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On the Benthic Invertebrate Megafauna at the Mid-Atlantic Ridge, in the Vicinity of the Charlie-Gibbs Fracture Zone

by

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Declaration of Authorship

I, Claudia Hannelore S. Alt, declare that this thesis titled, ‘ON THE BENTHIC INVERTEBRATE MEGAFAUNA AT THE MID-ATLANTIC RIDGE, IN THE VICINITY OF THE CHARLIE-GIBBS FRACTURE ZONE’ and the work presented in it are my own. I confirm that:

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"It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest sources of so much in life that makes life worth living."

Sir David Attenborough

"A scientist in his laboratory is not a mere technician: he is also a child confronting natural phenomena that impress him as though they were fairy tales."

Marie Curie

UNIVERSITY OF SOUTHAMPTON

Abstract

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Little is known about the fauna that inhabits non-chemosynthetic environments associated with mid-ocean ridges. This thesis investigates a ridge and fracture zone system to assess its influence as a barrier to faunal dispersal, and as a unique bathyal habitat. It also describes the ecology of megabenthic communities inhabiting a ridge. Sites were chosen on the Mid-Atlantic Ridge in the vicinity of the Charlie-Gibbs Fracture Zone, at a target depth of 2,500 m. Four superstations were chosen north and south of the Fracture Zone, on either side of the ridge. Different productivity levels and hydrographic features were characteristic for the northern and southern sites. In order to characterise the benthic megafauna 50 ha were trawled and 32,000 m^2 of seafloor were sampled with HD video footage, targeting both flat and 10 ° sloped habitats. Holothurians were the most abundant megafauna. In order to assess their evolutionary relationship 43 holothurian specimens were genetically studied by modelling five of their genes (16S, 18S, 28S, COI, H3) in a phylogenetic analysis. All four sites exhibited noticeably different faunal characteristics. The biomass was highest at the SE, and lowest at the NW site. Body sizes differed between sites for most taxa, that were sufficient in numbers to be compared between sites, most likely as a result of different adaptations to food supply. Differences in species richness were observed between the sampling methods, with the highest richness at the SE site in trawl samples, and highest at the NW and SW sites in the video survey. Species densities were highest at the northern sites with both methods. Differences in diversity were also observed, with trawl samples providing a higher taxonomic resolution than the video survey and showing highest diversity at the SE site and lowest at the NE site. Community composition was significantly different between sites. Variations in the composition of megabenthic assemblages were observed between flat and 10 ° sloped habitats, although the effect of slope appears to be site dependent. The genetic analyses revealed a close relationship between individuals from different families. The extent to which the Ridge acts as a faunal barrier was unclear as the southern sites lacked an obvious difference in community composition. Faunal differences to the north and south of the Fracture Zone, however, suggest that this feature is a barrier to dispersal. The contrasting megafaunal assemblages of the sites probably reflect a combination of environmental drivers including sediment type, phytodetrital quality, hydrography, and habitat complexity.

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TO MY MOM,
for raising me single handedly, while in full time employment,
for believing in me when others did not,
and for always being there.

FÜR MEINE MOM,
dafür, dass du mich alleine grossgezogen hast, während du Vollzeit gearbeitet hast, dafür dass du immer an mich geglaubt hast, wenn andere es nicht taten und dafür dass du immer für mich da bist.

Chapter 1

Introduction

1.1 A Selective Short History of Deep-Sea Research

Over the last century our understanding of the deep sea has improved greatly. Our current picture of the deep-sea ecosystem is the sum of successful research cruises, bright scientific minds and lots of luck. In 1818 Sir John Ross retrieved a large basket star (*Astrophyton*) on a sounding line from a depth of about 800 fathoms (about 1,600 m) (Menzies, 1965; Gage and Tyler, 1991). On voyages of the *Erebus* and *Terror* to the Southern Ocean James Clark Ross and J. Hooker collected animals from a water depth of 1,800 m, between 1839 and 1843 (Gage and Tyler, 1991). A series of expeditions to investigate the deep sea followed these early voyages, that began in the 1860s and 1870s. These include the H.M.S. *Lightning* in 1868, the H.M.S. *Porcupine* in 1865, and the H.M.S. *Blake* in 1870 (Menzies, 1965). The most important campaign, however, was undoubtedly the H.M.S. *Challenger* expedition, which circumnavigated the globe between 1872 and 1876. The *Challenger* expedition was the first of its kind, and set out with the sole aim to investigate the deep sea on a global scale (Gage and Tyler, 1991; Rice, 2010). The initial aim of this expedition was simply to discover how much life existed in the deep sea and how widely it was distributed. Apart from describing and cataloguing many new species, an understanding of the nutrition of deep-sea animals and their dependence on debris from the euphotic zone was also developed during this work (Anderson and Rice, 2006). In many respects, the *Challenger* expedition laid the foundations for the field of oceanography we know today (Gage and Tyler, 1991). Charles Wyville Thomson, the leading scientist on the H.M.S. *Challenger*, concluded that all main animal groups have representatives in the deep sea and that animal abundances decrease with increasing water depth (Tyler et al., 2001). He also suggested that animals became smaller in size with increasing depth, while recognising exceptions to this rule (Tyler et al., 2001). In general, his assumptions have held true, although we now know that these patterns are complex and can vary between different species and regions (Tyler et al., 2001). The *Challenger* expedition was followed by a series of major national campaigns, including the Danish round-the-world expedition *Galathea* (1950-1952), which furthered our understanding of the deep sea with its detailed taxonomic accounts. At a similar time, many Russian expeditions were commissioned (Sokolova, 2000); their work contributing greatly to our understanding of faunal distributions (Gage and Tyler, 1991).

The 1960s and 1970s saw major advances in deep-sea research led by American pioneers, focussing on deep-sea biodiversity (Hessler and Sanders, 1967; Sanders, 1968; Gage and Tyler, 1991). The use of newly developed epibenthic sledges and quantitative sampling gear, such as box corers, revealed, for the first time, the enormous diversity of smaller-sized benthic animals, meiofauna and macrofauna (Hessler and Sanders, 1967). Deep-sea research also benefitted from the development of submersibles and *in situ* digital photography (Tyler et al., 2001). Multidisciplinary approaches began in the 1970s and 1980s (Gage and Tyler, 1991) and were promoted by European funding and national programmes (Rice et al., 1994; Billett and Rice, 2001). These collaborations furthered our understanding of ecosystem functionality through simultaneously monitoring physical oceanographic conditions, particle fluxes, topography and fauna. One such project, ECOMAR (2006-2012), was a UK based multidisciplinary project with international collaborators that investigated the ecosystem of the Mid-Atlantic Ridge (Boyle, 2009). This thesis is based on research conducted within the ECOMAR framework.

1.2 Megafauna in the Deep Sea

Megafauna are loosely defined by size, either as large organisms that are easily visible in video footage and photographs, or as organisms that are > 1 cm in size (Dundas and Przeslawski, 2009; Wei et al., 2010). However, definition by size creates considerable ambiguity. Many juveniles are significantly smaller than their adult counterparts, and belong to the macrofauna classification, while other organisms, traditionally considered to be meiofauna, can grow to up to 10 cm in diameter, e.g. foraminifera of the class Xenophyophorea (Hughes and Gooday, 2004). Megafauna are divided further into subgroups; the term “pelagic” describing those individuals inhabiting the water column, “epipelagic” organisms immediately above the sediment, “epibenthic” organisms that reside at the sediment-water interface, and “infaunal” describes organisms within marine sediments, (Gage and Tyler, 1991).

1.2.1 Body Size

Body size is an important ecological parameter that is linked to faunal aspects such as metabolic rate (Brown et al., 2004), density (Ruhl, 2007), diversity (Rex and Etter, 1998), and community composition (Billett et al., 2001). In principle, the marine environment can support large body sizes as water is around 800 times denser than air (Humphries, 2007). However, there is a general trend of decreasing body size with increasing water depth in invertebrates (Rex et al., 2006), with the exception of gigantism in certain groups (Moran and Woods, 2012). There are several theories that explain the observed size-decrease in deep-sea organisms, most notable are the 'Size-Structure Hypothesis' by Thiel (1975) and the 'Optimal Size Model' by Sebens (1982). In the 'Size-Structure Hypothesis' it is recognised that larger body size has metabolic advantages as energy is used more efficiently. Nevertheless, a larger body requires a greater sustaining food resource. An energetic investment into larger sizes also has the likely trade-off of later reproductive development. Such an adaptation in low standing stock environments, can push the population below its effective population size (Thiel, 1975). Therefore, according to the 'Size-Structure Hypothesis' the small body size found in many deep-sea invertebrate species represents a balance between energy availability, metabolic rate, and reproductive success that is linked to population density (Thiel, 1975). The 'Optimal Size Model' is similar to the 'Size-Structure Hypothesis' involving a trade-off between energy cost in foraging, growth, reproduction, and the decrease in energy availability with greater depth (Sebens, 1982). However, an equilibrium between energy availability and usage is achieved by maximising the offset between energetic cost and energetic intake, with regard to the mass of an individual specimen. It is, therefore, predicted in the 'Optimal Size Model' that the optimum organism size will increase with habitat suitability (Sebens, 1982).

Further published data support a link between body size and shape not only in relation to food availability, and also water current regimes (Hildrew et al., 2007; Booth et al., 2008), where the orientation of fauna give information regarding the strength and direction of the current flow (Koehl, 1984). Various studies highlight the taxa-specificness of body size patterns, suggesting that a fit-all body size pattern in the deep sea may not exist. For example, it is generally reported that pelagic megafauna possess a larger size range than their benthic counterparts (MacPherson, 2003). Inflated body size has been observed in gastropods (Rex and Etter, 1998) that suggests advantages in resource competition and increased fecundity (Atkins and Hirst, 2007). However, a large body presents problems where strong currents cause dislodgment (i.e. large suspension feeders), in particular when current movements change unpredictably (Humphries, 2007).

An increase in the density of small individuals as a response to increased organic matter flux has been observed in ophiuroids at the Pacific Station M (Booth et al., 2008). Similar responses have also been reported for other benthic megafauna in the Pacific (Ruhl, 2007) and the Atlantic Oceans (Billett et al., 2001). It has been suggested that a smaller body size might reflect a limited supply of nutrients and the need to maintain a level of population density for successful reproduction (Sebens, 1982; Wei et al., 2010). However, a contradictory interpretation was made by Rex & Etter (1998) relating larger body size to decreased density and diversity, suggesting that limited nutrient availability supports fewer large animals rather than promoting numbers of smaller specimens (Rex and Etter, 1998). Two hypotheses have been put forward for polychaetes: the 'Juvenile Recruitment Hypothesis' and the 'Allometric Plasticity Hypothesis' (Paterson et al., 2006). The 'Juvenile Recruitment Hypothesis' suggests that smaller organism sizes can be observed in areas of seasonal or periodic phytodetrital flux, because new recruits are being attracted. The 'Allometric Plasticity Hypothesis' meanwhile, explains larger sizes in areas of little organic matter flux by delayed reproduction and an energy investment into larger body sizes, associating larger organism size with starvation mode (Paterson et al., 2006). This debate highlights our lack of understanding of the deep-sea environment and its driving forces. Body size can also be related to fecundity (White et al., 2007) and it has been suggested that size-frequency distributions can yield information about migration and recruitment of mobile fauna (Ruhl, 2007). While some species show seasonal growth, others demonstrate great intra-specific variability in growth rate between individuals measured over similar time periods, e.g. regular echinoids (Gage, 1992). Both of these cases, however, are considered an adaption to food availability in the deep sea.

1.2.2 Biomass

It was assumed initially that the deep sea could not host large megafaunal biomass, owing to their larger sizes and energy demands, particularly in comparison to meio- and macrofaunal biomass (Haedrich and Rowe, 1977). However, one of the first studies measuring and comparing the biomass of different size groups found this assumption to be incorrect (Haedrich and Rowe, 1977). Understanding biomass patterns is essential if we are to understand productivity-diversity relationships in the deep sea (Wei et al., 2010). Most research suggests that faunal biomass is positively related to particulate organic carbon flux and reflects the energy input into a system over time (Uiblein et al., 1996; Rex et al., 2006; Rowe et al., 2008; Wei et al., 2010). Hence, biomass is thought to decrease with depth and distance from land (Rex et al., 2006; Rowe et al., 2008; Wei et al., 2010). Wet weight provides a measure of general biomass patterns among different size classes. However, when comparing the biomass of different taxa within a system, wet weight is not appropriate (Lampitt et al., 1986). Ashfree dry weight or carbon weight are far more informative because they account for differences in body composition and water content (Lampitt et al., 1986). Biomass patterns in the deep sea vary between the different size categories. As depth increases, there is a more rapid decline in mega- and marcofaunal biomass, compared to that of bacteria and meiofauna (Rex et al., 2006; Wei et al., 2010). Bacteria constitute the only size group that does not show any apparent change in biomass with increasing depth (Wei et al., 2010). Currently, the effects of variables such as sediment grain size, bioturbation, oxygen, and organic composition on biomass remain poorly understood, although body size appears to govern the biomass more than abundance (Wei et al., 2010). While there appears to be a general global decrease in biomass with increasing depth, regional differences do occur, for example off the coast of New England (USA), where the highest megafaunal biomass was reported at depths of between 2,100 and 2,500 m (Haedrich et al., 1980).

1.2.3 Reproduction

In general, life-history patterns in the deep sea are similar to those found in shallow water, although a shift in the distribution of different types is noted (Young, 2003). For megafauna three main reproductive types have been identified: non-planktonic, lecithotrophy, and planktotrophy (Rundle et al., 2007). Although originally assumed to be common, seasonal reproduction is now thought to be the exception rather than the rule (Baillon et al., 2011). It has instead been suggested that increased organic matter flux and food-falls might be a controlling factor in activating the completion of gametogenesis (Young, 2003; Baillon et al., 2011). Internal and external fertilisation both occur in the deep sea, and their frequency varies between phyla. Internal fertilisation is common, but not universal, in gastropods, while in echinoderms external fertilisation is extremely common (Young, 2003). Brooding also occurs (e.g. in peracarids), although it is less common than larval development in the deep sea. ‘Herding’, or aggregations of individuals of the same species (Billett and Hansen, 1982), is reported more often in the deep sea than it is in coastal waters (Young, 2003). The success of fertilisation is increased when gametogenesis and spawning occur at the same time within an aggregation (Baillon et al., 2011). Lecithotrophic species generally produce fewer eggs than their planktotrophic counterparts (Ramirez Llodra, 2002) and the size of the eggs generally vary with depth (Young, 2003). Where larvae are produced, pelagic lecithotrophy is most common. Asexual reproduction, although rare, has also been reported in some megafauna (Bronsdon et al., 1997).

A recent study investigated misinterpretations that occur as a result of undersampling (i.e. the lack of continuous temporal sampling) (Baillon et al., 2011). Even when comparing the same species, during the same months, over several years, in the same location, discrepancies in gonadal development are reported (Baillon et al., 2011). Sites only 200 m apart showed significant differences in the development of gonads, suggesting that even at spatially small scales, there is large variation in reproductive stages. It is crucial that we understand reproduction because it is inexorably linked to the dispersal of species; those with shorter larval periods, such as ascidians, are assumed to have shorter dispersal ranges (Young et al., 1997).

1.2.4 Megafauna and their Environment

The relative importance of physical factors such as pressure (Young and Tyler, 1993), temperature (Childress et al., 1990), and substratum properties (Gray, 1974) for shaping communities is debated. Other authors suggest that such physical factors play only a minor role in the deep sea, in comparison to the influence of nutrient input (Soltwedel et al., 2009). The spatial distribution of some megafaunal species has been linked to phytodetritus availability (Lauerman and Kaufmann, 1998; Soltwedel et al., 2009); examples include the echinoid *Echinus affinis* in the northeast Atlantic (Campos-Creasey et al., 1994) and the ophuroid *Ophiura bathybia* at Station M, in the Pacific (Booth et al., 2008). Phytodetrital flux has been linked to the abundance, distribution, densities, biomass, and community structure of megafauna (Billett et al., 2001, 2010), as well as rates of key ecosystem processes, such as depths of bioturbation and respiration (Smith et al., 1997, 2008a). Based on the observations at the Pacific Station M, it has been inferred that a seasonal increase in phytodetrital flux can trigger aggregations of some mobile fauna, as well as an accelerated metabolic and biochemical response in benthic organisms (Lauerman and Kaufmann, 1998). These sudden structural community changes have been reported in the Pacific (Ruhl and Smith Jr, 2004) and the Atlantic Ocean (Billett et al., 2001), highlighting the rapid response of megafaunal assemblages to temporal changes. Phytodetritus is also considered to be one of the main causes for patchiness (Gage, 1996; Smith et al., 2008a). Generally, patchiness refers to the spatial distribution of specimens and species, and is modulated by physical and/or biological forcings (Tyler, 1995). Biogenic structures such as echiuran mounds, worm tubes, and various tracks and traces alter the seafloor micro-topography and modify sediment characteristics by increasing local environmental heterogeneity and creating faunal patchiness (Tyler, 1995; Gage, 1996; Roberts et al., 2000). Patchiness also influences the diversity of an area and can occur at scales of 10s of metres to kilometres (Levin et al., 2001; Parry et al., 2003; Levin and Dayton, 2009). Currents can influence directly faunal composition and benthic diversity on both regional and local scales (Levin et al., 2001). The flow regime of a habitat is suggested as one of the primary driving forces maintaining epibenthic biodiversity (Palardy and Witman, 2011). Moderate currents may enhance food supply by delivering organic matter and stimulating bacterial production. Furthermore, currents can also enhance the particulate flux for suspension feeders (Tyler, 1995). In regions affected by episodic disturbances, erosive flows create repeated opportunities for recolonisation. Constant reworking of the sediment in these environments ensure that the benthic fauna remain in an early successional state, favouring opportunistic behaviour and suppressing diversity (Levin et al., 2001). If currents are too strong, fauna can become detached and local scale habitats can be destroyed (Tyler, 1995). Vigorous near-bottom flows, in excess of 20 to 25 cm s^{-1}, potentially lower diversity through erosion of epifaunal species (Levin et al., 2001). Distinctive faunal assemblages are reported under high energy conditions such as these (e.g. Western Boundary Currents, Tyler (1995)). Water flow may also impact diversity indirectly by smoothing out the sediment habitat, hence reducing physical heterogeneity, and homogenising fauna by dispersing juveniles and subadults (Levin et al., 2001). Megafauna also play an important role in affecting the energy flow on a micro-scale (Roberts et al., 2000; Smith et al., 2008a), affecting current regimes in their immediate habitat through the formation of tubes or mounds that can divert current flow, influencing the local macro- and meiofauna.

The substratum type can determine the megafaunal taxa that dominate a habitat. Hard rock substrata, for example, are overwhelmingly inhabited by sessile fauna that attach to rock, while soft sediments are dominated by mobile deposit feeders (Ramirez Llodra et al., 2010). However, both substratum types have representatives of either group. Deposit feeders continually rework the sediment, which affects the sediment geochemistry and increases the habitat heterogeneity; these effects often depend on the feeding behaviour and locomotion of mobile deposit feeders (Roberts et al., 2000). Megafauna can change the substratum they inhabit at a localised scale through remineralisation, bioturbation, burial (Bett et al., 2001; Ruhl et al., 2008) and feeding methods (Roberts et al., 2000). This applies particularly to the local effects that holothurians have on soft sediment habitats. The orders Aspidochirotida and Apodida (epibenthic representatives of this group) decrease the stability of the sediment because they defecate on the sediment surface. This faecal matter not only increases the heterogeneity of the benthic surface layer, but also decreases the viscosity of the sub-layer (Roberts et al., 2000). Members of the order Dendrochirotida, on the other hand, are generally suspension feeders and allow for the accumulation of organic material, which increases the stability of the local sediment (Roberts et al., 2000). Burrowing holothurians of the order Molpadiida increase the vertical heterogeneity of the sediment, which in turn increases biodiversity (Roberts et al., 2000). Other megafauna, such as gorgonians, increase habitat heterogeneity by creating complex structures along the seafloor, however, the importance of such species increases as food supply and habitat heterogeneity decrease (Buhl-Mortensen et al., 2010). A study of deep-sea glass sponges at Station M in the Pacific showed that these animals provide an important habitat for specialised species, such as zoanthids, forminiferans and polychetes (Beaulieu, 2001). Zonation along the sponge stalks indicated a complex interaction amongst species occupying these micro-habitats (Beaulieu, 2001).

1.2.5 Organic Material Flux

Most benthic fauna in the deep sea are heterotrophic and depend upon delivery of organic material; a food source that originates from surface primary production (Smith et al., 2008a). With the exception of chemoautotrophic habitats, such as seeps and hydrothermal vents, there is no primary production in the deep sea (Gage and Tyler, 1991; Smith et al., 2008a). The main food sources are infrequent large food falls (Turner, 1973; Kemp et al., 2006), **P**articulate **O**rganic **C**arbon (POC) fluxes (Gage and Tyler, 1991; Gage, 2003) and **D**issolved **O**rganic **M**atter (DOM) (Kaiser et al., 2005).

Though small scale variations do occur, at a global scale, the amount of primary production reaching the seafloor does not differ significantly with latitude, based on the similarities observed in average primary production between the Pacific and Atlantic Oceans (Jahnke, 1996). The export ratio into the deep sea increases linearly with increased primary production in areas with production values of up to 200 g C m^2 yr^{-1} (Lampitt and Antia, 1997). Modelling based on satellite and sediment trap data shows that increased flux and export are characteristic of areas of high primary production such as continental margins and upwelling regions (Lutz et al., 2007). However, exceptions are found in the central northern Atlantic, Pacific and the Southern Ocean where the seafloor appears depleted of carbon (Lutz et al., 2007). It has been hypothesised that in areas where resuspension events occur, suspended particles from more energetic regions, such as nearby canyon systems (Baldwin et al., 1998), can be transported to less energetic areas. This additional influx represents a secondary source of carbon adding to that derived from the sea surface (Beaulieu and Baldwin, 1998). Movements of this nature are reported from the Pacific Station M up to 50 m above bottom (Beaulieu and Baldwin, 1998).

It was originally assumed that surface particles reach the deep sea at a near continuous rate (Menzies, 1965), however, it is now clear that particle flux varies both geographically and temporally throughout a yearly cycle (Lampitt and Antia, 1997; Gooday, 2002; Gage, 2003). Irrespective of an area's oligotrophic or eutrophic nature, seasonal signals in phytodetrital deposition have been reported in both margin areas and in the open ocean (Gooday, 2002). The lowest and highest fluxes have been recorded in polar regions (Lampitt and Antia, 1997). Generally, a higher proportion of primary production is exported in temperate regions compared to the tropics, the latter having a more consistent annual surface production (Gooday, 2002). The level of POC flux, its seasonal variability, and the composition of the settling material, are all influenced by biogeochemical processes in the water column (Beaulieu and Smith Jr, 1998; Lampitt et al., 2001). In the Northeast Atlantic about 2.4 % of the spring bloom production is reported to reach the seafloor (Gooday, 2002). Atlantic blooms have been recorded twice a year; a strong increase in spring/early summer and a weaker bloom in late summer (Billett et al., 1983; Levin and Gooday, 2003). Other interannual variations in POC flux are attributed to phenomena such as the El Niño Southern Oscillation in the Pacific, where concentrations of organic carbon and particulate nitrogen are diluted by siliceous plankton fluxes (Baldwin et al., 1998).

Seasonal fluxes of POC are of great importance to the deep-sea fauna and contribute to spatial heterogeneity in benthic assemblages (Gooday, 2002). Differences in bloom composition are reflected in the composition and characteristics of the phytodetritus reaching the seafloor (Billett et al., 1983; Beaulieu and Smith Jr, 1998; Gooday, 2002). Blooms earlier in the year in the Atlantic Ocean are nutrient driven and dominated by phytoplankton, in particular diatoms (Waniek et al., 2005a,b), whereas pulses later in the year, and weaker in intensity, are attributed to faecal pellets from copepods and salp swarms (Levin and Gooday, 2003). The phytodetrital composition on the seabed in the Pacific is classified into two main types: loosely cohesive and strongly cohesive, which derive from (old and new) diatom material and zooplankton mucous webs respectively (Beaulieu and Smith Jr, 1998). Although phytodetritus is heterogeneous, it tends to be dominated by either loosely or strongly cohesive phytodetritus (Beaulieu and Smith Jr, 1998).

The composition of POC affects the local fauna (Beaulieu and Smith Jr, 1998) and, although not consistent across all taxa, data suggest that the spatial distribution of megafauna correlates strongly with the distribution of detrital aggregates (Lauerman and Kaufmann, 1998). Elevated POC flux can increase faunal density and biomass after a four-week delay (Drazen et al., 1998). Furthermore, the sediment oxygen consumption of deep-sea fauna is strongly correlated to the seasonality in phytoplankton and POC flux (Drazen et al., 1998). At Station M a long-term shortage in food supply has been attributed to a decrease in plankton biomass as a response to increasing sea surface temperatures (Smith and Kaufmann, 1999). This decrease in plankton biomass, in turn, affects the re-processing and redistribution of particulate benthic material on the seafloor, particularly for mobile epibenthic megafauna (Kaufmann and Smith Jr, 1997).

1.3 Broad-Scale Faunal Patterns in the Deep Sea

Throughout history scientists have sought to find patterns in the geographic distributions for flora and fauna; a pursuit that has evolved into the scientific branch of biogeography. One of the earliest descriptions of distribution patterns was made by Edward Forbes. He hypothesised that continents and adjacent islands must have been connected in the past, because of the observed similarities in flora and fauna between them (discussed in Darwin (1859)). Forbes' theory found strong support following the formulation of continental drift theory several decades later (Wegener, 1929). This coming together of ideas vindicated Darwins theory that the distribution of species was driven by species dispersal that originated from a founder population (Darwin, 1859).

One of the first attempts to describe biogeographical patterns in marine environments was carried out by Ekman (1953). While he considered dispersal to be an important mechanism for increasing the distribution ranges of species, he also suggested that geomorphological features, such as ridge systems, may act as physical barriers to dispersal (Ekman, 1953). In recent years, interest in species level biogeography has grown following the ever increasing exploitation of the marine environment (McClain and Mincks Hardy, 2010). Today, biogeographic studies have become vital, as without detailed knowledge of the marine environment, effective conservation management is not possible. However, ambiguity has arisen in the interpretation of biogeographic distribution patterns as a result of differing theoretical concepts.

1.3.1 Biogeography: General Concepts

Marine ecologists endeavour to find characteristics typical for a habitat or region that can then be later applied, in a predictive manner, to similar study sites in the future. There is a vast body of literature on biogeography, which can be divided into ecological biogeography and historical biogeography (Crisci, 2001). While both areas of biogeography analyse the distribution of species, they focus on different causal mechanisms for the patterns observed. Historical biogeography assumes that original species distributions were modified by historical events (i.e. closure of the Central American Seaway (Knowlton and Weigt, 1998)), which result in the separation of populations that eventually lead to contrasting biogeographic regions (Crisci et al., 2006). In contrast, ecological biogeography, considers the importance of environmental conditions and ecological niches that result in respectively environmental constrains and functional types, both of which create different Ecoregions (Crisci et al., 2006). Historical biogeography can be further subdivided into dispersal and vicariance theories. Dispersal theories assume long distance dispersal, which eventually leads to the formation of genetically different populations, while vicariant biogeography assumes an initial wide-range of distribution, followed by the isolation of some populations through the formation of barriers (Sanmartín, 1997; Bartish et al., 2011). Unfortunately, historical and ecological biogeographers rarely combine their concepts to form an all encompassing, coherent picture of species dispersal (Crisci, 2001). Examples from the marine environment are discussed in detail in the following sections to highlight the contrasting biogeographical approaches.

1.3.2 Ecological Biogeography

The marine environment is complex as it is defined by both pelagic and benthic habitats that vary with depth (Gage and Tyler, 1991). Therefore, a selection of key environmental parameters must be chosen if distribution patterns are to be generalised. However, disagreement between authors regarding the importance of different environmental characteristics, often results in classification systems that are uncomplimentary.

Longhurst developed a system of biogeochemical provinces for pelagic ecosystems, following the ecological biogeography school. In this theory oceanographic factors, such as frontal zones and general circulation, are taken into account as well as chlorophyll concentrations and solar radiation (Longhurst, 2007). Four Biomes are described by Longhurst; the Westerly Winds, the Trade Winds, the Polar and the Ocean Coastal Biomes (Longhurst, 2007). Four of these biomes are represented in the Atlantic and Pacific oceans and three in the Indian Ocean and Southern Oceans (Longhurst, 2007). Biomes are further subdivided into a total of 150 provinces. While the biogeochemical province system is frequently used for pelagic studies, oceanographic characteristics of the upper ocean layer are only taken into account, although it has been suggested that the biomes also reflect underlying benthic communities through benthic-pelagic coupling (Longhurst, 2007).

Zoogeographic regions were proposed by Russian scientists and regard benthic fauna in the deep sea (Figure 1.1), whereby benthic species distributions were combined with environmental factors such as water temperature (Zezina, 1997; Mironov and Gebruk, 2006). Bathyal and abyssal regions vary substantially in their species distribution and therefore can be distinguished (Zezina, 1997). Particular species are considered representative for different regions and the importance of species-level identification is a prerequisite for this approach (Mironov and Gebruk, 2006). The bathyal zone extends between 200 and 3,000 m, and is further subdivided into the upper and lower bathyal regions, defined as between 200 to 700 m and 700 to 3,000 m respectively (Zezina, 1997). The abyssal zone is found below the bathyal zone, between 3,000 and 6,000 m (Vinogradova, 1997). Fauna in the east and west Atlantic are shown to be increasingly

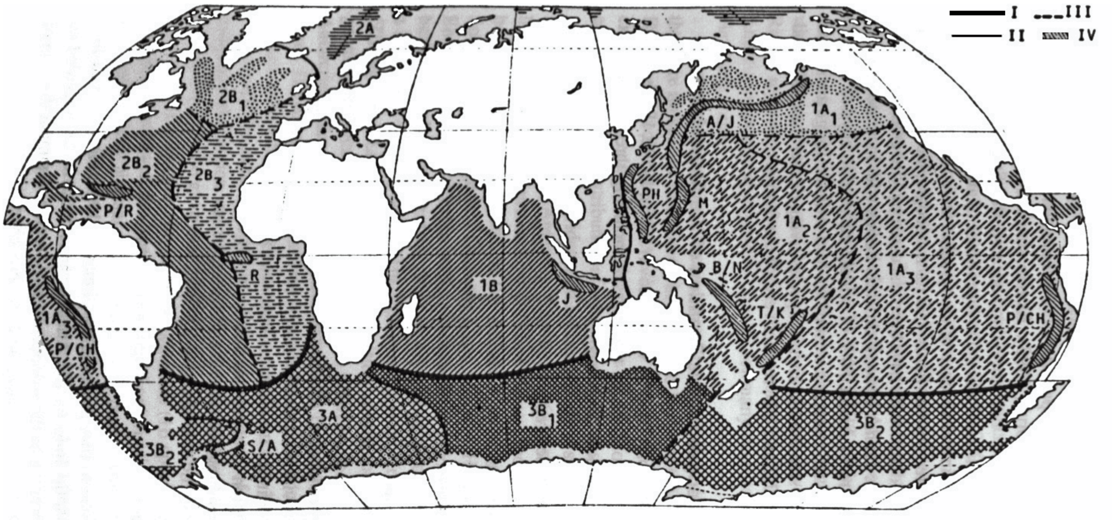


FIGURE 1.1: This map shows the different Zoogeographic regions as described by Vinogradova (1997) where; (I) defines different regions, (II) subregions, (III) abyssal provinces, and (IV) hadal provinces. 1A defines the Pacific subregion, 1B Indian subregion, 2A Arctic subregion, 2B Atlantic subregion, and 3B the Indian Ocean abyssal province. The subregions are further subdivided into provinces; 1A$_1$ North-Pacific abyssal province, 1A$_2$ West-Pacific abyssal province, 1A$_3$ East Pacific abyssal province, 2B$_1$ North Atlantic abyssal province, 2B$_2$ West Atlantic abyssal province, 2B$_3$ East-Atlantic abyssal province, 3B$_1$ Indian Ocean abyssal province, and 3B$_2$ Pacific abyssal province. Hadal provinces are described separately. The following hadal provinces are in proximity to the Pacific subregion: A/J Aleutian-Japan hadal provinces, PH Phillippine, M Mariana, B/N Bougainville - New Hebrides, T/K Tonga-Kermadec, P/CH Peru-Chile hadal provinces. In the Atlantic subregion the P/R Puerto-Rico hadal province, and the R province of the Romanche Trench are distinguished. Figure from Vinogradova (1997)

distinct with increasing depth Vinogradova (1997). While the two sides of the Atlantic share about 49 % of their species at depths shallower than 2,000 m, Vinogradova (1997) suggests that there is no similarity below 4,000 m, suggesting increasing geographic isolation with increasing water depth. In the upper bathyal region ten general areas with 13 subareas, and nine provinces are identified, whereas at lower bathyal depths only five areas with two subareas, and four provinces are recognised (Zezina, 1997). For the abyss Vingrodova proposes three regions, six subregions, and eight provinces (Vinogradova, 1997). Since the Vingrodova study, the classifications of the deep sea into biogeographic regions has progressed, with the inclusion of environmental data, such as salinity, oxygen and particle flux, that are combined to determine different biogeographic regions (Agostini et al., 2009). Thirty pelagic provinces and 38 benthic provinces were identified that are further subdivided into four depth ranges (Agostini et al., 2009). In addition, 10 hydrothermal vent provinces were subsequently recognised (Desbruyères et al., 2001; Van Dover et al., 2001; Ramirez Llodra et al., 2010; Rogers et al., 2012).

1.3.3 Historical Biogeography

In historical biogeography, molecular methods, such as phylogenetics, are often used to establish historic relationships. There are multiple approaches within historical biogeography; unfortunately these contrasting methods are often used in isolation, leading to a non-coherent conceptual framework (Crisci, 2001). Different approaches commonly used in historical biogeography include: phylogeography, phylogenetic biogeography, cladistic biogeography, parsimony analysis, centres of origin and dispersal, panbiogeography, and experimental biogeography (Crisci, 2001).

1.3.3.1 Dispersal Theory

An example of historical biogeography that focuses on dispersal theory is hydrothermal vents. The distribution of hydrothermal vents is linked to plate tectonics, and they are often found at spreading centres, such as the Mid-Atlantic Ridge (Tunnicliffe, 1991; Rogers et al., 2012). Evidence of hydrothermal vent communities have been found from as early as the Devonian, suggesting that the communities inhabiting them have evolved since this time (Walter, 1996). Although precise ages for individual vent fields have not been established, it is suggested that they are at least several decades old (Tunnicliffe, 1991). Often hydrothermal vent systems are several hundred kilometres apart and a high level of endemism can be observed (Tunnicliffe, 1991). However, within the recently established biogeographic regions, there are similarities in the dominant fauna (Ramirez Llodra et al., 2010; Rogers et al., 2012). Natural events, such as sporadic volcanism, can destroy entire vent system (Vrijenhoek, 2010) and so the question arises, how can species that thrive only in vent environments move between vent systems (Desbruyères et al., 2001; Van Dover et al., 2001)? It had been suggested that larval dispersal plays an important role and molecular data suggest a relatively linear stepping-stone dispersal along vent systems along ridge axes (Vrijenhoek, 2010).

1.3.3.2 Vicariant Theory

The holothurian family Elasipodida is entirely restricted to the deep sea, where it is widely distributed (Hansen, 1975). Within this family of holothurians, many species of the genus elpidiid occur predominantly in tropical regions, indicating that this area plays a key role in the distribution (Gebruk, 1994). Paleontological and morphological evidence suggests that members of this genus originated at bathyal depths in the Late Jurassic Tethys basin (Scotese et al., 1988; Gebruk, 1994), where it is thought that species of this genus were widely distributed. However, it is suggested that the Tethys-basin-population was divided into at least two different populations occurring in the Indo-Malayan and the tropical Caribbean seas as a result of the Tethys basin destruction (Gebruk, 1994).

1.4 Biodiversity in the Deep Sea

Biodiversity refers to all forms of biological diversity ranging from genes and species to higher taxa and communities (Magurran, 2004). Although the deep sea is considered diverse (Hessler and Sanders, 1967; Grassle and Mackiolek, 1992), the degree of diversity, as well as the abundance of organisms, can greatly vary in different parts of the ocean (Stuart et al., 2003). This variation in diversity reflects different environmental factors, including the organic matter flux, bottom-current velocity, and local topography (Stuart et al., 2003). The difficulties in comparing diversity measures between marine and terrestrial environments have caused considerable debate, as well as between shallow-water and deep-sea environments (Levin et al., 2001; Gray, 2001a). Most commonly, literature dealing with biodiversity distinguishes between three different scales of diversity; α (alpha), β (beta) and γ (gamma) diversity (Magurran, 2004; Rex and Etter, 2010). In marine sciences α refers to the local, within patch, diversity (Snelgrove and Smith, 2002), β diversity to species turnover, e.g. how many new species are found along a transect, and γ diversity to regional scale, based on individual samples from different patches within a region, for example within a basin (Snelgrove and Smith, 2002; Rex and Etter, 2010). Gamma diversity relates to larger scales than α diversity and is effectively made up by combining α and β diversity (Whittaker, 1960), and can also be referred to as landscape diversity (Levin et al., 2001) or geographic-scale diversity (Hunter and Gibbs, 2007).

1.4.1 Diversity Patterns

There are a number of studies that investigate diversity patterns in the deep sea, both in relation to latitude and bathymetry (Rex et al., 1993; Paterson and Lambshead, 1995; Gray, 2001a; Gage, 2004; Maciolek and Smith, 2009; Stuart and Rex, 2009). Although patterns have been found, they are not always consistent between different taxa. No patterns that could be applied universally to all species have been found, potentially because 1) different studies investigate different species, 2) studies utilise different sampling gears (Snelgrove and Smith, 2002), and 3) studies are carried out in different areas that are subject to contrasting environmental influences. It is clear that standardised sampling methods and species diversity indices are needed to understand fully the diversity patterns in the deep sea.

1.4.1.1 Bathymetric Diversity Patterns

Approximately 90 % of the known animal families occur in modern marine environments (Snelgrove and Smith, 2002). While it is commonly accepted that the deep sea contains a large number of species, it is strongly debated whether the deep sea is more diverse than shallow-water habitats (Snelgrove and Smith, 2002). One of the first studies to compare deep-sea to shallow water diversity was carried out by Sanders (1968). This study shows a much higher diversity in the deep sea than had previously been expected. Levin et al. (2001) also compared two study sites at the western North Atlantic that were sampled with similar gear, one in a coastal area, and one on the continental margin at the same locality. From this data it was found that the deep sea was more diverse than coastal regions (Sanders, 1968; Levin et al., 2001), however, other studies have concluded the contrary (Gray, 1997, 2001a). While the question of whether shallow waters are more diverse than the deep sea is debated, trends in bathymetric diversity have been identified.

