/B	2.73	5.16	1.57	1.42	4.13	21.92
AM/M	4.08	5.97	1.47	1.33	3.86	25.78
LH/F	4.60	6.41	1.46	1.20	3.83	29.62
5mm-1cm	3.23	5.28	1.45	1.34	3.82	33.44
FA/M	3.53	5.44	1.45	1.23	3.81	37.25
F/10	3.58	5.44	1.42	1.27	3.74	40.99
P/I	3.52	5.24	1.37	1.34	3.60	44.59
B/BB	3.95	5.44	1.32	1.14	3.48	48.06
2-5mm	1.35	3.15	1.27	1.66	3.33	51.39
F/100	1.36	3.02	1.19	1.62	3.14	54.53
B/SB	1.86	3.15	1.09	1.37	2.86	57.39
S/5	2.51	3.26	1.01	1.63	2.66	60.06

Groups 3.35m & 2.7m

Average dissimilarity = 50.23

	Group 3.35m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
6- 18m	2.85	3.02	1.95	1.48	3.88	3.88
FA/J	2.66	2.49	1.66	1.55	3.30	7.18
RF/I	4.35	3.60	1.60	1.41	3.19	10.38
1-2cm	1.74	2.69	1.60	1.40	3.18	13.56
B/BB	3.80	2.20	1.57	1.48	3.12	16.68
F/10	3.73	3.05	1.55	1.34	3.10	19.77
B/BV	0.98	2.45	1.53	1.32	3.05	22.82
≥6m	0.58	2.45	1.53	1.29	3.04	25.86
FT/S	0.64	2.45	1.52	1.32	3.03	28.90
FM/FS	0.65	2.45	1.52	1.32	3.03	31.93
LH/SP	0.84	2.45	1.52	1.36	3.02	34.95
FA/M	3.54	2.20	1.51	1.43	3.01	37.97
P/I	3.68	3.17	1.50	1.37	2.98	40.95
LH/F	4.53	2.36	1.47	1.44	2.94	43.89
P/E	2.84	1.55	1.43	1.37	2.84	46.73
<6m	2.36	0.33	1.42	1.28	2.83	49.56
<6m	4.10	2.31	1.42	1.30	2.83	52.39
AM/M	4.27	3.09	1.40	1.42	2.79	55.18
FT/B	2.43	0.47	1.33	1.36	2.65	57.83
FM/D	3.02	1.86	1.25	1.54	2.48	60.31



Groups 3.1m & 2.7m

Average dissimilarity = 58.98

	Group 3.1m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/10	4.82	3.05	2.72	2.14	4.61	4.61
FA/M	4.73	2.20	2.59	2.74	4.40	9.00
B/BB	4.73	2.20	2.59	2.74	4.40	13.40
6- 18m	4.78	3.02	2.50	1.26	4.24	17.64
AM/M	5.02	3.09	2.36	2.39	4.00	21.63
RF/I	5.15	3.60	2.24	1.75	3.80	25.43
FT/M	4.10	1.76	2.22	2.71	3.76	29.19
<6m	5.06	2.31	2.14	2.20	3.62	32.82
P/I	3.30	3.17	2.01	1.20	3.41	36.23
P/E	3.96	1.55	1.91	1.83	3.23	39.46
LH/F	4.61	2.36	1.90	1.98	3.22	42.68
FM/D	4.48	1.86	1.78	1.58	3.03	45.71
5mm-1cm	2.91	1.73	1.73	1.69	2.93	48.64
B/BV	0.00	2.45	1.58	1.07	2.68	51.32
≥6m	0.00	2.45	1.58	1.07	2.68	54.00
1-2cm	2.64	2.69	1.57	0.91	2.66	56.66
FM/FS	0.18	2.45	1.56	1.10	2.65	59.31
FT/S	0.18	2.45	1.56	1.10	2.65	61.96

Groups 3.3m & 2.7m

Average dissimilarity = 49.52

	Group 3.3m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
6- 18m	2.34	3.02	1.74	1.37	3.52	3.52
LH/F	4.60	2.36	1.74	1.64	3.51	7.03
FA/J	2.99	2.49	1.65	1.40	3.33	10.36
B/BB	3.95	2.20	1.64	1.77	3.31	13.67
<6m	2.80	0.33	1.62	1.28	3.27	16.94
P/E	3.10	1.55	1.55	1.35	3.13	20.07
<6m	3.99	2.31	1.54	1.46	3.10	23.17
1-2cm	1.70	2.69	1.53	1.48	3.08	26.25
FT/B	2.73	0.47	1.51	1.53	3.06	29.30
B/BV	1.00	2.45	1.51	1.35	3.05	32.35
FM/FS	0.38	2.45	1.49	1.44	3.01	35.36
FT/S	0.38	2.45	1.49	1.44	3.01	38.37
FA/M	3.53	2.20	1.49	1.56	3.01	41.38
≥6m	0.42	2.45	1.49	1.46	3.00	44.39
FM/D	3.42	1.86	1.48	1.64	2.99	47.38
RF/I	4.13	3.60	1.48	1.39	2.99	50.36
LH/SP	0.49	2.45	1.48	1.44	2.99	53.35
AM/M	4.08	3.09	1.46	1.48	2.95	56.30
F/10	3.58	3.05	1.40	1.46	2.83	59.13
P/I	3.52	3.17	1.34	1.43	2.70	61.84

Groups 3.2m & 2.7m

Average dissimilarity = 51.62

	Group 3.2m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FM/SS	5.16	0.47	2.50	3.92	4.85	4.85
FT/B	5.16	0.47	2.50	3.92	4.85	9.69
18m-2yrs	5.11	0.58	2.40	3.77	4.65	14.34
<6m	6.38	2.31	2.30	2.53	4.46	18.80
LH/F	6.41	2.36	2.29	2.43	4.44	23.24
5mm-1cm	5.28	1.73	1.94	2.23	3.75	26.99
FA/M	5.44	2.20	1.83	1.72	3.54	30.53
B/BB	5.44	2.20	1.83	1.72	3.54	34.08
AM/M	5.97	3.09	1.71	1.60	3.30	37.38
RF/I	6.38	3.60	1.69	1.40	3.28	40.66
<6m	3.15	0.33	1.66	2.05	3.21	43.87
FT/D	3.09	0.47	1.50	2.23	2.91	46.78
F/10	5.44	3.05	1.49	1.47	2.89	49.67
S/5	3.26	0.56	1.48	5.70	2.86	52.53
B/SB	3.15	0.67	1.42	2.18	2.75	55.28
2-5mm	3.15	0.80	1.41	1.62	2.74	58.02
P/I	5.24	3.17	1.36	1.46	2.63	60.64

Groups 3.35m & 2.6m

Average dissimilarity = 62.09

	Group 3.35m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/1K	0.03	5.94	3.14	2.38	5.05	5.05
1-2yr	0.11	5.94	3.09	2.31	4.97	10.02
RF/S	0.28	5.94	3.00	2.17	4.83	14.86
FM/SS	2.04	6.06	2.58	1.65	4.15	19.01
18m-2yrs	2.01	6.06	2.52	1.61	4.06	23.06
1-2cm	1.74	5.98	2.44	1.49	3.93	26.99
FA/M	3.54	6.06	2.34	1.51	3.76	30.75
B/BB	3.80	6.06	2.29	1.50	3.69	34.44
P/I	3.68	6.14	2.26	1.52	3.64	38.08
FT/D	2.06	5.94	2.21	1.51	3.55	41.64
AM/M	4.27	6.09	2.08	1.54	3.35	44.99
LH/F	4.53	6.10	2.02	1.51	3.25	48.24
<6m	4.10	0.91	1.91	1.37	3.08	51.32
RF/I	4.35	1.24	1.86	1.33	3.00	54.32
FM/D	3.02	0.00	1.71	1.69	2.76	57.08
F/10	3.73	1.08	1.66	1.28	2.68	59.75
P/E	2.84	0.00	1.63	1.69	2.62	62.38

Groups 3.1m & 2.6m

Average dissimilarity = 68.86

	Group 3.1m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/1K	0.00	5.94	3.26	2.00	4.73	4.73
1-2yr	0.26	5.94	3.13	1.81	4.54	9.27
FM/SS	1.05	6.06	3.01	1.55	4.37	13.64
RF/S	0.58	5.94	2.96	1.58	4.29	17.94
FA/M	4.73	6.06	2.95	1.54	4.29	22.22
B/BB	4.73	6.06	2.95	1.54	4.29	26.51
18m-2yrs	1.05	6.06	2.83	1.38	4.11	30.61
P/I	3.30	6.14	2.71	1.32	3.94	34.55
AM/M	5.02	6.09	2.66	1.62	3.86	38.41
1-2cm	2.64	5.98	2.58	1.27	3.75	42.17
FT/D	0.85	5.94	2.56	1.70	3.72	45.89
LH/F	4.61	6.10	2.46	1.57	3.57	49.46
FM/D	4.48	0.00	2.36	2.18	3.43	52.89
<6m	5.06	0.91	2.36	1.73	3.42	56.31
RF/I	5.15	1.24	2.26	1.61	3.29	59.59
F/10	4.82	1.08	2.21	1.50	3.21	62.80

Groups 3.3m & 2.6m

Average dissimilarity = 60.78

	Group 3.3m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1-2yr	0.04	5.94	3.08	2.38	5.06	5.06
F/1K	0.06	5.94	3.06	2.37	5.04	10.10
RF/S	0.10	5.94	3.05	2.31	5.02	15.12
FM/SS	2.17	6.06	2.39	1.54	3.93	19.04
18m-2yrs	2.23	6.06	2.35	1.51	3.87	22.92
1-2cm	1.70	5.98	2.30	1.52	3.78	26.70
FT/D	2.30	5.94	2.21	1.42	3.64	30.33
FA/M	3.53	6.06	2.15	1.46	3.54	33.87
B/BB	3.95	6.06	2.10	1.46	3.45	37.32
AM/M	4.08	6.09	2.07	1.55	3.40	40.72
LH/F	4.60	6.10	2.06	1.49	3.39	44.12
P/I	3.52	6.14	2.05	1.45	3.38	47.50
<6m	3.99	0.91	1.96	1.43	3.22	50.72
FM/D	3.42	0.00	1.93	1.79	3.18	53.90
RF/I	4.13	1.24	1.87	1.38	3.07	56.98
P/E	3.10	0.00	1.74	1.61	2.87	59.85
F/10	3.58	1.08	1.69	1.37	2.78	62.63

Groups 3.2m & 2.6m

Average dissimilarity = 56.70

	Group 3.2m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<6m	6.38	0.91	2.86	2.29	5.04	5.04
RF/I	6.38	1.24	2.71	2.15	4.78	9.81
1-2yr	0.00	5.94	2.52	2.35	4.45	14.26
F/1K	0.00	5.94	2.52	2.36	4.45	18.71
RF/S	0.00	5.94	2.52	2.36	4.45	23.16
5mm-1cm	5.28	0.91	2.27	1.91	4.00	27.15
F/10	5.44	1.08	2.26	1.86	3.99	31.14
FT/B	5.16	0.91	2.21	1.89	3.89	35.03
1-2cm	1.10	5.98	1.99	1.60	3.51	38.54
P/E	3.57	0.00	1.85	2.88	3.25	41.79
FM/D	3.52	0.00	1.82	2.82	3.21	45.01
LH/F	6.41	6.10	1.81	1.86	3.19	48.20
AM/M	5.97	6.09	1.74	1.79	3.07	51.27
FA/M	5.44	6.06	1.65	1.62	2.91	54.18
B/BB	5.44	6.06	1.65	1.62	2.91	57.09
2-5mm	3.15	0.00	1.64	2.30	2.90	59.99
FM/SS	5.16	6.06	1.61	1.64	2.83	62.82

Groups 2.7m & 2.6m

Average dissimilarity = 63.38

	Group 2.7m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1-2yr	0.00	5.94	3.43	2.75	5.42	5.42
F/1K	0.00	5.94	3.43	2.76	5.41	10.83
RF/S	0.00	5.94	3.43	2.76	5.41	16.25
FT/D	0.47	5.94	3.05	2.37	4.82	21.07
FM/SS	0.47	6.06	3.01	2.30	4.75	25.82
18m-2yrs	0.58	6.06	2.90	2.10	4.58	30.40
1-2cm	2.69	5.98	2.57	1.55	4.05	34.45
FA/M	2.20	6.06	2.19	1.41	3.46	37.91
B/BB	2.20	6.06	2.19	1.41	3.46	41.36
LH/F	2.36	6.10	2.11	1.38	3.33	44.69
AM/M	3.09	6.09	2.04	1.45	3.22	47.91
P/I	3.17	6.14	2.02	1.44	3.19	51.11
RF/I	3.60	1.24	1.87	1.37	2.95	54.06
6-18m	3.02	0.50	1.81	1.31	2.86	56.92
F/10	3.05	1.08	1.60	1.37	2.52	59.44
FA/J	2.49	0.74	1.49	1.52	2.34	61.79

Groups 3.35m & 0m

Average dissimilarity = 62.37

	Group 3.35m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/1K	0.03	4.70	2.99	2.47	4.80	4.80
1-2yr	0.11	4.73	2.96	2.43	4.75	9.55
RF/S	0.28	4.85	2.96	2.39	4.75	14.30
1-2cm	1.74	4.89	2.33	1.53	3.73	18.03
18m-2yrs	2.01	4.85	2.29	1.56	3.68	21.71
FM/SS	2.04	4.70	2.27	1.54	3.65	25.35
RF/I	4.35	0.46	2.22	1.82	3.57	28.92
<6m	4.10	0.17	2.22	1.87	3.56	32.48
FT/D	2.06	4.74	2.06	1.70	3.31	35.79
FA/M	3.54	4.71	2.02	1.41	3.24	39.02
B/BB	3.80	4.71	1.95	1.35	3.13	42.15
P/I	3.68	4.90	1.94	1.38	3.11	45.26
F/10	3.73	0.35	1.90	1.56	3.05	48.31
AM/M	4.27	4.88	1.74	1.48	2.80	51.10
LH/F	4.53	4.71	1.70	1.52	2.72	53.82
5mm-1cm	2.90	0.00	1.68	1.75	2.69	56.52
P/E	2.84	0.00	1.67	1.89	2.68	59.19
FM/D	3.02	0.49	1.52	1.78	2.44	61.63

Groups 3.1m & 0m

Average dissimilarity = 67.18

	Group 3.1m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/1K	0.00	4.70	3.11	1.93	4.62	4.62
1-2yr	0.26	4.73	2.99	1.77	4.45	9.08
RF/S	0.58	4.85	2.91	1.59	4.34	13.41
FM/SS	1.05	4.70	2.75	1.44	4.10	17.51
18m-2yrs	1.05	4.85	2.71	1.38	4.04	21.55
FA/M	4.73	4.71	2.60	1.25	3.87	25.42
B/BB	4.73	4.71	2.60	1.25	3.87	29.29
<6m	5.06	0.17	2.57	1.99	3.83	33.13
RF/I	5.15	0.46	2.53	1.89	3.77	36.89
FT/D	0.85	4.74	2.45	1.76	3.64	40.53
P/I	3.30	4.90	2.34	1.05	3.48	44.02
AM/M	5.02	4.88	2.33	1.28	3.47	47.49
1-2cm	2.64	4.89	2.32	1.05	3.46	50.95
F/10	4.82	0.35	2.28	1.39	3.40	54.35
6- 18m	4.78	0.46	2.27	1.42	3.37	57.72
P/E	3.96	0.00	2.15	2.68	3.20	60.92

Groups 3.3m & 0m

Average dissimilarity = 60.88

	Group 3.3m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/S	0.10	4.85	3.01	2.59	4.95	4.95
1-2yr	0.04	4.73	2.95	2.55	4.84	9.79
F/1K	0.06	4.70	2.91	2.50	4.78	14.57
<6m	3.99	0.17	2.26	1.91	3.71	18.28
RF/I	4.13	0.46	2.24	1.91	3.67	21.95
1-2cm	1.70	4.89	2.17	1.61	3.57	25.52
18m-2yrs	2.23	4.85	2.12	1.49	3.49	29.01
FM/SS	2.17	4.70	2.10	1.53	3.45	32.46
FT/D	2.30	4.74	2.04	1.51	3.35	35.81
F/10	3.58	0.35	1.97	1.77	3.24	39.05
5mm-1cm	3.23	0.00	1.90	1.85	3.11	42.17
P/E	3.10	0.00	1.80	1.77	2.95	45.12
FM/D	3.42	0.49	1.79	2.03	2.94	48.06
FA/M	3.53	4.71	1.73	1.22	2.84	50.90
P/I	3.52	4.90	1.72	1.36	2.83	53.73
AM/M	4.08	4.88	1.66	1.35	2.73	56.46
LH/F	4.60	4.71	1.64	1.25	2.69	59.15
B/BB	3.95	4.71	1.64	1.16	2.69	61.84

Groups 3.2m & 0m

Average dissimilarity = 55.13

	Group 3.2m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<6m	6.38	0.17	3.27	4.51	5.93	5.93
RF/I	6.38	0.46	3.15	3.61	5.70	11.64
5mm-1cm	5.28	0.00	2.73	3.88	4.95	16.59
FT/B	5.16	0.00	2.67	3.85	4.84	21.42
F/10	5.44	0.35	2.66	2.97	4.83	26.25
RF/S	0.00	4.85	2.43	3.47	4.42	30.67
1-2yr	0.00	4.73	2.37	3.18	4.29	34.96
F/1K	0.00	4.70	2.35	3.11	4.26	39.22
P/E	3.57	0.00	1.91	3.82	3.46	42.68
1-2cm	1.10	4.89	1.88	2.24	3.41	46.09
S/5	3.26	0.00	1.72	5.20	3.12	49.21
B/SB	3.15	0.00	1.70	2.75	3.08	52.29
<6m	3.15	0.00	1.70	2.75	3.08	55.37
FM/D	3.52	0.49	1.63	3.04	2.96	58.33
2-5mm	3.15	0.17	1.63	2.40	2.95	61.28