A peak in biodiversity has been reported for the bathyal zone between 2,000 and 3,000 m, however, a variety of bathymetric diversity patterns for different taxa have been shown. In a study of the northeast Atlantic, polychaete biodiversity was shown to peak at approximately 1,800 m water depth (Paterson and Lambshead, 1995), while in the tropical northern Atlantic peak diversity was reported at 2,000 m depth (Cosson-Sarradin et al., 1998). In a study of fauna bigger than 3 µm, collected with a box corer from 10 different sites in the northeast and northwest Atlantic, diversity peaks were recorded between 1,220 and 1,350 m and between 2,065 and 2,180 m water depths (Maciolek and Smith, 2009). Gastropods investigated along the Atlantic margin (northeast and northwest) with an epibenthic sledge peaked in diversity between 2,000 and 3,000 m (Stuart and Rex, 2009). These studies serve to highlight our lack of understanding of diversity patterns showing that bathymetric diversity patterns vary depending on study site (Stuart and Rex, 2009).

Numerous factors have been proposed as drivers of bathymetric diversity patterns, including oxygen (Rogers, 2000; Stuart and Rex, 2009) (diversity highly suppressed in oxygen depleted zones (Levin et al., 2001)), food supply (Smith et al., 2008a), hydrographic disturbance (Lambshead et al., 2001), geological- evolutionary processes (Brandt and Ebbe, 2009; Stuart and Rex, 2009), and sediment grain sizes (Etter and Grassle, 1992). However, the importance of the latter driver is debated (Maciolek and Smith, 2009). Conversely, it has been proposed that the reported peak in bathymetric species richness is a statistical artefact rather than an ecological occurrence, also referred to as 'mid-domain effect' (Colwell and Lees, 2000; Colwell et al., 2004; Gotelli et al., 2009).

1.4.1.2 Latitudinal Diversity Patterns

Latitudinal diversity patterns are as complex as thier bathymetric counterparts. In terrestrial ecology, a latitudinal biodiversity pattern has long been recognised, with biodiversity decreasing from the equator to the poles (Turner, 2004). Similar trends have also been recognised in shallow-water marine system (Gray, 1997). In the deep sea, a general trend of decreasing diversity in megafauna (e.g. gastropods, bivalves) and macrofauna (e.g. isopods) towards the poles has been suggested by numerous studies, although the legitimacy of this pattern has been questioned (Rex et al., 1993; Gray, 2001a,b; Ramirez Llodra et al., 2010). These studies have noted that such a trend is less pronounced in the Southern Ocean (Rex et al., 1993; Lambshead et al., 2000; Gray, 2001a,b) where species diversity has been reported to be very high (Gray, 2001b; Brandt and Ebbe, 2009). This increased diversity in the Southern Ocean has been explained by higher structural heterogeneity, and the age of the region (Gray, 2001b; Brandt and Ebbe, 2009). A poleward decrease in biodiversity has been observed in some holothurian dendrochirotid species, while other suspension feeders tend to show a decrease in diversity from the poles to the equator (Roberts et al., 2000). Molpadiida in contrast peak between 30 °C and 50 °C north and south, and are almost absent at the poles and the equator (Roberts et al., 2000).

While trends have been reported for species and sometimes groups there are no studies that suggest that there is a universal trend in either latitudinal or bathymetric diversity pattern. As particulate organic matter changes spatially and temporarily, a trend may become apparent across families if feeding guilds are considered.

1.4.2 Why is the deep sea so diverse?

Many hypotheses have been put forward to explain the diversity of the deep sea (Sanders, 1968; Gage, 1996; Cronin and Raymo, 1997). Theories dealing with this question can be divided into two main groups - those involving equilibrium and those involving disequilibrium processes (Gage and Tyler, 1991; Snelgrove and Smith, 2002).

1.4.2.1 Equilibrium Theory

According to equilibrium theories, finely tuned species coexist close to the carrying capacity of the system (Gage and Tyler, 1991). The environment that they inhabit exists at an ordered and harmonious equilibrium, to which the system returns following any perturbation (Wu and Loucks, 1995). An example of an equilibrium theory is the stability-time hypothesis (Sanders, 1968). The deep sea was long considered a very stable environment and, as such, it was reasoned that species had specialised to narrow niches that allowed numerous species to co-exist despite only a limited flux of organic matter (Sanders, 1968). However, it is now clear that many oceanographic variables in the deep sea are not as stable as first thought (Menzies, 1965; Tyler, 1995). While the deep sea exhibits a general stability in temperature and salinity (Snelgrove and Smith, 2002), with notable exceptions such as the Faroe Shetland Channel upper slope (Bullough et al., 1998), there can be large seasonal fluctuations in organic matter flux (Gooday, 2002; Smith et al., 2008b), and periods of intensive current activity (i.e. benthic storms) (Woodgate and Fahrbach, 1999). Temporal changes in diversity since the Pleiocene have been reported (ca. 2.5 million years ago), e.g. in benthic ostracods (Cronin and Raymo, 1997), suggesting that the deep sea is an environment that is climatically driven over geological times scales, for example during glacial-interglacial cycles (Hoffman et al., 1998; Broecker, 2002). Although there is clear evidence for temporal changes in the deep-sea environment, it has been suggested that an ecosystem can reach an equilibrium by stabilising density-dependent processes, such as recruitment and dispersal, at a more localised scale (Murdoch, 1994).

1.4.2.2 Disequilibrium Theory

Disequilibrium theories assume that faunal assemblages exist at an early successional stage through disturbance (e.g. predation), keeping them below the carrying capacity of the habitat, hence, increasing local diversity (Gage and Tyler, 1991; Snelgrove and Smith, 2002). This theory accounts for the influences of physical parameters on species and their interaction with the small-scale heterogeneity, as well as patchiness of the environment (Snelgrove and Smith, 2002). Benthic storms and small-scale disturbances (e.g. by megafauna) will temporarily and spatially disrupt communities and leave habitats at different successional stages (Snelgrove and Smith, 2002). Strong seasonal signals in phytodetrital flux are also considered as a source of disequilibrium in the deep sea (Snelgrove and Smith, 2002). Detrital deposition events are not, as previously thought, a continuous rain of particulate organic matter to the deep sea (Menzies, 1965), but instead occur in distinct events that deposit phytodetrital patches in clumped aggregates (Lauerman and Kaufmann, 1998). Phytodetrital patches promote a local increase in protein, carbohydrates and chloroplasti pigments (Thiel et al., 1988/1989) and also host a number of macrofaunal species (Vetter, 1998). Phytodetrital aggregates show considerable inter-patch chemical variability and support a range of megafaunal taxa (Thiel et al., 1988/1989). Patches range greatly in size (Teixido et al., 2002) and can reach km scales (David et al., 1997). Characteristics and levels of diversity differ between individual patches (Teixido et al., 2002) and their respective sizes have been linked to density dependent species recruitment (David et al., 1997). In a changeable environment, high biodiversity has the potential to reduce temporal variance and to increase the temporal mean, thus, high diversity could be a long-term insurance policy against natural environmental fluctuations (Loreau, 2000).

Finally, it is suggested that equilibrium and disequilibrium principles may not be mutually exclusive in deep sea environments (DeAngelis and Waterhouse, 1987; Wu and Loucks, 1995). It has been proposed that ecosystems are made up of a mosaic of distinct patches, that, on varying time scales, are influenced by both stabilising and destabilising environmental driving forces (Wu and Loucks, 1995). In this novel theory, at sufficiently large scales, systems approach an equilibrium state asymptotically (DeAngelis and Waterhouse, 1987). It is unlikely that any single factor drives the high diversity observed in the deep sea, as patterns are scale dependent (Snelgrove and Smith, 2002). Further data are required, ocean-wide, to improve our understanding of deep-sea diversity drivers, however, the greater the sample effort, the more complex the explanations are likely to become (Snelgrove and Smith, 2002).

1.4.3 Measuring Biodiversity

Described simply, biodiversity is “the variety of plant and animal life in the world or in a particular habitat, a high level of which is usually considered to be important and desirable.” (British Library, 2010). In practice, however, measuring and monitoring biodiversity is very complex and frequently results in debates and disagreements. In essence, all measures aim to compare biological communities in different areas or over time. All methods are based on three assumptions: 1) all species are equal, 2) all individuals are equal, and 3) abundance measures investigate the same units (e.g. species, feeding guilds, biomass) between different sites (Magurran, 2004).

There are many ways to define and measure biodiversity, for example, α diversity measures focus on aspects such as abundance (e.g. Fisher’s α), rarity (e.g. Gaston’s quartile criterion), and relationships between biomass and abundance (e.g. abc curves) (Clarke and Warwick, 1994; Magurran, 2004). β diversity is measured by comparing the differences between α diversities relative to γ diversity, where the latter describes the total species richness (Magurran, 2004), or by investigating differences in species composition between two or more α measures (Magurran, 2004). The particular biodiversity measure employed by a study depends on the type of samples available and the questions to be addressed. In the following sections, the diversity measures used in this study are further discussed. The term biodiversity is used as a combination of species richness and species evenness, which can be calculated with indices. Throughout this study, indices as well the species richness and species evenness are calculated separately to determine the drivers for observed diversity patterns.

1.4.3.1 Species Richness

Methods commonly used to express species richness in marine environments are rarefaction and species accumulation curves (Gage and Tyler, 1991; Gotelli and Colwell, 2001; Gray and Elliott, 2009). Apart from serving as α diversity measures for calculating the species richness of an area, these methods can also be used to estimate the similarity between two communities (as β diversity measure) (Colwell and Coddington, 1994; Chao et al., 2000; Gotelli and Colwell, 2001). Both rarefaction and species accumulation curves can be calculated using either the number of samples or the collected number of individuals. Sample based comparisons result in the aggregation of many individuals and often show lower species richness estimates, while a comparison against number of individuals tends to improve resolution (Gotelli and Colwell, 2001).

Rarefaction curves, developed by Sanders (1968), enable the comparison of species richness between different marine areas, independent of sample sizes. S is the expected number of species for a sample size of n individuals, ($E(S_n)$) (Sanders, 1968; Gage and May, 1993). This method was later modified by Hulbert (1971), after it was noticed that the Sanders' rarefaction tended to overestimate species numbers (Gray and Elliott, 2009). This modified technique aimed to show the expected number of species for a collection of n individuals or samples (Gotelli and Colwell, 2001; Snelgrove and Smith, 2002). Somewhat counterintuitively, rarefaction curves start at the right-hand side of a graph, at the expected species number, and move to the left as the number of individuals or samples decreases (Gotelli and Colwell, 2001). The rarefaction curve is produced by repeatedly calculating for progressively smaller numbers of individuals within a sample (Gray and Elliott, 2009). The steeper the curve produced, the greater the species richness of a community (Gray and Elliott, 2009). It is particularly useful in cases were only the number of individuals of each species is known without the knowledge of an area (Gray and Elliott, 2009). Species richness can be considerably overestimated when rarefaction curves are calculated for communities where individuals are aggregated (Magurran, 2004).

Species accumulation curves, or collectors curves, display the cumulative number of species in a successively pooled sample (Clarke and Warwick, 1994; Colwell and Coddington, 1994; Gotelli and Colwell, 2001). To create a species accumulation curve, different extrapolation methods are available, such as UGE, Chao 1 & 2, and Jacknife, although species accumulation curves can be calculated simply by using the number of species found (Colwell and Coddington, 1994). Most species accumulation curves are calculated through permutations, resulting in a smoothed accumulation curve (Clarke and Warwick, 1994; Gotelli and Colwell, 2001). These curves are read from the left-hand side to the right-hand side of a graph, showing elevated species numbers with increased sampling effort (Gotelli and Colwell, 2001). Furthermore, the asymptote of a species accumulation curve shows whether more species are to be expected in the event of an increase in sampling effort (Colwell and Coddington, 1994).

In this study, species richness was calculated using smoothed species accumulation curves. To reduce the bias of an unbalanced sampling effort, species richness was calculated based on number of individuals rather than the number of samples. This exercise had the added benefit of a greater resolution (Gotelli and Colwell, 2001). Species accumulation curves were chosen over rarefaction curves because there was a strong indication that individuals aggregated at one or more of the sample sites (Magurran, 2004). Furthermore, through utilisation of species accumulation curves, the success of sampling effort could be inferred.

1.4.3.2 Species Evenness

Species evenness describes the distribution of individual species within a community, where a high evenness is achieved through an even distribution of species in approximately equal abundance across a habitat. High evenness means low dominance and vice versa (Magurran, 2004). There are several models that calculate the evenness of samples which are discussed in detail in Magurran (2004). In this study however, the preferred evenness measure is the Whittaker Rank Abundance (Whittaker, 1972; Magurran, 2004), where species rank order is calculated against relative abundance (Ulrich et al., 2010). The Whittaker Rank Abundance Plot displays any of three possible curves: a) the geometric series, indicating a strong dominance, b) broken stick (Magurran, 2004), pointing towards random boundaries between niches, and c) log normal distribution, showing a relatively high level of evenness (Whittaker, 1972). This method is preferred, because the behaviour of the curves gives comprehensive information about a sample, making a decision as to whether datasets require transformation for subsequent analyses easier (the assumption is made that any sample that is not log normal needs transformation).

Furthermore, through employment of this method, an indication of rare species within a sample is also made (Magurran, 2004).

1.4.3.3 Diversity Indices

While there are many indices that can be used to calculate the diversity of a system, the parametric Simpson's diversity index and the non-parametric Shannon-Wiener diversity index are commonly used within the marine sciences (Magurran, 2004). The Simpson's diversity index is considered one of the most robust diversity indices, whereby the probability of two individuals from the same sample pool belonging to the same species is calculated (Rosenzweig, 1995; Magurran, 2004). One of the advantages of this method is its sample size independence, however, a drawback is its lack of sensitivity towards species richness and its strong weight towards dominant species (Rosenzweig, 1995; Magurran, 2004). In contrast, the Shannon-Wiener index is sensitive to changes in dominance (in terms of abundance), and weighs towards rare species (Whittaker, 1972; Chiarucci et al., 2011). Rare species are of considerable importance, in particular in deep-sea research where under-sampling often results in an incomplete snapshot of an area. In fact, it has been argued that rare species are one of the most informative measures as they can give an indication of the species that have not been sampled (Chao et al., 2000). However, a considerable drawbacks of the Shannon-Wiener index is the assumption that all species are represented within a sample (Magurran, 2004). This is of particular significance in deep-sea research where under-sampling is a common problem (Beck and Schwanghart, 2010). Other assumption for the Shannon-Wiener diversity index are that sampling is random and that communities are of unlimited size (Magurran, 2004). In general, this index increases either when the number of species becomes larger, or as the proportion of individuals of each species becomes more even (Gray and Elliott, 2009). In this study, both indices were used to compare the diversity between sites, as both indices complement each other in their focus (Gray, 2000).

The following work combines results from four years of field research at the Mid-Atlantic Ridge, in the vicinity of the Charlie-Gibbs Fracture Zone. The over-arching aim of this study was to explore a largely unknown area of the Mid-Atlantic Ridge and to compare four contrasting sites in the context of ecological aspects that have been introduced herein. This body of research focuses on invertebrate benthic megafauna that were sampled and analysed using three contrasting methodologies: trawling, video survey, and molecular analysis. I begin with an introduction to the study area, before guiding the reader through broad ecological comparisons (from trawl sample data in Chapter 3), down to small-scale variations between sites (through video surveys in Chapter 4). Following these sections, Chapter 5 critiques trawl and video survey methods, highlighting their pros and cons. After these ecological chapters, I present a detailed investigation into the phylogeny of holothurians; the most abundant benthic megafauna found at the Mid-Atlantic Ridge. The motivation behind this chapter is the unique molecular samples that were acquired through trawling and ROV sampling, which has led to a new line of investigation into this important class. Finally, a short synthesis concludes this thesis.

Chapter 2

The Mid-Atlantic Ridge around the Charlie-Gibbs Fracture Zone

2.1 Research Interest

Census **o**f **M**arine **L**ife (ComL) was a unique international effort to investigate life in the oceans. The main aims were to catalogue and count species in all oceans and to increase our understanding of the biggest ecosystem on Earth (Snelgrove, 2010). One of the work packages of ComL was MAR-ECO, a field project on "Patterns and Processes of the Ecosystems of the northern Mid-Atlantic Ridge" (Bergstad et al., 2008). The initial planning phase (2001-2003) was followed by the field phase (2003-2005) in which 16 different countries participated (Boyle, 2009). The main aim of MAR-ECO was to increase our understanding of the **M**id-**A**tlantic **R**idge (MAR) as an ecosystem, focussing on non-chemosynthetic environments. MAR-ECO sampled the MAR between the Azores and Iceland, with the aim to describe patterns of distribution, abundance and trophic structures of the fauna (Boyle, 2009).

As a contribution to MAR-ECO the UK NERC funded a consortium project of UK and international collaborators to investigate one area in greater detail (ECOMAR, 2012). ECOMAR (**Eco**systems of the **M**id-**A**tlantic **R**idge), a multidisciplinary project (2007-2012) including seven UK institutions, focussed on the Sub-Polar Front and **C**harlie-**G**ibbs **F**racture **Z**one (CGFZ) 50 to 56 °N. The main aims of the ECOMAR project were to determine the effect of the MAR on primary production, biomass and biodiversity of pelagic and benthic communities, and the coupling between them through the downward flux of organic matter. It also aimed to determine general patterns that might be applied to other mid-ocean ridge systems (ECOMAR, 2012). In order to address those questions four superstations were chosen in the vicinity of the CGFZ that were sampled over a four year field phase, between 2007 and 2010 (Figure 2.1). The two northern sites were situated about 137 km apart, while the southern sites were only about 73 km apart. The northern and southern sites were about 706 km away from each other to the east and about 777 km to the west. All stations targeted a depth around 2,500 m, either side of the CGFZ and MAR. The following chapter introduces our current knowledge of this area, ranging from its geology, to oceanography, and the biology in this area. However, as there was relatively little knowledge prior to the ComL research effort, some discussions are based on very recent findings, many of which have not been published yet. A large part of this data will be published in 2013 in a special volume by the Journal Deep-Sea Research II, which will be referenced accordingly.

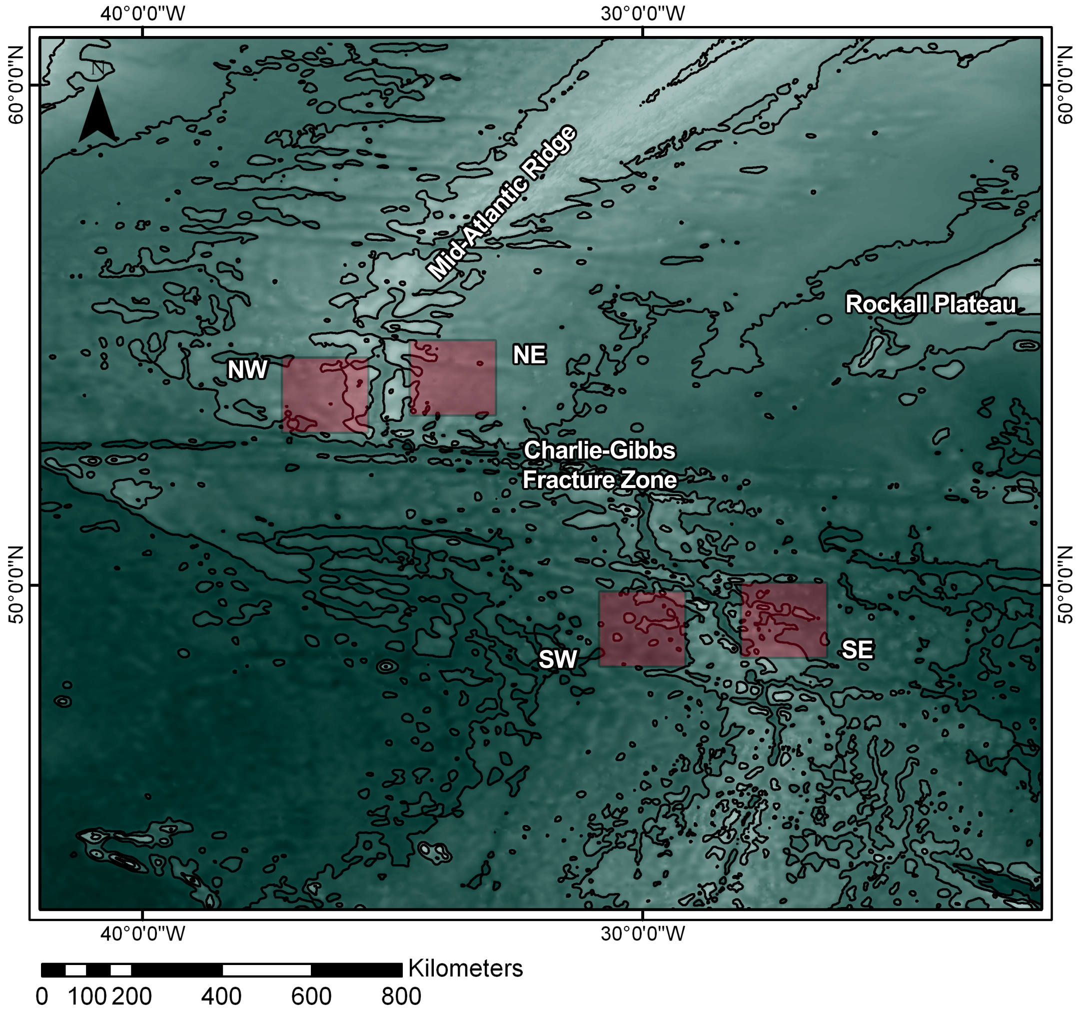


FIGURE 2.1: Map of the Charlie-Gibbs Fracture Zone and the Mid-Atlantic Ridge, indicating the four ECOMAR superstations at a target depth of around 2,500 m water depth. The distance between the northern sites is 137 km, between the southern sites 72 km, between the north and south sites to the east 706 km, and between the north and south sites to the West 777 km (± 100 m. 1,000 m contours are shown.). Map courtesy of Grant Duffy.

2.2 Geology

Mid-ocean ridges are ‘mountain ranges‘ that rise from the adjacent abyssal plains. The spreading centres at MORs are where new oceanic crust is formed and are part of the plate tectonic system (Gage and Tyler, 1991). These linear bathymetric highs make up about one third of the ocean floor by area (Seibold and Berger, 1996). The ridge crests may be elevated up to 2,500 m above the surrounding abyssal plains (Seibold and Berger, 1996). The crest is marked by a rough and rugged topography with shallow seamounts and hills (Seibold and Berger, 1996; Bergstad et al., 2008). Moving perpendicularly away from the crest, unevenness is gradually smoothed by sediment cover (Seibold and Berger, 1996). The sedimentation rate is typically very low (about 0.1 and 0.2 cm kyr^{-1} Gage and Tyler (1991)) in comparison to continental margins (about 20 cm kyr^{-1} Gage and Tyler (1991); Bergstad et al. (2008)); and the spreading rate varies from about 1 to 10 cm a year (Seibold and Berger, 1996).

The MAR divides the North Atlantic into two approximately equally sized basins (eastern and western basins) (Levin and Gooday, 2003; Tomczak and Godfrey, 2003). At the MAR the central rift is about 30 to 50 km wide and about 1 km deep (Seibold and Berger, 1996). The crest of the MAR is shallower than other ridges, such as those found in the Pacific, and becomes increasingly so towards Iceland, where it eventually rises above sea-level (Seibold and Berger, 1996; Tomczak and Godfrey, 2003). The height of the MAR affects the deep-water circulation in the Atlantic (Tomczak and Godfrey, 2003) and the pelagic fauna is assumed to differ significantly between the eastern and western basins (Longhurst, 2007). The MAR is interrupted along its length by fracture zones, such as the CGFZ, which can reach depths of 3,000 to 4,000 m below the ridge crest (Bergstad et al., 2008). Fracture zones are characterised by highly irregular bathymetry (Seibold and Berger, 1996). They are also seismically active as a result of the relative motion of the rigid blocks of oceanic crust on either side (Brown et al., 1992). The most northerly part of the MAR, which is situated north of the CGFZ is also referred to as Reykjanes Ridge.

2.3 Oceanography

2.3.1 Surface Waters

Ocean water circulation causes surface waters to be transported from the west to the east (Tomczak and Godfrey, 2003; Read et al., 2010). Though southward and northward movements also occur, it is pronounced on the western side of the Atlantic, while the eastern side is charcterised by higher eddy activity and low motion (Tomczak and Godfrey, 2003). As a result of freshwater supply from glaciers and icebergs, sea surface salinity decreases at high latitudes in the northern North Atlantic, producing a sharp gradient in salinity between the Labrador Current and the Gulf Stream, contributing to the formation of the Sub-Polar Front (Tomczak and Godfrey, 2003).

The Sub-Polar Front, which forms over the CGFZ, is defined by strong currents to the south and weaker currents to the north (Søiland et al., 2008). The southern part of the Sub-Polar Front is characterised by the North Atlantic Current, which emerges from the Gulf Stream and carries water over the ridge that eventually splits into a southern and a northern branch (Tomczak and Godfrey, 2003). The North Atlantic current, over the CGFZ, is characterised by energetic, long-lasting, and slow-moving eddies of a continuous succession (Miller, 2009). The northern branch of the North Atlantic Current has the CGFZ as a natural barrier towards the north, while the southern branch has meanders and eddies that pass close to the SE ECOMAR site and likely enhances spring productivity (Miller et al., submitted).

Recent data indicate that the MAR is a more effective barrier to ocean currents north of the CGFZ than the ridge to the south (Miller et al., submitted). It has also been suggested that around the southern ECOMAR sites the MAR is delineated by less variability in the small fronts (Miller et al., submitted). Over long periods, the mean surface velocity is slow at about 5 cm s^{-1}. The salinity in the upper 1,000 m tends to be higher south of the CGFZ compared to the north (Read et al., 2010). Furthermore, a weak mean eastward flow of subtropical water has been described over the southern sites, and a cooler subpolar mean westward flow over the northern sites (Read et al., 2010).

2.3.2 Deeper Waters

Overall, the CGFZ affects the deep-water hydrography of the area as two-thirds of the water mass transport occurs between 500 to 2,500 m (Read et al., 2010). Deeper water masses flow from the northeast Atlantic along the Reykjanes Ridge (the most northern part of the MAR) south-westward, until they reach the CGFZ through which the western Atlantic is reached, where water masses continue north-westward (Saunders, 1994; Tomczak and Godfrey, 2003; Hunter et al., 2007; Bower and von Appen, 2008; Søiland et al., 2008). This water mass is characterised by cold, oxygenated Iceland-Scotland-Overflow Water between 1,800 and 3,000 m water depth. Unexpectedly high bottom-water salinity south of the CGFZ suggests that some of the Iceland-Scotland-Overflow Water also mixes southwards (Read et al., 2010). Measurements of the deeper water along the CGFZ show a frequent directional change in water mass movement, with only a small positive annual average movement westward through the CGFZ (Read et al., 2010).

In 2007, CTD data were collected by Ms. Jane Read (OBE, National Oceanography Centre) on JC011 (Gooday et al., in press). CTD measurements between 2,113 and 2,777 m water depth covered the benthic sampling range (Table 2.1). There was little variation in temperature (2.93 to 3.20 °C), salinity (34.92 to 34.98 psu) or oxygen (281.20 to 282.43 µmol l^{-1}) (Table 2.3). Furthermore, data indicate that near-bottom flows at those depths, when forced to cross topography, cause enhanced local small scale turbulence (Dale and Inall unpublished).

TABLE 2.1: CTD data collected in 2007 at JC011. **press** = pressure, **temp** = temperature, **salin** = salinity. Data courtesy of Ms. Jane Read (Gooday et al., in press).

Site	**station number**	**press (dbart)**	**temp (°C)**	**salin (psu)**	**oxygen (µmol l^{-1})**	**Latitude**	**Longitude**
SE	JC011/016	2777	3.15	34.92	282.43	49° 04.83′N	27° 50.79′W
SE	JC011/025	1717	3.65	34.91	282.97	49° 02.20′N	27° 55.62′W
SW	JC011/034	1579	3.69	34.90	280.88	49° 53.26′N	28° 20.21′W
SW	JC011/036	2575	3.15	34.92	281.28	48° 45.80′N	28° 38.41′W
NW	JC011/066	1695	3.30	34.95	281.14	53° 48.15′N	35° 50.42′W
NW	JC011/069	2113	3.20	34.94	281.97	54° 09.01′N	36° 21.64′W
NW	JC011/070	2625	3.12	34.96	281.49	53° 59.74′N	36° 07.67′W
NE	JC011/090	1497	3.41	34.94	280.50	54° 00.00′N	34° 57.00′W
NE	JC011/091	2429	3.01	34.98	282.02	54° 00.00′N	34° 17.99′W
NE	JC011/099	2479	2.93	34.98	281.20	54° 00.00′N	33° 57.97′W

Apart from the Scotland-Iceland-Overflow Water, Arctic Bottom Water also characterises the area around the CGFZ. Arctic Bottom Water, which is the densest water in the world's oceans, is formed in the North Atlantic. However, only 4 Sv are carried outside of the Arctic and are referred to as Arctic Botton Water Overflow, which has an eastern and a western branch (Tomczak and Godfrey, 2003). The eastern overflow is mixed with surrounding water and carried southward into the eastern North Atlantic until it reaches the western Atlantic through the CGFZ, where it eventually joins the western overflow (Tomczak and Godfrey, 2003). The CGFZ is deep enough to allow this water to pass through below 3,000 m water depths (Tomczak and Godfrey, 2003). The bottom water that is found in the Atlantic basins is characterised by high salinity and high dissolved oxygen content (Tomczak and Godfrey, 2003).

2.4 Surface Water Primary Production

The Sub-Polar Front is characteristic for the ECOMAR study area and more nutrient rich waters were assumed to the north than to the south of the CGFZ. **P**rimary **p**roduction (PP) was compared between the northern and southern ECOMAR sites, between 1998 and 2010. Based on particle advection trajectories over a 400 km radius, the mean annual PP was confirmed to be higher over the northern sites (206 g C m^{-2} y^{-1}) compared to the southern ones (198 g C m^{-2} y^{-1}) (Tilstone et al., in prep). While the PP over the two northern sites showed no significant difference between the sites, a significant difference was observed over the southern sites, with a general decrease in PP over the SE site. This decrease in PP over the SE site has been associated with a decrease in micro- and nano-phytoplankton abundances and an increase in pico-phytoplankton abundance (Tilstone et al., in prep). The composition of pico- and nano phytoplankton in the surface waters differed significantly between the northern and southern ECOMAR sites. An enhanced biological activity was measured over the southern sites, which coincided with the Sub-Polar Front (Martinez-Vicente et al., 2011) (Table 2.3).

2.5 Information about the Pelagic Realm

Acoustic data were collected using a line-transect survey design by the St. Andrews team, lead by Dr. Martin Cox. Data were obtained at five frequencies (18, 38, 70, 120 & 200 kHz; one per panel) on the 2007 and 2009 cruises, using a multifrequency acoustic system. Following the cruise, an acoustic multi-frequency information algorithm was used to identify the dominant acoustic scatter in each assigned grid cell. This was achieved by using a combination of acoustic frequencies to maximise the depth to which the scatter type could be determined. Using the SIMFAMI algorithm, biovolumes (mm^{3} m^{-3}) were converted into mean zooplankton carbon concentrations (mg C m^{-3}) that were estimated between depths of 20 to 700 m. There was a significant north/south difference with noticeably higher carbon concentrations of zooplankton carbon standing stock in the south (Table 2.3). The highest carbon concentrations were related to euphausiids at all sites, followed by copepods, which showed a higher signal towards the south than the north. Another zooplankton signal identified was as large as the copepod signal, however, the identity of this zooplankton group has still to be determined (Dr. Martin Cox, *pers. comm.*). The greatest zooplankton biomass collected with pelagic trawling came from the NE site (Priede, 2009). In 2009, a large salp swarm also occurred at the SE site, with very high densities and biomass.

Zooplankton has been collected from different depths from the ECOMAR region and has been divided into mesopelagic zooplankton and bathypelagic/benthopelagic consumers (Letessier et al., 2012). The abundance of these groups differed between north and south, with higher abundances to the north supporting a PP increase north of the CGFZ (Letessier et al., 2012). However, species richness was greater at the southern sites (Priede, 2009). Species characteristic for the northern sites were *Sagitta* sp., Euchaetidae, *Themisto compressa* and *Sergestes arcticus*, while decapods *Sergia japonica*, *Parapasiphae sulcatifrons*, *Acanthephyra pelagica* and *Gennadas elegans* were typical for the southern sites (Letessier et al., 2012). The only species that was found in high abundances at all sites was the benthopelagic *Gnathophausia zoea*. Higher euphausiid species abundances were measured over the ridge compared to adjacent waters, and it has been hypothesised that niche availability is related to surface water temperatures (Letessier et al., 2009).

Data indicate that the energy transfer from the surface through the food web towards benthic communities might be driven by different micronektic communities and trophodynamics (Letessier et al., 2012). It has been suggested that differences in bloom seasonality are less important than yearly production rates (Letessier et al., 2012).

2.6 Particle Transport at the MAR

In order to measure the material flux from the surface waters, moorings with sediment traps were placed at the ECOMAR sites between 2007 and 2010. Unfortunately, some of the sediment traps failed. The information that was acquired from the remaining traps 1,000 m **a**bove **t**he **s**eafloor (ats) suggest the greatest total material flux occurred over the SW and NE sites, and the lowest material flux over the NW site (Table 2.2). Greater material flux was recorded in the traps set at 100 m ats (Table 2.2). This increase is considered a result of increased trap efficiency with increasing depth, rather than resuspension (Abell et al., submitted). It has been suggested that this could be caused by a greater clustering efficiency of particles with increasing depth. The traps 100 m ats might also get the additional flux from the ridge topography. However, conventionally it is believed that the traps 100 m ats are affected by resuspension from the benthic boundary layer (Lampitt et al., 2001). Based on the assumption that greater sediment flux is caused by resuspension, data on mean SFE (Table 2.2) show greater resuspension at the eastern sites, in particular the NE site, compared to the western sites.

In sediment traps 1,000 m ats the highest **O**rganic **C**arbon (OC) content was seen at the NW site and the lowest at the SE site (Table 2.2) (Abell et al., submitted). However, 100 m ats the OC availability changed to the highest at the SW site and the lowest at

Table 2.2: Sediment Trap Data; **MS** = **M**ean **S**ediment Trap sample weight (mg), **SFE** = Mean **S**ediment **F**lux **E**stimate (mg m^2 day), **OCF** = **O**rganic **C**arbon **F**lux (mg m^2 day), **OC %** = % of **O**rganic **C**arbon in Sediment Trap Sample. Data courtesy of R. Abell (*pers. comm.*).

Site	**Altitude**	**MS**	**MS SD**	**SFE**	**SFE SD**	**OCF**	**OCF SD**	**OC %**	**OC % SD**
SE	100	639.04	± 564.35	62.43	± 57.89	5.19	± 2.93	2.96	± 2.58
	1000	344.52	± 424.25	30.98	± 38.80	5.67	± 2.29	1.91	± 2.83
SW	100	558.75	± 698.85	46.05	± 50.91	6.24	± 6.43	2.75	± 3.53
	1000	403.53	± 408.33	32.75	± 35.39	7.40	± 6.74	2.26	± 2.69
NE	100	1086.54	± 991.62	106.50	± 86.24	2.22	± 2.16	2.72	± 2.42
	1000	440.62	± 484.20	51.72	± 59.81	7.52	± 9.01	1.89	± 1.99
NW	100	404.76	± 501.62	42.00	± 45.14	5.78	± 12.15	1.57	± 2.08
	1000	101.71	± 153.77	10.80	± 17.45	13.40	± 17.13	0.69	± 0.85

the NE site. A north/south pattern in energy flux was not obvious in the sediment trap data, despite the greater PP measured over the northern sites (Table 2.3).

Although no clear seasonal signal could be observed, patterns and peaks of export were recorded in traps from both trap depths, at all four sites. The average organic carbon flux during the ECOMAR field phase (summer 2007 to summer 2010) for the 100 m traps (above the seafloor) was 2.9 mg m^{-2} day^{-1}, and for the 1,000 m traps (above the seafloor) was 1.8 mg m^{-2} day^{-1}.

Altimeter data collected on the moorings were used to investigate the source regions of particles. These were modelled based on the assumption of a constant speed, with three different sinking speeds being tested (10 m day^{-1}, 50 m day^{-1}, 100 m day^{-1}). Particles were tracked backwards in time from the time of sample collection to their presumed source at the surface. The northern and southern moorings had source regions with little, if any, overlap, even at the slowest sinking rate. This suggests a divide between the northern and southern sites by the Sub-Polar Front. Between the southern sites even the fastest sinking rate showed strongly overlapping regions, indicating that there are no clear distinctions between the source regions (Table 2.3). In contrast, the source regions for the NW and NE sites were more distinct, especially at the fastest sinking rate (Dale and et al., submitted).

2.7 Benthic Food Webs

The main aim of ECOMAR was to investigate the non-hydrothermal vent environment at the MAR, and although bathymetry data did not indicate any presence of hydrothermal vents, bathymetry resolution was not very high and further confirmation was needed. A high dependence of benthic and benthopelagic fauna on photosynthetic primary production, without any hydrothermal vent input, was confirmed by measuring δ^{13} C and δ^{34} S, in a selection of common species at the ECOMAR sites (Reid et al., in press). A strong trophic discrimination was found with a δ^{13} C analysis between consumers and potential food sources. It has been suggested that this strong discrimination indicates that reworking of organic carbon occurs before assimilation by benthic fauna (Reid et al., in press). Tropic guilds could be differentiated with δ^{13}C and δ^{15}N analyses, with a particular strong signal between mobile predators/scavengers and deposit feeders (Reid et al., in press).

2.8 Substrate

As a result of the **C**arbon **C**ompensation **D**epth (CCD) the sediment types on mid-ocean ridges vary with depth (Tomczak and Godfrey, 2003). The MAR has a shallow summit and a deep CCD, causing a different sediment composition (foraminiferan and coccolithophorid oozes) on higher parts of the ridge than the surrounding abyssal plains (Tyler, 1995; Thistle, 2003). Sediment is derived either from terrigenous or marine biogenic sources, although some sediment particles originate from volcanoes (Brown et al., 1989; Tyler, 1995; Seibold and Berger, 1996; Thistle, 2003). Biogenic sediment is predominantly made up of the shells of dead planktonic marine organisms (Brown et al., 1989; Thistle, 2003). Marine organisms, notably planktonic foraminiferans, coccolithophores and pteropods, produce calcium carbonate shells, while diatoms, radiolarians and silicoflagellates produce silica (opal) shells (Brown et al., 1989; Thistle, 2003). In areas under high biogenic surface production the sea bed consists of carbonate ooze above the CCD, and siliceous ooze and red clays below the CCD (Tyler, 1995; Seibold and Berger, 1996). Sediments containing > 30 % biogenic components are referred to as biological oozes (or calcerous/siliceous ooze), while red clay has < 30 % biogenic ooze, is devoid of calcareous material, and forms below the CCD (Brown et al., 1989; Gage and Tyler, 1991). Large-scale processes control sediment composition and uniformity over hundreds of square km (Thistle, 2003). At smaller spatial scales, organic material derived from surface production (Tyler, 1995), together with faunal structures and traces (Seibold and Berger, 1996) can cause patchiness.