Groups 2.7m & 0m

Average dissimilarity = 63.35

	Group 2.7m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/S	0.00	4.85	3.42	3.14	5.40	5.40
1-2yr	0.00	4.73	3.32	2.92	5.24	10.65
F/1K	0.00	4.70	3.30	2.86	5.20	15.85
FT/D	0.47	4.74	2.95	2.66	4.66	20.51
18m-2yrs	0.58	4.85	2.82	2.85	4.45	24.95
FM/SS	0.47	4.70	2.80	2.65	4.42	29.38
RF/I	3.60	0.46	2.27	2.08	3.59	32.96
1-2cm	2.69	4.89	2.23	1.23	3.52	36.48
F/10	3.05	0.35	1.97	2.29	3.11	39.59
FA/M	2.20	4.71	1.94	1.55	3.06	42.65
B/BB	2.20	4.71	1.94	1.55	3.06	45.71
LH/F	2.36	4.71	1.88	1.69	2.97	48.68
6- 18m	3.02	0.46	1.87	1.36	2.95	51.64
AM/M	3.09	4.88	1.69	1.43	2.67	54.31
P/I	3.17	4.90	1.64	1.36	2.59	56.89
<6m	2.31	0.17	1.59	2.35	2.52	59.41
B/BV	2.45	0.40	1.53	1.35	2.41	61.82

Groups 2.6m & 0m

Average dissimilarity = 39.47

	Group 2.6m	Group 0m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FA/M	6.06	4.71	2.11	1.74	5.34	5.34
B/BB	6.06	4.71	2.11	1.74	5.34	10.68
FM/SS	6.06	4.70	2.10	1.74	5.33	16.02
LH/F	6.10	4.71	2.09	1.74	5.30	21.32
AM/M	6.09	4.88	2.08	1.69	5.27	26.59
18m-2yrs	6.06	4.85	2.07	1.70	5.25	31.84
P/I	6.14	4.90	2.07	1.69	5.24	37.07
F/1K	5.94	4.70	2.05	1.70	5.20	42.28
1-2yr	5.94	4.73	2.05	1.69	5.19	47.47
FT/D	5.94	4.74	2.05	1.69	5.18	52.65
1-2cm	5.98	4.89	2.04	1.66	5.16	57.81
RF/S	5.94	4.85	2.03	1.68	5.14	62.95

Groups 3.35m & -2m

Average dissimilarity = 62.23

Species	Group 3.35m	Group -2m	Av.Diss	Diss/SD	Contrib%	Cum.%
	Av.Abund	Av.Abund				
F/1K	0.03	3.55	2.88	2.53	4.63	4.63
1-2yr	0.11	3.55	2.82	2.44	4.53	9.16
RF/S	0.28	3.55	2.71	2.21	4.35	13.51
RF/I	4.35	0.33	2.56	2.23	4.11	17.63
<6m	4.10	0.33	2.41	1.98	3.87	21.50
F/10	3.73	0.33	2.16	1.76	3.47	24.97
FM/SS	2.04	3.60	2.12	1.43	3.40	28.38
18m-2yrs	2.01	3.60	2.04	1.41	3.28	31.66
FM/D	3.02	0.00	2.04	2.09	3.27	34.93
1-2cm	1.74	3.55	1.99	1.31	3.20	38.13
P/E	2.84	0.00	1.94	2.12	3.12	41.24
FA/J	2.66	0.00	1.86	1.67	2.99	44.24
FA/M	3.54	3.60	1.86	1.27	2.98	47.22
B/BB	3.80	3.60	1.78	1.21	2.87	50.09
5mm-1cm	2.90	0.33	1.76	1.74	2.83	52.92
P/I	3.68	3.60	1.74	1.32	2.80	55.71
FT/D	2.06	3.55	1.72	1.55	2.76	58.48
6- 18m	2.85	0.00	1.68	1.32	2.70	61.18

Groups 3.1m & -2m

Average dissimilarity = 70.84

Species	Group 3.1m	Group -2m	Av.Diss	Diss/SD	Contrib%	Cum.%
	Av.Abund	Av.Abund				
F/1K	0.00	3.55	3.09	1.71	4.36	4.36
FA/M	4.73	3.60	3.04	1.51	4.30	8.66
B/BB	4.73	3.60	3.04	1.51	4.30	12.95
1-2yr	0.26	3.55	2.93	1.53	4.13	17.09
RF/I	5.15	0.33	2.81	1.91	3.97	21.05
FM/D	4.48	0.00	2.78	2.98	3.92	24.97
<6m	5.06	0.33	2.75	1.89	3.89	28.86
RF/S	0.58	3.55	2.73	1.31	3.85	32.71
AM/M	5.02	3.60	2.72	1.87	3.84	36.55
FM/SS	1.05	3.60	2.68	1.18	3.79	40.34
F/10	4.82	0.33	2.61	1.52	3.69	44.02
6- 18m	4.78	0.00	2.55	1.31	3.60	47.62
18m-2yrs	1.05	3.60	2.55	1.13	3.60	51.22
P/E	3.96	0.00	2.47	3.45	3.49	54.71
P/I	3.30	3.60	2.41	1.02	3.40	58.11
LH/F	4.61	3.60	2.29	1.51	3.23	61.34

Groups 3.3m & -2m

Average dissimilarity = 60.81

Species	Group 3.3m	Group -2m	Av.Diss	Diss/SD	Contrib%	Cum.%
	Av.Abund	Av.Abund				
1-2yr	0.04	3.55	2.80	2.53	4.60	4.60
F/1K	0.06	3.55	2.78	2.52	4.57	9.17
RF/S	0.10	3.55	2.77	2.42	4.55	13.72
RF/I	4.13	0.33	2.57	2.32	4.23	17.95
<6m	3.99	0.33	2.47	2.06	4.06	22.01
FM/D	3.42	0.00	2.29	2.21	3.77	25.79
F/10	3.58	0.33	2.23	2.00	3.67	29.46
P/E	3.10	0.00	2.07	1.91	3.40	32.86
FA/J	2.99	0.00	2.04	1.80	3.36	36.22
5mm-1cm	3.23	0.33	1.99	1.84	3.28	39.50
FM/SS	2.17	3.60	1.93	1.44	3.17	42.67
18m-2yrs	2.23	3.60	1.90	1.42	3.13	45.80
<6m	2.80	0.00	1.86	1.49	3.07	48.87
1-2cm	1.70	3.55	1.75	1.30	2.88	51.75
FT/D	2.30	3.55	1.73	1.26	2.85	54.60
FT/B	2.73	0.33	1.69	1.50	2.78	57.38
6- 18m	2.34	0.00	1.63	1.42	2.68	60.06

Groups 3.2m & -2m

Average dissimilarity = 57.33

	Group 3.2m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/I	6.38	0.33	3.58	7.01	6.25	6.25
<6m	6.38	0.33	3.58	7.01	6.25	12.50
F/10	5.44	0.33	2.98	3.87	5.20	17.70
5mm-1cm	5.28	0.33	2.89	3.97	5.04	22.74
FT/B	5.16	0.33	2.82	3.91	4.91	27.65
P/E	3.57	0.00	2.17	4.60	3.78	31.43
FM/D	3.52	0.00	2.14	4.37	3.73	35.17
F/1K	0.00	3.55	2.12	4.30	3.70	38.87
RF/S	0.00	3.55	2.12	4.30	3.70	42.57
1-2yr	0.00	3.55	2.12	4.30	3.70	46.27
FA/J	3.15	0.00	1.93	2.96	3.37	49.63
B/SB	3.15	0.00	1.93	2.96	3.37	53.00
2-5mm	3.15	0.00	1.93	2.96	3.37	56.37
<6m	3.15	0.00	1.93	2.96	3.37	59.73
S/5	3.26	0.15	1.86	6.98	3.25	62.98

Groups 2.7m & -2m

Average dissimilarity = 62.27

	Group 2.7m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/1K	0.00	3.55	3.22	3.02	5.17	5.17
RF/S	0.00	3.55	3.22	3.02	5.17	10.34
1-2yr	0.00	3.55	3.22	3.02	5.17	15.51
FT/D	0.47	3.55	2.76	3.05	4.43	19.94
RF/I	3.60	0.33	2.67	3.02	4.28	24.22
FM/SS	0.47	3.60	2.65	4.42	4.26	28.48
18m-2yrs	0.58	3.60	2.51	3.85	4.04	32.51
F/10	3.05	0.33	2.25	3.22	3.62	36.13
6-18m	3.02	0.00	2.22	1.32	3.56	39.69
1-2cm	2.69	3.55	1.95	1.01	3.13	42.82
FA/J	2.49	0.00	1.84	1.31	2.96	45.78
FM/FS	2.45	0.00	1.81	1.31	2.91	48.70
FT/S	2.45	0.00	1.81	1.31	2.91	51.61
LH/SP	2.45	0.00	1.81	1.31	2.91	54.53
B/BV	2.45	0.00	1.81	1.31	2.91	57.44
≥6m	2.45	0.00	1.81	1.31	2.91	60.35