Table 2.3: Summary of Data Collected from Other ECOMAR Research Groups

Equipment	**Measurement Taken**	**NW Site**	**NE Site**	**SW Site**	**SE Site**
Satellite	Primary Production	206 g C m^{-2} y^{-1}	206 g C m^{-2} y^{-1}	198 g C m^{-2} y^{-1}	198 g C m^{-2} y^{-1}
	Difference between East & West Sites	non	non	Sig. higher than SE	Sig. lower than SW
	Surface Meanders & Eddies	Absent	Absent	Absent	Present
Sediment traps 1,000 m ats	Organic Carbon	17.13 mg m^2 day^{-1}	9.01 mg m^2 day^{-1}	6.74 mg m^2 day^{-1}	2.29 mg m^2 day^{-1}
	Sediment Flux	10.80 mg m^2 day^{-1}	51.72 mg m^2 day^{-1}	32.75 mg m^2 day^{-1}	62.43 mg m^2 day^{-1}
100 m ats	Organic Carbon	12.15 mg m^2 day^{-1}	2.16 mg m^2 day^{-1}	6.43 mg m^2 day^{-1}	2.93mg m^2 day^{-1}
	Sediment Flux	42.00 mg m^2 day^{-1}	106.80 mg m^2 day^{-1}	46.05 mg m^2 day^{-1}	30.98 mg m^2 day^{-1}
	Modelled Source region	discrete	discrete	Overlap with SE	Overlap with SW
CTD	Depth	2,500 m	2,400 m	2,600 m	2,700 m
	Temperature	3.12 °C	2.96 °C	3.15 °C	3 °C
	Oxygen	281.49 micro mol l^{-1}	281.90 micro mol l^{-1}	281.28 micro mol l^{-1}	282.43 micro mol l^{-1}
	Salinity	34.96	34.98	34.92	34.92
Megacorer	Sediment type	Mud	Mud	Silt/Clay	Silt/Clay
	Signs of Burrowing	Present	Present	Present	Present
	Observed Phytodetritus	Spring	Spring	Spring & late Summer	Spring & late Summer
	Pteropod shells	Non	Non	Abundant	Abundant
	Stratification	Yes	Yes	No	No
RMT	Zooplankton				
	Richness	Lower	Lower	Higher	Higher
	Abundance	Higher	Higher	Lower	Lower
Acoustic multi-frequency survey	Mg C m^{-3}	Lower	Lower	Higher	Higher

2.8.1 ECOMAR Sediment

At the ECOMAR sites megacore samples were collected on all cruises, with the exception of the NW site in 2007. The sediments at the paired northern and southern sites showed distinctive characteristics, but eastern and western sites were very similar.

The northern sites were characterised by very fine, soft mud (Table 2.3). They showed a surficial light brown mud layer of about 18 cm, and 10 to 15 cm, at the NE and NW sites, respectively (Priede, 2007, 2009). Below the upper layer a dark layer of variable depth was reported, averaging 5 cm in thickness, which was followed by a layer of grey mud (Figure 2.2). While both sites had extremely soft sediment, the NW site was slightly more so. The extreme softness of the sediment at the NW site is speculated to have caused a lower success rate in collecting megacore samples at this site (Priede, 2009). Megacore samples from both the NE and NW sites lacked a phytodetritus layer on the sediment surface in 2007 and 2009, while such a layer was reported in 2010 (Priede, 2007, 2009; Priede and Bagley, 2010). The 2007 and 2009 cruises were carried out around late July/August, and the 2010 cruise around early June, suggesting a spring bloom deposition event at the northern sites. Both sites also showed evidence of burrowing megafauna in the sediment cores. It has also been speculated that the surficial brown upper layer at the northern sites might have been deposited during the Holocene, which would suggest a sediment accumulation rate of about 2 cm ky^{-1} (Priede, 2009). Furthermore, in cores from the NE site large numbers of sponge spicules were reported in the upper 10 cm, while at the NW site the sediment appeared to have high pore water content (Priede and Bagley, 2010).

Compared to the northern sites, sediments at the southern sites were slightly coarser and of a silt/clay consistency, with increased sand fraction compared to the northern sites (Priede, 2009; Priede and Bagley, 2010). Unlike cores collected from the northern sites, the southern sites did not show any signs of sediment banding, but were instead characterised by a light brown, grainy, homogenous sediment layer (Figure 2.2) (Priede, 2009). Both southern sites had large numbers of pteropod tests with a patchy distribution on the sediment surface that were absent from deeper layers (Priede, 2007, 2009). On JC048 (2010) dark grey patches were observed several cm into the sediment which were found to contain large numbers of pteropod tests (Priede and Bagley, 2010). Phytodetritus patches several mm thick were observed at both southern sites on all three cruises (Priede, 2007, 2009; Priede and Bagley, 2010). Both southern sites showed evidence of burrowing megafauna (Priede and Bagley, 2010). In 2009 the phytodetritus layer and the pteropod test deposit at the SE site were reported as denser compared to the SW site (Priede, 2009).

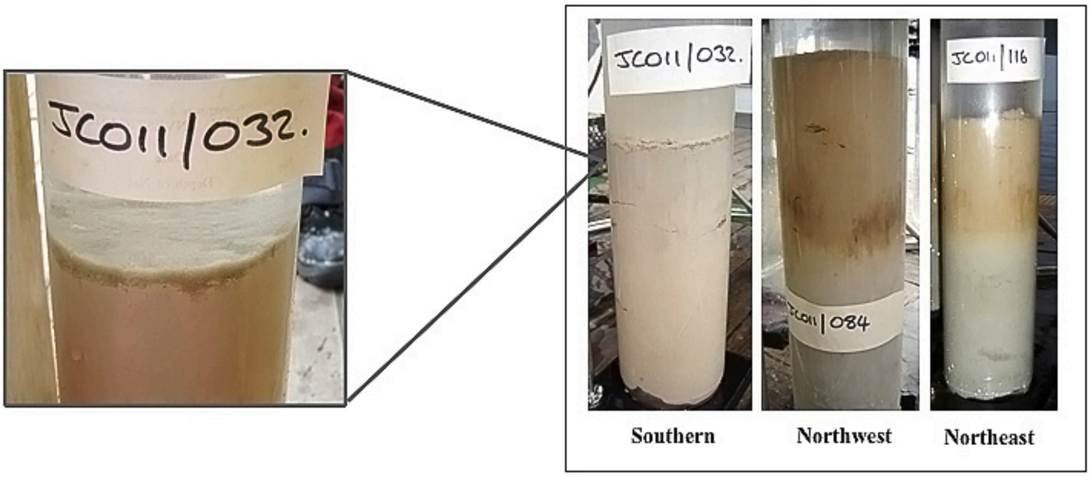


FIGURE 2.2: Sediment profiles for the southern sites, the northwest and northeast, on the right hand side. On the left hand side, a layer of phytodetritus on the sediment surface from the SE Site, which was absent from the northern sites during late summer sampling. Photo courtesy of Dr. Alan Hughes.

2.9 Benthic Invertebrate Megafauna

2.9.1 Biology at the Northern MAR, in Non-Chemosynthetic Habitats

Prior to the MAR-ECO project only very little was known about the biology of mid-ocean ridges (Tyler, 1995). A faunal transition between 800 and 1,000 m water depth had been observed on the northern MAR (Copley et al., 1996). Most of our ecological knowledge from the Mid-Atlantic Ridge results from the first MAR-ECO field phase.

Data show that benthic assemblages at the MAR are distinct between the Azores and the CGFZ, with the CGFZ further divided into zones between 1,263 to 1,916 m, and 2,350 and 3,512 m depth (Gebruk et al., 2010). The distribution of some megafauna, such as holothurians, appears to be random around the CGFZ (Felley et al., 2008). The topography of the ridge is very heterogenous and fauna is dominated by invertebrates such as echinoderms (49.5 %), sponges (18.2 %) and anthozoans (16.7 %) (Gebruk et al., 2010). Many new species were discovered, including echinoids (Mironov, 2008), ophiuroids (Martynov and Litvinova, 2008), asteroids (Dilman, 2008) and holothurians (Gebruk, 2008). The hard substratum is dominated by sessile organisms (Felley et al., 2008).

Fish abundance and biomass are highest in the benthic boundary layer, indicating a bathypelagic fish assemblage (Sutton et al., 2008). Outside the benthic boundary layer, abundance is lowest at 2,300 m. It is suggested that the increased biomass and abundance in the benthic boundary layer is caused by increased bathypelagic food sources on the ridge, compared with the surrounding abyssal plains (Sutton et al., 2008). Scavenging fish were observed to form three depth related assemblages between 924 and 1,198 m, 1,569 and 2,355 m, and 2,869 and 3,420 m, and are all dominated by different individual fish species (King et al., 2006).

2.9.2 Biogeography of the MAR, in the Vicinity of the CGFZ

According to the biogeochemical provinces by Longhurst, the area around the CGFZ is in the Atlantic Westerly Winds Biome. South of the CGFZ is the **N**orth **A**tlantic **S**ub**t**ropical (NAST) Gyral Province (Longhurst, 2007), which has typically weak winter mixing and short winter phytoplankton blooms, dominated by coccolithophorids (Longhurst, 2007). This province is further subdivided into NAST-E and NAST-W, with the MAR as a natural barrier. *Sargassum* seaweed is very abundant in the surface waters to the west of the MAR, while almost absent to the east (Longhurst, 2007). Chlorophyll is generally low compared to other provinces, with the highest concentrations in March to April; concentrations tend to be higher in the NAST-E than in the NAST-W (Longhurst, 2007). North of the CGFZ is the North Atlantic Drift Province (Longhurst, 2007), which is characterised by strong winter mixing and a strong spring bloom that is followed by a smaller bloom in late summer (Longhurst, 2007).

The area of the MAR, around the CGFZ has been recognised as a boundary for species confined to either the eastern or western basins of the North Atlantic (Vinogradova, 1997; Longhurst, 2007). Vinogradova (1997) classified the CGFZ as part of the North-Atlantic Abyssal Province, which puts most cold water species at the limit of their distribution around the CGFZ (Zezina, 1997). On its western slope a zone has been identified at 2,000 m depth that contains a similar number of species as the western and eastern Atlantic (Mironov and Gebruk, 2006). This area also corresponds to the western boundary of the coral species *Flabellum* found in the eastern Atlantic, and the eastern boundary for a barnacle *Cirripedia* species found in the western Atlantic (Mironov and Gebruk, 2006).

The recent GOODS report splits the ocean into pelagic and benthic provinces (Agostini et al., 2009). The pelagic zone to the north of the CGFZ falls within the Subarctic Atlantic Province, which reaches from 200 to 4,500 m depth, and the area to the south falls within the North Atlantic Current, which affects depths between 100 to 5,000 m water depth. According to the GOODS report (Agostini et al., 2009) the entire benthic North Atlantic, between 3,500 and 6,500 m, belongs to North Atlantic Deep Water Province, which characteristically has temperatures of 2 to 3 °C, salinity of 34.5 to 35 psu, and dissolved oxygen of over > 5 ml l^{-1}. The lower bathyal province between 800 and 3,000 m is classified as Northern North Atlantic Province, which typically has water temperatures of 3 to 4 °C, a salinity of 34.6 to 35 psu, and dissolved oxygen of over > 5 ml l^{-1} (Agostini et al., 2009).

In all three biogeographical schemes, the CGFZ is a significant feature that divides the MAR into different provinces (Agostini et al., 2009; Longhurst, 2007; Mironov and Gebruk, 2006). However, in the GOODS report this is only true for the pelagic realm, and no differences are identified in bathyal benthic provinces on the eastern and western flanks of the MAR (Agostini et al., 2009). In contrast the biogeochemical provinces and the zoogeographic regions both recognise the ridge as a barrier between the eastern and western Atlantic Ocean. The GOODS classification, however, recognises the MAR as distinct from other bathyal habitats in the Atlantic (Agostini et al., 2009).

2.10 Working Hypotheses

This thesis is part of the ECOMAR effort to increase our understanding of the ecosystem around the Charlie-Gibbs Fracture Zone. Data collected within the ECOMAR field phase, between 2007 and 2010, are analysed in detail and contribute further to our understanding of this region. Data for this thesis were collected with three distinct methods (trawling, video survey, molecular analysis). One of the most striking differences between these methods is the area they can sample. The following testable hypotheses were addressed within this work :

- Biomass, as measure of energy input, does not differ between the southern and northern sites in benthic megafauna.
- Biomass, as measure of energy input, does not differ between the eastern and western site in benthic megafauna.
- Body sizes of benthic megafauna do not differ between the south and the north.
- Body sizes do not differ in benthic megafauna between east and west.
- No particular species is dominant at any site, suggesting an even species distribution.
- There is no difference in diversity in benthic megafauna between the southern and northern sites.
- There is no difference in diversity in benthic megafauna between the western and eastern sites.

- There is no difference in the community composition of benthic megafaunal between the southern and northern sites.
- There is no difference in the community composition of benthic megafaunal between the eastern and western sites .
- Small-scale habitat variations do not affect benthic community composition of megafauna assemblages at the MAR.
- The taxonomic relationship of benthic megafauna at the MAR are resolved.
- The new species *Peniagone coccinea*, *Laetmogone billetti*, *Molpadia* sp. nov. are not genetically distinct from other holothurians found at the MAR.
- *Gephyrothuria alcocki* does not belong to the Order Molpadiida.

Chapter 3

Trawling Benthic Megafauna at the Mid-Atlantic Ridge

3.1 Introduction

Variations in energy supply, such as those observed over the ECOMAR sites north and south of the **C**harlie-**G**ibbs **F**racture **Z**one (CGFZ), are considered potential drivers for biodiversity changes in benthic invertebrate megafauna and are also thought to affect body size, density, and biomass (Thurston et al., 1994; Billett et al., 2001; Wigham et al., 2003a,b). These variations can occur spatially and temporarily and have been associated with benthic community shifts at abyssal depths (Billett et al., 2001; Ruhl, 2008). The presence of geological features such as the CGFZ and the **M**id-**A**tlantic **R**idge (MAR) can potentially act as dispersal barriers and therefore, may also result in differing community composition.

Deep-sea benthic communities may experience major changes in biodiversity, body size, density and biomass over time and space (Glover et al., 2010). There is evidence for such changes at sites in the abyssal Atlantic (Billett et al., 2001) and Pacific (Ruhl, 2008), where orders of magnitude shifts in the density of common megafaunal species between sampling years are primarily associated with changes in the chemical composition of settling particles (Kiriakoulakis et al., 2001). The increase in the density of some taxa, and the decrease in others, led to the community shifts observed at the abyssal **P**orcupine **A**byssal **P**lain (PAP) (Billett et al., 2010) and the Pacific Station M (Ruhl, 2007, 2008). Besides changes in biodiversity and community composition, median body sizes are negatively correlated with higher density (Ruhl, 2008). Changes in the biology and ecology of megafauna also occur spatially and are associated with changes in particle flux quality. Decreases in biomass, abundance, and size with depth are believed to be a result of decreasing food availability rather than higher pressure (Sibuet et al., 1989; Rex et al., 2006). Spatial and temporal variation in food availability to benthic organisms reflects surface plankton dynamics and variable degrees of remineralisation during sinking (Thurston et al., 1994). In general, food availability is considered to be the most important ecological driver affecting the distribution of benthic fauna in the deep sea (Lampitt et al., 1986; Galéron et al., 2000; Smith et al., 2008a; Billett et al., 2010).

Benthic invertebrate megafauna are restricted in their mobility as adults. Some can swim or float but this probably occurs only over very short distances and as a means to locate food patches (Jones et al., submitted; Rogacheva et al., acceptedb). Instead, invertebrate megafauna generally depend on larvae for their dispersal (Young et al., 1997). It is likely that geological features such as ridges and fracture zones act as barriers to larval dispersal. A genetic study of dispersal of the bivalve *Deminucula atacellana* revealed that this species has the capacity to disperse over thousands of kilometres within the same depth range, and that the effect of depth on dispersal range is stronger than that of distance (Zardus et al., 2006). Although there is evidence that submarine ridges are not effective barriers to mobile bathyal fish (White et al., 2010) and mobile abyssal crustaceans (Menzel et al., 2010), the deep trough of the CGFZ does appear to act as a barrier to fish dispersal (White et al., 2010). The barrier created by the CGFZ might represent an oceanographic rather than a geological hurdle since water masses cross the ridge through the CGFZ in fluctuating directions, although with an overall westward tendency (Saunders, 1994). The current movement possibly could prevent larvae from moving either north or south at some depths, although it might facilitate east to west movement. Finally, the movement of the Scotland-Iceland overflow water from the eastern Reykjanes Ridge to the western side (Saunders, 1994; Bower and von Appen, 2008) provides a potential path for larval exchange from the NE to the NW site.

Trawl samples were collected at three (NW, NE, SE; all at about 2,500 m depth) of the four ECOMAR sites. A semi-balloon otter trawl (OTSB) was used to obtain the samples. This is smaller than commercial trawls and therefore ideal for trawling in restricted areas, such as those found at the MAR (Priede et al., in prep). The OTSB yields large qualitative samples, providing material for detailed taxonomic analyses as well as size and weight data for individual specimens.

3.2 Methods

3.2.1 Sampling

Trawl samples were collected during RRS James Cook cruises 11 (JC011; 13 July to 18 August 2007) and 37 (JC037; 1 August to 9 September 2009) at three ECOMAR sites ($\sim$ 2,500 m): southeast (48 ° 58 ′N, 27 ° 51 ′W), northeast (54 ° 05 ′N, 33 ° 58 ′W), and northwest (54 ° 19 ′N, 36 ° 01 ′W) (Figure 2.1, page 24). The samples were obtained using a 13.7 m long **s**emi-**b**alloon **o**tter **t**rawl (OTSB) with a single warp (Thurston et al., 1994; Priede et al., 2010). The effective opening width of the OTSB is about 8.6 m, and the net is composed of 43 mm and 37 mm stretch mesh netting, reducing to 13 mm stretch mesh in the cod end (Thurston et al., 1994). The average trawling speed was between 2 and 2.5 knots (Priede, 2007, 2009), which is the ideal speed for collecting both mobile and non-mobile animals at the water sediment interface (Priede et al., 2010). During JC011 (2007), one successful trawl was collected at the **s**outh**e**ast (SE) and **n**orth**w**est (NW) sites and three trawls from the **n**orth**e**ast (NE) site (Table 3.1). During JC037 (2009) a further three trawls were obtained from the SE and NW sites (Table 3.1).

3.2.2 Processing

The invertebrates were separated from the fish and sorted into major taxonomic groups onboard the RRS James Cook. The wet weight of the major taxa was measured with a S182 Marine Scale (POLS hf, Iceland). Specimens were fixed in 4 % borax-buffered formaldehyde solution, and preserved in 70 % ethanol.

Species were identified to the closest possible taxonomic unit (led by Antonina Rogacheva). Unfortunately, small aggregating holothurians collected at the NE site were damaged and it was not possible to identify them to species level. They are referred to as Elpidiidae mix. This mix included *Kolga nana*, *Peniagone azorica*, *Peniagone longipapillata*, *Ellipinion delagei* and *Ellipinion alani*. In the laboratory, individuals were measured to the closest mm using an electronic calliper.

Table 3.1: Successful trawls from the Mid-Atlantic Ridge collected in 2007 from JC011, and in 2009 from JC037, with detail on station numbers, collection dates, trawling locations, trawling depths, total areas trawled, and the site in relation to the Charlie-Gibbs Fracture Zone. Co-ordinates and depths are given for the start and end position of each trawl.

Station No.	**Date**	**Latitude**	**Longitude**	**Depth** (m)	**Area trawled** (ha)	**Site**
JC011/023	21.07.2007	48° 54.59′N	27° 50.00′W	2718	3	SE
		49° 15.85′N	27° 50.00′W	2734		
JC011/075	05.08.2007	53° 51.10′N	36° 11.36′W	2615	4	NW
		54° 06.02′N	36° 07.20′W	2630		
JC011/101	10.08.2007	54° 06.33′N	33° 58.27′W	2405	6	NE
		53° 47.47′N	34° 02.89′W	2435		
JC011/106	11.08.2007	54° 05.68′N	33° 58.54′W	2410	6	NE
		54° 46.94′N	34° 03.02′W	2445		
JC011/111	12.08.2007	54° 05.68′N	33° 58.54′W	2404	6	NE
		53° 47.71′N	34° 02.83′W	2430		
JC037/015	10.08.2009	49° 05.04′N	27° 50.70′W	2750	2	SE
		49° 06.59′N	27° 49.84′W	2750		
JC037/019	11.08.2009	49° 04.64′N	27° 50.66′W	2754	4	SE
		49° 07.16′N	27° 50.30′W	2724		
JC037/027	18.08.2009	49° 04.79′N	27° 50.29′W	2755	5	SE
		49° 07.86′N	27° 50.51′W	2702		
JC037/061	28.08.2009	54° 13.04′N	36° 04.07′W	2598	5	NW
		54° 09.83′N	36° 05.58′W	2619		
JC037/067	29.08.2009	54° 13.07′N	36° 04.03′W	2598	5	NW
		54° 09.96′N	36° 04.08′W	2625		
JC037/070	30.08.2009	54° 13.00′N	33° 58.54′W	2604	4	NW
		54° 10.53′N	36° 05.24′W	2615		

3.2.3 Analyses

Analyses were carried out on the major taxa in the trawl samples. Species that were not collected reliably by trawling were excluded. These included macrofaunal annelids, echiurans and nemerteans, which are traditionally collected in cores owing to their small size. Actinarians, gorgonians, crinoids and ascidians were also excluded because they are associated with hard rock substratum and are by-catches of the sampling method.

The wet weight obtained on the ship was converted into ash-free dry weight and carbon weight based on conversion factors published by Lampitt et al. (1986). Conversion factors were not available for all the taxonomic groups and so were estimated for some taxa; the same conversion factors were used for cnidarians and asteroids, sipunculans and holothurians, and pycnogonids and ophiuroids. Molluscs were estimated to have conversion factors halfway between crustaceans and asteroids (Table 3.2). Carbon weight was used to compare the sites, as it best reflects the amount of energy used by major taxonomic groups in a particular area. Ash-free dry weight was used to compare with other studies.

Table 3.2: Conversion factors used to convert collected fresh **w**et **w**eight (WW) to **a**sh **f**ree **d**ry **w**eight (AFDW) and **o**rganic **c**arbon (OC) weight. Conversion factors are based on Lampitt et al. (1986), and were estimated for cnidarians, sipunculans, pycnogonids and molluscs.

Taxa	**Conversion factor from fresh WW to AFDW**	**Conversion factor from fresh WW to OC**
Asteroids	27.11	9.05
Holothurians	3.64	2.78
Echinoids	19.94	6.20
Ophiuroids	43.23	8.67
Crustaceans	11.28	16.83
Pycnogonids	43.23	8.67
Molluscs	20.00	12.00
Cnidaians	27.11	9.05
Sipunculans	3.64	2.78

A few species were sufficiently abundant for their sizes to be compared between sites. Species were grouped into different size classes: holothurians, the sipunculan *Sipunculus norvegicus*, and the echinoid *Urechinus naresianus* were grouped into 10 mm size classes, while asteroids were placed into 5 mm size classes. In the case of holothurians and sipunculans, size refers to body length; in echinoids it refers to the length of the oral side. For asteroids, both the arm length and the interradius were measured, but because many arms were damaged, the size of the interradius (excluding arms) was used for size comparison between sites.

Biomass, density and diversity were compared using the non-parametric Kruskal-Wallis analysis, which was used because data were not normally distributed, and sample not of equal size. Differences in size distributions were compared using the Kolmogorov Smirnov test, which was used because it makes no prior assumption about the distribution of data. Both analyses were done in the R programming environment (R Development Core Teams, 2009). In order to visualise the ranges of biomass, density and diversity they were plotted with their standard deviation. However, when compared to other studies, these measures were plotted with their standard error, to show the 95 % confidence interval, which made it easier to asses any differences to other studies.

The evenness for different samples was determined using a Whittaker Rank Abundance plot (Whittaker, 1972), calculated using the R programming environment (R Development Core Teams, 2009) (Section 1.4.3.2). This method is preferred because the shape of the curve makes it easier to decide whether data need to be transformed and how many rare species are present (Magurran, 2004). Pielous evenness J' was also calculated, using Primer 6 (Clarke and Warwick, 1994), to enable comparison with other studies. Species richness was taken as the number of species in a given area (Gray, 2000) and was calculated with a species accumulation curve using the Sobs parameter in Primer 6 (Clarke and Warwick, 1994) (Section 1.4.3.1). Sobs was calculated using the number of individuals. The Shannon-Wiener and the Simpson indices were also calculated in Primer 6. The Simpson index emphasises rare species and the Shannon-Wiener index places more weight on dominant species (Magurran, 2004) (Section 1.4.3.3). In order to calculate these metrics, the numbers of elpidiids (i.e. the Elpidiidae mix) were split equally between the five component species, yielding the highest possible evenness and hence the highest possible diversity, making this approach conservative.

In order to investigate similarities between sites a one-way ANOSIM, a non-metric **m**ultidimensional **s**caling **a**nalysis (MDS), and a hierarchical cluster analysis, were carried out using Primer 6 (Clarke and Warwick, 1994). The cluster analysis was then overlain onto the MDS plot. All data were square root transformed for multivariate analyses. The ANOSIM was run with the maximum number of possible permutations (5,775), using site as factor. Multivariate analyses were based on a Bray-Curtis similarity matrix. A one-way SIMPER analysis was run in Primer 6, based on Bray-Curtis similarity with a cut off for low contributions at 90 %. This analysis shows a) the % similarity of the assemblages between individual hauls, factored by site; and b) the % average dissimilarity between sites, in terms of species composition.

Species lists for each site (all trawl samples combined) were compared to identify the species only found at one site (termed unique species). To avoid counting errors, this was done automatically using a custom Matlab programme (Matlab version r2010b, Mathworks). The numbers of species unique to each site were divided into the number of unique species for particular taxa (asteroids, crustaceans, echinoids, holothurians and ophiuroids).

3.3 Results

A total of 21,959 individuals represented 153 taxa. Of these individuals, 14,131 (64.4 %) were holothurians, 2,821 (12.8 %) asteroids, 2,587 (11.8 %) ophiuroids, 829 (3.8 %)

crustaceans, 695 (3.2 %) echinoids, 437 (2 %) pycnogonids, 338 (1.5 %) sipunculans, and 121 (0.6 %) molluscs.

3.3.1 Biomass

The SE had the highest total **w**et **w**eight (WW) and the NW the lowest (Table 3.4). Although the differences in total WW between the sites were not significant (Kruskal-Wallis: chi-squared = 0.85, df = 2, p = 0.66), individual taxa contributed in varying degrees to this total (Table 3.4). Holothurians dominated WW at all three sites, contributing in similar proportions to the total WW at the NE and SE sites (NE: 72 %, SE: 73 %), with a lower proportion at the NW site (44 %). Each site also yielded a high WW of asteroids (NE: 19 %, SE: 13 %, NW: 12 %), though this was less pronounced than that of the holothurians. The WW of holothurians and asteroids differed between sites, but this variation was not significant (Table 3.4). There was also a higher WW of cnidarians at the SE site (6 %), echinoids at the NW site (23 %), and sipunculans at the NE site (1 %) (Table 3.4). The WW of echinoids, ophiuroids, pycnogonids, cnidarians and sipunculans differed significantly between sites (Table 3.3 & 3.4).

Table 3.3: Results from a Kruskal-Wallis analysis, testing for the biomass differences of the individual taxonomic groups between sites, with their respective chi-squared value, degrees of freedom (df), and the p value. Highlighted in bold are those groups that differed significantly in biomass between sites.

Taxonomic Groups	**Kruskall-Wallis Results**
Asteroids	Chi-squared = 5.296, p = 0.07, df = 2
Holothurians	Chi-squared = 5.212, p = 0.07, df = 2
Echinoids	**Chi-squared = 7.849, p < 0.05, df = 2**
Ophiuroids	**Chi-squared = 8.909, p < 0.05, df = 2**
Crustaceans	Chi-squared = 1.296, p = 0.52, df = 2
Pycnogonids	**Chi-squared = 7.076, p < 0.05, df = 2**
Molluscs	Chi-squared = 0.212, p = 0.90, df = 2
Cnidaians	**Chi-squared = 7.681, p < 0.05, df = 2**
Sipunculans	**Chi-squared = 7.076, p < 0.05, df = 2**

As the composition of different taxa was very different and there were large differences in the proportions of these taxa between stations, comparison of wet weight biomass did not reflect the energy availability within the megabenthos at each site. In order to overcome this problem, all WW biomass was converted to **O**rganic **C**arbon **W**eight (OCW) (Table 3.2 & 3.4). Although the difference between sites was less pronounced, the same general trend was seen with the lowest total OCW at the NW site and the highest at the SE site (Kruskal-Wallis: chi-squared = 1.18, df = 2, p = 0.55) (Table 3.4).

Differences in biomass between samples were most pronounced in the case of the sipunculan *Sipunculus norvegicus* and the pycnogonid *Colossendeis colossea.* At the NW site large variations in biomass were observed among molluscs (caused by the variable presence of the large octopod *Grimpoteuthis* sp.), crustaceans (caused by variability in Reptantia indet. and *Munidopsis* sp.), and echinoids (caused by *Urechinus naresianus* and *Tromikosoma koehleri*).

The high standard deviations in biomass at the SE site was caused by the sipunculan *Sipunculus norvegicus* and the pycnogonid *Colossendeis colossea.* At the NW site high standard deviations were observed in molluscs (caused by the variable presence of *Grimpoteuthis* sp.), crustaceans (caused by variability in Reptantia indet. and *Munidopsis* sp.), and echinoids (caused by *Urechinus naresianus* and *Tromikosoma koehleri*).

TABLE 3.4: The **O**rganic **C**arbon **W**eight (OCW) of the major taxonomic groups, converted from **W**et **W**eight (WW) based on conversion factors published in Lampitt et al. (1986). Values are presented in g ha^{-1}, with the respective **S**tandard **D**eviation (SD).

Weight Unit	**Taxonomic Groups**	**SE**	**SD**	**NW**	**SD**	**NE**	**SD**
WW	Asteroidea	695	± 335	392	± 205	952	± 171
	Holothuroidea	3,976	± 2,151	1,419	± 476	3,564	± 2,362
	Echinoidea	**27**	**± 26**	**764**	**± 1,181**	**67**	**± 22**
	Ophiuroidea	**12**	**± 7**	**92**	**± 33**	**3**	**± 1**
	Crustacea	195	± 112	198	± 282	108	± 14
	Pycnogonida	**22**	**± 32**	**222**	**± 131**	**2**	**± 2**
	Mollusca	85	± 69	149	± 227	160	± 45
	Cnidaria	**349**	**± 244**	**< 1**	**± 1**	**6**	**± 3**
	Sipuncula	**101**	**± 125**	**27**	**± 18**	**225**	**± 77**
	Total	5,460	± 3,101	3,263	± 2,555	4,975	± 2,697
OCW	Asteroidea	63	± 30	35	± 19	86	± 15
	Holothuroidea	111	± 60	39	± 13	99	± 66
	Echinoidea	**2**	**± 2**	**47**	**± 73**	**4**	**± 1**
	Ophiuroidea	**1**	**± 1**	**8**	**±3**	**0**	**± 0**
	Crustacea	33	± 19	33	± 47	18	± 2
	Pycnogonida	**2**	**± 3**	**19**	**± 11**	**0**	**± 0**
	Mollusca	10	± 8	18	± 27	6	± 5
	Cnidaria	**32**	**± 22**	**0**	**± 0**	**0**	**± 0**
	Sipuncula	**3**	**± 3**	**1**	**± 1**	**6**	**± 2**
	Total	255	± 42	201	± 32	221	± 42

3.3.2 Density

Total population density was greatest at the NE site (815.5 individuals ha^{-1}) and lowest at the NW site (270.0 individuals ha^{-1}) (Table 3.5). However, the difference in total density observed between sites was not statistically significant (Kruskal-Wallis: density: chi-squared = 3.45, df = 2, p = 0.18). Taxonomic groups that showed significant differences between sites included asteroids, holothurians, echinoids, ophiuroids, pycnogonids and cnidarians (Table 3.5). The greatest densities of cnidarians and asteroids were observed at the SE site. Echinoids, ophiuroids and pycnogonids dominated densities at the NW site and holothurians were dominant at the NE site (Table 3.5). As in the case of biomass, the high variation in sipunculan densities at the NE site was caused by variable numbers of *Sipunculus norvegicus.* Variability in the mean densities of particular taxa at the NW site was caused by *Bathybiaster vexillifer* and *Porcellanaster ceruleus* among asteroids, *Gephyrothuria alcocki* and *Benthodytes gosarsi* among holothurians, Sipuncula sp. B among sipunculans, *Stereomastis nanus* among crustaceans, and Bivalvia sp. A among molluscs. Variation in ophiuroid densities was principally caused by *Ophiacantha aculeata* and *Ophiura ljungmani*, while *Urechinus naresianus* was mainly responsible for variations in echinoid densities (Table A.1).

TABLE 3.5: Table representing the densities from the trawl data. The densities are presented as number of individuals ha^{-1}, with the **S**tandard **D**eviation (SD). Highlighted in bold are those groups that differed significantly between the sites.

Taxonomic Group	**SE**	**SD**	**NW**	**SD**	**NE**	**SD**
Asteroidea	**102.9**	**± 32.7**	**48.3**	**± 193.3**	**26.4**	**± 2.1**
Holothuroidea	**153.9**	**± 38.3**	**17.4**	**± 69.5**	**753.3**	**± 175.6**
Echinoidea	**3.8**	**± 0.9**	**22.9**	**± 91.7**	**12.7**	**± 3.2**
Ophiuroidea	**16.8**	**± 12.3**	**132.5**	**± 529.8**	**3.4**	**± 0.8**
Crustacea	21.8	± 13.4	18.5	± 74.1	9.9	± 1.0
Pycnogonida	**2.6**	**± 3.5**	**23.4**	**± 93.5**	**0.3**	**± 0.3**
Mollusca	4.6	± 4.1	2.6	± 10.5	1.0	± 0.7
Cnidaria	**30.6**	**± 9.8**	**0.1**	**± 0.3**	**0.2**	**± 0.2**
Sipuncula	6.3	± 1.5	7.5	± 6.8	8.3	± 17.4
Total	343.3	± 12.9	273.3	± 118.8	815.5	± 26.4

3.3.3 Body Size

A number of species occurred in sufficient densities at most sites for a detailed comparison to be made of body size distributions. Of all species that could be compared

Gephyrothuria alcocki was the only one that exhibited no size differences between any sites (Figure 3.1, Table 3.6). The size distribution between the other species varied greatly. *Freyella elegans* was the only species that differed significantly in its size distribution between all sites, having the largest specimens at the NW and the smallest at the NE site (Figure 3.2, Table 3.6). *Sipunculus norvegicus* was similar in size at the two northern sites but significantly smaller at the SE site. *Molpadia* aff. *blakei* and *Hymenaster* cf. *coccinatus* were significantly larger at the NE site, compared to the other sites, which showed no differences. *Psychropotes depressa* and *Porcellanaster ceruleus*, on the other hand, were significantly larger at the NW site, compared to the NE and SE sites (Figure 3.1 & 3.2, Table 3.6). Although only collected in sufficient numbers from two sites, *Benthodytes gosarsi*, *Bathybiaster vexillifer*, *Hyphalaster inermis*, and *Urechinus naresianus* all had significantly greater size distributions at the NW site (Figure 3.1 & 3.2, Table 3.6).

Table 3.6: Results for the Kolmogorov-Smirnov analysis, comparing the size distributions of individual species between sites. Highlighted in bold are species that differed significantly in size between sites.

Species	**Sites Compared**	**Kolmogorov-Smirnov D**	**p value**
Molpadia aff. *blakei*	**SE < NE**	**0.87**	**< 0.01**
	SE < NW	0.22	0.69
	NW < NE	**0.92**	**< 0.01**
Gephyrothuria alcocki	SE < NE	0.21	0.74
	SE < NW	0.24	0.10
	NE < NW	0.38	0.15
Psychropotes depressa	NE < SE	0.57	0.19
	SE < NW	**0.78**	**< 0.0001**
	NE < NW	**0.92**	**< 0.01**
Pseudostichopus peripatus	SE < NE	0.19	0.72
	SE < NW	**0.37**	**< 0.05**
	NE < NW	0.42	0.08
Benthodytes gosarsi	**SE < NW**	**0.60**	**< 0.001**
Sipunculus norvegicus	**SE < NE**	**0.49**	**< 0.001**
	SE < NW	**0.38**	**< 0.05**
	NW < NE	0.28	0.158
Freyella elegans	**NE < SE**	**0.80**	**< 0.001**
	SE < NW	**0.45**	**< 0.001**
	NE < NW	**0.81**	**< 0.001**
Bathybiaster vexillifer	**NW < NE**	**0.28**	**< 0.001**
Hymenaster cf. *coccinatus*	**SE < NE**	**0.67**	**< 0.001**
	NW < SE	0.26	0.99
	NW < NW	**0.85**	**< 0.05**
Porcellanaster ceruleus	**SE < NW**	**0.47**	**< 0.001**
	NE < SE	0.29	0.09
	NE < NW	**0.73**	**< 0.001**
Hyphalaster inermis	**SE < NW**	**0.33**	**< 0.05**
Urechinus naresianus	**NE < NW**	**0.82**	**< 0.001**

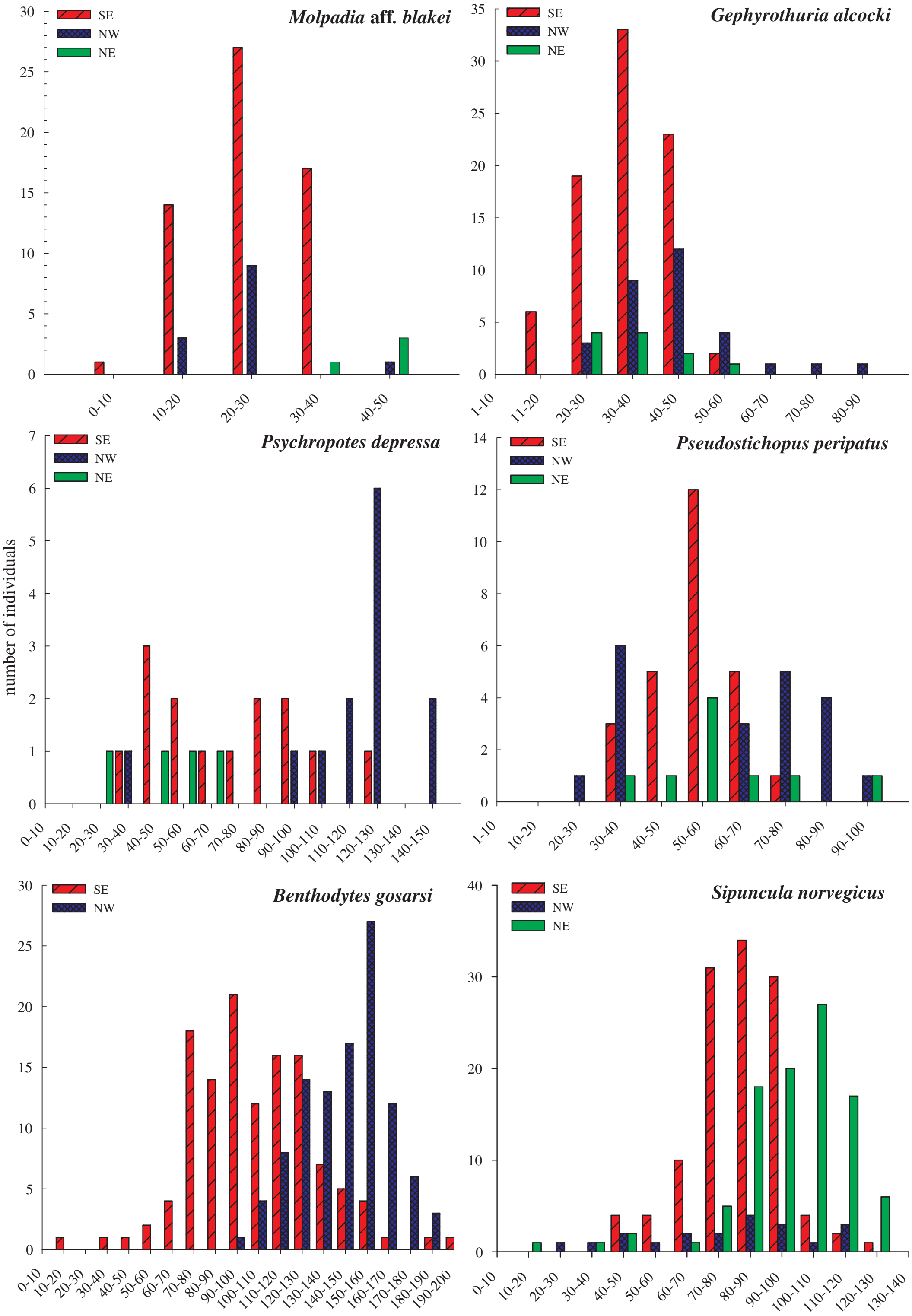


FIGURE 3.1: Size Frequencies of select holothurians (*Molpadia* aff. *blakei*, *Gephyrothuria alcocki*, *Psychropotes depressa*, *Pseudostichopus peripatus*, and *Benthodytes gosarsi*) and the sipunculan *Sipunculus norvegicus*. Species are compared between all three sites, apart from *Benthodytes gosarsi* where only NW and SE data were available. Species are grouped in 10 mm size groups. Size refers to the length of the specimen.