Groups 2.6m & -2m

Average dissimilarity = 36.32

	Group 2.6m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
AM/M	6.09	3.60	2.09	1.68	5.74	5.74
FM/SS	6.06	3.60	2.08	1.67	5.71	11.45
FA/M	6.06	3.60	2.08	1.67	5.71	17.17
B/BB	6.06	3.60	2.08	1.67	5.71	22.88
18m-2yrs	6.06	3.60	2.08	1.67	5.71	28.59
P/I	6.14	3.60	2.05	1.62	5.65	34.25
LH/F	6.10	3.60	2.04	1.60	5.61	39.85
1-2cm	5.98	3.55	2.01	1.63	5.55	45.40
1-2yr	5.94	3.55	2.00	1.61	5.51	50.91
FT/D	5.94	3.55	2.00	1.61	5.50	56.41
F/1K	5.94	3.55	2.00	1.61	5.50	61.91

Groups 0m & -2m

Average dissimilarity = 31.50

	Group 0m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1-2cm	4.89	3.55	1.60	1.83	5.08	5.08
F/1K	4.70	3.55	1.59	1.73	5.04	10.11
P/I	4.90	3.60	1.58	1.77	5.03	15.14
1-2yr	4.73	3.55	1.58	1.75	5.03	20.17
FT/D	4.74	3.55	1.58	1.77	5.02	25.20
RF/S	4.85	3.55	1.58	1.83	5.01	30.20
AM/M	4.88	3.60	1.57	1.77	5.00	35.20
FA/M	4.71	3.60	1.57	1.67	4.99	40.20
LH/F	4.71	3.60	1.57	1.67	4.99	45.19
B/BB	4.71	3.60	1.57	1.67	4.99	50.18
FM/SS	4.70	3.60	1.57	1.67	4.97	55.16
18m-2yrs	4.85	3.60	1.56	1.77	4.94	60.10

Appendix 9.1. Average Similarity :Biomass –weighted

Group 0m

Average similarity: 44.25

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	0.05	3.31	2.17	7.48	7.48
AM/M	0.05	3.18	2.22	7.18	14.66
18m-2yrs	0.05	2.66	1.42	6.02	20.68
LH/F	0.04	2.61	1.89	5.91	26.59
1-2cm	0.05	2.61	1.62	5.91	32.50
B/BB	0.04	2.61	1.90	5.89	38.39
FT/D	0.04	2.43	1.78	5.49	43.88
FA/M	0.04	2.42	1.80	5.47	49.34
S/20	0.04	2.13	1.95	4.81	54.16
RF/S	0.05	2.04	0.98	4.62	58.78
FM/SS	0.03	1.70	0.95	3.85	62.62

Group 3.35m

Average similarity: 42.51

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
LH/F	0.05	3.23	1.99	7.60	7.60
AM/M	0.05	2.81	1.83	6.62	14.21
P/I	0.06	2.79	1.46	6.57	20.78
FA/J	0.05	2.04	1.13	4.80	25.58
RF/I	0.03	2.03	1.48	4.77	30.35
S/5	0.03	1.77	1.35	4.16	34.51
<6m	0.03	1.73	1.24	4.07	38.58
5mm-1cm	0.03	1.68	0.97	3.95	42.53
<6m	0.03	1.64	0.93	3.85	46.38
FT/D	0.03	1.56	1.18	3.67	50.04
B/BB	0.03	1.46	0.98	3.44	53.48
S/10	0.02	1.45	1.83	3.41	56.89
P/E	0.02	1.35	1.14	3.17	60.06



Group 3.1m

Average similarity: 70.86

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
RF/I	0.03	4.35	5.55	6.14	6.14
6- 18m	0.03	4.00	3.69	5.65	11.78
F/10	0.03	4.00	3.69	5.65	17.43
LH/F	0.03	3.90	3.88	5.50	22.93
AM/M	0.03	3.89	5.88	5.50	28.43
<6m	0.03	3.49	15.72	4.92	33.35
B/BB	0.03	3.44	23.05	4.86	38.21
FA/M	0.03	3.40	39.62	4.79	43.01
FM/D	0.03	3.22	2.59	4.54	47.55
FT/M	0.03	2.89	2.08	4.09	51.64
S/20	0.02	2.45	16.56	3.45	55.09
5mm-1cm	0.02	2.40	39.62	3.39	58.48
P/E	0.03	2.40	1.36	3.38	61.86

Group 3.3m

Average similarity: 48.93

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
LH/F	0.07	3.35	1.85	6.84	6.84
P/I	0.07	3.04	2.30	6.22	13.06
AM/M	0.05	2.95	1.87	6.03	19.09
5mm-1cm	0.05	2.35	1.33	4.80	23.88
RF/I	0.04	2.27	1.80	4.64	28.52
B/BB	0.05	2.27	1.77	4.63	33.15
FA/J	0.06	2.22	1.26	4.54	37.69
F/10	0.03	2.09	1.81	4.28	41.97
<6m	0.06	1.91	1.03	3.90	45.86
<6m	0.03	1.85	1.43	3.78	49.64
FA/M	0.03	1.82	1.48	3.71	53.35
FT/B	0.04	1.69	1.32	3.45	56.80
S/5	0.05	1.64	1.44	3.36	60.16

Group 3.2m

Average similarity: 77.04

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
LH/F	0.09	5.03	10.32	6.53	6.53
AM/M	0.09	5.01	10.30	6.50	13.04
5mm-1cm	0.09	4.97	10.40	6.45	19.49
P/I	0.08	4.67	8.48	6.06	25.55
RF/I	0.07	4.09	10.34	5.30	30.85
<6m	0.07	4.09	10.34	5.30	36.16
FA/M	0.07	4.03	10.28	5.23	41.38
B/BB	0.07	4.03	10.28	5.23	46.61
F/10	0.07	4.03	10.28	5.23	51.84
FM/SS	0.07	4.00	10.47	5.19	57.02
FT/B	0.07	4.00	10.47	5.19	62.21

Group 2.7m

Average similarity: 70.39

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
6- 18m	0.08	4.30	4.95	6.10	6.10
RF/I	0.08	4.30	4.95	6.10	12.20
1-2cm	0.08	4.18	5.01	5.94	18.15
P/I	0.09	4.17	5.03	5.93	24.07
FA/J	0.10	4.14	5.03	5.89	29.96
FM/FS	0.08	4.11	5.04	5.84	35.80
FT/S	0.08	4.11	5.04	5.84	41.64
LH/SP	0.08	4.11	5.04	5.84	47.48
B/BV	0.08	4.11	5.04	5.84	53.31
≥6m	0.08	4.11	5.04	5.84	59.15
AM/M	0.08	3.20	4.73	4.55	63.71

Group 2.6m

Average similarity: 45.05

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
P/I	0.08	3.82	2.45	8.49	8.49
LH/F	0.08	3.82	2.45	8.48	16.97
AM/M	0.08	3.02	1.91	6.70	23.67
FM/SS	0.08	3.02	1.91	6.70	30.36
FA/M	0.08	3.02	1.91	6.70	37.06
B/BB	0.08	3.02	1.91	6.70	43.75
18m-2yrs	0.08	3.02	1.91	6.70	50.45
1-2cm	0.08	3.01	1.92	6.68	57.13
FT/D	0.08	3.01	1.93	6.67	63.80

Group -2m

Average similarity: 83.46

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
FM/SS	0.04	6.16	13.01	7.38	7.38
FA/M	0.04	6.16	13.01	7.38	14.76
AM/M	0.04	6.16	13.01	7.38	22.14
P/I	0.04	6.16	13.01	7.38	29.51
LH/F	0.04	6.16	13.01	7.38	36.89
B/BB	0.04	6.16	13.01	7.38	44.27
18m-2yrs	0.04	6.16	13.01	7.38	51.65
FT/D	0.04	5.97	10.12	7.16	58.81
1-2cm	0.04	5.97	10.12	7.16	65.96

## Appendix 9.2 Average Dissimilarity: Biomass-weighted

Groups 0m & 3.35m

Average dissimilarity = 62.93

	Group 0m	Group 3.35m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/S	0.05	0.02	2.51	1.47	3.99	3.99
18m-2yrs	0.05	0.03	2.45	1.61	3.90	7.88
1-2cm	0.05	0.03	2.39	1.51	3.80	11.69
P/I	0.05	0.06	2.33	1.48	3.69	15.38
AM/M	0.05	0.05	2.22	1.51	3.53	18.91
FA/J	0.03	0.05	2.09	1.36	3.33	22.24
1-2yr	0.03	0.01	1.86	1.24	2.95	25.19
S/20	0.04	0.03	1.80	1.43	2.86	28.05
FM/SS	0.03	0.02	1.78	1.24	2.83	30.88
5mm-1cm	0.01	0.03	1.75	1.15	2.78	33.67
LH/F	0.04	0.05	1.74	1.19	2.76	36.43
FT/D	0.04	0.03	1.71	1.36	2.71	39.14
B/BB	0.04	0.03	1.68	1.23	2.67	41.81
FA/M	0.04	0.02	1.67	1.24	2.66	44.47
LH/SP	0.03	0.02	1.64	1.14	2.60	47.07
F/1K	0.03	0.00	1.60	1.03	2.55	49.62
<6m	0.01	0.03	1.55	0.99	2.46	52.08
F/10K	0.03	0.02	1.55	1.01	2.46	54.54
S/5	0.01	0.03	1.47	1.26	2.33	56.87
FM/P	0.02	0.03	1.44	1.30	2.29	59.17
RF/I	0.01	0.03	1.43	1.14	2.27	61.44

Groups 0m & 3.1m

Average dissimilarity = 56.31

	Group 0m	Group 3.1m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/S	0.05	0.01	2.21	1.55	3.92	3.92
18m-2yrs	0.05	0.01	2.14	1.83	3.80	7.72
P/I	0.05	0.02	1.92	1.92	3.41	11.13
RF/I	0.01	0.03	1.87	1.80	3.33	14.46
6- 18m	0.01	0.03	1.84	1.93	3.27	17.73
F/10	0.01	0.03	1.82	1.76	3.24	20.96
1-2cm	0.05	0.02	1.81	1.49	3.22	24.18
1-2yr	0.03	0.00	1.77	1.35	3.14	27.32
AM/M	0.05	0.03	1.76	2.12	3.12	30.44
FT/D	0.04	0.01	1.75	1.66	3.11	33.56
FM/SS	0.03	0.01	1.69	1.73	2.99	36.55
<6m	0.01	0.03	1.66	1.84	2.95	39.50
FA/J	0.03	0.02	1.61	1.72	2.86	42.36
F/1K	0.03	0.00	1.58	1.20	2.80	45.16
P/E	0.00	0.03	1.48	1.50	2.63	47.79
6m - 1yr	0.03	0.01	1.43	1.50	2.55	50.33
B/BB	0.04	0.03	1.37	1.93	2.43	52.77
FA/M	0.04	0.03	1.37	1.78	2.43	55.20
LH/F	0.04	0.03	1.37	1.81	2.43	57.62
F/10K	0.03	0.01	1.34	1.17	2.39	60.01

Groups 3.35m & 3.1m

Average dissimilarity = 52.85

	Group 3.35m	Group 3.1m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
P/I	0.06	0.02	1.97	1.85	3.73	3.73
FA/J	0.05	0.02	1.97	1.43	3.72	7.45
AM/M	0.05	0.03	1.73	1.55	3.28	10.74
6- 18m	0.02	0.03	1.71	1.56	3.24	13.98
F/10	0.03	0.03	1.57	1.36	2.97	16.94
<6m	0.03	0.00	1.56	0.99	2.96	19.90
5mm-1cm	0.03	0.02	1.53	1.40	2.90	22.80
LH/F	0.05	0.03	1.53	1.49	2.89	25.69
FT/M	0.02	0.03	1.51	1.52	2.86	28.55
FA/M	0.02	0.03	1.45	1.37	2.74	31.29
RF/I	0.03	0.03	1.43	1.52	2.71	34.00
B/BB	0.03	0.03	1.42	1.31	2.68	36.68
B/SB	0.02	0.01	1.41	1.07	2.67	39.35
FM/P	0.03	0.01	1.37	1.45	2.59	41.94
18m-2yrs	0.03	0.01	1.37	1.14	2.59	44.52
FM/D	0.02	0.03	1.33	1.41	2.51	47.04
2 - >5cm	0.01	0.01	1.29	1.14	2.44	49.48
<6m	0.03	0.03	1.29	1.41	2.44	51.92
FT/I	0.02	0.01	1.27	1.36	2.40	54.32
1-2cm	0.03	0.02	1.26	1.23	2.38	56.70
P/E	0.02	0.03	1.22	1.28	2.32	59.01
FT/D	0.03	0.01	1.22	1.39	2.31	61.33

Groups 0m & 3.3m

Average dissimilarity = 62.56

	Group 0m	Group 3.3m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<6m	0.01	0.06	2.37	1.26	3.79	3.79
FA/J	0.03	0.06	2.37	1.38	3.78	7.58
5mm-1cm	0.01	0.05	2.25	1.45	3.60	11.18
P/I	0.05	0.07	2.23	1.45	3.56	14.74
LH/F	0.04	0.07	2.21	1.60	3.53	18.27
RF/S	0.05	0.00	2.11	1.33	3.37	21.63
AM/M	0.05	0.05	1.97	1.42	3.15	24.78
18m-2yrs	0.05	0.03	1.92	1.50	3.07	27.85
S/5	0.01	0.05	1.90	1.15	3.04	30.90
1-2cm	0.05	0.01	1.82	1.31	2.92	33.81
FT/B	0.01	0.04	1.82	1.36	2.91	36.72
FT/D	0.04	0.04	1.82	1.36	2.90	39.63
B/BB	0.04	0.05	1.68	1.39	2.68	42.31
B/SB	0.00	0.04	1.66	1.09	2.65	44.96
FM/P	0.02	0.04	1.64	1.36	2.62	47.58
1-2yr	0.03	0.00	1.63	1.19	2.60	50.18
RF/I	0.01	0.04	1.54	1.37	2.46	52.65
FM/SS	0.03	0.03	1.52	1.29	2.43	55.08
<6m	0.01	0.03	1.49	1.35	2.38	57.46
F/10	0.01	0.03	1.48	1.38	2.37	59.82
F/1K	0.03	0.00	1.41	1.03	2.26	62.08

Groups 3.35m & 3.3m

Average dissimilarity = 55.07

	Group 3.35m	Group 3.3m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FA/J	0.05	0.06	2.54	1.39	4.61	4.61
P/I	0.06	0.07	2.39	1.45	4.35	8.95
<6m	0.03	0.06	2.38	1.24	4.31	13.27
LH/F	0.05	0.07	2.23	1.49	4.05	17.32
AM/M	0.05	0.05	2.09	1.40	3.79	21.11
5mm-1cm	0.03	0.05	2.08	1.29	3.78	24.89
FM/P	0.03	0.04	1.85	1.30	3.36	28.25
S/5	0.03	0.05	1.83	1.12	3.33	31.58
B/BB	0.03	0.05	1.80	1.35	3.27	34.86
FT/B	0.02	0.04	1.78	1.28	3.24	38.10
B/SB	0.02	0.04	1.73	1.08	3.13	41.23
FT/D	0.03	0.04	1.72	1.36	3.12	44.35
AM/L	0.02	0.03	1.57	0.80	2.85	47.20
18m-2yrs	0.03	0.03	1.56	1.15	2.84	50.03
FT/I	0.02	0.02	1.41	1.12	2.56	52.60
FA/M	0.02	0.03	1.41	1.18	2.55	55.15
F/10	0.03	0.03	1.40	1.20	2.55	57.70
2 - >5cm	0.01	0.03	1.35	0.64	2.45	60.15

Groups 3.1m & 3.3m

Average dissimilarity = 49.70

	Group 3.1m	Group 3.3m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
<6m	0.00	0.06	2.47	1.27	4.98	4.98
FA/J	0.02	0.06	2.38	1.43	4.80	9.77
P/I	0.02	0.07	2.10	1.42	4.23	14.00
LH/F	0.03	0.07	2.08	1.92	4.19	18.19
5mm-1cm	0.02	0.05	1.76	1.34	3.53	21.72
S/5	0.01	0.05	1.69	1.00	3.39	25.12
FT/D	0.01	0.04	1.69	1.41	3.39	28.51
FM/P	0.01	0.04	1.65	1.46	3.32	31.83
FT/B	0.01	0.04	1.63	1.27	3.28	35.11
B/SB	0.01	0.04	1.63	1.24	3.28	38.39
2 - >5cm	0.01	0.03	1.59	0.90	3.21	41.60
AM/M	0.03	0.05	1.55	1.35	3.13	44.73
B/BB	0.03	0.05	1.43	1.35	2.88	47.61
FM/D	0.03	0.03	1.41	1.23	2.84	50.45
P/E	0.03	0.03	1.26	1.41	2.54	52.99
AM/L	0.01	0.03	1.24	0.65	2.50	55.49
FT/I	0.01	0.02	1.14	1.42	2.29	57.78
6- 18m	0.03	0.02	1.10	1.22	2.22	60.00
FM/SS	0.01	0.03	1.07	1.05	2.15	62.15