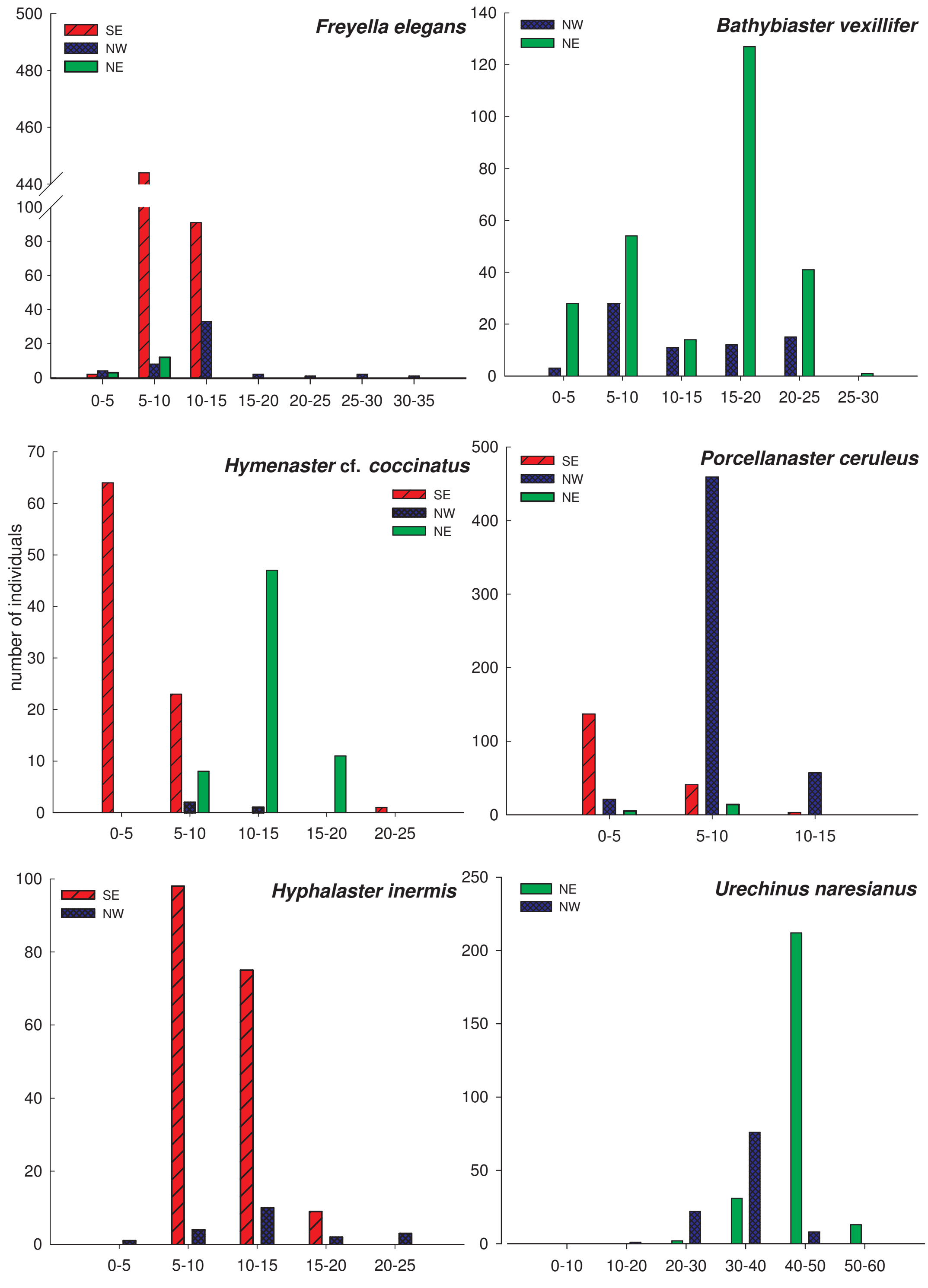


FIGURE 3.2: Size Frequencies of selected asteroids (*Freyella elegans*, *Bathybiaster vexillifer*, *Hymenaster* cf.*coccinatus*, *Porcellanaster ceruleus*, and *Hyphalaster inermis*) and the echinoid *Urechinus naresianus*. Asteroids are grouped in 5 mm size groups, with size referring to the radius. *Urechinus naresianus* is grouped in 10 mm size groups, here size refers to the length of the oral side. Only undamaged body parts were measured.

3.3.4 Diversity

3.3.4.1 Species Richness

The species accumulation rate differed between the sites, with the highest species richness observed at the SE site where 4,233 individuals were assigned to 96 different species (Figure 3.3). At the NW site a similar number of individuals (4,313) represented only 69 species, and at the NE site, where the highest number of individuals (12,716 individuals) was recorded, only 60 species were recognized (Figure 3.3). An asymptote was not reached at any site, suggesting that an increased sampling effort would yield more species. The higher species richness at the SE site was driven by higher species numbers among holothurians, asteroids, ophiuroids, cnidarians, and molluscs compared to the northern sites. Echinoids and sipunculans showed greater species richness at the NW site.

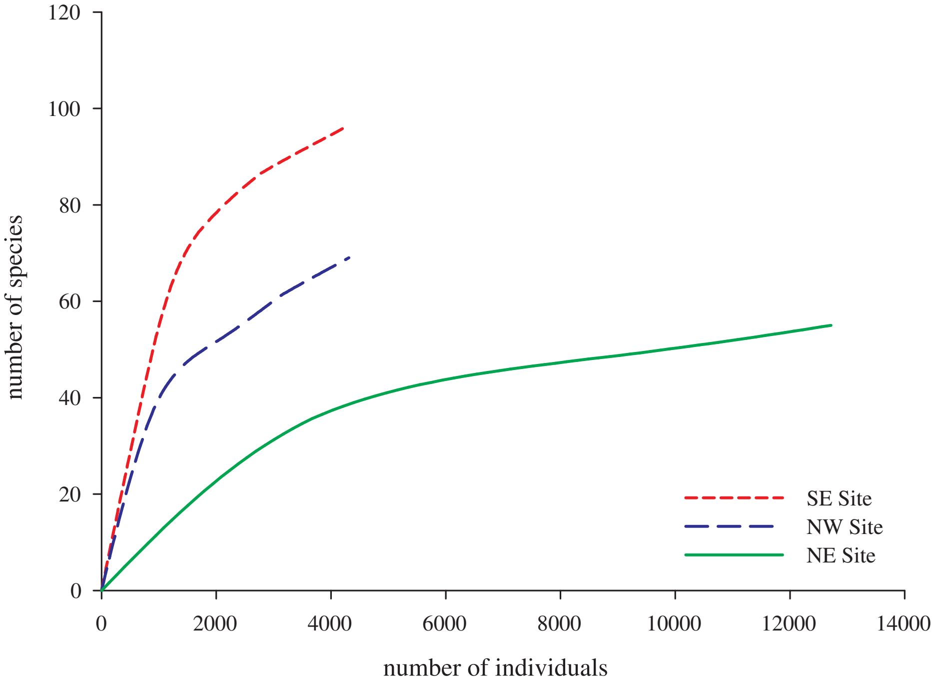


FIGURE 3.3: Species accumulation curves for all sites, based on raw data with the number of species plotted against the number of individuals collected at each site.

3.3.4.2 Species Rank Abundance

Samples from the NE site formed a geometric series in the Whittaker Rank Abundance plot, which suggests a strong numerical dominance by either one or several species (Figure 3.4). The dominance observed at the NE site was related to the superabundance of elpidiid holothurians (the 'Elpidiidae mix') with densities of about 4,000 individuals ha^{-1}. The asteroid *Bathybiaster vexillifer* was also found in high densities at the NE site. In contrast, samples from the NW and SE sites formed a log normal distribution, indicating a relatively high evenness at both sites. The shape of the curves also indicated that the SE site had the greatest number of rare species (Figure 3.4).

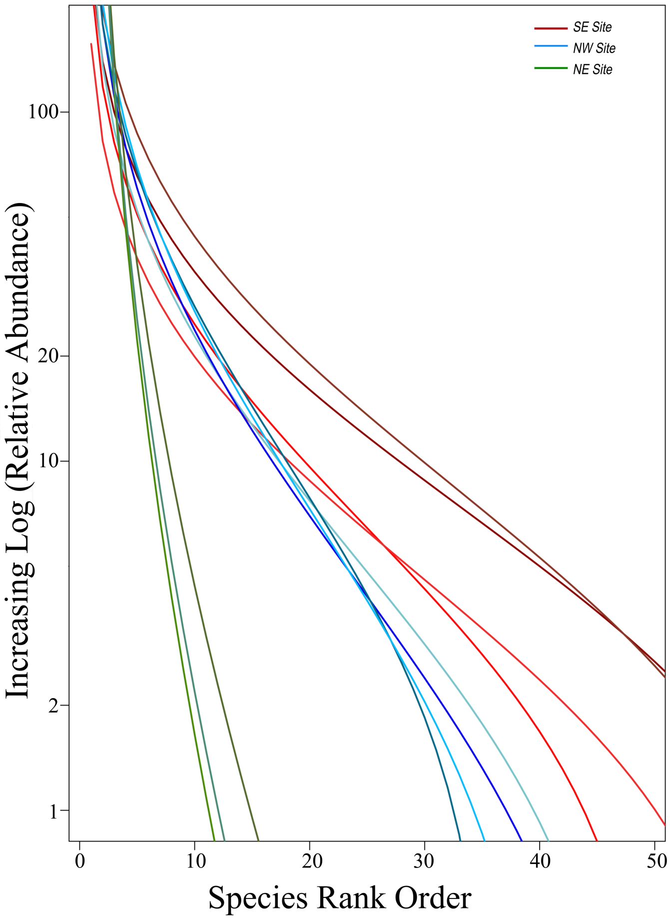


Figure 3.4: Whittaker Rank Abundance Plot. The most common species are on the left hand side on the x-axis, and the rare species on the far right. Lines represent individual trawls. Red lines are replicates from the SE site, blue lines from the NW site, and green lines from the NE site.

3.3.4.3 Combined Diversity

Both Simpson's Index and the Shannon-Wiener index revealed significantly different diversities between sites (Kruskal-Wallis: chi-squared = 8.91, df = 2, p = < 0.05) (Figure 3.5), with highest values at the SE site and lowest values at the NE site. The difference in diversity between the northern sites is less pronounced with the Simpson index, which is most likely because this index puts more weight on rare species.

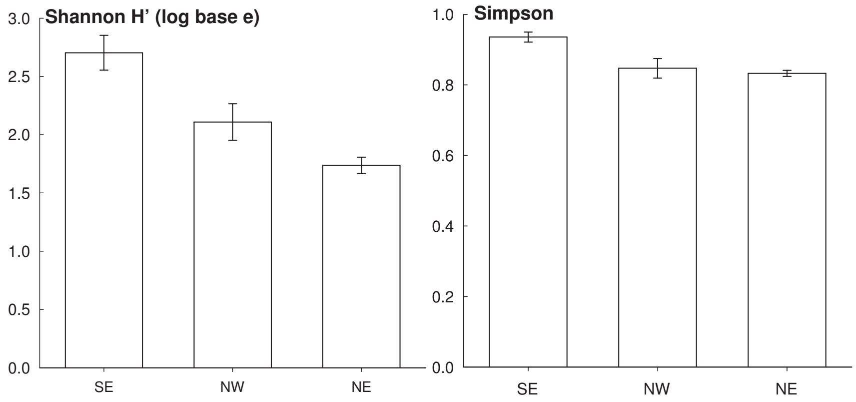


FIGURE 3.5: Shannon-Wiener and Simpson analyses, with standard deviations. SE n=4, NW n=4, NE n=3

3.3.5 Community Composition

The community composition differed significantly between sites (ANOSIM $p < 0.01$, Global R = 1), with each site being equally dissimilar (about 20 %) to all other sites. On the other hand, each trawl grouped strongly with others from its respective site. The within-site similarity of replicated trawl samples was over 60 % at the NE and NW sites respectively, while replicates from the SE site formed two distinct clusters, each with 60 % similarity.

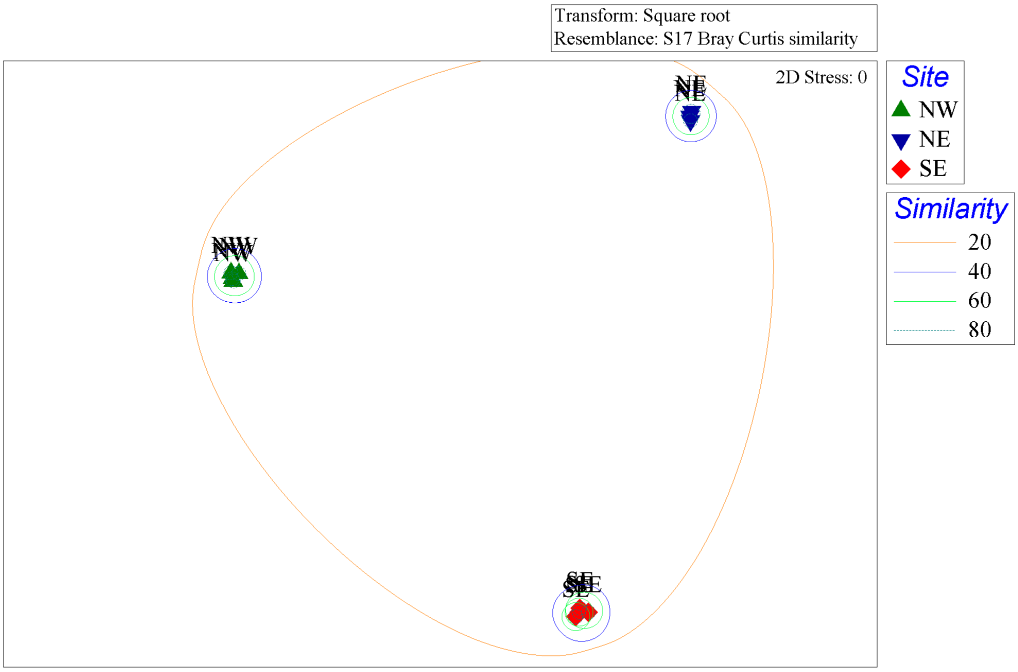


FIGURE 3.6: Multidimensional Scaling Plot, based on Bray-Curtis Similarity test, after standardisation by total. Circles represent the similarity of individual samples to all other samples, based on the cluster overlay, where green shows a 60 % similarity and blue a 80 % similarity.

At the SE site the multivariate pattern was dominated by three holothurians (*Staurocucumis abyssorum*, *Benthodytes gosarsi*, *Gephyrothuria alcocki*), three asteroids (*Porcellanaster ceruleus*, *Hymenaster membranaceus*, *Hyphalaster inermis*), one crustacean (*Munidopsis rostrata*), and one cnidarian (*Heteropolypus* cf. *insolitus*) (Table 3.7). The NW site was principally characterised by four ophiuroids (*Ophiura ljungmani*, *Ophiacantha aculeata*, *Ophiura irrorata*, *Ophiocten hastatum*), two asteroids (*Porcellanaster ceruleus*, *Freyella elegans*), one holothurian (*Benthodytes gosarsi*) and one crustacean (*Stereomastis nanus*). Multivariate patterns at the NE site were dominated by two holothurians (Elpidiidae mix, *Paelopatides grisea*), three asteroids (*Bathybiaster vexillifer*, *Hymenaster* cf. *coccinatus*, *Porcellanaster ceruleus*), two echinoids (*Urechinus naresianus*, *Echinosigra phiale*) and one crustacean (*Stereomastis nanus*) (Table 3.7). The only species that occurred at all sites and was identified as an important component of the community by the SIMPER test was the asteroid *Porcellanaster ceruleus*, although it was ranked differently at different sites (Table 3.7).

Table 3.7: SIMPER results for each site showing the eight most important species that cause the dissimilarities between sites, with the % contribution of each taxonomic unit for the sites.

SE Site	**%**	**NW Site**	**%**	**NE Site**	**%**
Porcellanaster ceruleus	10.78	*Ophiura ljungmani*	18.23	Elpidiidae mix	52.22
Hymenaster membranaceus	6.69	*Porcellanaster ceruleus*	10.94	*Bathybiaster vexillifer*	7.23
Staurocucumis abyssorum	6.16	*Ophiacantha aculeata*	7.91	*Urechinus naresianus*	5.14
Benthodytes gosarsi	5.24	*Azygocypridina imperialis*	6.42	*Stereomastis nanus*	5.07
Gephyrothuria alcocki	5.00	*Ophiura irrorata*	5.66	*Hymenaster* cf. *coccinatus*	3.92
Hyphalaster inermis	4.63	*Benthodytes gosarsi*	4.74	*Echinosigra phiale*	3.09
Munidopsis rostrata	4.61	*Ophiocten hastatum*	4.29	*Paelopatides grisea*	2.78
Benthothuria funebris	4.03	*Stereomastis nanus*	3.64	*Porcellanaster ceruleus*	2.04

3.3.6 Unique Species

A total of 25 species was unique to the SE site, while noticeably fewer species were only found at the northern sites (3 and 4 unique species at the NE and NW sites, respectively). At the SE site most of the unique species were asteroids, holothurians and ophiuroids (Table 3.8). At the northern sites the unique species comprised a holothurian, two echinoids and an ophiuroids (NW) and two echinoids and an asteroid (NE) (Table 3.8).

Table 3.8: The number of unique species among different major taxa at each site.

Taxonomic Group	**SE Site**	**NW Site**	**NE Site**
Asteroidea	8	0	2
Holothuroidea	10	1	1
Echinoidea	1	2	0
Ophiuroidea	5	1	0
Crustacea	1	0	0
Pycnogonida	0	0	0
Sipuncula	0	0	0
Total	**25**	**4**	**3**

3.4 Discussion

3.4.1 Environmental Controls on Assemblage Composition

Density, biomass and body size are linked to food availability (Thiel, 1975; Sibuet et al., 1989; Thurston et al., 1994; Billett et al., 2001; Rex et al., 2006), which in turn is related to surface primary productivity (Thurston et al., 1994; Wigham et al., 2003a,b; Billett et al., 2010). Since surface productivity is higher at the northern than at the southern sites (Letessier et al., 2012; Tilstone et al., in prep), it was hypothesised that these faunal characteristics would exhibit a corresponding pattern. In fact, data show that there were no differences in biomass (Table 3.4) and density (Table 3.5) between sites. However, species had a tendency to be larger at one of the northern sites, with a significant differentiation between the NE and NW sites for most species (Figure 3.1 & 3.2). The exception was *Gephyrothuria alcocki*, which showed no difference in size distribution between any sites.

Despite the absence of a significant trend in total biomass and total density between sites, some differences were observed, though they were not positively correlated with organic carbon flux. The NW site yielded the lowest total biomass and total density (Table 3.4 & 3.5) despite the fact that the organic carbon flux in sediment traps set 100 and 1,000 m above the seafloor was highest at this site (Abell et al., submitted). A lack of correlation between organic carbon flux and biomass/density is reported also for abyssal depths (Thurston et al., 1994) and suggests that factors other than organic carbon input drive megafaunal community structures at the ECOMAR sites. Although there were no differences in total biomass and total density, significant differences were observed in individual taxonomic groups between sites.

Although total values were lower, the NW site had a significantly greater biomass and density of echinoids, ophiuroids and pycnogonids than the other sites (Table 3.4 & 3.5). Here, the most common echinoid was the deposit-feeder *Urechinus naresianus*. Its great densities and significantly larger body size at the NW site (Figure 3.2, Table 3.6) suggest this species thrived as a result of the high organic matter flux (Abell et al., submitted). Ophiuroids were characterised by high densities of *Ophiura ljungmani*, which is considered an omnivore although it feeds predominantly on material from surface waters such as flocculent organic material, diatoms, coccolithophores and foraminifera (Pearson and Gage, 1984). It is assumed that, like *U. naresianus*, the ophiuroid *O. ljungmani* benefited from the increased organic matter availability at the NW site. The pycnogonid *Colossendeis colossea* also dominated the NW site in density. This species is a carnivore and so unlikely to have benefitted directly from the increased organic carbon flux (Ruppert et al., 2004). In the absence of more information about the ecology of *C. colossea*, it is unclear why it was more common in the NW.

Holothurian biomass was fairly similar between sites (particularly the SE and NE), but the NE site showed significantly greater densities, reflecting the abundance of small deposit-feeding elphidiids (the Elpidiidae mix: *Kolga nana*, *Peniagone azorica*, *Peniagone longipapillata*, *Ellipinion delagei* and *Ellipinion alani*). Although individual elphidiid species have distributional ranges that extend beyond the ECOMAR sites (Rogacheva et al., accepteda), with the exception of *Ellipinion delagei*, they were restricted to the NE site in the present study. The organic carbon content of the sediment was lowest at the NE site, which is surprising in view of the high densities of deposit-feeding holothurians. However, the sediment flux in traps set at 100 m above the seafloor was greater than at other sites (Abell et al., submitted), which might indicate the occurrence of re-suspension events caused by elevated current velocities. These conditions could have been favourable or unfavourable to some species, *Kolga hyaline*, for example, has been suggested to thrive in environments characterised by the periodic accumulation of phytodetritus, irregular topography and strong bottom currents (Billett and Hansen, 1982). Rogacheva (2011) proposed recently that *Kolga nana* and *K. hyalina* are synonyms, supporting the idea of an energetic environment at the NE site. Because the Eplidiidae mix is restricted mostly to the NE site, no between-site size comparisons were possible. However, other deposit-feeding holothurians, such as *Psychropotes depressa*, *Pseudostichopus peripatus* and *Benthodytes gosarsi*, were significantly larger at the NW site (Figure 3.1, Table 3.6), which is consistent with the elevated organic matter flux observed in the sediment traps (Abell et al., submitted). *Gephyrothuria alcocki* was the only holothurian that did not show size differences between any of the sites (Table 3.6); why this should be is unclear. *Molpadia* aff. *blakei* was the only holothurian that was largest at the NE site (Table 3.6). The infaunal habitat of this species provides potential shelter from any disturbances occurring on the sediment surface. It may have a similar diet to *M. musculus*, a deposit feeder (McClintic et al., 2008) living on refractory material (Reid et al., in press). We speculate that the infaunal mode of life of *M.* aff. *blakei* allows this species to attain larger sizes. The infaunal deposit-feeding sipunculan *Sipunculus norvegicus* was also larger at the NE site (Figure 3.1, Table 3.6). This species also feeds on refractory material (Reid et al., in press), suggesting that, while they compete with each other for space and resources, *M.* aff. *blakei* and *S. norvegicus* avoid competition with the superabundant surface deposit-feeding elpidiids. Although sipunculan densities were similar between sites, the larger size of *S. norvegicus* led to a significantly greater biomass at the NE site. It is generally assumed that megafauna decreases in size with increasing depth, in the absence of gigantism (Rex et al., 2006). As the NE site was the shallowest site (Table 3.1), it might explain the observed size variation, although the sites sampled varied only slightly in depths (ranging about 350 m in depth).

At the SE site, cnidarians had a significantly higher biomass and density and were dominated by the suspension feeder *Heteropolyus* cf. *insolitus.* This species was absent from the northern sites. While the organic carbon availability was similar between the eastern sites, the sediment flux was noticeably lower at the SE (Abell et al., submitted). Furthermore, the sediment at the SE site was coarser, possibly providing a better substratum for *H.* cf. *insolitus* (Priede, 2007). Asteroids were significantly denser at the SE site, despite similar biomass between sites (Table 3.4). *Hymenaster membranaceus* dominated in density at the SE site but was absent at the northern sites, which is puzzling because it also occurs in the Rockall Trough (Pain et al., 1982) and therefore has a fairly wide distribution. Although *H. membranaceus* is considered a predator/scavenger based on stomach content analyses (Howell et al., 2003), a polyunsaturated-fatty-acid analysis also revealed a dependence on fresh organic carbon (Reid et al., in press). As this species lives partially buried in the sediment (Pain et al., 1982), it is not clear why it thrived at the SE site, where a high abundance of pteropod shells might inhibit the burrowing ability and the organic carbon availability was reduced (Abell et al., submitted). The size distribution of *H. membranaceus* could not be compared between sites, but other asteroid species were significantly smaller at the southern sites (Figure 3.2, Table 3.6). The largest specimens of *Freyella elegans*, *Porcellanaster ceruleus* and *Hyphalaster inermis* were found at the NW site, while *Hymenaster* cf. *coccinatus* and *Bathybiaster vexillifer* were significantly larger at the NE site. *Freyella elegans*, a suspension feeder, would have benefitted from the greater organic matter availability at the NW site. *Porcellanaster cereuleus* and *Hyphalaster inermis* are both sub-surface mud (deposit) feeders (Howell et al., 2002; Reid et al., in press), a feeding strategies that might avoid direct resource competition with *Ophiura ljungmani* and *Urechinus naresianus*, which are abundant at the NW site. Similarly, it is possible that *Bathybiaster vexillifer* avoids competition with the Elpidiidae mix at the NE site by feeding in sub-surface layers (Reid et al., in press). It is not clear why *Hymenaster* cf. *coccinatus*, a surface deposit feeder, reaches its largest size at the NE site.

3.4.2 Influences on Body Size

In general, no clear trend was observed between surface production, biomass, density and body size. Individual species appear to benefit from different environmental conditions. Observed taxon-specific size differences might be caused by a combination of feeding mode, organic matter availability, and level of disturbance. Species feeding on fresh detritus, including deposit feeders (*Pseudostichopus peripatus*, *Psychropotes depressa*, *Benthodytes gosarsi*), mud eaters (*Porcellanaster ceruleus*, *Hyphalaster inermis*) and filter feeders (*Freyella elegans*), tended to have their largest representatives at the NW site. If larger body size bestows metabolic or competitive advantages (Rex and Etter, 1998), then the larger size of species feeding on fresh detritus at the NW site might be driven by energy availability. In contrast, burrowers (*Molpadia* aff. *blakei*, *Sipunculus norvegicus*) and predators/scavengers (*Hymenaster* cf. *coccinatus*, *Bathybiaster vexillifer*) were largest at the NE site, where the sediment flux was greatest in traps located at 100 and 1,000 m above the seafloor. As mentioned above, this might reflect re-suspension events, possibly caused by occasional strong currents. A burrowing life style would allow protection from such disturbances. It is unclear why benthic scavengers are larger at the NE site. A potential nursery ground for scavenging amphipods has been identified at this site, possibly reflecting greater food availability for a scavenging diet (Horton et al., in press). Although more data are needed to support their existence, putative disturbance events at the NE site might provide scavengers with such food resources. It is unclear what drives the smaller body sizes at the SE site. Oxygen and temperature do not differ noticeably between sites (Gooday et al., in press), and size distributions do not appear to reflect any particular feeding strategy. The most likely explanation is that small sizes are a result of lower organic carbon availability compared to the other sites. Although megafaunal sizes decrease with increasing depths on a global scale (Rex et al., 2006), it is unlikely that the 300 m difference between the SE and NE sites was responsible for the smaller body sizes observed at the former.

3.4.3 Comparison with Other Studies

Biomass and density data from the MAR sites were compared to model predictions at comparable depths (Wei et al., 2010) (Figure 3.7). Biomass at the MAR was greater than predicted for their respective depths at all ECOMAR sites (Figure 3.7). Fish are included in the model predictions, but not in the present dataset. The inclusion of ECOMAR fish data (Cousins et al., submitted) would increase the discrepancy between biomass predictions and measurements. The megafaunal density at the NW and SE ECOMAR sites was close to the predictions for their respective depths, but slightly higher at the NE site (Figure 3.7). Compared to actual data from similar depths in the **P**orcupine **S**ea**b**ight (PSB), the total wet weight and density were lower at the MAR (Lampitt et al., 1986). Echinoderm data were available from the eastern and western continental slopes (Haedrich et al., 1980; Billett, 1991; Howell et al., 2004). The **a**sh **f**ree **d**ry **w**eight (AFDW) of echinoderms was higher at the MAR compared to the PSB (Figure 3.7). Similar to the PSB, the high biomass at the eastern ridge sites was driven mainly by holothurians; echinoids also accounted for a substantial proportion of biomass at the NW site (Table 3.4). MAR densities, however, were lower than those at the PSB (Figure 3.7), consistent with the slightly lower mean vertical export fluxes at the MAR (0.658 0.26 g C m^{-2} y^{-1}) and those measured near the PSB on the Porcupine Abyssal Plain (0.905 g C m^{-2} y^{-1}) (Priede and et. al., submitted).

It is unclear why echinoderm biomass is higher but density lower at the MAR compared to the PSB. A possible contributing factor could be the sampling gear. Although both areas were trawled, the PSB was also sampled using an epibenthic sledge (Lampitt et al., 1986). Different gears can yield different catch rates (Gage and Bett, 2005). Alternatively, echinoderm densities may have been higher at the PSB, but body sizes smaller and therefore biomass lower. Echinoderm biomass at the New England slope was similar to the NW and SE sites (Figure 3.7). The NE site showed a somewhat reduced biomass compared to the New England continental slope. The New England biomass data are based on preserved wet weight (Haedrich et al., 1980), while the present study reports fresh wet weight. Biomass decreases after fixation (by about 40 to 70 %, Billett *pers. comm.*) and hence values from the MAR would have been even lower than those from the New England slope, given comparable methods. Echinoderm densities on the New England slope (Haedrich et al., 1980) were similar to those reported in the present study, rather than being lower as predicted by the lower energy availability at the MAR (Figure 3.7). Although the New England slope was sampled with an OTSB trawl, data were pooled with shrimp trawl data (Haedrich et al., 1980). The combination of two different trawls might have reduced the total density counts. Furthermore, periodically elevated bottom current velocities (benthic storms) at the nearby abyssal HEBBLE site could possibly have influenced megafauna at shallower depths on the New England slope.

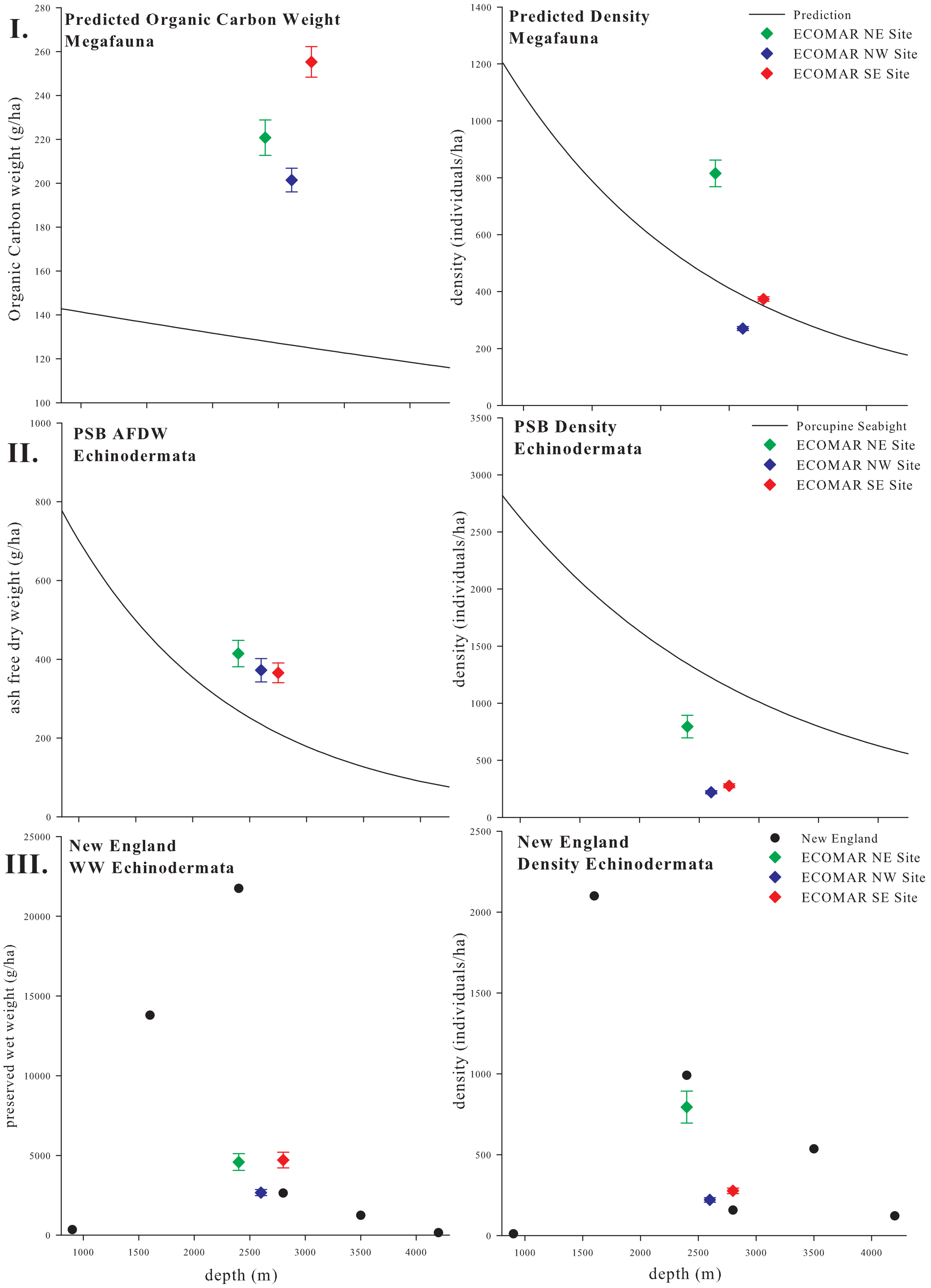


FIGURE 3.7: Comparison of MAR data to other studies: I. Organic carbon weight (g ha^{-1}) and density (ind. ha^{-1}) values for megafauna at ECOMAR sites compared with model predictions for similar depths (Wei et al., 2010). II. Comparison of biomass and density data for echinoderms at ECOMAR sites and comparable depths at the **P**orcupine **S**ea**b**ight (PSB) (Lampitt et al., 1986). III. Comparison of biomass and density data for echinoderms at ECOMAR sites and comparable depths on the New England continental slope (Haedrich et al., 1980). Error bars represent standard errors.

In summary, the MAR yielded higher megafaunal biomass and density values than expected for depths around 2,500 m compared with the global estimated average (Wei et al., 2010). The total, megafauna biomass and density measured at the MAR was lower than reported from the PSB (Billett, 1991; Howell et al., 2002). This reduced biomass at the MAR can be explained by the higher input of organic matter at the continental slope sites compared to the ridge, which further lacks down-slope inputs from shelf sea sediments. However, when comparing only MAR echinoderm data to the New England slope (Haedrich et al., 1980) and the PSB (Billett, 1991; Howell et al., 2002), the picture changes. Echinoderm biomass is greater at the MAR compared to the PSB, while being very similar to the New England slope though noticeably lower at the NE site at comparable depth. Density at the MAR is lower than the PSB, but very similar to the New England slope values. It is not clear whether the density of the New England slope is reduced by possible disturbances emanating from the HEBBLE site. Given its distant location from continents and the resulting limited export flux, however, the MAR is characterised by benthic megafauna density and biomass that would be expected for its setting.

3.4.4 Biodiversity and Species Composition

Overall, the SE site was significantly more diverse than the northern sites (Figure 3.5). In order to understand this difference, the two components of diversity, species richness and evenness, as well as the Shannon-Wiener diversity index, are compared with the New England slope echinoderm data (Haedrich et al., 1980) (Figure 3.8). The species richness at the northern sites was slightly lower than values from the New England slope, while the SE site was similar to the New England slope. The higher species richness at the SE, compared to the other MAR sites, was also reflected in the number of species that were unique to this site, while the northern sites had many more species in common (Table 3.8). Evenness, on the other hand, is very similar between the NW site and the New England slope, while being slightly elevated at the SE, and depressed at the NE site (Figure 3.8). The low evenness at the NE site reflected the numerical dominance of the Elpidiidae mix. The elpidiids may have depressed species richness at this site by outcompeting other species (Matabos et al., 2008; Yemane et al., 2010; Baccaro et al., 2012). The diversity at the NE and SE sites appeared to reflect contrasting factors. Low diversity at the NE site reflects low evenness, while high diversity at the SE site reflects high species richness (Figure 3.8). If we are correct in inferring the existence of occasional strong currents at the NE site, this provides one possible explanation for depressed diversity. Low diversity has been associated with elevated current velocities at the HEBBEL site (Rex and Etter, 2010). It is unlikely that temperature, oxygen, or salinity influenced the diversity patterns at the ECOMAR sites, as they vary little between sites (Table 2.3, page 2.3). Species groups (Elpidiidae mix) and species (e.g. *Hymenaster membranaceus*) that were particularly abundant at a specific site, tended to be either absent or rare at other sites. Although it has been speculated that larvae might migrate from the NE to the NW site via the Scotland-Iceland Overflow Water (Saunders, 1994; Bower and von Appen, 2008), there is no conclusive evidence for a strong exchange of benthic invertebrate species across the Ridge. Equally, dispersal between the SE and the northern sites appears very limited. Apart from the possible dispersal barrier created by the CGFZ, differences in environmental conditions between the sites might also contribute to the differences in megafaunal community composition and structure. Temperature and oxygen were similar, but sediment characteristics at the southern and northern sites were noticeably different (Table 2.3, page 2.3). Although depth varied by only 356 m between sites, some species have a reported depth range of only 200 m (Howell et al., 2002) and so bathymetry (hydrostatic pressure) may have limited the distribution for some species. Finally, the ridge creates a very heterogeneous habitat, and although trawl samples were taken on soft sediment, surrounding rocky outcrops can alter the hydrography on a microhabitat scale, which can also affect the distribution of some species (Auster et al., 1991).

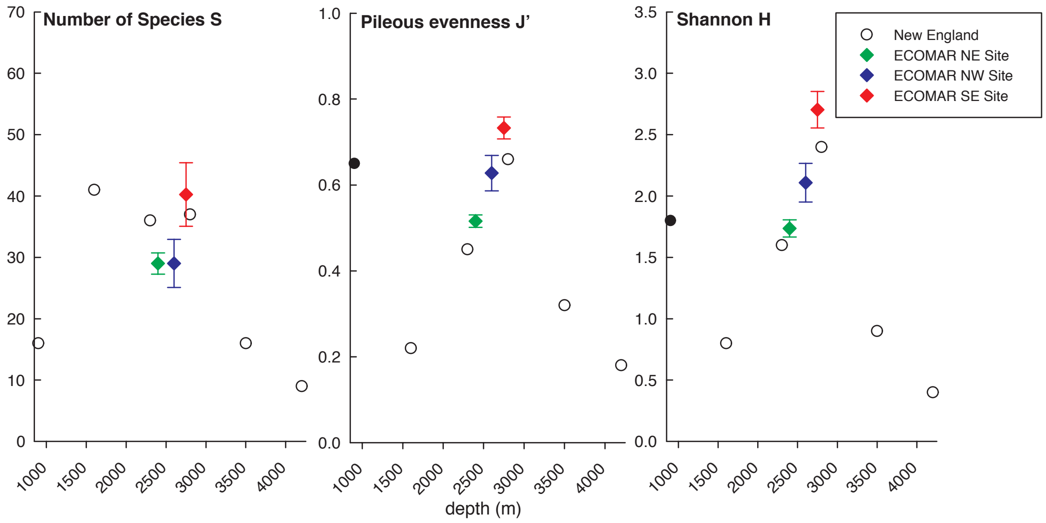


FIGURE 3.8: Comparison of species richness, Pileou's evenness and Shannon-Wiener Diversity Index for echinoderms at ECOMAR sites and the New England slope (Haedrich et al., 1980). Error bars represent standard errors. The Elphidiid mix was divided equally between the five component species in order to calculate J' and H'.

3.4.5 Species Depth Ranges

Considering only species presence/absence data, the greatest faunal similarity is between the MAR and PAP/PSB area, which have 26 species in common (Billett, 1991; Howell et al., 2002). Fewer species were shared with the Rockall Trough (10 species) (Gage, 1986), European Atlantic (9 species) (Sibuet, 1979), New England (8 species) (Haedrich et al., 1980), Greenland Sea (5 species) and the Labrador Sea (2 species) (Sibuet, 1979). Species belonging to some groups, e.g. scavenging fishes, may occur shallower on the Mid-Atlantic Ridge than on the continental margins as a response to reduced food supply (King et al., 2006). The benthic megafauna described in this study include 36 species for which depth ranges are available from other areas (Figure 3.9 & 3.10). Of these, 14 occurred at different depths at ECOMAR sites compared with continental margin settings in the NE and NW Atlantic. Four species occurred at shallower depths in the PSB/PAP area than the MAR, namely the ophiuroid *Ophiacantha aculeata* (755 to 815 m), and the holothurians *Bathyplotes natans* (770 to 1,572 m), *Mesothuria maroccana* (1,431 to 2,315 m) and *Paelopatides grisea* (1,484 to 2,315 m) (Figure 3.10). In contrast, the holothurian *Staurocucumis abyssorum* occurred at around 4,810 m on the PAP, deeper than the individuals sampled at ECOMAR. Asteroids *Styracaster armatus* (3,310 to 4,400 m), *Freyella elegans* (3,640 to 4,849 m), *Hyphalaster inermis* (3,749 to 4,849 m), and *Dytaster grandis* (3,749 to 4,880 m) all occurred deeper at PSB/PAP than ECOMAR. Two of these species, *Freyella elegans* and *Hyphalaster inermis*, have been reported on the European Atlantic margin spanning a wider depth range than observed at the MAR and PSB/PAP sites (Figure 3.10). All species that were reported from the PSB were also found in the Rockall Trough, apart from the echinoid *Echinus alexandri* and *Echinosigra phiale* (Figure 3.9). The depth range of the holothurian *Benthothuria funebris* was slightly deeper in the Rockall Trough than at the ECOMAR sites, but falls within the range reported from the PAP/PSB. The echinoid *Echinus alexandri* occurred at shallower depth in the Rockall Trough (1,300 to 2,300 m) and the New England slope (1,270 to 1,947 m) than in our samples (Figure 3.9). The asteroid *Porcellanaster ceruleus* was the only species found at all sites. Its range is slightly deeper in the Greenland Sea (3,000 to 5,000 m) than on the MAR and shallower on the New England continental slope (1,270 to 1,947 m) (Figure 3.10), but this probably represents sampling bias, especially since the global depth range for *Porcellanaster ceruleus* is very large. On the New England slope the sea spider *Colossendeis collossea* is reported at shallower depths (1,380 to 1,947 m), together with the ophiuroid *Ophiomusium lymani* (393 to 2,481 m). The latter is found in the Rockall Trough across a depth range encompassing the MAR and the New England slope sites. The echinoid *Aeropsis rostrata* occurs deeper on the New England continental slope (3,244 to 3,740 m) than at the ECOMAR SE site. In conclusion, there is no evidence that the MAR causes any bathymetric displacement of species. Those species that appear to show displacement in other studies are most likely absent from the MAR depths because of sampling bias (different sampling gear and speed or mesh sizes) or because they are rare around the MAR area that was sampled.

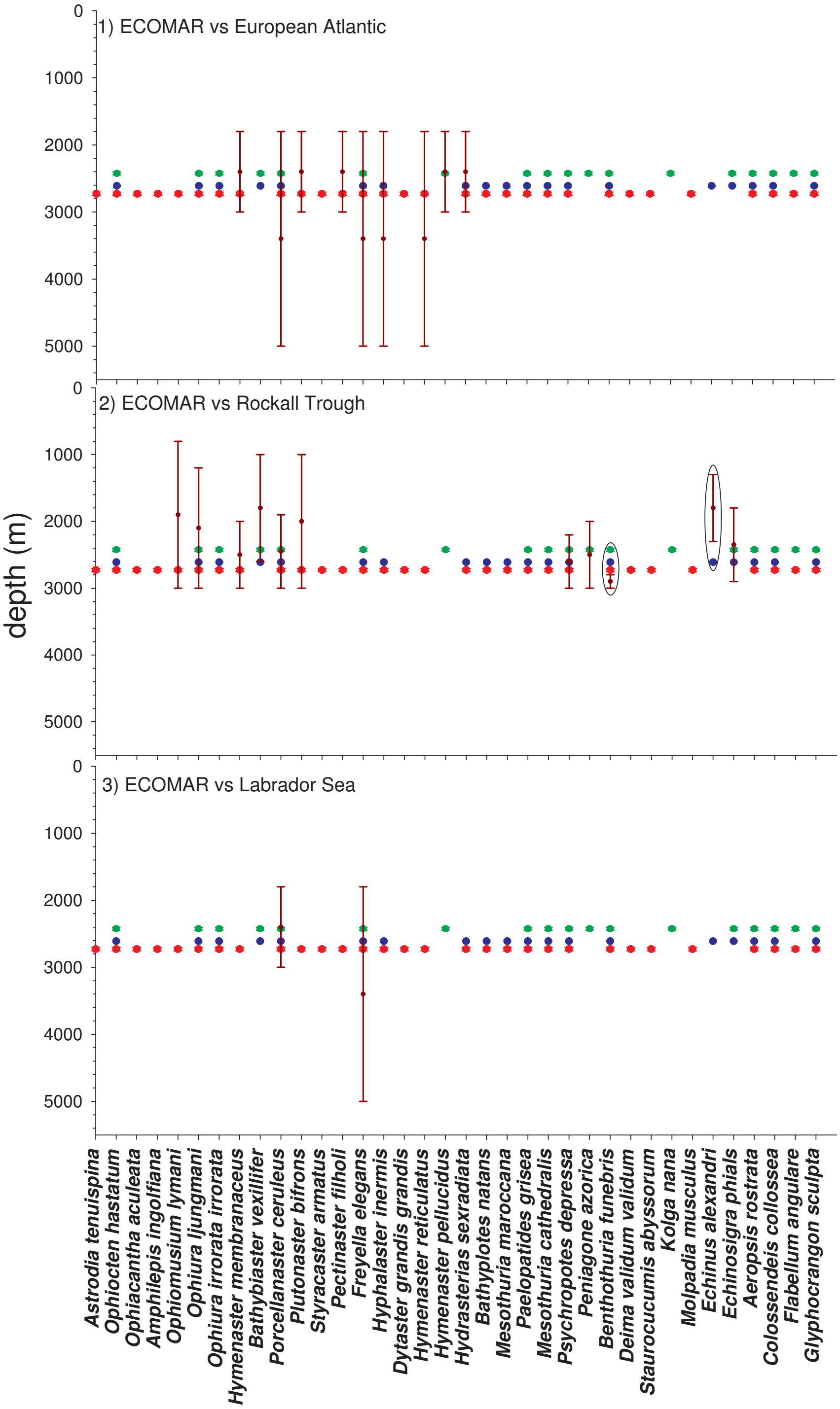


Figure 3.9: Discrete species absence/presence data for the ECOMAR sites are plotted at their respective depth (red-SE, blue-NW, green-NE). The ECOMAR species plots are the same for each graph. Overlain are the depth ranges of the species from other areas in the North Atlantic. 1) European Atlantic (Sibuet, 1979); 2) Rockall Trough (Gage, 1986); and 3) Labrador Sea (Sibuet, 1979); where the error bars represent the reported depth range of each study. Ellipses indicate species that are displaced at the ridge compared to other studies.

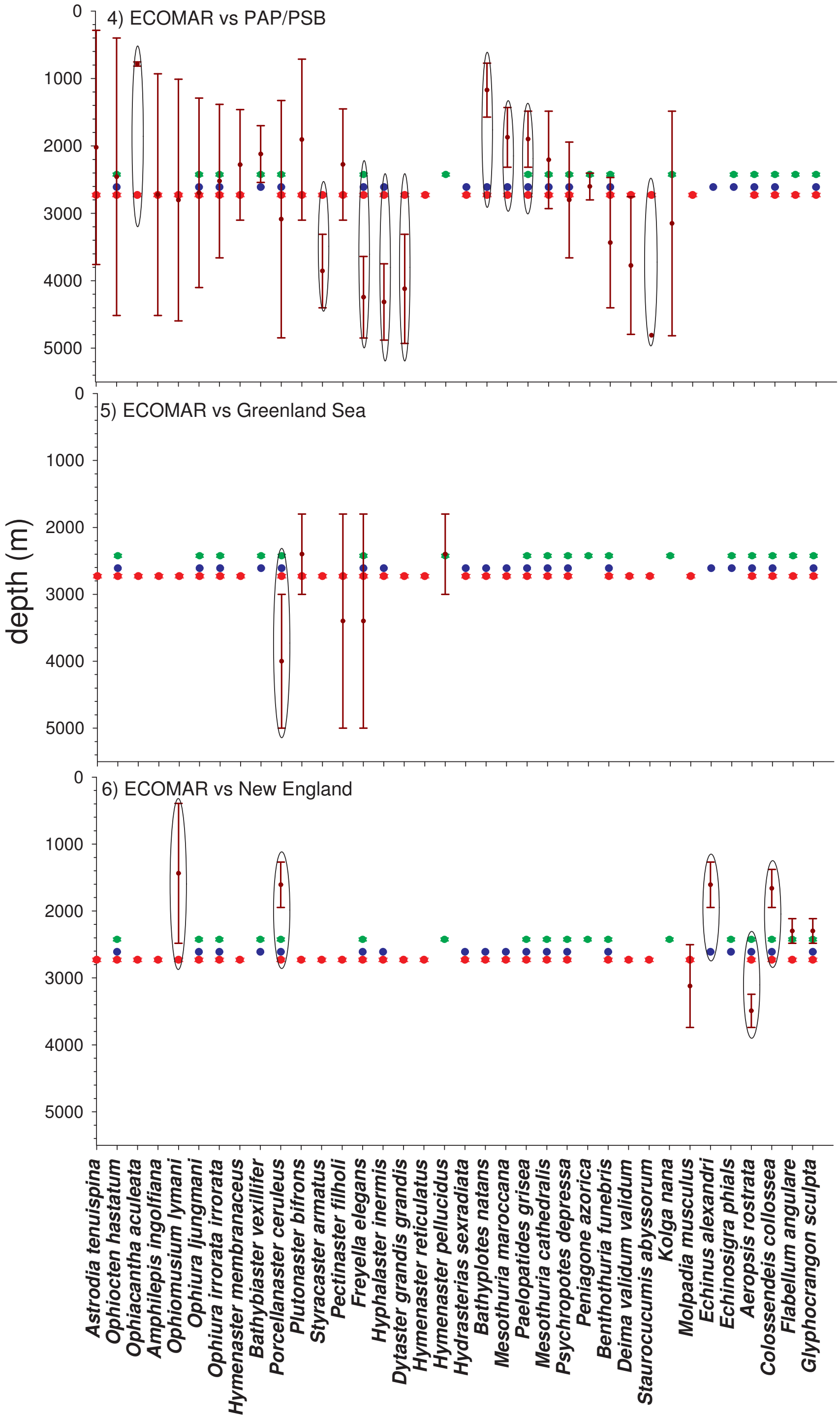


FIGURE 3.10: Discrete species absence/presence data for the ECOMAR sites are plotted at their respective depth (red-SE, blue-NW, green-NE). The ECOMAR species plots are the same for each graph. Overlain are the depth ranges of the species from other areas in the North Atlantic. 4) PAP and PSB Billett (1991) for holothurians, and Howell et al. (2002) for asteroids; 5) Greenland Sea (Sibuet, 1979) 6) Continental slope south of New England (Haedrich et al., 1980). where the error bars represent the reported depth range of each study. Ellipses indicate species that are displaced at the ridge compared to other studies.

3.5 Conclusions

Despite the relatively small distances between ECOMAR sites, in particular the northern sites, the community composition and diversity of benthic megafauna differed significantly. Substantial differences in community composition between the northern sites suggest that the Scotland-Iceland Overflow Water does not act as a dispersal route across the Ridge. Biomass and density were similar between the sites but size distributions differed significantly. The SE site has the greatest number of unique species, suggesting that the CGFZ acts as more efficient barrier to dispersal than the Ridge. Environmental differences may contribute most to the observed differences in community structures between sites. Compared to continental margins, the MAR shows no bathymetric displacement of benthic invertebrate megafauna. The heterogeneity of benthic assemblages over small spatial scales should be considered in the design of marine protected areas on the MAR.

Chapter 4

ROV Video Survey on Invertebrate Megafauna Distribution at the MAR

4.1 Introduction

According to 'the theory of spatial heterogeneity' communities become more complex and diverse the more heterogeneous and complex the physical environment is (Pianka, 1966). The level at which habitat complexity is investigated gives information on communities at different scales. Habitat heterogeneity at a macro-scale, for example, refers to features such as topographic relief and other geological features (Pianka, 1966). Such features are often associated with speciation events, in which ridge structures create a barrier to gene flow between two populations that can eventually lead to the evolution of two separate species (Zardus et al., 2006). Habitat heterogeneity at a micro-scale, on the other hand, refers to features of about the same size as the investigated organisms (Pianka, 1966). Although faunal distributions can be assessed through trawling at a broad scale, it does not give any information about variations at macro- or micro-scale (Malatesta et al., 1992). The distribution of benthic megafauna are driven by microhabitat features (Rex, 1981; Auster et al., 1991), such as sediment types (Grassle et al., 1975), hydrodynamic features (Christiansen and Thiel, 1992), and fine-scale biogenic structures (Zajac, 2008). These microhabitats can affect the diversity, density, and species composition of the entire area.

Several aspects are recognised today that influence microhabitats and create fine-scale patches. As a result of the food limitations in the deep sea, microhabitats can be created through phytodetritus patches (Lampitt, 1985), which in turn can increase local diversity

(Snelgrove, 1999). Species distributions have also been correlated with sediment types (Rex, 1981), which can be influenced and changed through bioturbating epifauna, which in turn affect local infauna (McClain and Barry, 2010). Other factors affecting habitat structures are hydrodynamic features which range in scale over several km (i.e. benthic storms, Woodgate and Fahrbach (1999)) to a few cm. Small-scale hydrodynamic changes can be caused by either rocky outcrops (Grassle et al., 1975) or non-motile structure-forming fauna, such as corals (Buhl-Mortensen et al., 2010), sponges (Beaulieu, 2001) and xenophyophores (Hughes and Gooday, 2004). These features affect the current flow of their immediate surrounding, creating patches with different environmental characteristics to the background habitat, i.e. creating strong currents, food patches, shelter, and habitat (Buhl-Mortensen et al., 2010). Mounds and tubes that are created by mobile fauna also affect the local hydrology, and can also provide surfaces ideal for the aggregating phytodetritus (McClain and Barry, 2010). Biogenic structures are associated with increased diversity in soft sediment communities (Zajac, 2008), suggesting a greater diversity with increasing habitat complexity.

The complexity of habitats cannot be sampled by conventional methods. It is, therefore, important to get visual information of an area (Grassle, 1991). New habitats have frequently been discovered in the deep sea and their classification would have been difficult without the visualisation of characteristic features (Ramirez Llodra et al., 2010). Images and videos have become very important in understanding deep-sea habitats as “a picture is worth a thousand worms” (Solan et al., 2003). It is a non-destructive sampling method that can give concurrent information on habitats, such as habitat heterogeneity, while also allowing quantification of faunal diversity, densities, distribution and behaviour, i.e. predation, feeding (Bett et al., 1995), locomotion, burrowing, and intra-specific interactions, e.g. pairing (Tyler et al., 1992).

Inter-specific species associations can also be observed, such as the holothurian *Pseudostichopus* sp. and the foraminifera *Discospirina tenuissima* (Gooday et al., in press), and the holothurian *Deima validum* and a polynoid polychaete *Harmothoe bathydomus* (Shields et al., accepted). Video and photographic systems range greatly in size and shape, depending on their target (Bett, 2003; Smith and Rumohr, 2005), and they capture observations that would otherwise be lost (Gage and Bett, 2005). In the Atlantic, for example, aggregations of small holothurians could be observed, with some individuals clustering around phytodetrital patches (Billett and Hansen, 1982). Long-term monitoring studies have also greatly benefitted from camera systems and allowed for the description of community changes (Glover et al., 2010) that were linked to the quality of phytodetritus reaching the sea floor in the Atlantic (Bett et al., 2001) and the Pacific (Ruhl, 2008). The effects of large scale disturbances can also be quantified through visual tools (Glover et al., 2010), regardless of whether these disturbances are natural, such as benthic storms (Woodgate and Fahrbach, 1999), or man made, such as trawling (Bett et al., 2001) or oil drilling (Jones et al., 2011).

The previous chapter highlights the absence of significant patterns in biomass and density in trawl samples. This observation, in combination with sediment trap data and surface primary production (Table 2.2, page 30), indicate an absence of significantly different productivity regimes on the benthos north and south of the **C**harlie-**G**ibbs **F**racture **Z**one (CGFZ). It is also apparent, from trawl data, that the ECOMAR sites have very different community compositions. In this chapter a detailed survey of the MAR, with state-of-the-art technology was combined with a sound sampling design. Best quality imaging technology available (HD video cameras, digital recordings) was combined with precise ROV navigation, in order to investigate the levels of habitat heterogeneity in soft sediment communities at the ECOMAR sites NW, NE, SW and SE of the Charlie-Gibbs Fracture Zone.

4.2 Methods

Samples were collected from the **M**id-**A**tlantic **R**idge (MAR) at bathyal depth as part of the ECOMAR project. Four stations were targeted **s**outh**e**ast (SE), **s**outh**w**est (SW), **n**orth**e**ast (NE), and **n**orth**w**est (NW) of the CGFZ (Figure 2.1, page 24).

Video transects were obtained in 2010 onboard the RRS ***James Cook*** (JC) with the National Marine Facilities **R**emotely **O**perated **V**ehicle (ROV) *Isis.* The ROV was equipped with two **h**igh-**d**efinition (HD) colour video cameras (Insite Mini Zeus), a 3-chip colour standard-definition video (Insite Pegasus), digital still camera (Insite Scorpio) and Hydrargyrum medium-arc iodide (HMI) lighting. A set of two parallel lasers (100 mm apart) was mounted on each HD camera for scaling. One HD camera was mounted vertically on the tool tray with a HMI light mounted at an angle to illuminate the field of view (1.5 m separation). The other HD camera was mounted on a pan-and-tilt unit at the front of the ROV. This was used to take zoomed-in oblique video images to help with species identifications. Only the vertical HD camera was used for analyses. The ROV was equipped with both ultra-short baseline navigation (Sonardyne medium frequency USBL) to provide absolute global position (accuracy approximately ± 10 m) and Doppler velocity log navigation (RDI DVL 1200 kHz) to provide very accurate relative position (accuracy ± 0.1 m).

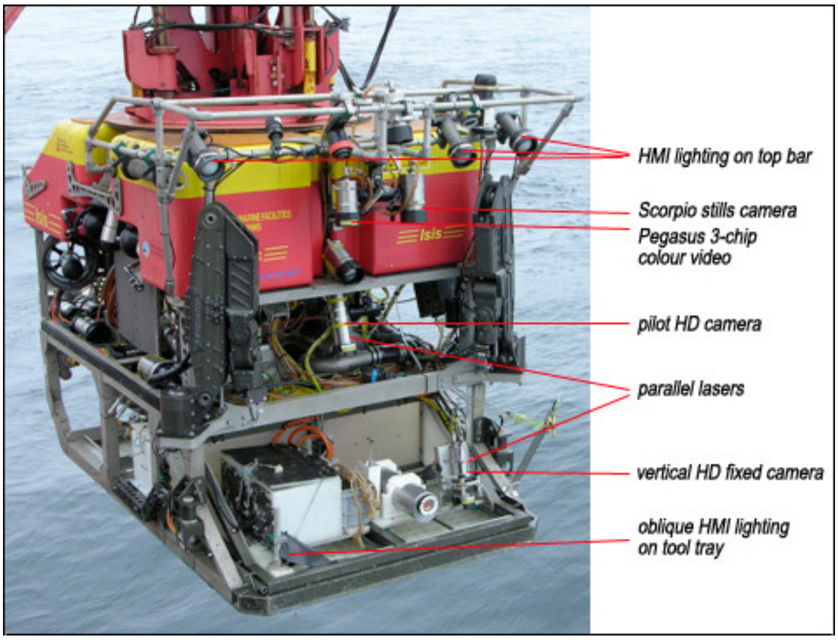
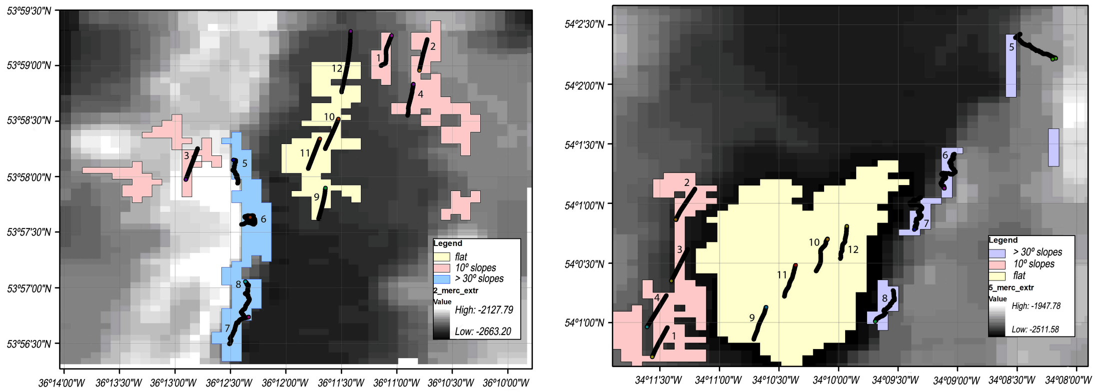


FIGURE 4.1: Image of the *Isis* ROV, with captions showing the positions of the equipment used for the video transect survey. Picture by Marsh Youngbluth.

During every transect the ROV was run in a straight line, on a set bearing, at a constant speed (0.13 ms^{-1}) and at the same set altitude (2 m). The ROV was flown maintaining Doppler lock on the seafloor, enabling very precise control. Transect width (2 m; max variation ± 0.1 m) was maintained over an uneven seafloor by adjusting ROV altitude in 50 mm steps to ensure that parallel laser beams projected onto the seafloor (100 mm apart on the seafloor) were constantly the same distance apart on the screen (5 % of screen width). Over the 500 m long transect, this technique imaged 1,000 m^2 of seafloor and 2,000 m^3 of overlying suprabenthic water. HD video was recorded (AJA KiPro) and stored as full resolution digital files on a hard drive (DroboPro).

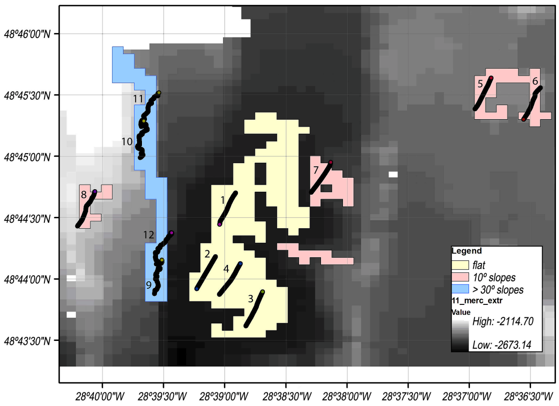
4.2.1 Survey Design

The survey was designed by Dr. Daniel O. B. Jones, from the National Oceanography Centre, Southampton. The design was based on bathymetry data collected on RRS JC011 ECOMAR cruise in 2007 with a Kongsberg EM120 swath bathymetry system. Within each study site two habitats were identified: flat (0-2° slope) and 10° slope (8-12° slope) (Figure 4.3). The area of each habitat was delineated by polygons using ArcGIS (version 10, ESRI). For each habitat in turn, polygons were selected (largest area first) until > 0.5 km^2 of seabed were covered, all remaining polygons were removed automatically. Within the selected polygons 100 lines were generated starting at random start points, lines were 500 m long and 15° heading, along the ridge axis. All lines that intersected with polygon boundaries were removed. Four non-overlapping lines were picked at random from the remaining lines, for each habitat. These four lines became the ROV sampling transects. The sampling unit for all analyses was a 500 m long ROV transect, resulting in a total of 32 sampling units.

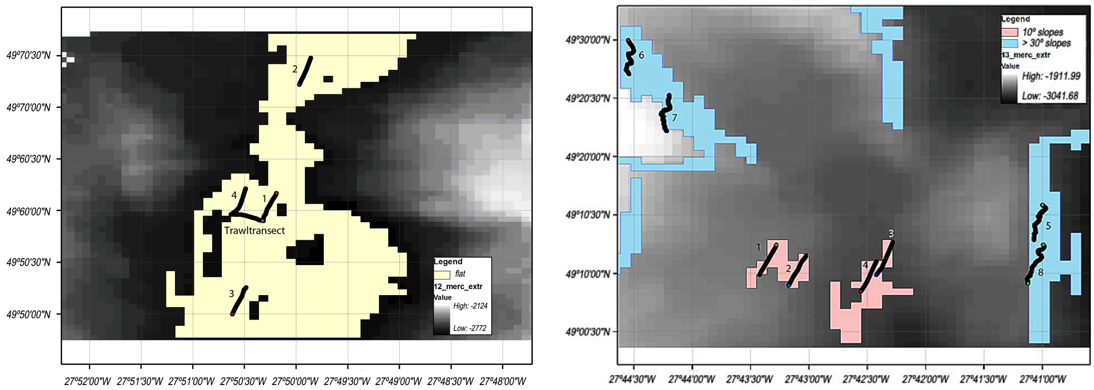


(a) Transect lines at the NW site.

(b) Transect lines at the NE site.



(c) Transect lines at the SW site



(d) Transect lines at the SE site, flat area.

(e) Transect lines at the SE site, 10 degree area.

FIGURE 4.2: Map showing the transect lines at all sites. Red areas indicate slopes between 8 and 12 degrees. Yellow areas show flat terrain. The exact position for the transects can be found in Table 4.1 (page 72). The different grey shades show different depth ranges, with the lightest grey shade at 1,911 m depth and the darkest shade at 3,041 m depth. For the purpose of this study, the blue area should be ignored. Maps courtesy of Dr. D.O.B. Jones.

Table 4.1: ROV transects, with transect name, site, habitat type, starting and end positions of each transect, and date the transects were recorded. The site refers to the location relative to the Charlie-Gibbs Fracture Zone. As all transects are of equal length and same altitude, they each cover 1,000 m^2 of benthos.

Transect	**Site**	**Habitat**	**Position**	**Latitude**	**Longitude**	**Date**
A02_01	NW	10°slope	start	53° 59.00′N	36° 11.15′W	06.06.2010
			end	53° 59.26′N	36° 11.05′W	
A02_02	NW	10°slope	start	53° 58.97′N	36° 10.82′W	06.06.2010
			end	53° 59.23′N	36° 10.73′W	
A02_03	NW	10°slope	start	53° 57.96′N	36° 12.89′W	05.06.2010
			end	53° 58.22′N	36° 12.79′W	
A02_04	NW	10°slope	start	53° 58.56′N	36° 10.91′W	06.06.2010
			end	53° 58.82′N	36° 10.82′W	
A02_09	NW	flat slope	start	53° 57.62′N	36° 11.71′W	05.06.2010
			end	53° 57.88′N	36° 11.61′W	
A02_10	NW	flat slope	start	53° 58.25′N	36° 11.64′W	05.06.2010
			end	53° 58.52′N	36° 11.54′W	
A02_11	NW	flat slope	start	53° 58.56′N	36° 10.91′W	05.06.2010
			end	53° 58.82′N	36° 10.82′W	
A02_12	NW	flat slope	start	53° 58.77′N	36° 11.50′W	01.06.2010
			end	53° 59.31′N	36° 11.42′W	
A05_01	NE	10°slope	start	53° 59.73′N	34° 11.54′W	11.06.2010
			end	53° 59.99′N	34° 11.44′W	
A05_02	NE	10°slope	start	54° 00.86′N	34° 11.33′W	11.06.2010
			end	54° 00.61′N	34° 11.27′W	
A05_03	NE	10°slope	start	54° 00.35′N	34° 11.38′W	11.06.2010
			end	54° 00.23′N	34° 11.27′W	
A05_04	NE	10°slope	start	53° 59.98′N	34° 11.57′W	11.06.2010
			end	54° 00.23′N	34° 11.46′W	
A05_09	NE	flat slope	start	53° 59.86′N	34° 10.72′W	11.06.2010
			end	54° 00.13′N	34° 10.61′W	
A05_10	NE	flat slope	start	54° 00.22′N	34° 10.46′W	11.06.2010
			end	54° 00.70′N	34° 10.10′W	
A05_11	NE	flat slope	start	54° 00.22′N	34° 10.46′W	11.06.2010
			end	54° 00.47′N	34° 10.37′W	
A05_12	NE	flat slope	start	54° 00.55′N	34° 90.98′W	11.06.2010
			end	54° 00.80′N	34° 90.86′W	
A11_01	SW	flat slope	start	48° 44.45′N	28° 39.04′W	18.06.2010
			end	48° 44.71′N	28° 38.91′W	
A11_02	SW	flat slope	start	48° 43.91′N	28° 39.20′W	16.06.2010
			end	48° 44.17′N	28° 39.07′W	
A11_03	SW	flat slope	start	48° 43.63′N	28° 38.83′W	16.06.2010
			end	48° 43.89′N	28° 38.71′W	
A11_04	SW	flat slope	start	48° 43.87′N	28° 39.02′W	16.06.2010
			end	48° 44.12′N	28° 38.90′W	

table continues ...

Transect	**Site**	**Habitat**	**Position**	**Latitude**	**Longitude**	**Date**
A11_05	SW	10 °slope	start	48 ° 45.38 ′N	28 ° 36.95 ′W	19.06.2010
			end	48 ° 45.64 ′N	28 ° 36.83 ′W	
A11_06	SW	10 °slope	start	48 ° 45.30 ′N	28 ° 36.55 ′W	19.06.2010
			end	48 ° 45.56 ′N	28 ° 36.42 ′W	
A11_07	SW	10 °slope	start	48 ° 44.69 ′N	28 ° 38.28 ′W	18.06.2010
			end	48 ° 44.95 ′N	28 ° 38.15 ′W	
A11_08	SW	10 °slope	start	48 ° 44.45 ′N	28 ° 40.19 ′W	18.06.2010
			end	48 ° 44.71 ′N	28 ° 40.06 ′W	
A12_01	SE	flat slope	start	49 ° 50.91 ′N	27 ° 50.32 ′W	24.06.2010
			end	49 ° 60.17 ′N	27 ° 50.19 ′W	
A12_02	SE	flat slope	start	49 ° 70.23 ′N	27 ° 49.99 ′W	23.06.2010
			end	49 ° 70.48 ′N	27 ° 49.86 ′W	
A12_03	SE	flat slope	start	49 ° 50.00 ′N	27 ° 50.62 ′W	24.06.2010
			end	49 ° 50.26 ′N	27 ° 50.48 ′W	
A12_04	SE	flat slope	start	49 ° 50.96 ′N	27 ° 50.62 ′W	23.06.2010
			end	49 ° 60.22 ′N	27 ° 50.49 ′W	
A13_05	SE	10 °slope	start	49 ° 00.98 ′N	27 ° 43.42 ′W	27.06.2010
			end	49 ° 10.24 ′N	27 ° 43.29 ′W	
A13_06	SE	10 °slope	start	49 ° 00.89 ′N	27 ° 43.16 ′W	27.06.2010
			end	49 ° 10.15 ′N	27 ° 43.03 ′W	
A13_07	SE	10 °slope	start	49 ° 10.01 ′N	27 ° 42.41 ′W	26.06.2010
			end	49 ° 10.27 ′N	27 ° 42.28 ′W	
A13_08	SE	10 °slope	start	49 ° 00.85 ′N	27 ° 42.55 ′W	26.06.2010
			end	49 ° 10.11 ′N	27 ° 42.41 ′W	

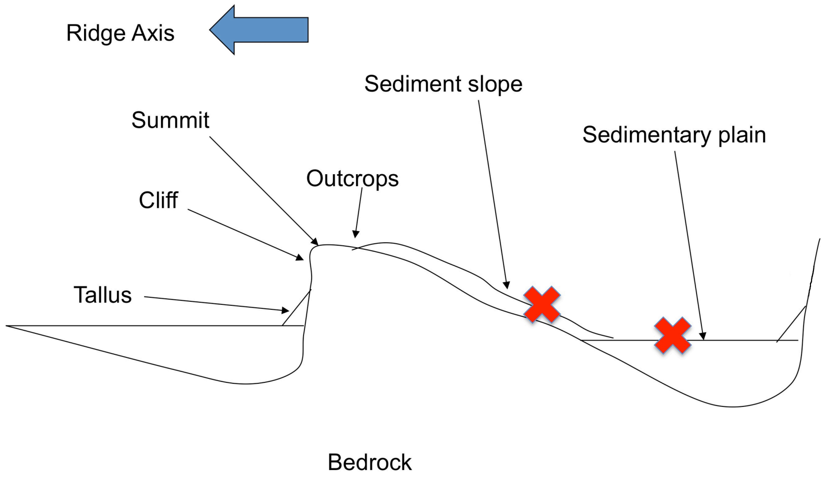


FIGURE 4.3: Image showing the terraced structure of the ridge. Red crosses indicate the flat and 10 degree terrain sampled. Schematic courtesy of Dr. Andy Dale.

4.2.2 Video Processing

Transect lengths were standardised to 500 m using smoothed Doppler velocity log data and by applying a combined routine in Matlab (version 2009a MathWorks, Inc). A CTD sensor was mounted on the ROV. Data on temperature, salinity and pressure from the ROV mounted CTD sensor were extracted using REDAS (version Idronaut S.R.L. 5.43) for each transect, and plotted using SigmaPlot 11.0 (Appendix D).

For analysis HD video was displayed on a 27 inch monitor using Quicktime Pro (version 7, Apple Inc.). Identifications and abundance counts were made to the closest possible taxonomic unit, using the HD video footage. Identifications were based on a species guide that had been created on the ship with the help of taxonomic experts (Appendix E). One still frame was extracted every second, from each video transect, using Final Cut Pro (X 10.0 Apple Inc.), and given a unique ID code. Data were quality controlled based on abundance data collected from the HD videos. The frames containing each occurrence of every species were automatically extracted using a programme written in the R software environment (R Development Core Teams, 2009), the code for this was written by the author and her supervisor Dr. D.O.B. Jones. These were manually screened to check for consistency in identification and to validate counts. Once this was completed, taxonomic experts checked and confirmed species identities where necessary.