Groups 0m & 3.2m

Average dissimilarity = 58.79

	Group 0m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
5mm-1cm	0.01	0.09	3.51	3.22	5.96	5.96
<6m	0.01	0.07	2.71	2.50	4.60	10.57
FT/B	0.01	0.07	2.68	2.40	4.55	15.12
RF/I	0.01	0.07	2.65	2.35	4.51	19.63
F/10	0.01	0.07	2.64	2.39	4.49	24.12
LH/F	0.04	0.09	2.30	1.50	3.92	28.04
AM/M	0.05	0.09	2.07	1.33	3.52	31.56
B/SB	0.00	0.05	1.98	1.58	3.37	34.94
<6m	0.01	0.05	1.81	1.47	3.07	38.01
RF/S	0.05	0.00	1.73	1.40	2.94	40.95
P/I	0.05	0.08	1.72	1.21	2.93	43.88
FM/SS	0.03	0.07	1.71	1.12	2.90	46.78
1-2cm	0.05	0.00	1.65	1.43	2.80	49.58
18m-2yrs	0.05	0.07	1.62	1.21	2.75	52.33
FA/J	0.03	0.05	1.61	1.39	2.74	55.07
FA/M	0.04	0.07	1.61	1.17	2.74	57.81
B/BB	0.04	0.07	1.55	1.14	2.63	60.45

Groups 3.35m & 3.2m

Average dissimilarity = 51.58

	Group 3.35m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
5mm-1cm	0.03	0.09	2.59	1.57	5.01	5.01
AM/M	0.05	0.09	2.42	1.60	4.68	9.70
FM/SS	0.02	0.07	2.35	1.82	4.55	14.25
18m-2yrs	0.03	0.07	2.34	1.80	4.53	18.78
FA/M	0.02	0.07	2.21	1.71	4.28	23.06
FT/B	0.02	0.07	2.20	1.60	4.26	27.32
LH/F	0.05	0.09	2.17	1.39	4.21	31.53
F/10	0.03	0.07	2.11	1.58	4.09	35.62
<6m	0.03	0.07	2.11	1.76	4.09	39.71
B/BB	0.03	0.07	2.04	1.51	3.96	43.66
RF/I	0.03	0.07	2.00	1.64	3.87	47.54
P/I	0.06	0.08	1.99	1.29	3.86	51.40
FA/J	0.05	0.05	1.76	1.45	3.41	54.81
B/SB	0.02	0.05	1.67	1.37	3.24	58.05
<6m	0.03	0.05	1.63	1.36	3.17	61.22

Groups 3.1m & 3.2m

Average dissimilarity = 52.22

	Group 3.1m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
5mm-1cm	0.02	0.09	3.02	6.60	5.77	5.77
FM/SS	0.01	0.07	2.67	3.96	5.11	10.89
FT/B	0.01	0.07	2.64	3.86	5.06	15.95
P/I	0.02	0.08	2.56	5.35	4.90	20.85
18m-2yrs	0.01	0.07	2.53	4.06	4.85	25.70
LH/F	0.03	0.09	2.50	4.31	4.78	30.48
AM/M	0.03	0.09	2.49	4.39	4.76	35.24
<6m	0.00	0.05	1.97	1.57	3.77	39.01
<6m	0.03	0.07	1.79	2.78	3.43	42.44
FA/M	0.03	0.07	1.79	2.71	3.42	45.86
B/BB	0.03	0.07	1.77	2.70	3.39	49.25
B/SB	0.01	0.05	1.73	1.45	3.31	52.56
FA/J	0.02	0.05	1.60	1.36	3.06	55.61
F/10	0.03	0.07	1.59	2.42	3.04	58.65
RF/I	0.03	0.07	1.56	2.55	3.00	61.65

Groups 3.3m & 3.2m

Average dissimilarity = 42.65

	Group 3.3m	Group 3.2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
5mm-1cm	0.05	0.09	1.98	1.37	4.65	4.65
<6m	0.06	0.05	1.91	1.48	4.47	9.12
AM/M	0.05	0.09	1.86	1.40	4.35	13.47
18m-2yrs	0.03	0.07	1.85	1.60	4.34	17.81
FA/J	0.06	0.05	1.85	1.46	4.33	22.13
FM/SS	0.03	0.07	1.81	1.58	4.25	26.38
P/I	0.07	0.08	1.80	1.44	4.22	30.60
LH/F	0.07	0.09	1.77	1.19	4.14	34.74
FT/B	0.04	0.07	1.76	1.50	4.12	38.86
<6m	0.03	0.07	1.62	1.46	3.80	42.67
FA/M	0.03	0.07	1.61	1.44	3.78	46.45
B/BB	0.05	0.07	1.58	1.39	3.70	50.15
F/10	0.03	0.07	1.55	1.51	3.63	53.78
B/SB	0.04	0.05	1.53	1.35	3.59	57.38
RF/I	0.04	0.07	1.52	1.51	3.56	60.93

Groups 0m & 2.7m

Average dissimilarity = 66.01

	Group 0m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
≥6m	0.00	0.08	3.07	3.02	4.65	4.65
6- 18m	0.01	0.08	3.01	3.11	4.56	9.21
B/BV	0.01	0.08	2.91	2.90	4.41	13.62
RF/I	0.01	0.08	2.89	2.66	4.38	18.00
FM/FS	0.01	0.08	2.83	2.45	4.28	22.28
FT/S	0.01	0.08	2.83	2.45	4.28	26.56
FA/J	0.03	0.10	2.70	1.62	4.09	30.65
LH/SP	0.03	0.08	2.30	1.47	3.49	34.14
F/100	0.00	0.06	2.17	3.02	3.29	37.43
F/10	0.01	0.06	2.01	2.37	3.05	40.48
AM/L	0.01	0.06	1.93	2.47	2.92	43.40
P/I	0.05	0.09	1.89	1.34	2.87	46.26
1-2cm	0.05	0.08	1.80	1.31	2.73	48.99
18m-2yrs	0.05	0.00	1.78	1.68	2.70	51.69
AM/M	0.05	0.08	1.78	1.44	2.70	54.38
RF/S	0.05	0.00	1.62	1.35	2.45	56.83
LH/F	0.04	0.05	1.51	1.49	2.29	59.12
5mm-1cm	0.01	0.05	1.49	1.06	2.26	61.38

Groups 3.35m & 2.7m

Average dissimilarity = 61.68

	Group 3.35m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
LH/SP	0.02	0.08	2.96	2.68	4.80	4.80
≥6m	0.01	0.08	2.94	2.53	4.77	9.57
FT/S	0.01	0.08	2.89	2.39	4.69	14.25
FM/FS	0.01	0.08	2.89	2.39	4.68	18.94
1-2cm	0.03	0.08	2.87	2.53	4.65	23.59
B/BV	0.01	0.08	2.81	2.26	4.56	28.15
6- 18m	0.02	0.08	2.78	2.28	4.51	32.66
FA/J	0.05	0.10	2.71	1.76	4.40	37.05
RF/I	0.03	0.08	2.22	1.76	3.59	40.64
P/I	0.06	0.09	2.14	1.41	3.47	44.11
AM/M	0.05	0.08	2.02	1.62	3.27	47.38
F/100	0.01	0.06	1.90	2.52	3.08	50.46
AM/L	0.02	0.06	1.82	1.80	2.95	53.41
5mm-1cm	0.03	0.05	1.64	1.32	2.66	56.07
<6m	0.03	0.04	1.63	1.16	2.64	58.71
LH/F	0.05	0.05	1.59	1.46	2.58	61.29

Groups 3.1m & 2.7m

Average dissimilarity = 59.77

	Group 3.1m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
≥6m	0.00	0.08	3.31	5.89	5.55	5.55
FA/J	0.02	0.10	3.27	3.57	5.46	11.01
B/BV	0.00	0.08	3.21	5.61	5.38	16.39
FM/FS	0.00	0.08	3.16	5.58	5.29	21.67
FT/S	0.00	0.08	3.16	5.58	5.29	26.96
LH/SP	0.01	0.08	2.76	5.59	4.61	31.57
P/I	0.02	0.09	2.73	5.36	4.57	36.14
1-2cm	0.02	0.08	2.58	5.50	4.32	40.46
F/100	0.00	0.06	2.24	5.38	3.75	44.21
AM/L	0.01	0.06	2.07	4.93	3.46	47.66
6- 18m	0.03	0.08	1.98	4.40	3.31	50.97
RF/I	0.03	0.08	1.90	4.69	3.18	54.15
AM/M	0.03	0.08	1.82	1.75	3.05	57.20
B/SB	0.01	0.04	1.46	1.01	2.45	59.65
<6m	0.00	0.04	1.35	0.81	2.26	61.91