4.2.3 Analyses

A number of taxa were excluded from statistical analyses. These included taxa that were infaunal, too small (< 1 cm), or not benthic species, such as fish and jellyfish. All observations that could not be identified to at least phylum level, and where it was unclear whether they were organisms or traces, were also excluded. Notes on these observations were made and they comprised about 17 % of the total count. Small gastropods and bivalves were excluded because they could not be distinguished with certainty from pteropod shells. However, all species were included in the species catalogue (Appendix E). Of the species included many could not be identified to species level. The level of taxonomic identification that was possible was highlighted in the names of the indet. taxa, which were differentiated in the analyses between different indet. spp. Two species, belonging to two different orders, are too similar in shape to be distinguished in videos; they are henceforth referred to as Urechinidae/Hemiasteridae complex. All taxonomic units, regardless of their level of identification, were treated as species; i.e. counts of Holothurian (Class) indet. were treated in the same way as *Staurocucumis abyssorum.* This method has been successfully applied in other studies (Gutt and Piepenburg, 2003; Jones et al., 2007; Soltwedel et al., 2009). The greatest possible taxonomic resolution is maintained by treating indet. spp. and individual species as undifferentiated, previous results suggest that the analyses are not distorted by this method.

In order to check the evenness of the different transects, a Whittaker Rank Abundance plot (Magurran, 2004) was calculated using the R programming environment (R Development Core Teams, 2009) (Section 1.4.3.2). This method was preferred because the shape of the curve made it easier to judge whether data needed to be transformed and to determine where most rare species occurred (Magurran, 2004). The difference between species richness and standing stock in this study are only subtly different, as the area sampled between transects and sites were comparable. While species richness refers to number of species for a given number of sampled individuals; standing stock refers to the number of species in a given area (Gray, 2000). Species richness was calculated with a species accumulation curve, using the S estimator in Primer 6 (Clarke and Warwick, 1994) (Section 1.4.3.1). Standing stock was compared using the non-parametric Kruskal-Wallis analysis in the R programming environment, because data were not normally distributed (R Development Core Teams, 2009). The Shannon-Wiener and the Simpson indices were also calculated in Primer 6 (Section 1.4.3.3), and calculations are based on the abundance data for taxa in each transect. Both indices were used to cover patterns for rare and dominant species; Shannon-Wiener is weighted towards rare species, while the Simpson Index concentrates on dominant species (Magurran, 2004). The diversity measures of superstations and habitats were tested for normality with the Shapiro-Wilk Normality Test, resulting in the Shannon-Wiener index tested for significance with the parametric two-way ANOVA (factoring habitat and site), while the Simpson index was compared with the non-parametric Kruskal-Wallis test. Both tests were carried out in the R programming environment (R Development Core Teams, 2009).

Before multivariate analyses commenced the dataset was square-root transformed as the majority of transects lacked a clear log normal distribution associated with an even species distribution in the Whittaker Rank Abundance plot (Figure 4.5). In order to investigate similarities between sites a one-way ANOSIM, a non-metric multidimensional scaling analysis (MDS) and a hierarchical cluster analysis were carried out using Primer 6 (Clarke and Warwick, 1994), where the cluster results were overlain onto the MDS graph. A one-way SIMPER analysis was run in Primer 6, based on Bray-Curtis similarity with a cut off for low contributions at 90 %. This analysis shows a) the % similarity of the assemblages between individual transects, factored by site and habitat respectively; and b) the % average dissimilarity between sites, in terms of species composition. Species densities were analysed with a non-nested PERMANOVA (Bray-Curtis similarity, 999 permutations) using the vegan library (Oksanen, 2011) in the R environment (Clarke and Warwick, 1994), factoring site and habitat.

4.3 Results

4.3.1 Environmental Observations

The density of pteropod shells was notably greater at the southern sites, while being virtually absent in the north. At the SW site these pteropod shells were distributed densely throughout most transects. At the SE site pteropod shells were more prominent on flat habitats and only occurred in patches in transects taken on slope habitat. Furthermore, benthic ripples were seen at the seafloor upon initial arrival at the SW site, which appeared to be absent at the other sites. Several dead sponges were observed on the seabed at the NE site, which, although seen at other sites, occurred more frequently at the NE.

4.3.2 Species Richness

Similar species numbers were observed at the eastern and western sites of the ridge, respectively. The species accumulation rate differed between the sites and was noticeably greater at the southern sites (Table 4.2). The slowest rate in which new species were collected was found at the NW site, while the fastest accumulation rate was observed at the SW site. At the SW site less than half the individuals sampled represented the same number of species observed at the NW site. A similar trend was observed between the NE and SE sites.

Table 4.2: Species richness at all four sites.

Site	**No of Taxa**	**No. of Individuals**
NW	104	15,071
NE	73	12,078
SW	104	7,372
SE	73	7,688

Between habitats the species accumulation rates were similar at the northern sites, while a faster accumulation rate was observed for sloped habitats at the southern sites (Figure 4.4). Although the least number of individuals were sampled at the SW site at sloped habitat, they represented the highest number of species (Figure 4.4). In contrast, at the SE site in flat habitat the least number of species were represented by the highest numbers of individuals (with the exception of the NW sloped habitat) (Table 4.3). Although all species accumulation curves level off, none reaches an asymptote, suggesting that more sampling would be required in order to encounter all species from the different sites (Figure 4.1).

TABLE 4.3: Species richness in each habitat from each site.

Site	**Habitat**	**No of Species**	**No. of Individuals**
NW	flat	69	3,274
	10 °	82	11,797
NE	flat	66	6,287
	10 °	65	5,781
SW	flat	70	5,942
	10 °	85	1,430
SE	flat	62	6,295
	10 °	52	1,393

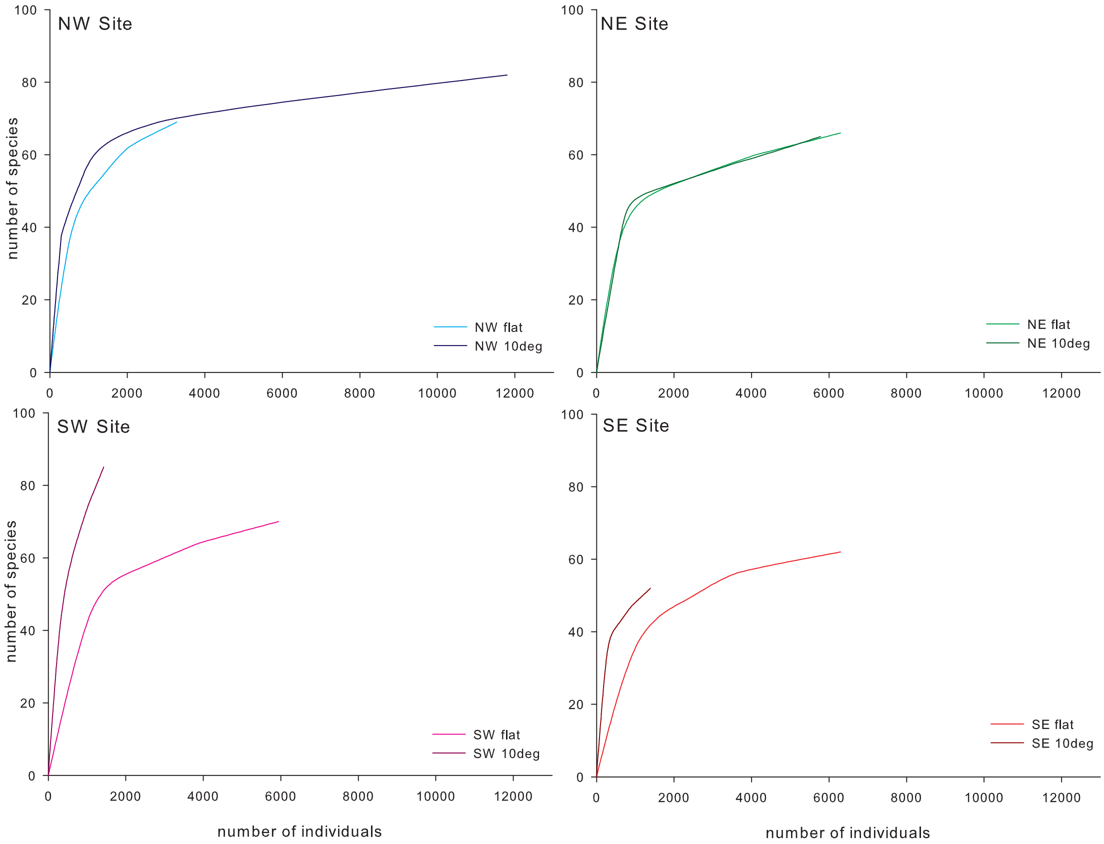


FIGURE 4.4: Species accumulation curve for each site, with every site being differentiated between flat and 10 degree habitats. Data shown are based on raw data with the number of species against the number of individuals collected at each site. Every habitat was sampled with four transects, at each site.

4.3.3 Standing Stock

A total of 32,000 m^2 of HD video footage were analysed, and 302,480 still frames were produced for later reference. A total of 55,192 individual specimens were counted, representing nine phyla and 156 different taxonomic units (Table 4.4). Every transect covered an area of 1,000 m^2, and the same number of transects were taken at each habitat and site. Hence, standing stock refers to the number of individuals in 8,000 m^2 area sampled when comparing sites, while for habitats it is measured for 4,000 m^2. The areas were not standardised to 1,000 m^2 because the resolution would have been compromised.

Overall, echinoderms were the most abundant phylum at the ECOMAR study area and dominated the standing stock of the eastern ridge sides (Table B.1). Also high in abundance were sponges that were particularly dense at the NW site, and foraminiferans, which dominated the standing stock at the SW site (Table 4.4). The relatively low abundance for annelids reflected the fact that they are normally too small to be counted in videos. Only those species large enough, e.g. Polynoidae (Family) indet., were included (Table B.1, page 147). Low standing stock in arthropods are assumed to be caused by their ability to move out of the visual view.

High standing stock of sponges, echinoderms and foraminiferans characterised the NW site. High numbers in porifera were caused by the Hexactinellida (Class) sp. BJ and Hexactinellida (Class) indet. in all transects. One transect at the NW site showed unusually high abundances, which also included high numbers of *Pheronema* sp. A, Rossellidae sp. I and Hexactinellida (Class) sp. AO (Table B.1, page 147). The dominance in echinoderms at the NW site resulted from a large standing stock of regular echinoids Urechinidae/Heminasteridae complex and *Urechinus naresianus*, and in ophiuroids from Ophiuroidea (Class) indet., Ophiuroidea (Class) sp. E and Ophiuroidea (Class) sp. F. High numbers in foraminiferans at the NW site were caused by the foraminiferans *Syringammina fragillissima* and *Discospirina tenuissima* at the NW03 transect. The NE site also had a high standing stock of echinoderms (Table 4.4); with high numbers of the aggregating holothurian *Kolga nana*, and irregular echinoid *Pourtalesia* (Genus) indet. A high standing stock in sponges were mainly observed for Hexactinellida (Class) sp. BJ at the NE site. Sponges Porifera (Phylum) indet. and Rossellidae sp. I, and foraminiferans *Discospirina tenuissima* occurred in high abundance at the SW site. Finally, the SE site was characterised by the echinoid *Pourtalesia* (Genus) indet. and foraminifera *Discospirina tenuissima* (Table B.1, page 147).

Although differences in standing stock were observed between sites, they did not differ statistically (Kruskal-Wallis: chi-squared = 2.9 , df = 3, p = 0.41). At the southern sites, transects from 10 ° slope terrain showed a noticeably lower standing stock than the flat terrain (Table 4.3). At the northern sites, on the other hand, the standing stock did not differ much between the habitats at the NE site, while showing noticeably greater standing stock at the 10 ° habitat. Between-site variations in standing stock were greater in slope than flat habitats, although those differences were not statistically significant (Kruskal-Wallis: chi-squared = 0.01 , df = 1, p = 0.92).

TABLE 4.4: The standing stock (individuals 8,000 m^{-2}) of different Phyla between sites, including the total number of observations for each Phyla and from each site, at the MAR, displayed from most common to least common Phylum.

Phylum	**NW Site**	**NE Site**	**SW Site**	**SE Site**	**Total**
Echinodermata	4,642 (30 %)	25,394 (93 %)	840 (12 %)	3,871 (50 %)	34,747
Porifera	6,918 (45 %)	1,331 (5 %)	1,480 (20 %)	814 (11 %)	10,543
Foraminifera	2,925 (19 %)	126 (> 1 %)	3,759 (51 %)	2,143 (28 %)	8,953
Cnidaria	500 (3 %)	153 (1 %)	959 (13 %)	533 (7 %)	2,145
Hemichordata	39 (> 1 %)	44 (> 1 %)	120 (2 %)	221 (3 %)	424
Nemertea	300 (> 1 %)	6 (> 1 %)	4 (> 1 %)	6 (> 1 %)	316
Annelida	132 (1 %)	44 (> 1 %)	29 (> 1 %)	21 (> 1 %)	226
Arthropoda	38 (> 1 %)	17 (> 1 %)	71 (1 %)	58 (1 %)	184
Mollusca	3 (> 1 %)	5 (> 1 %)	83 (1 %)	22 (> 1 %)	113
Bryozoa	2 (> 1 %)	0 (> 1 %)	3 (> 1 %)	0 (> 1 %)	5
Total	**15,499**	**27,120**	**7,348**	**7,689**	57,656

4.3.4 Species Rank Abundance

The highest level of evenness and the greatest number of rare species occurred at three transects from the NW site (NW03, NW11, NW12) (Figure 4.5). One transect from the SE site (SE02) and three from the NE site (NE10, NE11, NE12) showed high levels of dominance compared to other transects. The echinoid *Pourtalesia* (Genus) indet. dominated transect SE02 in numbers, and the transects NE10, NE11 and NE12 were dominated by the holothurian *Kolga nana*. In general, there was no clear pattern for all the transects, as they ranged in shape from log-normal curves (3 from NW site, 3 from SW site, 2 from NE site) to geometric series (24 remaining transects) (Figure 4.5). A geometric series is caused by the dominance of some species and low levels of evenness, whereas log-normal curves suggest high evenness within the transect (Whittaker, 1972). Based on a high number of transects forming a geometric series, it was decided to transform the data (square root) for subsequent MDS, cluster, SIMPER and PERMANOVA analyses.

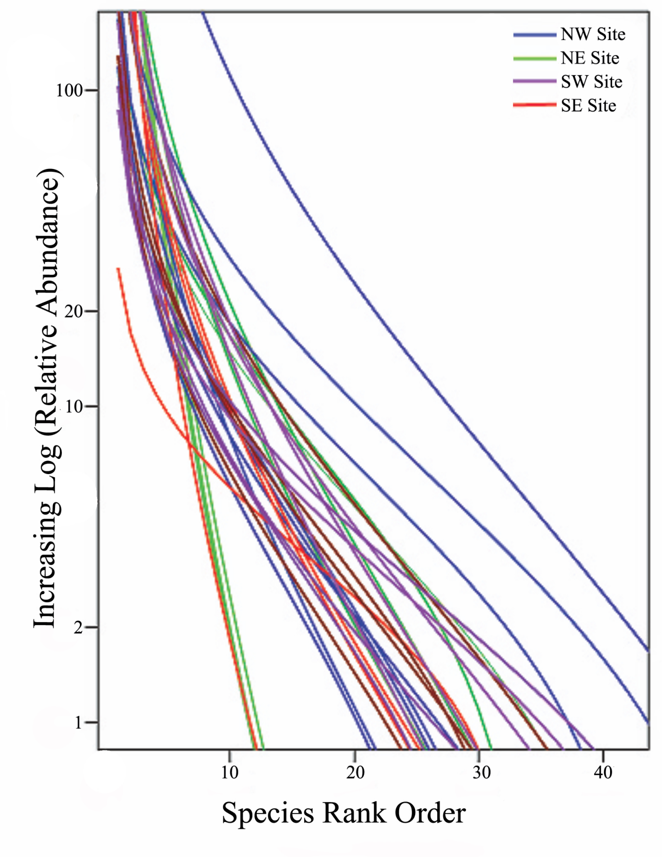


FIGURE 4.5: Whittaker Rank Abundance Plot: The most common species are found on the left hand side on the x axis, and rare species on the far right. Lines represent individual transects.

4.3.5 Diversity

Although small-scale differences could be observed, they were not significant between either sites (Kruskall-Wallis: chi-squared = 3.43, df = 3, p = 0.33) or habitats (Kruskal-Wallis: chi-squared = 2.9, df = 1, p = 0.09) with the Simpson index (Table 4.5). While a significant difference in diversity between the sites (ANOVA: F-value = 1.91, df = 3, p = 0.15) was also absent in the Shannon-Wiener analysis, a significant difference between habitats was measured (ANOVA: F-value = 8.57, df = 1, $p < 0.01$). A two-way ANOVA on the Shannon-Wiener results revealed a strong interaction between habitats and sites (F-value = 6.99, df = 3, $p < 0.01$), suggesting that the variation observed in diversity between habitats was site dependent.

Table 4.5: Differences in diversity between habitats and sites with the respective standard deviation; Simpson and Shannon-Wiener indices

Index	**Habitat**	**NW Site**	**NE Site**	**SW Site**	**SE Site**
Simpson	flat	0.85 ± 0.05	0.60 ± 0.20	0.65 ± 0.13	0.39 ± 0.15
	10 ° slope	0.74 ± 0.05	0.69 ± 0.23	0.82 ± 0.09	0.83 ± 0.08
	Site	0.80 ± 0.08	0.64 ± 0.20	0.73 ± 0.14	0.61 ± 0.26
Shannon-Wiener	flat	2.45 ± 0.28	1.69 ± 0.55	1.79 ± 0.37	1.12 ± 0.42
	10 ° slope	1.91 ± 0.10	1.96 ± 0.63	2.46 ± 0.33	2.44 ± 0.40
	Site	2.18 ± 0.35	1.83 ± 0.57	2.12 ± 0.48	1.78 ± 0.80

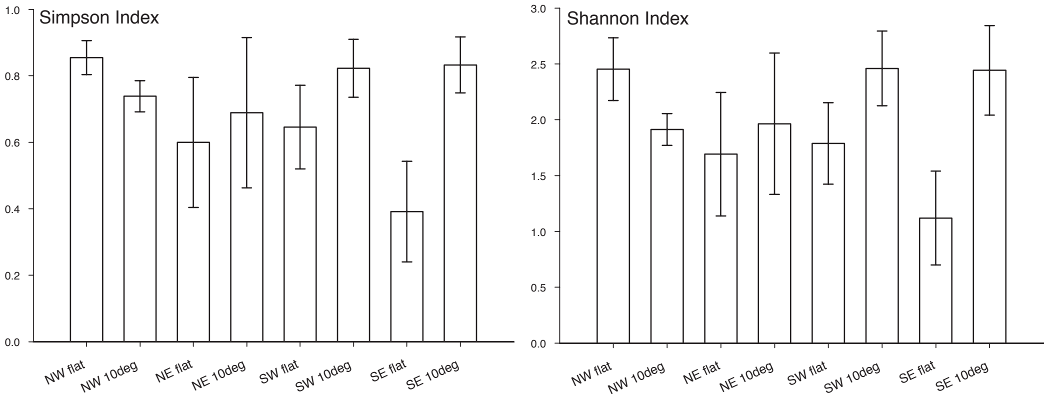


Figure 4.6: Diversity indices. Simpson and Shannon-Wiener analyses, with their standard deviation based on four replicates for each habitat at every site.

4.3.6 Community Composition

Five distinct clusters were apparent in a MDS that compared the community composition between all transects. The northern transects clustered by site into NE and NW; and the southern sites formed three further clusters (Figure 4.7). The majority (13 transects) of the southern transects grouped together in a main cluster, and two further clusters were formed by two SE transects (SE02 & SE01) and one SW transect (SW06), respectively (Figure 4.7). The community composition varied significantly between sites (PERMANOVA: Pseudo-F = 15.91, df = 3, p = < 0.001), and between habitats (PERMANOVA: Pseudo-F = 5.70, df = 2, p = < 0.001). The interaction between sites and habitats was also very significant (PERMANOVA: Pseudo-F = 3.91, df = 3, p = < 0.001), suggesting that the differences in community composition between habitats was site dependent.

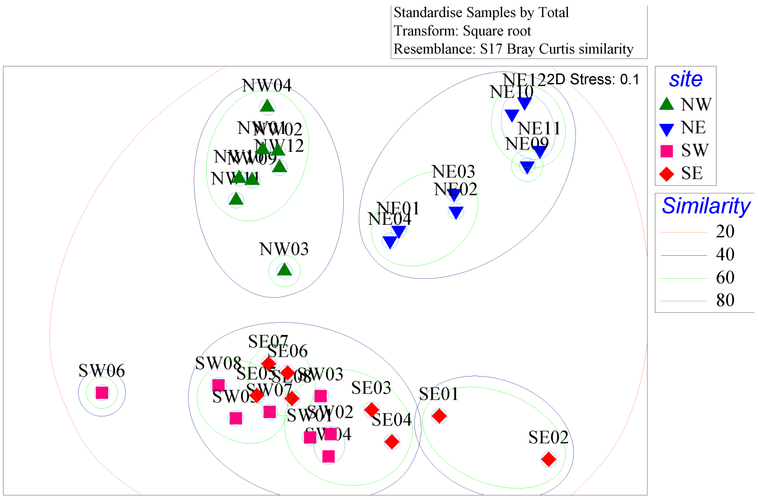


FIGURE 4.7: Multidimensional Scaling Plot, based on Bray-Curtis Similarity, after square root transformation. Circles represent the similarity of individual samples to all other samples, based on a cluster overlay.

While there is a clear separation between the northern sites the southern sites lack such a divide, though a west/east trend can be observed. The transects collected from the northern sites showed the least within-site variation, with 60.1 % similarity between the transects from the NE and NW sites, respectively (Table 4.6). At the southern sites, the within-site similarity of transects was lower than those at the northern sites (Table 4.6). With the exclusion of the three transects that form two distinct clusters at the southern sites (Figure 4.7), the similarity in community composition between transects from the SE and SW sites equals the within-site-similarity of the northern sites. The community composition between habitats showed least variation at the NE site and greatest variation at the SE site (Table 4.6). Differences in community composition between habitats were generally lower at the southern sites, and within-habitat similarities varied between 50.3 % and 76.7 % (Table 4.6).

At the NW site transect 03 stands out in the MDS plot, with only 40 % similarity to other transects from this site. NW03 showed unusually high densities with over 11,000 individuals in 1,000 m^2, while the other transects averaged about 700 individuals in each transect (Figure 4.8). Although data were square root transformed, the effect of such high abundances were not entirely removed. A further cause for the observed difference could be the distant location of this transect, relative to the others (Figure 4.2). The NE site had the clearest within-site habitat distinction. At the NE site the NE09 transect appeared to be somewhat different in community composition, compared to the other transects. It is not clear what distinguishes this transect from the others at the NE site. The positioning of the NE transects to one another is not unlike the geographic position they were collected from (Figure 4.2).

Table 4.6: The similarity of the replicates within each site, and within each habitat of every site, together with the overall similarity between habitats from each site. Measures are based on the Bray-Curtis similarity.

Sites	**Within-Site**	**Habitat**	**Replicate**	**Habitat**
NW	60.1 %	flat	68.1 %	58.2 %
		10 °	57.3 %	
NE	60.1 %	flat	65.2 %	72.0 %
		10 °	68.7 %	
SW	53.7 %	flat	76.7 %	46.4 %
		10 °	50.3 %	
SE	48.8 %	flat	65.2 %	40.1 %
		10 °	56.1 %	

Both northern sites were more similar in community compositions between habitat types than the southern sites (Figure 4.8). The southern sites showed a stronger separation by habitat than site. Hence, community compositions appear more distinct based on habitat type rather than site in the south. At the SW site, the SW06 transect was distinct from the other transects at the site, which was mainly caused by an overall higher abundance of sponges. This transect was characterised by some meters of hard rock substratum, in the form of boulders and pebbles on the seabed. Although the transects were run over flat habitats, it was impossible to predict such small scale variation based on the available bathymetry data, prior to the survey design. Finally, at the SE site two transects (SE01 & SE02) appeared to vary in their species composition to the extent that they only shared about 20 % in species composition with the other transects from the site (Figure 4.8). Differences in those transects (SE01 & SE02) were mainly caused by a high abundance of *Pourtalesia* (Genus) indet. and fewer observations of *Discospirina tenuissima* compared to the other flat transects at the SE site (SE03 & SE04). A clear gradient can be observed at the southern sites that indicates species composition was more habitat than site dependent (Figure 4.8).

Taxonomic units contributing to the dissimilarity in species composition between sites show three taxa in common for all sites (Porifera (Phylum) indet., Hexactinellida (Class) indet., *Discospirina tenuissima*). These taxa all contributed to the total average dissimilarity between the four ECOMAR sites. The northern sites shared four important taxa (*Urechinus naresianus*, Urechinidae/Hemimasteridae complex, Ophiuroidea (Class) indet., Hexactinellid sp. BJ), as did the southern sites (*Flabellum angulare*, Enterproneusta sp. B, *Peniagone* (Genus) indet., *Syringammina fragillissima*).

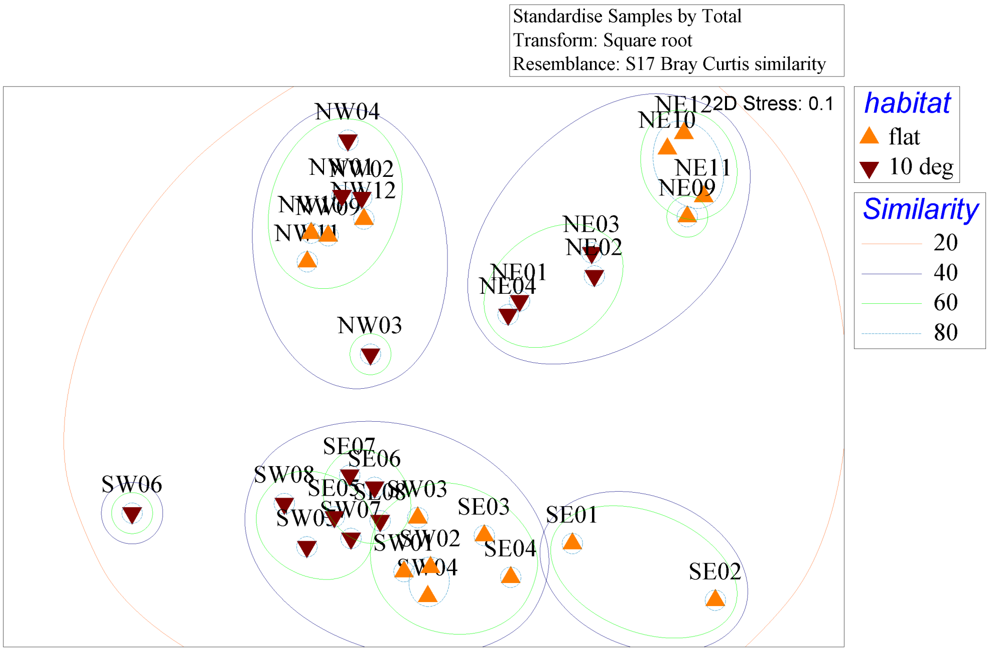


FIGURE 4.8: Multidimensional Scaling Plot, highlighting differences in community composition between flat and 10 ° slope habitats, from each site.

The Hydroidolina (Subclass) indet. contributed to the dissimilarity in species composition at the NW, SW and SE sites, but not the NE site, while the *Pourtalesia* (Genus) indet. was important at the two eastern sites, and the Holothurian (Class) indet. at the NE and SW sites. All sites were characterised by two uniquely important taxa with the exception of the NW site, where three taxa contributed to the average dissimilarity to the other sites (Table 4.7).

Between habitats taxa contributing to differences were similar at the northern sites (Table 4.8). At the NW site both habitats had the same taxa (Urechinidae/Hemimasteridae complex, *Urechinus naresianus*, Porifera (Phylum) indet., Hexactinellida (Class) indet., Ophiuroidea sp.), but they differed in their rank of importance. A similar pattern was observed at the NE site. The majority of important taxa were the same in the two habitats (*Kolga nana*, Urechinidae/Hemimasteridae complex, Hexactinellida (Class) indet., Porifera (Phylum) indet.), apart from Ophiuroidea (Class) indet., which occurred only at the NE flat site, and Hexactinellida (Class) indet. which occurred only at the NE 10 ° slope. At the southern sites the differences between habitats were more noticeable. In both cases only two taxa were the same between habitats (SW: Hydroidolina (Subclass) indet., Porifera (Phylum) indet.; SE: *Discospirina tenuissima*, Porifera (Phylum) indet.), while three taxa contributed uniquely to the different habitats at both sites (Table 4.8). Overall, the species composition in flat habitats were more similar between the sites (66.7 %) than the 10 ° slope habitats (59.3 %).

TABLE 4.7: SIMPER results for each site showing the 11 most important species that differentiate sites, with the % contribution of each species.

NW Site	%	**NE Site**	%	**SW Site**	%	**SE Site**	%
Urechinus naresianus	15.2	*Kolga nana*	39.3	Porifera (Phylum) indet.	16.5	*Discospirina tenuissima*	12.9
Urechinidae/Hemimasteridae complex	12.5	Urechinidae/Hemimasteridae complex	8.0	*Discospirina tenuissima*	12.7	Porifera (Phylum) indet.	11.0
Porifera (Phylum) indet.	11.5	Ophiuroidea (Class) indet.	7.1	Hydroidolina (Subclass) indet.	7.7	Hydroidolina (Subclass) indet.	7.6
Hexactinellida (Class) indet.	7.5	*Pourtalesia* (Genus) indet.	6.1	*Flabellum angulare*	5.7	Enterproneusta sp. B	7.1
Ophiuroidea (Class) indet.	7.2	Porifera (Phylum) indet.	5.9	Hexactinellida (Class) indet.	4.7	*Flabellum angulare*	5.4
Ophiuroid sp. E	4.7	Hexactinellida (Class) indet.	5.5	Enterproneusta sp. B	3.8	Hexactinellida (Class) indet.	5.3
Discospirina tenuissima	4.1	Hexactinellida sp. BJ	3.0	*Peniagone* (Genus) indet.	3.5	*Hydraasterias sexradiata*	4.7
Hydroidolina (Subclass) indet.	3.5	*Urechinus naresianus*	3.0	Holothurian (Class) indet.	3.5	*Peniagone* (Genus) indet.	4.4
Hydroidolina sp. A	3.3	*Discospirina tenuissima*	2.1	Scaphopod (Class) indet.	3.2	Cnidaria (Phylum) indet.	3.8
Hexactinellida sp. BJ	3.2	*Hymenaster* (Genus) indet. A	2.0	Elpidiidae (Family) indet.	3.0	*Pourtalesia* (Genus) indet.	3.6
Ophiuroidea sp. F	2.7	Holothurian (Class) indet.	2.0	*Syringammina fragillissima*	2.9	*Glyphocrangon sculpta*	2.5

TABLE 4.8: SIMPER results for the different habitats at each site showing the 5 most important species that are responsible for the dissimilarities between sites, with the % contribution of each taxonomic unit.

	NW Site	%	**NE Site**	%	**SW Site**	%	**SE Site**	%
flat	*Urechinus naresianus*	14.0	*Kolga nana*	26.9	*Discospirina tenuissima*	23.2	*Discospirina tenuissima*	15.0
	Urechinidae/Hemimasteridae complex	9.3	*Pourtalesia* (Genus) indet.	9.5	Porifera (Phylum) indet.	10.9	*Pourtalesia* (Genus) indet..	14.6
	Porifera (Phylum) indet.	9.2	Urechinidae/Hemimasteridae complex	7.0	*Flabellum angulare*	8.7	Hydroidolina (Subclass) indet.	8.0
	Ophiuroidea (Class) indet.	9.0	Porifera (Phylum) indet.	6.1	Hydroidolina (Subclass) indet.	5.5	Enterproneusta sp. B	7.1
	Hexactinellida (Class) indet.	7.1	Ophiuroidea (Class) indet.	5.6	*Syringammina fragillissima*	4.5	Porifera (Phylum) indet.	6.1
10 °	Urechinidae/Hemimasteridae complex.	16.7	*Kolga nana*	19.7	Porifera (Phylum) indet.	22.3	Porifera (Phylum) indet.	16.8
	Urechinus naresianus	14.2	Porifera (Phylum) indet.	8.6	Hydroidolina (Subclass) indet.	8.4	Hexactinellida (Class) indet.	8.3
	Porifera (Phylum) indet.	12.6	*Pourtalesia* (Genus) indet.	8.5	Hexactinellida (Class) indet.	7.8	*Flabellum angulare*	8.0
	Hexactinellida (Class) indet.	7.3	Urechinidae/Hemimasteridae complex	8.1	Scaphopod (Class) indet.	6.2	*Discospirina tenuissima*	8.0
	Ophiuroidea (Class) indet.	6.4	Hexactinellida (Class) indet.	6.8	Elpidiidae (Family) indet.	6.0	*Peniagone* (Genus) indet.	5.5

4.4 Discussion

4.4.1 Standing Stock

The southern transects were characterised by pteropod shells covering the seafloor. This sometimes made it difficult to distinguish species and it is very likely that some species were overlooked. The pteropod shell cover was more dense at the SW site, and was relatively sparse at the SE site on the 10 ° slopes. Comparing these two areas, there was no indication that the specimen count increased noticeably in areas where these shells were almost absent, suggesting that the numbers are a realistic representation. Epibenthic megafauna occurred in greater abundance at the two stations north of the CGFZ than the south (Table 4.4), though the difference between sites was not significant. The absence of a significant trend in density between the sites is not surprising, as temperature, salinity, and pressure did not show any noticeable variations in the ROV CTD profiles (Appendix C). Neither were any significant differences in organic matter flux measured between the sites from 2007 to 2010 (Table 2.2, page 30). The standing stock of benthic megafauna generally decreases with depth on a large scale (Lampitt et al., 1986; Rex et al., 2006; Wei et al., 2010), and although density decreased somewhat with increasing depths in the present study, the 600 m variation in sampling depth are too little to show such global trends.

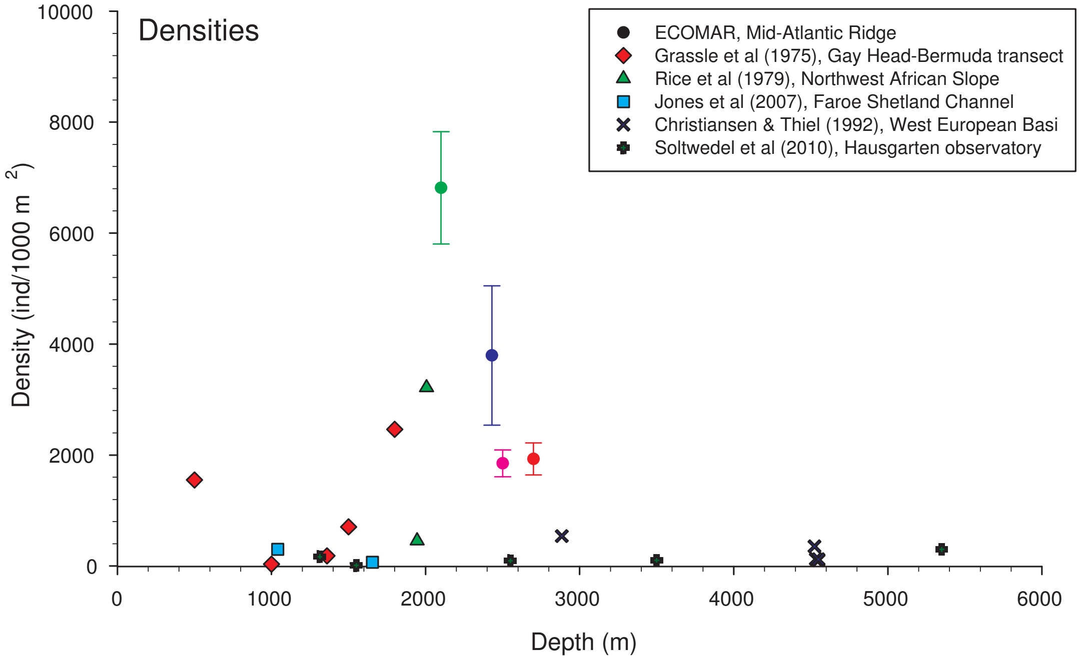


FIGURE 4.9: Mean density (individuals 1,000 m^{-2}) of the ECOMAR sites with standard error bars, compared to other study areas. ECOMAR sites are presented individually, with colours consistent with previous figures (green - NE, blue - NW, pink - SW, red - SE). References are named in the legend together with the study area.

The standing stock from the MAR was compared to other studies that used imaging technology to estimate the density of epibenthic fauna (Figure 4.9). The majority of studies reported densities of less than 800 individuals 1,000 m^{-2} (Grassle et al., 1975; Rice et al., 1979; Christiansen and Thiel, 1992; Jones et al., 2007; Soltwedel et al., 2009), while all densities at the MAR were greater than 1,000 individuals 1,000 m^{-2}. Two sites from the Gay Head Bermuda transect showed comparable densities to the southern ECOMAR sites, although these sites were over 1,000 m shallower (Grassle et al., 1975). The NW site from the MAR compared in density to the Northwest African Slope (Rice et al., 1979), while the NE site exceeded the densities of any other reported study area. The high density observed at the NE site was characterised by aggregations of the deposit feeding holothurian *Kolga nana.* Aggregations of *Kolga hyalina* have been reported from the **P**orcupine **S**ea**b**ight (PSB). At the PSB *Kolga hyalina* showed signs of very early gonadal development and similar size distributions, both useful reproductive adaptations suitable for unstable environments, or r-selected life history (Billett and Hansen, 1982). A revision of the genus *Kolga* shows that *Kolga nana* and *Kolga hyalina* are the same species (Rogacheva, 2011). Although detailed analyses of *Kolga nana* are lacking from the MAR, observations of similar size distributions imply a similar life-history at the MAR. The presence of *Kolga nana* at the NE site might point towards disturbance events at that site.

In general, the standing stock of the MAR was greater than expected for their respective depths. It is believed that this, in part, is caused by improved imaging technology that allows for better species counts, and also because the density measures presented for the ECOMAR area are based on replicates and not only individual transects. Although the density pattern at the MAR might be driven partially by depth, it is believed that other factors also play a role. These factors cannot be identified within the scope of this study, but it is speculated that they might be caused by differences in the quality of organic matter input (Kiriakoulakis et al., 2001) or disturbance events that could effect some sites.

4.4.2 Biodiversity

One of the greatest challenges in analysing video footage is the identification of specimens down to species level. Despite the HD video quality used in this study, there was a limit to the detail that could be seen in videos recorded at 2 m altitude. All individuals in this study were identified to the lowest possible taxonomic unit. However, the actual diversity in the ECOMAR area is almost certainly higher than reported here, as organisms (morphotypes) could often only be identified confidently down to family or genus level, and might encompass several species. The species accumulation curves also suggest that more sampling effort would increase the number of species at all sites (Figure 4.4). The biodiversity at the MAR did not differ significantly between sites (Table 4.5). The diversity at the western sites was marginally higher, with less variations between transects, but no clear overall pattern could be observed. On a global scale biodiversity has been reported to decrease from the equator to the Arctic (Rex et al., 1993; Ramirez Llodra et al., 2010). However, no such northward decrease in biodiversity could be observed in the present study, most likely because the scale in this study is too small to see global trends.