Groups 3.3m & 2.7m

Average dissimilarity = 58.81

	Group 3.3m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FM/FS	0.00	0.08	2.81	3.33	4.78	4.78
FT/S	0.00	0.08	2.81	3.33	4.78	9.56
≥6m	0.00	0.08	2.80	3.28	4.76	14.32
LH/SP	0.00	0.08	2.78	3.18	4.73	19.05
B/BV	0.02	0.08	2.62	2.35	4.45	23.50
1-2cm	0.01	0.08	2.54	2.97	4.31	27.81
6- 18m	0.02	0.08	2.39	2.67	4.06	31.87
FA/J	0.06	0.10	2.33	1.54	3.96	35.83
AM/L	0.03	0.06	2.14	3.13	3.65	39.47
<6m	0.06	0.04	1.99	1.29	3.39	42.86
P/I	0.07	0.09	1.89	1.50	3.22	46.08
F/100	0.01	0.06	1.83	3.41	3.11	49.19
LH/F	0.07	0.05	1.80	1.57	3.05	52.25
RF/I	0.04	0.08	1.75	1.72	2.98	55.22
5mm-1cm	0.05	0.05	1.69	1.40	2.88	58.10
AM/M	0.05	0.08	1.69	1.66	2.87	60.98

Groups 3.2m & 2.7m

Average dissimilarity = 52.90

	Group 3.2m	Group 2.7m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FM/FS	0.00	0.08	2.52	5.86	4.77	4.77
FT/S	0.00	0.08	2.52	5.86	4.77	9.54
LH/SP	0.00	0.08	2.52	5.86	4.77	14.30
B/BV	0.00	0.08	2.52	5.86	4.77	19.07
≥6m	0.00	0.08	2.52	5.86	4.77	23.84
1-2cm	0.00	0.08	2.40	5.08	4.54	28.38
6- 18m	0.01	0.08	2.30	4.24	4.34	32.72
FM/SS	0.07	0.00	2.19	3.71	4.13	36.85
FT/B	0.07	0.00	2.19	3.71	4.13	40.98
18m-2yrs	0.07	0.00	2.19	3.71	4.13	45.11
5mm-1cm	0.09	0.05	2.09	2.09	3.95	49.06
LH/F	0.09	0.05	1.93	2.10	3.65	52.71
AM/L	0.00	0.06	1.78	5.86	3.37	56.08
FA/J	0.05	0.10	1.77	1.69	3.35	59.43
<6m	0.07	0.02	1.71	3.67	3.23	62.66



Groups 0m & 2.6m

Average dissimilarity = 56.17

	Group 0m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
F/1K	0.03	0.08	2.76	1.70	4.92	4.92
1-2yr	0.03	0.08	2.69	1.66	4.78	9.70
FM/SS	0.03	0.08	2.68	1.67	4.77	14.47
RF/S	0.05	0.08	2.66	1.56	4.73	19.20
18m-2yrs	0.05	0.08	2.57	1.53	4.58	23.78
1-2cm	0.05	0.08	2.52	1.50	4.49	28.28
LH/F	0.04	0.08	2.51	1.51	4.47	32.74
FA/M	0.04	0.08	2.49	1.62	4.44	37.18
FT/D	0.04	0.08	2.48	1.57	4.41	41.59
P/I	0.05	0.08	2.48	1.47	4.41	46.00
AM/M	0.05	0.08	2.47	1.53	4.40	50.40
B/BB	0.04	0.08	2.46	1.61	4.37	54.77
S/20	0.04	0.04	1.64	1.56	2.92	57.70
FA/J	0.03	0.01	1.56	1.20	2.78	60.48

Groups 3.35m & 2.6m

Average dissimilarity = 67.16

	Group 3.35m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/S	0.02	0.08	3.34	2.02	4.98	4.98
F/1K	0.00	0.08	3.32	1.96	4.94	9.92
1-2yr	0.01	0.08	3.27	1.90	4.86	14.78
1-2cm	0.03	0.08	3.06	1.73	4.55	19.33
18m-2yrs	0.03	0.08	2.96	1.74	4.40	23.74
FM/SS	0.02	0.08	2.90	1.65	4.31	28.05
P/I	0.06	0.08	2.75	1.55	4.09	32.14
FA/M	0.02	0.08	2.71	1.50	4.04	36.18
B/BB	0.03	0.08	2.67	1.51	3.97	40.15
FT/D	0.03	0.08	2.64	1.58	3.93	44.08
AM/M	0.05	0.08	2.62	1.56	3.89	47.98
LH/F	0.05	0.08	2.51	1.48	3.74	51.72
FA/J	0.05	0.01	1.90	1.15	2.83	54.55
S/20	0.03	0.04	1.67	1.52	2.49	57.04
<6m	0.03	0.01	1.66	1.07	2.47	59.51
5mm-1cm	0.03	0.01	1.51	0.99	2.25	61.76

Groups 3.1m & 2.6m

Average dissimilarity = 65.73

	Group 3.1m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1-2yr	0.00	0.08	3.24	2.03	4.92	4.92
F/1K	0.00	0.08	3.21	1.98	4.89	9.81
RF/S	0.01	0.08	3.01	1.77	4.59	14.39
FM/SS	0.01	0.08	2.85	1.59	4.34	18.73
FT/D	0.01	0.08	2.80	1.57	4.27	22.99
P/I	0.02	0.08	2.76	2.04	4.20	27.20
18m-2yrs	0.01	0.08	2.67	1.47	4.07	31.27
LH/F	0.03	0.08	2.53	2.32	3.84	35.11
1-2cm	0.02	0.08	2.43	1.33	3.70	38.81
AM/M	0.03	0.08	2.37	1.86	3.61	42.42
B/BB	0.03	0.08	2.35	1.64	3.57	45.99
FA/M	0.03	0.08	2.35	1.62	3.57	49.56
6- 18m	0.03	0.00	1.85	1.69	2.82	52.38
FM/D	0.03	0.00	1.80	1.87	2.73	55.11
RF/I	0.03	0.01	1.76	1.46	2.68	57.79
F/10	0.03	0.01	1.74	1.48	2.64	60.43

Groups 3.3m & 2.6m

Average dissimilarity = 64.71

	Group 3.3m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1-2yr	0.00	0.08	3.01	1.88	4.65	4.65
RF/S	0.00	0.08	2.99	1.86	4.63	9.28
F/1K	0.00	0.08	2.99	1.85	4.62	13.89
1-2cm	0.01	0.08	2.53	1.51	3.91	17.80
FT/D	0.04	0.08	2.45	1.48	3.79	21.59
P/I	0.07	0.08	2.45	1.51	3.79	25.38
18m-2yrs	0.03	0.08	2.40	1.53	3.70	29.08
LH/F	0.07	0.08	2.38	1.49	3.68	32.77
FM/SS	0.03	0.08	2.35	1.48	3.63	36.40
<6m	0.06	0.01	2.29	1.28	3.54	39.94
B/BB	0.05	0.08	2.29	1.49	3.54	43.47
AM/M	0.05	0.08	2.26	1.43	3.49	46.96
FA/J	0.06	0.01	2.25	1.27	3.48	50.44
FA/M	0.03	0.08	2.22	1.45	3.43	53.87
5mm-1cm	0.05	0.01	2.02	1.25	3.12	56.99
S/5	0.05	0.01	1.80	1.10	2.78	59.77
B/SB	0.04	0.01	1.62	1.14	2.50	62.27

Groups 3.2m & 2.6m

Average dissimilarity = 57.81

	Group 3.2m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
5mm-1cm	0.09	0.01	3.28	2.77	5.67	5.67
<6m	0.07	0.01	2.60	2.33	4.50	10.18
F/10	0.07	0.01	2.55	2.25	4.40	14.58
RF/I	0.07	0.01	2.54	2.16	4.39	18.97
FT/B	0.07	0.01	2.54	2.32	4.39	23.36
1-2yr	0.00	0.08	2.52	1.87	4.37	27.73
F/1K	0.00	0.08	2.52	1.88	4.36	32.09
RF/S	0.00	0.08	2.52	1.88	4.36	36.46
1-2cm	0.00	0.08	2.35	1.66	4.06	40.52
AM/M	0.09	0.08	2.06	1.43	3.56	44.08
FA/M	0.07	0.08	1.84	1.73	3.18	47.26
B/BB	0.07	0.08	1.84	1.73	3.18	50.45
FT/D	0.04	0.08	1.84	1.52	3.18	53.62
FM/SS	0.07	0.08	1.83	1.76	3.17	56.80
18m-2yrs	0.07	0.08	1.83	1.76	3.17	59.97
LH/F	0.09	0.08	1.77	1.26	3.06	63.03

Groups 2.7m & 2.6m

Average dissimilarity = 69.87

	Group 2.7m	Group 2.6m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FA/J	0.10	0.01	2.94	2.16	4.21	4.21
6- 18m	0.08	0.00	2.90	2.65	4.14	8.36
FM/FS	0.08	0.00	2.82	2.65	4.03	12.39
FT/S	0.08	0.00	2.82	2.65	4.03	16.42
B/BV	0.08	0.00	2.82	2.65	4.03	20.45
≥6m	0.08	0.00	2.82	2.65	4.03	24.48
LH/SP	0.08	0.00	2.81	2.61	4.01	28.49
RF/I	0.08	0.01	2.76	2.39	3.95	32.44
FM/SS	0.00	0.08	2.38	1.77	3.40	35.85
18m-2yrs	0.00	0.08	2.38	1.77	3.40	39.25
1-2yr	0.00	0.08	2.37	1.77	3.39	42.64
F/1K	0.00	0.08	2.37	1.77	3.39	46.03
RF/S	0.00	0.08	2.37	1.77	3.39	49.42
FT/D	0.03	0.08	2.10	1.51	3.00	52.43
LH/F	0.05	0.08	2.03	1.63	2.90	55.33
F/100	0.06	0.00	1.99	2.65	2.85	58.18
AM/M	0.08	0.08	1.97	1.84	2.82	61.00