The only diversity data available for comparison were from the Arctic and the **F**aroe-**S**hetland **C**hannel (FSC) (Jones et al., 2007; Soltwedel et al., 2009). The Arctic region is considered to be low in species diversity, though it has been suggested that this generalisation has to be taken with caution (Piepenburg, 2005). However, the diversity at the MAR is evidently higher than any of the transects in the FSC and at the Hausgarten observatory (Figure 4.10). All of these areas were characterised by high levels of habitat heterogeneity, similar to that at the MAR. However, the HAUSGARTEN site and the FSC comprise passages for large water masses, creating highly dynamic local hydrography that are believed to depress diversity (Jones et al., 2007; Soltwedel et al., 2009). Hydrodynamic profiles taken at the ECOMAR sites suggest an absence of such highly dynamic local hydrographic features (Dale and et al., submitted). Based on the assumption that the Arctic is generally less diverse, the elevated diversity at the MAR was expected and it is assumed that the biodiversity of the MAR is not unusual for its depth.

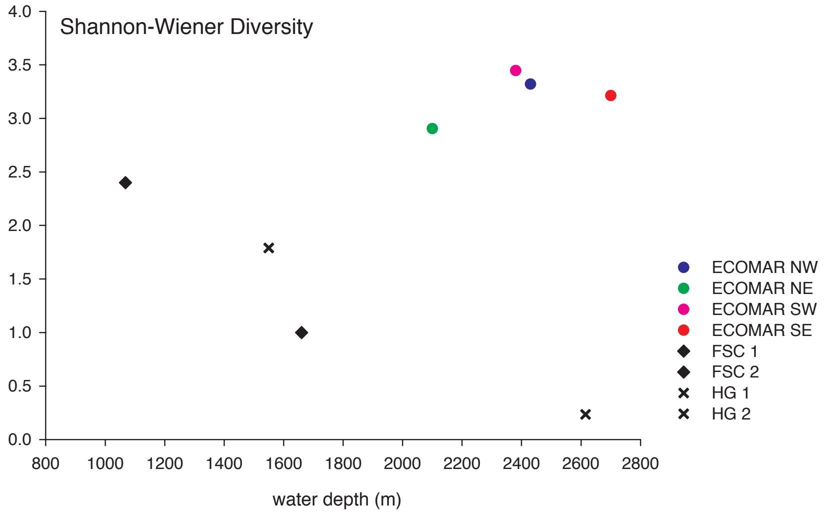


FIGURE 4.10: Shannon-Wiener diversity compared to other studies. Data from the Faroe-Shetland Channel (FSC) (Jones et al., 2007) and HAUSGARTEN observatory close to Svalbard (Soltwedel et al., 2009).

4.4.3 Community Composition

All ECOMAR sites vary significantly in community compositions (Figure 4.7). The most distinct differences in community composition were seen between the northern and southern sites, followed by the division of the northern sites. The species distribution ranges varied depending on species. The distribution of the holothurian *Kolga nana*, for example, was entirely restricted to the NE site of this study. The echinoids *Urechinus naresianus* and the Urechinidae/Hemimasteridae complex were found in great abundances at the northern sites and virtually absent at the southern sites, while the echinoid *Pourtalesia* (Genus) indet. was restricted to the eastern sites of the ridge and completely absent from the western sites. The Hexactinellida sp. BJ was particularly abundant in the northern sites and rare at the southern ones, and the *Peniagone* (Genus) indet. occurred at all sites except the NW site, which was characterised by high abundances of Ophiuroidea (Class) indet. and Nemertea (Phylum) indet., which were rare at other sites. While virtually absent in the north *Flabellum angulare*, Enteropneusta sp. B, and arthropods *Munidopsis rostrata* and *Glyphocrangon sculpta* were observed in almost all transects to the south.

Differences in faunal composition reported between the Rockall Trough and the FSC, which are separated by the Wyville-Thomson Ridge, were attributed to hydrographic parameters such as water temperature (Bett et al., 2001). Although minor differences in temperature and salinity were seen between the northern and southern ECOMAR sites (temperatures to the south 0.2 ° C higher, salinity 0.1 lower [Table 2.1, page 27]), it is very unlikely that these small variations affected the community composition at the MAR.

In a study investigating two areas at similar depth, 100 km apart, with very similar hydrographic characteristics, differences in community composition were attributed, in part, to sediment characteristics (Rex, 1981). Differences in sediment were observed also at the MAR (finer-grained muddy sediments to the north, coarser sediments to the south) (Figure 2.2, page 34). At the southern sites the sediment could not be distinguished further, whereas at the northern sites the sediment from the NW site was described as slightly finer than that of the NE site (Priede, 2007). Although sediment characteristics have only been considered secondary drivers for community changes in some areas (Jones et al., 2007; Soltwedel et al., 2009), they might contribute to differences in communities observed at the MAR.

Similar to this study, a north-south divide is also reported at the FSC and attributed to a combination of physical factors, such as sediment type, habitat heterogeneity and primary organic carbon availability (Jones et al., 2007). Habitat heterogeneity can be increased by geological and biogenous structures. As all transects were collected on soft sediment, habitat heterogeneity caused by geological features is not a likely driver for differences in species composition in this study. Biogenous structures can be further divided into 1) living biogenic, non-motile fauna that increase local habitat heterogeneity (Rex, 1981; Buhl-Mortensen et al., 2010), and 2) secondary structures that are caused by the movement of mobile fauna (McClain and Barry, 2010). The presence of pteropod shells at the southern sites, for example, increased the local biogenic habitat (Zajac, 2008). By increasing the habitat heterogeneity to the south these shells might have contributed to the north-south divide observed at the MAR. Biogenic structures that were created by bioturbation covered more % area at the SE and NW sites (Bell et al., in press), increasing habitat heterogeneity at those sites, which might have contributed to the observed community compositions. Taxa that contributed to the differences in community composition at each site included a number of biogenous structure-forming taxa (Table 4.7), such as sponges (Beaulieu, 2001), sea pens, Alcyoniidae cnidarians and xenophyophores (Buhl-Mortensen et al., 2010). In general, each site had structures that increased habitat heterogeneity which in turn increase diversity (Zajac, 2008). In the absence of any difference in diversity between sites, it is assumed that the habitat heterogeneity between the sites was similar, although caused by different biogenic structures.

Studies have shown that the quality of organic carbon play a role in structuring communities (Kiriakoulakis et al., 2001; Wigham et al., 2003a). Although no data were available on the chemical composition of the organic carbon, the source regions of particles collected by the sediment traps were modelled by Dr. Andy Dale (Section 2.6). The pattern of the source region was very similar to those of the community compositions reported here. The two northern sites had distinct source regions that were restricted to the NE and NW respectively, while the southern sites showed overlapping source regions. It is unclear what the implications are, but it is hypothesised that the source regions reflect differences in the composition of material reaching the benthos, hence affecting their species composition, but this remains speculation as no further data were available.

Differences in community composition have been reported between the European Basin and Icelandic Basin (Christiansen and Thiel, 1992). The stronger currents present in the Icelandic basin were reflected by greater abundances of resuspension feeders that were strongly anchored to the seafloor, such as pennatulids. In areas of weaker currents resusupension feeders, such as sponges and crinoids, tended to be more fragile (Christiansen and Thiel, 1992). Both southern sites had five suspension feeders identified as important to community composition, while at the NW site eight suspension feeders were identified (Table 4.7). In contrast, the NE site only had three suspension feeders. Although some species could not be identified beyond phylum level the NW site appeared to have the most fragile population of suspension feeders with three ophiuroid species, followed by the SW site with *Syringammina fragilissima*. At the SE site there is still a representation of fragile suspension feeder in form of Hydroidolina (subclass) indet., while the NE site had arguably less fragile suspension feeders as Hexactinellida sp. BJ was small with little surface area.

Finally, differences in community composition could be driven also by distance and barriers to dispersal. The similarities in community composition reflect the distance between sites, with the greatest similarity observed between the sites closest together (the southern sites), and the greatest distinction between those with the greatest distance to one another (northern and southern sites). The ridge between the southern sites does not elevate as high into the water column as at the northern ridge and might, therefore, be less of a dispersal barrier. Between the northern and southern sites, current flow through the CGFZ could prevent dispersal.

4.4.4 Fine-Scale Habitat Variability

The species accumulation rate between habitats differed between the northern and southern sites. While the northern sites showed very similar patterns between habitats, the southern sites had a faster species accumulation rate in sloped areas (Figure 4.4). A noticeable difference in diversity was observed between the habitats at the SE and NW sites, which were not observed at the NE and SW sites. Diversity between habitats differed significantly with the Shannon-Wiener diversity index, with a strong interaction between sites and habitats pointing towards site dependent diversity differences. The absence of a statistically significant difference with the Simpson index is likely an artefact caused by the statistical approach, as both indices showed the same general pattern (Figure 4.6). The community composition between flat and sloped terrain was also significantly different and showed a strong interaction between sites and habitats, suggesting that differences in community composition between habitats was site dependent (Figure 4.8). The northern sites varied less in species composition between habitats, compared to the southern sites. It is unclear why variations between habitats were more prominent at some sites and absent from others. The MAR forms a complex habitat with soft-sediment communities forming only part of the bigger structure (Priede et al., in prep), and fine-scale habitat heterogeneity likely drives spatial distributions of benthic communities (Auster et al., 1991), leading to differences in community compositions.

The within-site variability of the transects was greater at the southern sites, while transects from the northern sites were to over 60 % similar to those from their respective sites (Table 4.7). At the southern sites there was no clear division between the east and the west (Figure 4.7), and transects were more similar in community composition based on habitat rather than site (Table 4.6). The within-site variability suggests that the distribution of fauna might be more patchy at the southern sites. It has been suggested that the more distant locations are from each other, the more distinct their community is (McClain et al., 2011). In this study most transects were relatively evenly distributed (Figure 4.4). Two transects that were located farther away (NE3 and SW08), did not show any particular difference in species composition compared to other transects from their site (Figure 4.7). It is therefore not likely that the distance between the transects plays an important role in the observed within-site variation in species composition. Small-scale environmental features, such as temperature, salinity, and pressure can also affect species distributions (Auster et al., 1991). The CTD profiles (Appendix C), however, did not pick up any trend that would suggest that environmental conditions varied between habitats (three profiles that showed differences had not been calibrated appropriately).

Fauna forming biogenic structures that enhance habitat heterogeneity, such as xenophyophores and sponges (Beaulieu, 2001; Buhl-Mortensen et al., 2010), were present at all the sites and habitats (Table 4.8). However, there was no apparent trend suggesting that there were more or less of these fauna in either habitat. Equally, there is no apparent difference in the distribution of deposit and suspension feeders. Often high levels of habitat heterogeneity are associated with increased diversity (Zajac, 2008). In this study significant differences in diversity were seen between habitats, with the exception of the NW site, diversity tended to be greater in sloped terrain (Table 4.5). Assuming that greater habitat heterogeneity drives diversity one might speculate that the habitat in sloped terrain is more complex, because diversity tended to be higher. However, with videos only displaying the immediate soft sediment analysed and the resolution of bathymetry data where one pixel reflects 9 m, this remains speculation as the habitat structure outside the field of view could not be assessed. One factor that could not be accounted for, for example, was the distance of individual transects to rocky outcrops. Such obstacles can cause fine-scale turbulences, which may affect nearby fauna. For example, Levin and Thomas (1988) found that xenophyophores were more abundant immediately behind the rim of the caldera of a Pacific submarine volcano. These giant protists also often occur in high densities on sloped terrain (Levin, 1994; Hughes and Gooday, 2004). In this study xenophyophores were particularly abundant at the SW site in flat habitat, which suggests that those transects might have been nearby rocky structures.

Variations in species distribution can also be caused by differences in sediment structure (Rex, 1981; Auster et al., 1991). Spatial variations in sediment type have been shown to control the local distribution in macrofauna at the Rockall Trough and the Faroe-Shetland Channel (Bett et al., 2001). Potential fine-scale variations in sediment might also cause a variation in megafaunal distributions. Although differences in sediment were observed between sites, no variation was noticed at a scale that would distinguish the two habitat types. At the SE site pteropod shell cover was a lot denser at the flat terrain compared to the slope. However it is not clear whether that could have impacted the community composition, as pteropods were abundant in both habitat types at the SW site that also showed significant differences between habitats. The relative similarity in community composition between habitats in the north suggest that drivers, other than slope, might also cause observed fine-scale spatial variations. One possible factor could be the patchy distribution of phytodetrital deposits, which were observed in mega core samples (Figure 2.2). The spatial distribution of some species has been correlated to such aggregates in the Pacific (Lauerman and Kaufmann, 1998).

4.5 Conclusion

Except for the southern sites, the community composition between the sites was significantly different. The eastern sites of the ridge were dominated by echinoderms in density, whereas the western sites were dominated by poriferans and foraminiferans. The ridge might act as dispersal barrier to the northern sites, but there was no evidence for it to affect the dispersal for species from the southern sites. The CGFZ, on the other hand is more likely to act as effective dispersal barrier between the northern and southern sites of the ECOMAR area. Between the sites there was no significant difference in diversity, while between habitats a significant difference was picked up with the more sensitive Shannon-Wiener index. No such significant difference in diversity between habitats was picked up with the Simpson index and more investigation is needed to conclude whether a slope of about 10° incline affects biodiversity. Although the diversity between habitats remains speculation, the community composition between habitats was significantly different at the southern sites, while not significantly different for the northern sites. It remains unclear what causes this discrepancy between the northern and southern sites.

Chapter 5

Assessing Benthic Communities Imaging vs. Trawling

Deep-sea research is heavily dependent on trawling and video surveys to investigate the benthic and benthopelagic environment, as highlighted by their frequent use over the past four decades (Rice et al., 1979; Billett and Hansen, 1982; Rice et al., 1986, 1994; Billett et al., 2001; Smith et al., 2008a; Priede et al., 2010). The following chapter compares trawl and video data collected at the MAR. The advantages and disadvantages of trawling and video survey will be discussed, in addition to a synthesis demonstrating the potential information gained by combining these methods.

5.1 The Efficiency of Collecting Ecological Information: Trawling vs Video

5.1.1 Species Richness

Within the ECOMAR framework a unique dataset of video and trawl data makes it possible to compare the fidelity of both sampling methodologies in their estimation of species richness. The most striking difference between these methods is their spatial extent. Trawl samples tend to cover areas in the region of hectares, while video surveys sample areas on the metre ^{2} scale. The quality of trawl and video data analyses, presented in this thesis, was greatly improved by analysis of samples collected by both methods, being carried out by the same ecologist (C. H. S. Alt) and the same taxonomist (A. Rogacheva). Such a personnel-limited approach reduced the inherent inconsistencies of subjective species identification. The wider sampling area obtained by trawling led to an expectation that greater species richness would be found with this method. However, an inspection of the species numbers between methods shows a surprisingly high species number from the video survey in comparison to trawling (Table 5.1). Furthermore, when standardised to the same area the video survey appears much more efficient in determining species richness. It is speculated here that two main considerations explain the high species richness in video samples: 1) differences in target size, and 2) differences in the type of fauna targeted.

TABLE 5.1: Table representing the number of species and number of megafaunal individuals collected by trawls (2007 & 2009) and by the video survey (2010). On the right side is the theoretical species accumulation rate, had both surveys sampled 1 ha area.

Gear	**Site**	**Area Sampled**	**Number of Species**	**Number of Individuals**	**Number of Species ha^{-1}**	**Number of Individual ha^{-1}**
Trawl	NW	4 ha	69	4,312	17	1,078
	NE	3 ha	55	12,716	18	4,239
	SE	3 ha	96	4,233	24	1,058
Video	NW	8,000 m^2	104	15,071	130	18,839
	NE	8,000 m^2	73	12,078	91	15,098
	SE	8,000 m^2	73	7,688	91	9,610
	SW	8,000 m^2	104	7,372	130	9,215

5.1.1.1 Target Fauna

Trawls can only be used in areas of flat sedimentary plains, absent of any obstructions such as rocky outcrops. This greatly restricts potential sampling areas of complex geomorphological structures such as the MAR. Furthermore, the damage to fragile specimens through this sampling method is substantial. An example of the damage caused was observed in trawl samples from the NE site, where large numbers of small gelatinous holothurians were entangled in the trawl mesh. Most specimens from this haul were too damaged to be identified to species level, forcing a grouping of these individuals to be simply grouped into an Elpidiidae mix, which could only be refined to a mixture of five different species, thanks to the limited number of less damaged specimens (Section 3.2.2.). The sampling of highly fragile fauna is not possible by trawling, as the destructive nature of this technique leaves little identifiable remains of delicate body structures such as that of xenophyophores (Hughes and Gooday, 2004) or enteropneusts (Jones et al., submitted); thus, trawling often gives an incomplete account of species within an area. However, when trawls are flown too close to the sediment surface, sometimes small amounts of sediments are entrained. Within the sediments some larger infauna specimens are captured, which can give a unique insight into the infaunal species composition of an area that would otherwise not be accessible.

In contrast to the shortcomings of trawling, a great benefit of video surveys is their ability to assess rough terrain. Even when sampling soft sedimentary plains, video surveys can target specimens that would otherwise be missed by trawls, as fragile specimens are not damaged by this sampling method (i.e. the aforementioned xenophyophres and enteropneusts). Other species that are more readily sampled with this method include sponges and other sessile fauna that are anchored to the seabed. Infaunal traces can be observed with video or imaging techniques, but classification of such species remains elusive. A significant restriction associated with this technique, however, is the inability to identify specimens down to species level (often it is difficult even to estimate the family level). Although, with an ROV survey, it is possible to collect specific individuals for identification, this time-intensive procedure allows only a small selection of samples to be justifiably collected. High quality video material is, therefore, critical to the identification of different morpho-types. However, it is not currently possible, through video surveying alone, to distinguish morpho-types that represent different species from those that merely present the morphological plasticity of one species, often leading to the overestimation of species richness within an area.

5.1.1.2 Target Size

The size of net mesh restricts the target size of trawl samples. The trawl opening has a net mesh wider than the cod end (Section 3.2.1.). It is difficult to target species smaller than the net mesh near the trawl opening, as they often become lost in transit to the cod end. This also makes it difficult to quantify the catch success rate of species with smaller body size. Video surveys do not suffer from such restrictions of specimen target sizes, in particular when high definition camera equipment is available, as was the case in this study (Section 4.2.). However, problems arise when video quality becomes of such high fidelity that species not belonging to the targeted megafauna can be visualised. In such cases it is crucial to define the lower target size prior to analysis.

In conclusion, one of the greatest advantages of trawl samples is the ability to identify specimens down to species level, while video surveys can overestimate species richness, as morphological plasticity cannot be accounted for. The variation observed in species richness estimates presented here (Table 5.1) shows a higher species richness from videos. The identification bias in this study is greatly reduced, owing to specimen identification being carried out by the same persons that worked up the trawl and video samples. It is thought that the difference in species richness between methods is too high to be accounted for entirely by morphological plasticity (Table 5.1). Data presented here indicate that advantages in being able to identify specimens down to species level, do not outweigh the inclusion of fragile specimens and species that are anchored to the sediment. Data suggest that a survey with high quality video footage gives a more reliable account of epibenthic species richness when compared to a trawl survey of the same area.

5.1.2 Density

The distance a trawl covers over the seabed during a single pass can be estimated thanks to advanced sensors. This information, combined with details of the effective net opening gives an estimate of the area being trawled. However, the inability to reliably collect smaller specimens and the occasional collection of infaunal specimens (also reducing the area of the benthopelagic realm sampled) makes trawling only semi-quantitative (Gage and Bett, 2005). It is further recognised that trawling tends to underestimate densities (Bett et al., 2001). Here, trawl and video density data are compared to highlight the extent to which these two methods differ in estimating density. Density that was standardised to the number of individuals per hectare has been compared for major taxonomic groups, to highlight differences in the sampling success rate for these two methods (Table 5.2).

TABLE 5.2: Densities of major megafaunal taxa calculated from video and trawl data (individuals ha^{-1}). The proportion of each taxon within a site is expressed in % of the total count, the most noticeable discrepancies between methods are highlighted in bold.

Gear	**Taxa**	**NW**	**SD**	%	**NE**	**SD**	%	**SE**	**SD**	%
Trawl	Asteroidea	48.3	± 193.3	18.2	26.4	± 2.1	3.3	102.9	± 32.7	30.5
	Holothuroidea	17.4	± 69.5	6.6	753.3	± 175.6	93.9	153.9	± 38.3	45.7
	Echinoidea	22.9	± 91.7	**8.6**	12.7	± 3.2	**1.6**	3.8	± 0.9	**1.1**
	Ophiuroidea	132.5	± 529.8	50.0	3.4	± 0.8	0.4	16.8	± 12.3	5.5
	Crustacea	18.5	± 74.1	7.0	9.9	± 1.0	1.2	21.8	± 13.4	6.5
	Pycnogonida	23.4	± 93.5	**8.8**	0.3	± 0.3	**0.0**	2.6	± 3.5	**0.8**
	Mollusca	2.7	± 10.5	1.0	1.0	± 0.7	0.1	4.6	± 4.1	1.4
	Cnidaria	0.1	± 0.3	**0.0**	0.2	± 0.2	**0.0**	30.6	± 9.8	**2.9**
Total		265.8	± 70.6		807.2	± 638.5		337	± 37.7	
ROV	Asteroidea	120.0	± 13.6	1.9	230.0	± 28.5	0.7	187.5	± 23.6	3.3
	Holothuroidea	1,306.3	± 173.1	20.3	28,998.8	± 5120.5	90.7	396.3	± 27.5	7.0
	Echinoidea	2,543.8	± 519.5	**39.5**	1,795.0	± 374.1	**5.6**	4,208.8	± 1,484.5	**74.6**
	Ophiuroidea	1,832.5	± 373.5	28.4	716.3	± 275.7	2.2	43.8	± 18.2	0.8
	Crustacea	30.0	± 5.2	0.5	21.3	± 2.8	0.1	68.8	± 11.9	1.2
	Pycnogonida	17.5	± 7.1	**0.3**	0.0	± 0.0	**0.0**	3.8	± 2.7	**0.1**
	Mollusca	3.8	± 2.2	0.1	6.3	± 1.4	0.0	27.5	± 15.9	0.5
	Cnidaria	588.8	± 64.5	**9.1**	215.0	± 14.3	**0.7**	705.8	± 52.5	**12.5**
Total		6,442.7	± 585.0		31,982.7	± 937.6		5,642.3	± 243.7	

Total density estimates differed significantly (Kruskal-Wallis: chi-squared = 11.86, df = 1, $p < 0.0001$) between the two sampling methods (Table 5.2). The most noticeable differences were observed for echinoids, which were ranked the most abundant species within the video survey at the NW and SE sites, while only ranking respectively as 4th and 7th most abundant taxa within trawl samples. Most echinoids from the ECOMAR area were hard-shelled and very fragile (Appendix E), the majority of specimens were damaged through trawling and could not be quantified. Density estimates based on video data are considered more reliable for this class. Similar disparity between sampling results was also observed in cnidarians, though not as pronounced as in echinoids (Table 5.2). However, this variation in density found between methods is to be expected, as sessile cnidarians cannot be targeted effectively through trawling. Pycgnogonids were the only taxa ranked at greater abundance in the trawl samples, in comparison to video surveying; their slender body types often being unintentionally overlooked in video footage (Table 5.2).

Overall, the high numerical dominance of holothurians at the NE site was confirmed with both sampling methods. However, the ranks in density between the NW and SE sites differed between trawling and video survey. This result shows that data collected from a previously unknown area can be greatly biased by the survey instrumentation used. The greater numbers in the video survey confirm that trawls underestimate densities (Bett et al., 2001) and suggest that a video survey capture the density of species more reliably.

5.1.3 Diversity

The diversity values derived from the video surveys and trawl samples did not significantly differ between sites (Kruskall-Wallis: chi-squared = 1.7, df = 1, p = 0.1907). The diversity in the trawl hauls was driven by high species richness at the NW and SE sites and low levels of evenness at the NE site. In contrast, the diversity in the video survey is thought to be a result of the level of species richness at all sites. A significant difference in diversity between sites was observed in the trawl samples, but not in the video survey. However, when both diversity datasets were combined, there was no significant difference in diversity between sites (Kruskall-Wallis: chi-squared = 6.81, df = 3, p-value = 0.08).

The two sampling techniques differ in their reliability for estimating diversity. Although trawling is biased towards larger specimens, diversity measures derived from trawl samples are more accurate than those derived from video surveys, at least in part because it is easier to discriminate between species in trawled material than in video images. Variations in diversity between samples from the same sites were smaller in trawl samples (Figure 5.1). One of the main difficulties regarding imaging techniques is the low level of identification that can be achieved. While critical features such as spicules can be investigated under a microscope in trawl samples (e.g. in sponges, Janussen et al. (2004) and holothurians, Rogacheva et al. (accepteda)), only relatively large external morphological features can be observed in video transects. Morphological 'type-specimens' that are differentiated in videos may actually encompass several species, while specimens collected with trawls can often still be identified even when damaged.

As discussed above, video and trawling techniques target different species, and neither can sample all megafauna. Some species can only be 'sampled' in video surveys: those too fragile to be collected (e.g. xenophyophores, Levin (1994) or enteropneusts, Osborn et al. (2011)), those anchored in the sediment (e.g. sponges, Beaulieu (2001)), or too small to be targeted with trawls (e.g *Discospirina* spp., Gooday et al. (in press)). Other species collected with trawls that are either underrepresented (e.g. *Hymenaster* spp.) or absent (e.g. *Molpadia* spp., Amaro et al. (2010)) in video surveys are either covered by sediment or have burrowed into it. Ideally, a video survey along a transect should be followed by a trawl; a combination method that has been applied with epibenthic sledges (Rice et al., 1979), so that species can be identified with both molecular and morphological taxonomy. Unfortunately, time and resource constraints often make such a thorough approach unfeasible.

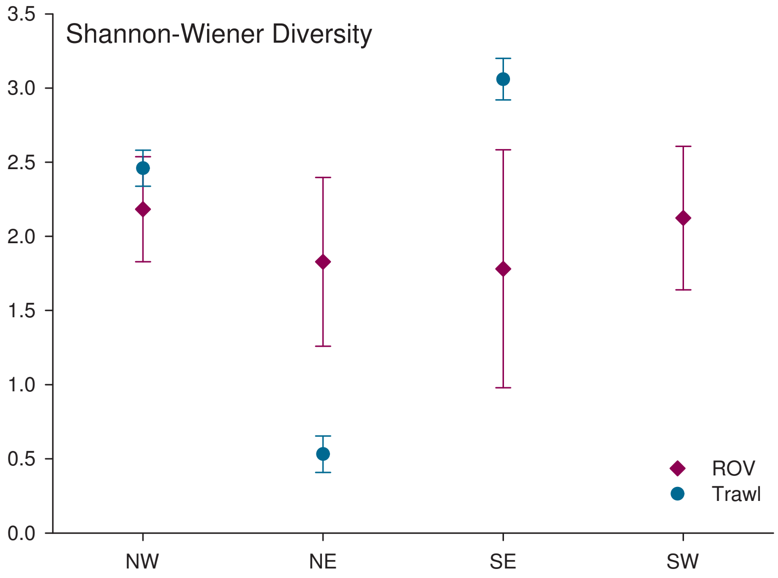


FIGURE 5.1: The Diversity from the trawl and video survey, compared between the different ECOMAR sites, with their respective standard deviation.

5.2 Variability in Benthic Megafauna Communities

5.2.1 Variability in Time

The higher estimates of density obtained via the video surveying method when compared to trawling employed (Section 5.1.2.) was expected as trawls are restricted by their mesh size and previous studies have been shown to underestimate densities (Bett et al., 2001; Gage and Bett, 2005). However, many patterns are observed in the data presented in Table 5.2 and not all can be attributed to sampling biases mentioned above.

At the NW site the densities of pycnogonids were lower in the video survey (2010) than in the trawl samples (2007 & 2009), numbers ranged between 32 (in 2007) and 142 (in 2009) specimens ha^{-1} in trawl samples, while their density in the video transects was between 1 and 9 individuals ha^{-1} (2010). It is considered unlikely that these differences were caused by faunal patchiness of pycnogonids, as it is assumed that the randomised design of the video survey (in 2010) would have identified such patches, especially with such high densities in the previous year. These data, therefore, suggest that the population size itself fluctuated within the 4-year period. However, as a caveat, counts of pycnogonids were disproportionately low in the video survey; therefore this lower density may be, at least in part, a result of their slight body type making their visualisation in video footage difficult. This drawback of video analyses likely explains the scarcity of this taxon at the NE and SE sites, where densities were so low that this class could have been overlooked in the video records.

In addition to the pycnogonids, other taxa suggested shifts in density at the NW site over time (Figure 5.2). With regard to taxa from the trawls, asteroid densities decreased from 292 individual ha^{-1} in 2007 to an average of 181 individuals ha^{-1} in 2009, molluscs decreased from 25 individuals ha^{-1} in 2007 to an average of 6 individuals ha^{-1} in 2009, while arthropods, holothurians and ophiuroids showed little apparent variation in density between 2007 and 2009. Changes in community structure over time have also been reported in abyssal environments, at the **P**orcupine **A**byssal **P**lain (PAP) site in the Atlantic (Billett et al., 2010) and at the Pacific station M (Ruhl, 2008). Megafaunal species, that were previously considered rare, became very abundant and vice versa. Other species changed less dramatically in their density, while some did not appear to change at all (Ruhl, 2008; Billett et al., 2010). Two species that were associated with the '*Amperima* event' at the PAP (Bett et al., 2001), were also abundant at the NW site: *Ophiocten hastatum*, and *Colossendeis colossea*, support the possibility of a community shift.

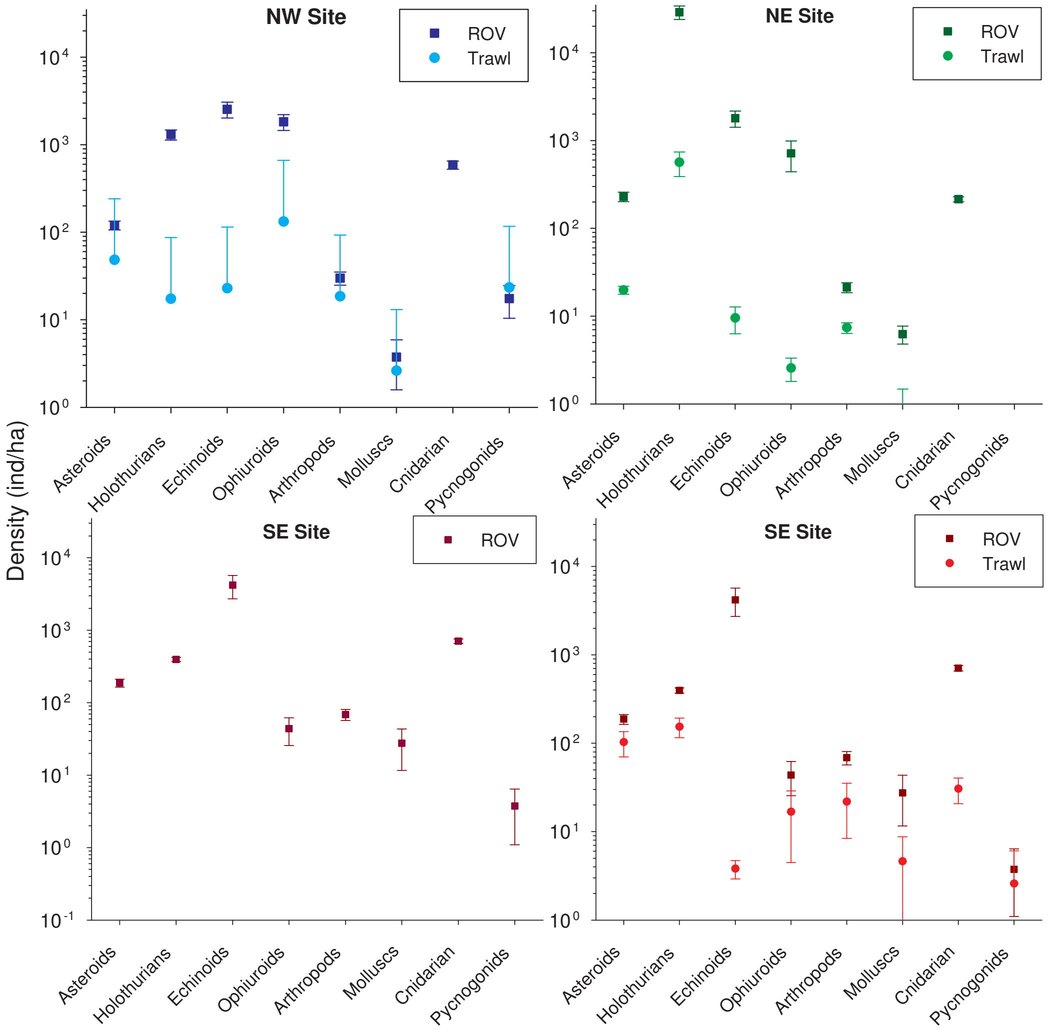


FIGURE 5.2: Densities (individuals ha^{-1}) from trawl and video survey from every site. Results are plotted on a logarithmic y-axis, with their standard deviation.

At the PAP and station M shifts were associated with changes in phytodetrital quality, information which is not available for the current study. At the PAP pycnogonids were strongly affected by this parameter, as were ophiuroids, holothurians, and asteroids (Billett et al., 2001). Although changes in density have been seen for most megafaunal species at the PAP (Billett et al., 2010), some species clearly have a greater ability to respond to changes in quantity and quality of the nutrition than others (Ruhl, 2008). At the PAP changes in megafaunal density were observed between 1994 and 1996 (Billett et al., 2001). No sampling was carried out in 1995 therefore a change in density occurring over just one year cannot be discounted. Although a community shift at the NW site is considered the most likely explanation for the results presented here, this interpretation must be treated with caution as other factors may also explain the discrepancies in density for some taxa. The low densities in crustaceans at the NW site in 2010 may also be a result of their mobility, with disturbance caused by ROV movement likely invoking a flight response. The visual field of the cameras was only 2 m wide, while the trawl net opening was over 8 m wide, making it more likely that escaping animals would be captured in the trawl than observed in the video survey. Furthermore, discrepancies in asteroid numbers were potentially caused by specimens obscured by sediment. Finally, some molluscs (i.e. cephalopods) are mobile enough to flee the visual field. A more important consideration is that the smallest molluscs were excluded from the analysis of ROV records, as they could not be distinguished reliably from the very abundant pteropod shells at the southern sites.

5.2.2 Variability in Space

All ECOMAR sites were significantly different from each other in community composition in both trawl and video survey, though the SW site was only sampled in 2010 (ROV survey) and showed no significant difference from the SE site (Section 4.3.6). The greater similarity between transects of different sites in the video survey, is likely a result of a more balanced sampling design in the 2010 survey (Table 5.3).

Table 5.3: The similarity of the sites to one another based on benthic megafauna community composition, calculated with a Bray-Curtis analysis, and highlighting distances between sites.

Sites	Distance	Trawl	ROV	ANOSIM
SE & SW	72 km		47.9 %	
NW & NE	137 km	22.9 %	37.0 %	
NE & SE	706 km	11.3 %	28.4 %	ROV: $p < 0.05$, Global R = 0.79
NW & SE	706 km	20.0 %	31.0 %	Trawl: $p < 0.05$, Global R = 1

It is clear from this study that a multitude of processes govern variations in community composition, although the dominant driving factor remains unclear. Differences in sediment characteristics, surface primary production and hydrography between sites were observed, however, no definite environmental drive could be discerned. Despite extensive research into deep-sea communities over the last few decades, it remains undecided within what geographical range similar species assemblages are expected to occur. Several studies have highlighted the patchiness of megafaunal species distributions through their observed random distribution along transect lines (Lauerman et al., 1996). Furthermore, it is shown that even within the same area, communities change significantly over time (Ruhl, 2008; Billett et al., 2010). While data presented here suggest that it is likely that these spatial and temporal changes also apply to the MAR no previous study has been carried out that investigates community change over distance, as a result of limitations to dispersal. Within ECOMAR, some predominantly benthic megafauna were shown to 'drift' with the currents between feeding grounds (Jones et al., submitted), or to actively 'swim' (Rogacheva et al., acceptedb). These pelagic excursions, however, appear to only be effective over short distances. Larval dispersal is difficult to monitor in the open ocean and can often only be inferred through faunal distributions (Howell et al., 2002). Yet many species considered 'cosmopolitan' are often found to comprise several genetically different cryptic species (O'Loughlin et al., 2011). While some megafaunal species have evolved the ability to disperse over very large distances, such cases remain rare. The differences in community composition between the ECOMAR sites, reflect the distances between them (Table 5.3). It is therefore suggested that the differences observed in ECOMAR are at least in part a function of site proximity (Figure 2.1, page 24). Other factors that likely played a role in shaping the community composition between the southern and northern sites include productivity regimes, sediment types, and possible disturbance events.

Evidence for past disturbance events was found at the northern sites, in particular the NE site. Megacore samples from 2010 were characterised by sponge spicules in the sediment surface layer. It is speculated that these spicules were spread along the seabed by strong currents (Priede and Bagley, 2010). This interpretation was further supported by the presence of the holothurian *Kolga nana* at the NE site. *Kolga* spp. are also reported at the HAUSGARTEN observatory (Soltwedel et al., 2009) and **P**orcupine **S**ea**b**ight (PSB) (Billett and Hansen, 1982), and in both cases their occurrence is associated with high energy environments. Aggregations of *Kolga nana* occur at both the NE site, and between 2,755 and 4,080 m in the PSB. These aggregations have clear reproductive advantages, particularly because this species shows early gonadal development, ideal for opportunistic species that exploit disturbance events (Billett and Hansen, 1982). The presence of *Kolga nana*, *Ophiocten hastatum* and *Ophiura ljungmani* highlight the likelihood of occasional disturbance events at both northern sites. While the NW site may be affected by community changes similar to the '*Amperima*' event at the PAP, the NE site may be subject to benthic storms. The southern sites, in contrast, were characterised by a thin phytodetritus layer and high numbers of pteropod shells, both observed throughout the study interval (Section 2.8, page 31). The phytodetritus layer was observed in August (Priede, 2007, 2009) and in June (Priede and Bagley, 2010) at the southern sites indicating two possible organic carbon pulses, while at the NE site a small phytodetritus layer was only reported in June 2010 (Priede and Bagley, 2010).

The greater variation in density observed between trawl samples has several potential causes, most notably is the lack of replicate trawls at the NW site in 2007. A number of inherent factors within the trawling process affect the size and composition of the catch, in particular the trawling speed and its interaction with the seafloor. Minor changes in either of these aspects can affect the catch-rate (Gage and Bett, 2005). Furthermore, when a trawl touches the seabed it accumulates sediment, which can block the mesh, resulting in the retention of organisms normally not targeted by this method. Therefore, consistency between trawl replicates is poorer than repeat video transects, as technology for video surveying allows for a precise regulation of altitude and speed. In this study the replication between the video surveys was significantly more balanced with eight transects at each site, while trawl replicates were carried out up to two years apart, adding a temporal influence. Video surveys reveal the fine-scale distribution of animals on the seafloor whereas trawls integrate their catch over the entire sampling area. As a result of the inconsistencies described for trawls they are not considered truly quantitative (Gage and Bett, 2005).