Groups 0m & -2m

Average dissimilarity = 48.27

	Group 0m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/S	0.05	0.04	2.35	1.92	4.86	4.86
1-2cm	0.05	0.04	2.16	2.04	4.47	9.33
18m-2yrs	0.05	0.04	2.11	1.52	4.38	13.71
F/1K	0.03	0.04	2.09	1.29	4.33	18.04
1-2yr	0.03	0.04	2.07	1.40	4.29	22.33
P/I	0.05	0.04	2.03	1.91	4.21	26.54
AM/M	0.05	0.04	1.97	1.73	4.07	30.61
FA/J	0.03	0.00	1.89	1.43	3.91	34.52
FM/SS	0.03	0.04	1.86	1.07	3.85	38.37
FT/D	0.04	0.04	1.80	1.40	3.72	42.09
FA/M	0.04	0.04	1.62	1.16	3.36	45.45
LH/F	0.04	0.04	1.60	1.21	3.31	48.76
B/BB	0.04	0.04	1.59	1.20	3.29	52.05
LH/SP	0.03	0.00	1.53	1.05	3.16	55.21
F/10K	0.03	0.00	1.45	0.97	3.01	58.22
S/20	0.04	0.02	1.45	1.41	3.00	61.22

Groups 3.35m & -2m

Average dissimilarity = 65.01

	Group 3.35m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
RF/S	0.02	0.04	3.14	2.43	4.83	4.83
F/1K	0.00	0.04	3.04	2.17	4.67	9.50
1-2yr	0.01	0.04	3.00	2.12	4.62	14.11
1-2cm	0.03	0.04	2.72	1.84	4.19	18.30
18m-2yrs	0.03	0.04	2.51	1.59	3.86	22.16
FA/J	0.05	0.00	2.44	1.41	3.76	25.92
FM/SS	0.02	0.04	2.44	1.58	3.75	29.67
FA/M	0.02	0.04	2.17	1.39	3.34	33.01
P/I	0.06	0.04	2.16	1.34	3.33	36.34
AM/M	0.05	0.04	2.09	1.51	3.22	39.56
FT/D	0.03	0.04	2.02	1.46	3.11	42.67
B/BB	0.03	0.04	1.99	1.19	3.07	45.73
5mm-1cm	0.03	0.00	1.94	1.22	2.98	48.72
<6m	0.03	0.00	1.92	1.12	2.95	51.66
LH/F	0.05	0.04	1.80	1.33	2.77	54.43
S/5	0.03	0.00	1.72	1.39	2.65	57.08
RF/I	0.03	0.00	1.69	1.35	2.61	59.69
B/SB	0.02	0.00	1.59	0.95	2.44	62.13

Groups 3.1m & -2m

Average dissimilarity = 56.95

	Group 3.1m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
1-2yr	0.00	0.04	2.86	5.85	5.01	5.01
F/1K	0.00	0.04	2.83	4.75	4.97	9.98
RF/S	0.01	0.04	2.57	4.08	4.52	14.50
6- 18m	0.03	0.00	2.57	4.69	4.51	19.01
RF/I	0.03	0.00	2.43	4.65	4.26	23.27
FM/SS	0.01	0.04	2.39	3.71	4.19	27.46
F/10	0.03	0.00	2.33	3.63	4.09	31.55
FM/D	0.03	0.00	2.30	3.26	4.04	35.59
FT/D	0.01	0.04	2.25	2.54	3.94	39.53
18m-2yrs	0.01	0.04	2.16	4.26	3.80	43.33
FT/M	0.03	0.00	2.08	2.93	3.65	46.99
<6m	0.03	0.00	2.05	3.10	3.60	50.59
P/E	0.03	0.00	2.01	2.12	3.53	54.12
1-2cm	0.02	0.04	1.70	2.95	2.99	57.11
P/I	0.02	0.04	1.41	2.06	2.47	59.58
5mm-1cm	0.02	0.00	1.29	2.59	2.26	61.84

Groups 3.3m & -2m

Average dissimilarity = 63.63

	Group 3.3m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FA/J	0.06	0.00	2.97	1.54	4.67	4.67
<6m	0.06	0.00	2.79	1.35	4.38	9.05
1-2yr	0.00	0.04	2.65	2.26	4.17	13.22
RF/S	0.00	0.04	2.64	2.21	4.14	17.36
F/1K	0.00	0.04	2.63	2.19	4.13	21.49
5mm-1cm	0.05	0.00	2.54	1.57	3.99	25.49
LH/F	0.07	0.04	2.24	2.00	3.52	29.01
S/5	0.05	0.00	2.20	1.24	3.46	32.47
P/I	0.07	0.04	2.09	1.44	3.28	35.75
FT/D	0.04	0.04	2.08	1.51	3.26	39.01
FT/B	0.04	0.00	1.98	1.37	3.10	42.12
1-2cm	0.01	0.04	1.93	1.59	3.04	45.15
B/SB	0.04	0.00	1.91	1.19	3.00	48.15
RF/I	0.04	0.00	1.90	1.80	2.99	51.14
FM/P	0.04	0.00	1.88	1.23	2.96	54.10
F/10	0.03	0.00	1.80	1.72	2.82	56.92
18m-2yrs	0.03	0.04	1.78	1.56	2.80	59.72
AM/M	0.05	0.04	1.78	1.57	2.79	62.51

Groups 3.2m & -2m

Average dissimilarity = 59.55

	Group 3.2m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
5mm-1cm	0.09	0.00	4.07	11.30	6.83	6.83
RF/I	0.07	0.00	3.25	4.60	5.46	12.29
<6m	0.07	0.00	3.25	4.60	5.46	17.75
F/10	0.07	0.00	3.21	4.53	5.40	23.15
FT/B	0.07	0.00	3.17	4.52	5.33	28.47
FA/J	0.05	0.00	2.27	1.76	3.81	32.29
B/SB	0.05	0.00	2.27	1.76	3.81	36.10
<6m	0.05	0.00	2.27	1.76	3.81	39.91
LH/F	0.09	0.04	2.27	3.17	3.81	43.72
AM/M	0.09	0.04	2.25	3.13	3.79	47.51
F/1K	0.00	0.04	2.00	4.72	3.36	50.86
RF/S	0.00	0.04	2.00	4.72	3.36	54.22
1-2yr	0.00	0.04	2.00	4.72	3.36	57.58
S/5	0.04	0.00	1.93	10.19	3.24	60.82

Groups 2.7m & -2m

Average dissimilarity = 74.53

	Group 2.7m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
FA/J	0.10	0.00	4.20	8.07	5.64	5.64
6- 18m	0.08	0.00	3.65	5.39	4.89	10.53
FM/FS	0.08	0.00	3.55	5.44	4.76	15.29
FT/S	0.08	0.00	3.55	5.44	4.76	20.05
LH/SP	0.08	0.00	3.55	5.44	4.76	24.81
B/BV	0.08	0.00	3.55	5.44	4.76	29.57
≥6m	0.08	0.00	3.55	5.44	4.76	34.33
RF/I	0.08	0.00	3.49	5.33	4.68	39.00
AM/L	0.06	0.00	2.51	5.44	3.37	42.37
F/100	0.06	0.00	2.51	5.44	3.37	45.73
F/10	0.06	0.00	2.48	5.03	3.33	49.07
P/I	0.09	0.04	2.07	2.99	2.77	51.84
FM/SS	0.00	0.04	1.87	3.54	2.51	54.35
18m-2yrs	0.00	0.04	1.87	3.54	2.51	56.87
F/1K	0.00	0.04	1.85	3.42	2.48	59.35
RF/S	0.00	0.04	1.85	3.42	2.48	61.82

Groups 2.6m & -2m

Average dissimilarity = 45.92

	Group 2.6m	Group -2m				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
AM/M	0.08	0.04	2.66	2.60	5.79	5.79
FM/SS	0.08	0.04	2.65	2.61	5.78	11.57
FA/M	0.08	0.04	2.65	2.61	5.78	17.35
B/BB	0.08	0.04	2.65	2.61	5.78	23.13
18m-2yrs	0.08	0.04	2.65	2.61	5.78	28.91
1-2cm	0.08	0.04	2.64	2.50	5.75	34.66
1-2yr	0.08	0.04	2.63	2.50	5.74	40.39
FT/D	0.08	0.04	2.63	2.50	5.73	46.13
F/1K	0.08	0.04	2.63	2.51	5.73	51.86
RF/S	0.08	0.04	2.63	2.51	5.73	57.59
P/I	0.08	0.04	2.59	2.29	5.65	63.24