Chapter 6

Systematic Clarification of Holothurians from the MAR

6.1 Introduction

Holothurians are a very diverse and abundant group of megafauna in the deep sea (Billett, 1991; Gebruk, 1994; Pawson, 2007; Gebruk et al., 2010) that are considered very important in horizontal transport and vertical mixing of sediments (Billett, 1991; Ginger et al., 2001), and therefore, play a vital role in carbon burial. Based on ossicle fossil evidence it has been suggested that holothurians have been around since the Silurian (Gilliland, 1993). One of the best-preserved whole specimens found is placed in the Devonian (Lehman, 1958). As a result of this Class having been around for such a long time they show great morphological diversity. This morphological variability causes much debate when considering their taxonomic classification system (Billett, 1991). Today, there are an estimated 1,400 known holothurian species belonging to six orders: Aspidochirotida Grube (1840); Elasipodida Théel (1882), 1882; Molpadiida Haeckel (1896); Dendrochirotida Grube (1840); Apodida Brandt (1835); and Dactylochirotida Pawson and Fell (1965) (Pawson, 2007). Of those, only the Elasipodida is restricted entirely to the deep sea (Hansen, 1975), while the Aspidochirotida has a strong representation there (Solís-Marín, 2003). Some of the families and genera have frequently been revisited morphologically, in the attempt to clarify their taxonomic positioning in relation to other holothurians (Kerr, 2001; Kerr and Kim, 2001). Kerr and Kim (2001) assessed the relationship of holothurian families by analysing recognised morphological features and by creating a phylogeny based on those morphological characteristics. They excluded some families such as the Gephyrothuriidae, owing to their taxonomic uncertainty. Such exclusions and reclassifications of genera or even entire families (Heding,

1935) are a continuous problem in holothurian taxonomy. Most studies of holothurian phylogeny concentrate on coastal species and genera (Uthicke and Benzie, 2001; Hoareau and Boissin, 2010). This is a problem for research into deep-sea holothurians as new species are frequently being discovered (Gage, 1985; Gage and Billett, 1986; Gebruk et al., 2003; Gebruk, 2008; O'Loughlin et al., 2011). Solís Marín revised the systematics of the Synallactidae family, clarifying the position of species with morphological data and the 16S mitochondrial gene (Solís-Marín, 2003). Another recent study looked into holothurian species from the Antarctic, analysing the relationship of individual species within different genera (O'Loughlin et al., 2011).

All attempts to understand holothurian systematics with molecular methods have been primarily based on single mitochondrial genes combined with morphological characteristics (O'Loughlin et al., 2011; Solís-Marín, 2003). While this has increased our understanding to some extent, there is still a lot of uncertainty. Mitochondrial DNA alone is not ideal for phylogenetic purposes, and conclusions drawn can be misleading, especially without any prior knowledge of the history of that particular gene in a particular group of animals (Rubinoff and Holland, 2005). Each gene codes for hundreds and thousands of characters, which determine its position in relation to other species. Mitochondrial genes only carry information about the maternal line and are highly variable within species, while nuclear genes diverge much slower, but might not give an ideal resolution down to species level (Rubinoff and Holland, 2005). Therefore, a combination of different genes should be used to determine the relationship of species. In the present study the systematics of holothurians is approached by looking at the molecular information in more detail and by combining nuclear and mitochondrial DNA fragments. I successfully amplified the histone 3 gene (H3) for the first time in holothurians and propose this gene as a valuable additional tool in understanding holothurian taxonomy. I concentrate on deep-sea species in this study, as there has not been much research into understanding their relationships on a molecular level, despite there being a great need for it.

6.2 Methods

6.2.1 Taxa

Samples of holothurians were collected from the Mid-Atlantic Ridge as part of the ECOMAR project between 2007 and 2010 (Table D.1, page 164) (ECOMAR, 2012). The specimens were collected from four sites at the Mid-Atlantic Ridge, to the southeast (48 ° 58 ′N, 27 ° 51 ′W), southwest (48 ° 48 ′N, 28 ° 38 ′W), northeast (54 ° 05 ′N, 33 ° 58 ′W), and northwest (54 ° 19 ′N, 36 ° 01 ′W) of the Charlie-Gibbs Fracture Zone (see Figure 2.1, page 24). Additional sequences were obtained from the National Centre for Biotechnology Information (NCBI). Genetic sequences were obtained from the NCBI genbank for five species, which had 2 or more genes sequenced: *Pseudostichopus villosus* (16S DQ777098, COI AF486436, 18S DQ777086, 28S DQ777088), *Bohadschia vitiensis* (16S FJ223868, COI EU848267, 18S AY133477), *Holothuria edulis* (16S EU220806, COI EU220830, 18S AY133471), *Holothuria forskali* (16S GQ214740, COI GQ214762, 18S AY133470), *Psychropotes longicauda* (16S DQ777099, 18S Z80956). In order to have representatives of all orders, some material was also obtained from the PP. Shirshov Institute of Oceanography, Moscow; *Molpadia borealis*, *Molpadia blakei*, *Acanthotrochus mirabilis*, and a species of *Ypsilothuria*. In total, 47 specimens from 13 families, representing all six orders of holothurians were analysed in this phylogenetic study.

6.2.2 DNA Extraction, Amplification and Sequencing

A phenol-chloroform protocol (as described by Hoelzel (1998)) was used for DNA extraction. Where this did not yield enough DNA, a QIAGEN DNeasy extraction kit was used, following the manufacturers protocol. For the genes 18S, 28S, 16S and H3, primers were designed using Oligo v2.0 (see Table 6.1). All H3 sequences in this study are new to science. No previous study has analysed the histone gene for holothurians. It was included in this study because it is highly conserved and therefore, complements the other genes used in this study. For COI a hybrid primer was used as described by Hoareau and Boissin (2010).

Table 6.1: Primers used in this study are listed, indicating the size of the target DNA strand, and the origin of the primers

Gene	Primers	Fragment Size	Primer Origin
16Sf	TGACCGTGCAAAGGTAGC	406bp	this study
16Sr	GAGGTCGCAAACCCTTCT	406bp	this study
18Sf	TCTGGAGGGCAAGTCTGG	546bp	this study
18Sr	ATCCTGGTGGTGCCCTTC	546bp	this study
28Sf	CGCAGAATAAGTGGGAGG	436bp	this study
28Sr	TTTTTGACACCCCTTGCG	436bp	this study
COIf	ACTGCCCACGCCCTAGCAATGA TATTTTTTATGGTNATGC	656bp	(Hoareau and Boissin, 2010)
COIr	TCGTGTGTCTACGTCCATTCCT ACTCTRAACATRTG	656bp	(Hoareau and Boissin, 2010)
H3f	AAATAGCYCGTACYAAGCAGAC	338bp	this study
H3r	ATTGAATRTCYTTGGGCATGAT	338bp	this study

Amplification was achieved with the QIAGEN Multiplex PCR Master Mix. The PCR mix for the genes 28S, 18S, 16S and COI contained 0.2 µM of each forward and reverse primer, 1x QIAGEN Multiplex PCR Master Mix and 1 µg template DNA in a final 20 µl reaction volume. For H3, 0.5x QIAGEN Q-Solution was included also in the final 20 µl reaction volume. The PCR amplification conditions were as follows: 94 °C for 15:00 min, followed by 35 cycles at 94 °C for 00:30 min, 50 °C (for 16S, 18S and 28S) and 48 °C (for COI and H3) for 01:30 min, 72 °C for 01:00 min, and a final extension at 60 °C for 10:00 min. In total, 39 different species were successfully sequenced (Table D.1, page 164). PCR products were purified using QIAGEN QIAquick Purification Kit®as per manufacturers protocol and sequenced.

6.2.3 Species and Outgroup Selection

The selection of outgroups in a phylogenetic study is crucial and will affect the final result (Milinkovitch and Lyons-Weiler, 1998). In the present study the aim was to resolve relationships at order and family level while maintaining sufficient resolution at species level. Hence, it was important to find an outgroup related closely enough to the investigated species to show relationships at species level, while being distant enough to resolve relationships at higher taxonomic levels.

Initially, *Staurocucumis abyssorum* was used as outgroup because of its resemblance to the oldest whole fossil specimen yet described (Lehman, 1958). The fossil species *Palaeocucumaria hunsrückiana* was given its name because of its morphological similarities to the modern Cucumariidae family. In an extensive study that investigates holothurian deposits, fossil evidence is compared with modern specimens. The order Dendrochirotida is considered to be the oldest living order today (Gilliland, 1993). However, after analyses were run, it was apparent that this outgroup did not give the desired resolution at higher taxonomic levels. Hence, the analyses were re-run with non-holothurian echinoderms from the NCBI genbank: the echinoid *Strongylocentrotus purpuratus* (16S X12631.1, 18S L28056.1, 28S AF212171.1, COI HM542410.1, H3 NW001293040.1), the *Evasterias troscheli* asteroid (16S DQ297090.1, 18S DQ060788.1, 28S DQ273706.1, COI GQ902422.1, H3 DQ676909.1), and the *Pisaster ochraceus* asteroid (16S DQ297110.1, 18S DQ060813.1, 28S DQ273718.1, COI HM542339.1, H3 X07503.1). At species level most groupings remained very similar regardless of the outgroup. However, where appropriate dissimilarities/similarities are discussed for the different outgroups, in later sections.

6.2.4 Alignment and Analysis

Sequences were mounted and aligned with GENEIOUS (Drummond et al., 2010) and ClustalW (Larkin et al., 2007). The evolutionary models used for the molecular data in the Bayesian analyses were obtained from MrModelTest 2.2 (Nylander, 2004), choosing the AIC criterion (see Table 6.2). A bayesian analysis was carried out using MrBayes 3.1.2. (Ronquist and Huelsenbeck, 2004). Individual genes were run for 400,000 generations each, and 1,000 generations were discarded as burn-in. The datasets were then combined, using their respective evolutionary model and unlinking the genes. The combined analysis was run for 2 million generations with 5,000 generations discarded as burn-in.

Table 6.2: Models are listed as chosen by MrModel. Protein coding genes COI and H3 are split into their codon position for maximum accuracy.

Gene	**Evolutionary Model**
16S	GTR+I+G
18S	GTR+G
28S	GTR+G
COI pos 1	GTR+I+G
COI pos 2	GTR+I
COI pos 3	GTR+I+G
H3 pos 1	GTR+I
H3 pos 2	JC
H3 pos 3	GTR+G

6.3 Results

6.3.1 Combined Analyses

In total 2,248 base pairs were analysed, consisting of 338bp from 16S, 575bp from 18S, 359bp from 28S, 653bp from COI, and 323bp from H3. The values on the nodes indicate the support value based on 2,000,000 generations run in MrBayes.

In total, 37 nodes have support values with 31 showing ≥ 95 % support (Figure 6.1). Two distinct clades are formed: the Elasipodida clade, excluding *Deima validum*, and a non-Elasipodida clade that has representatives of all other orders, including *Deima validum*. The orders Dendrochirotida and Dactylochirotida are strongly grouped together, forming a minor clade together with the Apodida representative *Acanthotrochus* *mirabilis.* This group forms a cluster with *Gephyrothuria alcocki* (low support 0.85). *Gephyrothuria alcocki* did not form this cluster when *Staurocucumis abyssorum* was used as outgroup; it fell basal to all other holothurians, except the Apodida, Dendrochirotida and Dactylochirotida representatives. The relationships within the Aspidochirotida order are unresolved; the family Holothuriidae forms a separate group to the *Pseudostichopus* species from this study, while the position of *Pseudostichopus villosus* is unclear. *Deima validum* and *Benthothuria funebris* are grouped together with good support, even though, at present, those two species belong to the orders Elasipodida and Aspidochirotida, respectively. Within the major Elasipodida clade there is a subdivide between the family Elpidiidae, and the families Psychropotiidae and Laetmogonidae. The family Elpidiidae is further distinguished between *Peniagone* spp. and other Elpidiidae members of this study. Within the minor *Peniagone* clade, the species *Peniagone azorica* and *Peniagone islandica* do not appear as clearly distinct species (low support 0.94). This low support for *Peniagone azorica* and *Peniagone islandica* is also seen when using *Staurocucumis abyssorum* as outgroup.

6.3.2 Individual Gene Analysis

The most successful amplification rate was achieved in the 16S gene with 39 successful amplifications. This was followed by 28S with 38 sequences, COI with 35 sequences, H3 with 33 sequences, and 18S with 32 sequences (Table D.1, page 164).

6.3.2.1 16S Gene

Similar to the consensus tree, a strongly supported non-Elasipodida clade is formed, including *D. validum.* The low support (0.82) in which *D. validum* is grouped together with *B. funebris* (Figure 6.2), is not seen in the analysis using *S. abyssorum* as outgroup (0.99). *Molpadia* spp. form a low supported clade (0.63), which did not change with a different outgroup (0.73). The order Aspidochirotida forms distinct groups within this major clade, grouping members from the family Holothuriidae together, and the *Pseudostichopus* species of this study. *Pseudostichopus* spp. form a sister clade to all other non-Elasipodida members. *P. villosus* forms a minor clade with *G. alcocki*, *S. abyssorum*, and *A. mirabilis.* The relationship between the orders Dendrochirotida and Dactylochirotida remains unresolved for this gene because amplification of the *Ypsilothuria* sp. was not achieved. Unlike the consensus tree, Elasipodida (except *D. validum*) representatives do not form a distinct clade in this gene. *Peniagone* spp., members of the families Psychropotiidae and Laetmogoniidae, and non-*Peniagone* Elpidiidae species form their respective, distinct sister clades. These clades form sister clades to one-another and to

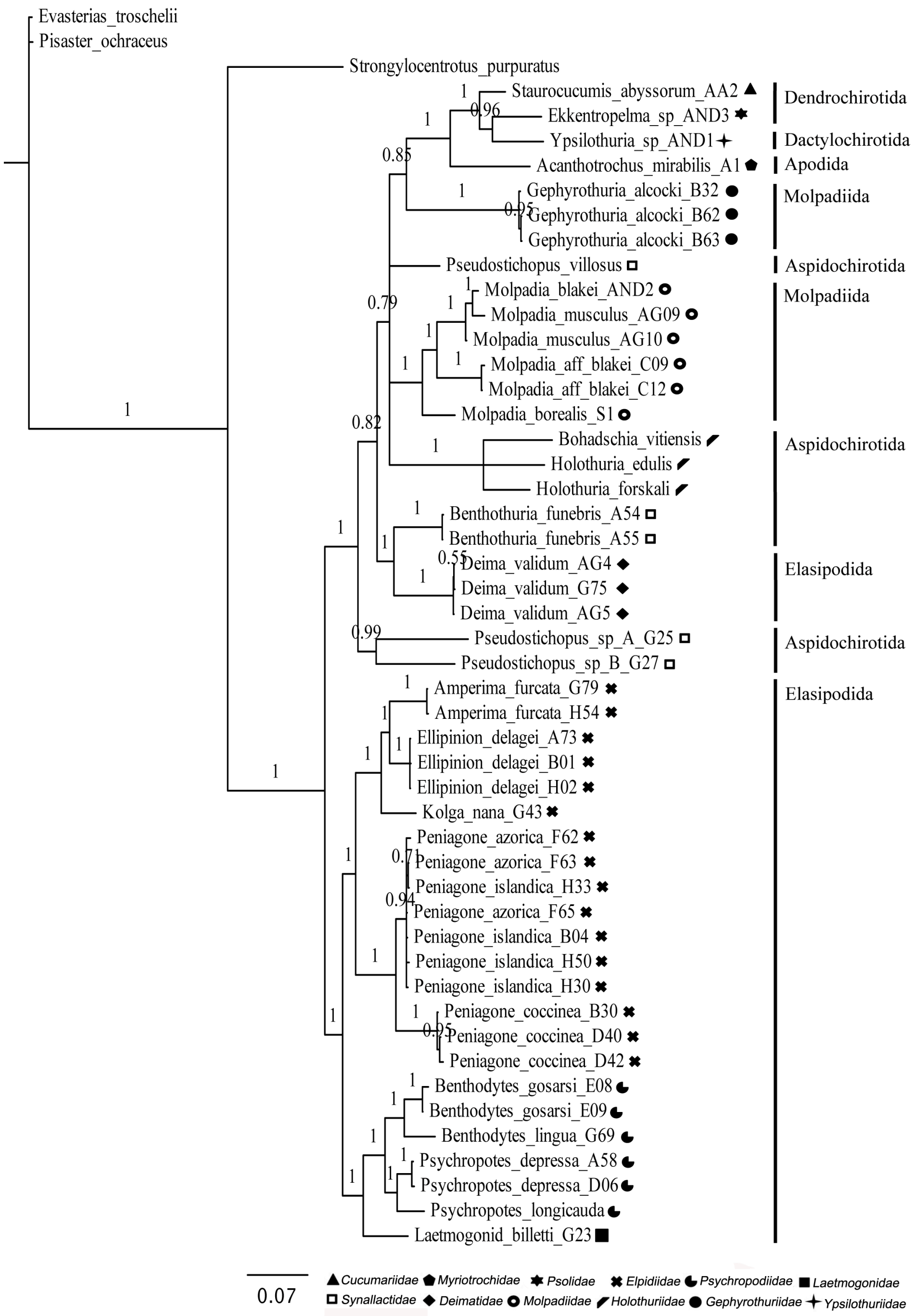


FIGURE 6.1: Consensus Tree. Numbers after each species name refer to their individual sample code, and symbols show their families, which are listed below the table. Vertical bars on the right hand side highlight different orders.

the non-Elasipodida clade (Figure 6.2). *Peniagone* species form one clade that distinguishes *P. coccinea* as different species, but fails to do so for *P. islandica* and *P. azorica*. The same grouping for this genus was formed, regardless of the outgroup.

6.3.2.2 28S Gene

The 28S tree, similar to the 16S and consensus trees, forms a major non-Elasipodida clade that includes *Deima validum* (Figure 6.3), though with low support (0.72). *D. validum* forms a minor clade with *Benthothuria funebris* and *Acanthotrochus mirabilis*, latter being grouped directly with *D. validum*. This minor clade forms with low support with both outgroup variations (0.77/0.73). *Molpadia* spp. are grouped together in a minor clade with strong support. Within the major clade, the *Pseudostichopus* species of this study form a low supported (0.72), minor sister clade to all other non-Elasipodida species (Figure 6.3). When using *Staurocucumis abyssorum* as outgroup, this minor clade of *Pseudostichopus* forms a strongly supported sister clade to Elasipodida species. Similar to the 16S tree, Elasipodida representatives form three distinct sister clades to the major non-Elasipodida clade. The best supported clade is formed by Elpidiidaes that exclude *Peniagone* species. *Peniagone* species form a weakly supported clade with the echinoid *Strongylocentrotus purupatus*. The *Peniagone* branch does not distinguish between individual species in the 28S gene and is only weakly supported (0.84) with asteroids and an echinoid as outgroup. In contrast, this *Peniagone* branch is well supported with *S. abyssorum* as outgroup. The representatives of the families Psychopodiidae and Laetmogoniidae form a weakly supported (0.56) minor clade, in which the positioning of *Benthodytes lingua* and *B. gosarsi* E09 appear unresolved. With *S. abyssorum* as outgroup, this clade is absent and *Laetmogone billetti* is positioned basally to all other Elasipodida species, leaving the position of *Benthotyes* spp. and *Psychropotes depressa* unresolved.

6.3.2.3 COI Gene

In the COI gene shallow-water representatives of the order Aspidochirotida fall basal to all deep-sea representatives of this study (Figure 6.4). The deep-sea representatives form one major clade that is not very well supported (0.81). Within this clade the positions of *Ekkentropelma* sp. and *Ypsilothuria* sp. are unresolved. The COI gene is the only gene in which a big clade is formed that includes all Elasipodida (0.74). *Deima validum* still forms a minor clade with *Benthothuria funebris*, latter being directly grouped with *Pseudostichopus* sp. A (0.92). This minor clade has little support (0.67) with the presented outgroups (Figure 6.4). With *Staurocucumis abyssorum* as outgroup this

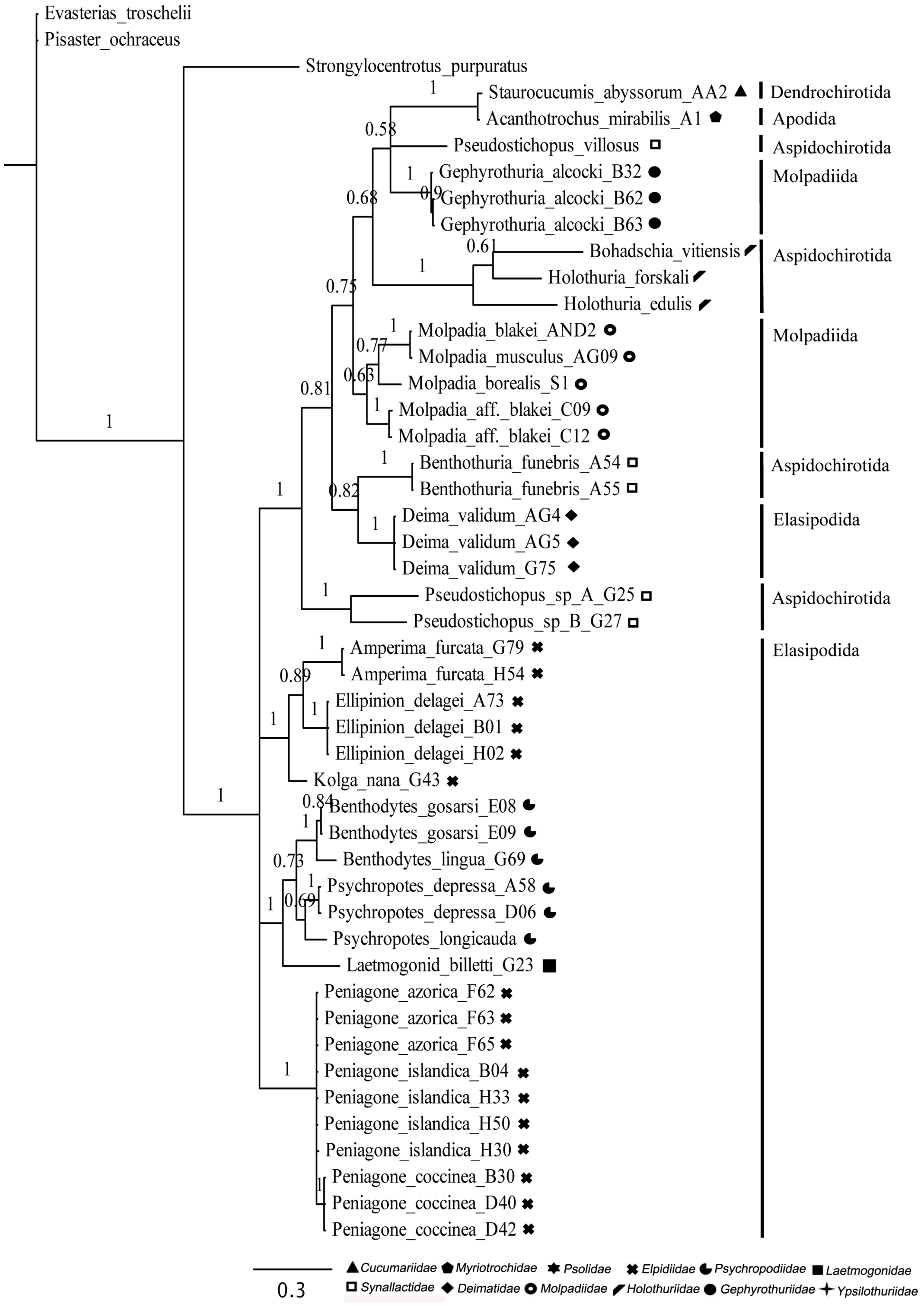


FIGURE 6.2: 16S Tree. Numbers after each species name refer to their individual sample code, and symbols show their families, which are listed below the table. Vertical bars on the right hand side highlight different orders.

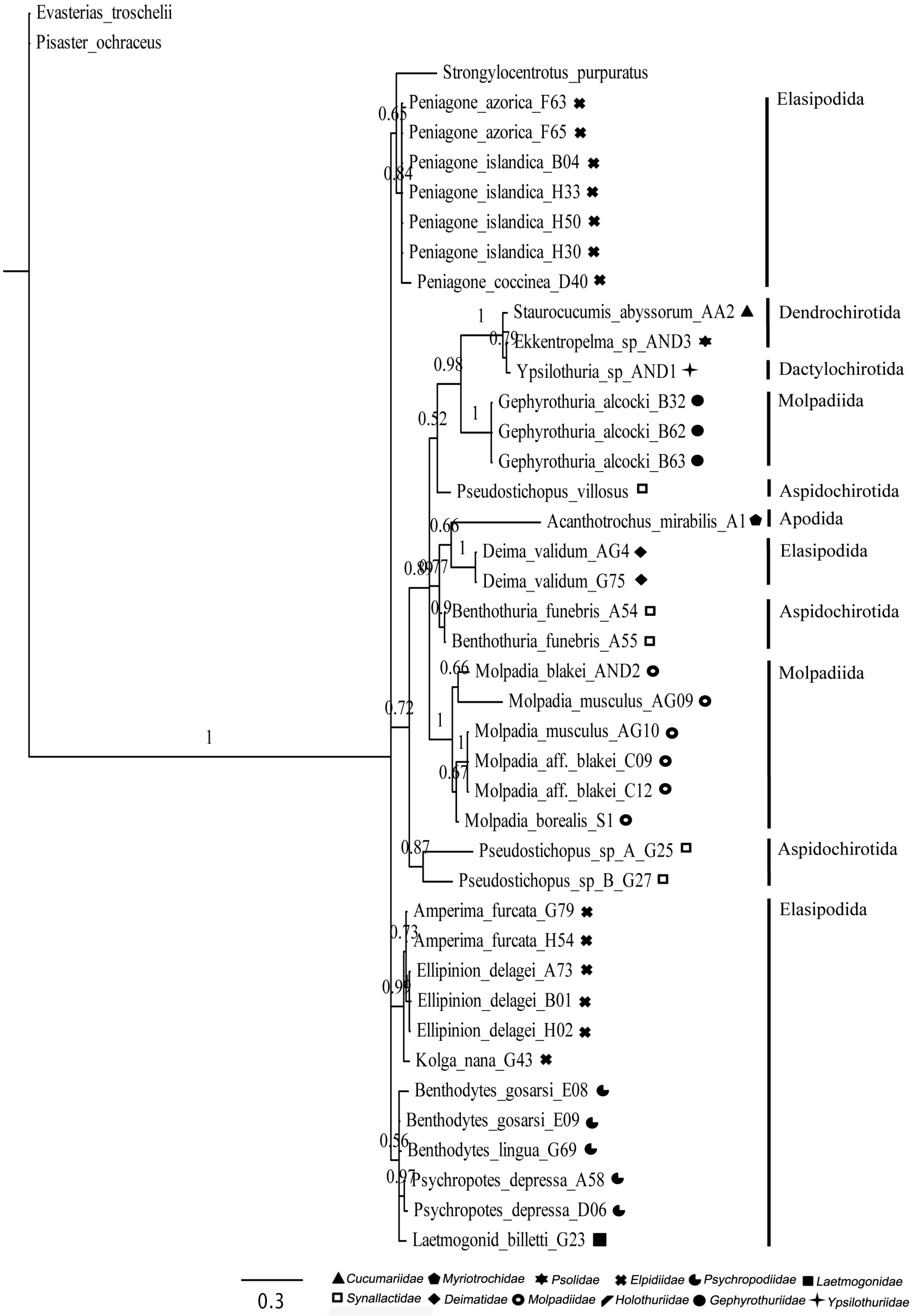


FIGURE 6.3: 28S Tree. Numbers after each species name refer to their individual sample code, and symbols show their families, which are listed below the table. Vertical bars on the right hand side highlight different orders.

minor clade is absent, and although *B. funebris* and *Pseudostichopus* sp. A are still grouped together, they have even less support (0.6). The position of *Deima validum* remains unresolved with *S. abyssorum* as outgroup. The division between the families Elpidiidae, and Psychropotiidae and Laetmogoniidae is strong (Figure 6.4). The family Laetmogoniidae forms a weak cluster (0.93) with the family Psychropotiidae. There is a strong separation of *Peniagone* spp. from other Elpidiidae members. Though the separation of *Ellipinion delagei* from *Kolga nana* and *Amperima furcata* is weak (0.93), there is good support for this division with *S. abyssorum* as outgroup. The grouping of *K. nana* with *E. delagei* only finds low support, regardless of outgroup (0.65/0.94). Sister to the Elasipodida clade are the weakly supported grouping of *Gephyrothuria alcocki* and *Staurocucumis abyssorum* (0.57), and a clade that includes all *Molpadia* spp., together with *Pseudostichopus* sp. B (0.62).

6.3.2.4 H3 Gene

The H3 tree is least similar to the consensus tree. Three major sister clades are formed, non of which is well supported (Figure 6.5). One of these clades groups *Peniagone islandica* and *Peniagone azorica* together with the families Laetmogoniidae and Psychropotiidae. This grouping was also found when *Staurocucumis abyssorum* was used as outgroup, and finds low support regardless of the outgroup (0.54/0.81). Another clade groups all non-*Peniagone* Elpidiidae together (0.89). Within this smaller clade, *Amperima furcata* and *Ellipinion delagei* are paired together (0.8). These two sister clades form one larger clade when *S. abyssorum* was used as outgroup (0.99). Finally, the largest clade is formed by all remaining species (Figure 6.5). Within this clade the positions of *Pseudostichopus* sp. A, *Pseudostichopus* sp. B, *Acanthotrochus mirabilis*, and *Peniagone coccinea* D42 are unresolved. The position of these species were also unresolved with *S. abyssorum* as outgroup. Within this major clade a well supported *Molpadia* clade is formed, as well as one including the representatives of the orders Dendrochirotida and Dactylochirotida. H3 is the only gene in which *Deima validum* and *Benthothuria funebris* do not form a minor clade. *Benthothuria funebris* is paired up with *Gephyrothuria alcocki*, leaving *Deima validum* in an unresolved position. With *S. abyssorum* as outgroup, these three species form one, low supported (0.63) clade, although *B. funebris* and *G. alcocki* are paired up regardless of the outgroup.

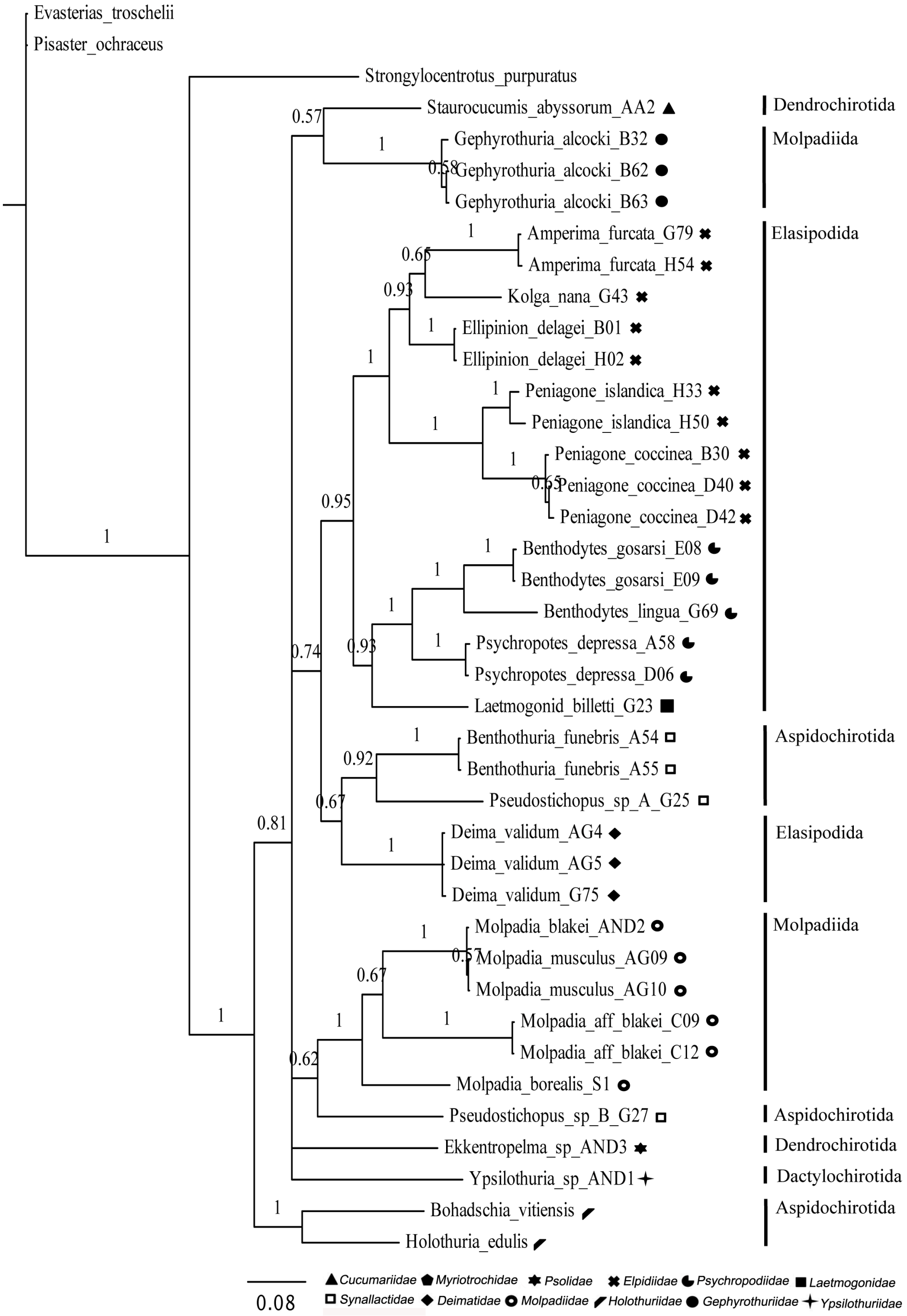


FIGURE 6.4: COI Tree. Numbers after each species name refer to their individual sample code, and symbols show their families, which are listed below the table. Vertical bars on the right hand side highlight different orders.

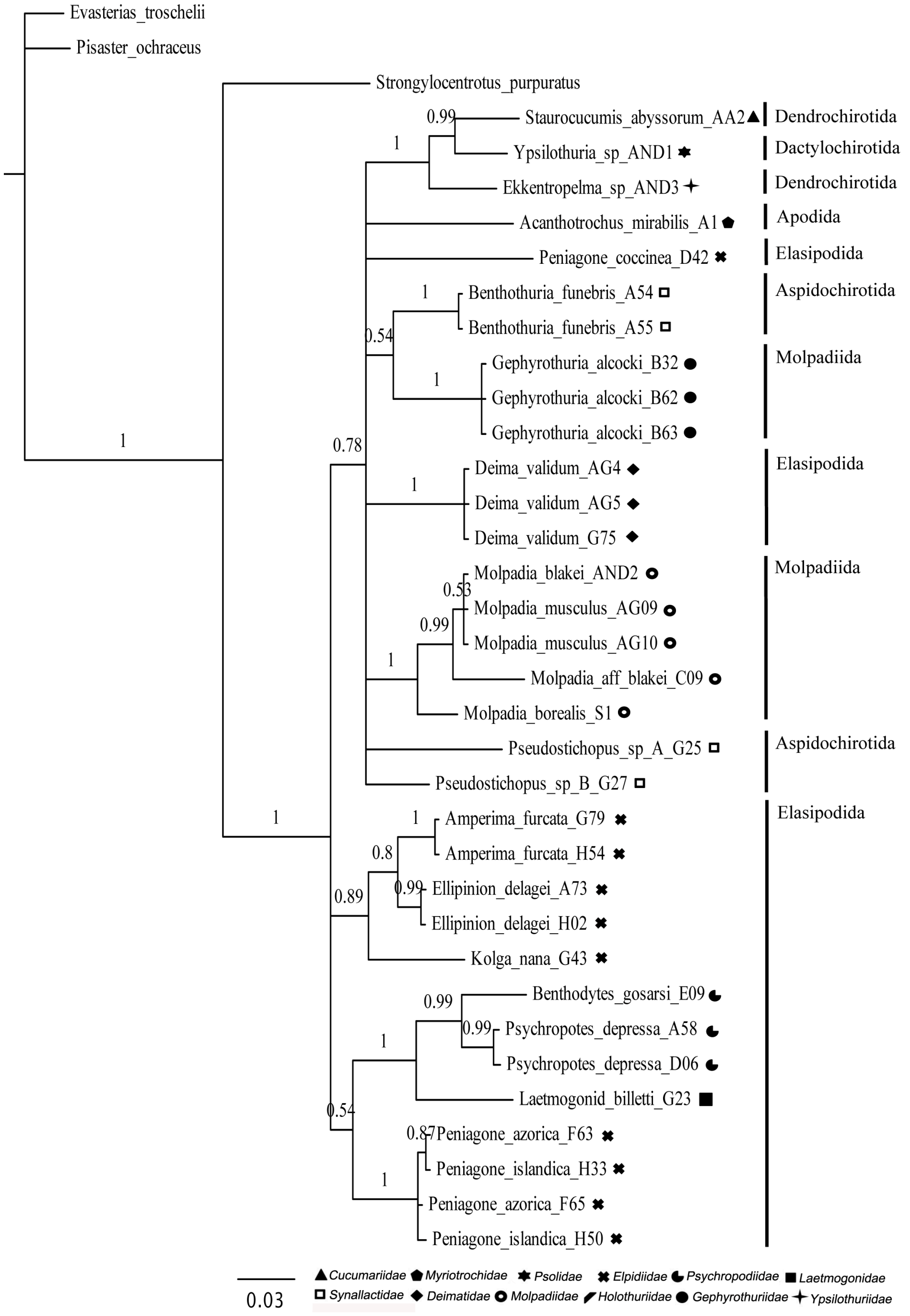


Figure 6.5: H3 Tree. Numbers after each species name refer to their individual sample code, and symbols show their families, which are listed below the table. Vertical bars on the right hand side highlight different orders.

6.3.2.5 18S Gene

The 18S tree is most similar to the consensus tree (Figure 6.6). Two major clades are formed in the 18S tree, dividing the Elasipodida from the non-Elasipodida (except *Deima validum*). Within the Elasipodida clade *Laetmogone billetti* falls basally to all other Elasipodida, which are further divided between the families Elpidiidae and Psychropotiidae. The division between these two families is only weakly supported, regardless of outgroup (0.63/0.57). Within the Elpidiidae clade *Peniagone* spp. fall into a sister clade to the other Elpidiidae species. No differentiation between *Peniagone islandica* and *Peniagone azorica* is apparent, though the support for this *Peniagone* branch is low with both outgroups (0.89/0.83). *Amperima furcata* falls basally to *Kolga nana* and *Ellipinion delagei*, latter pairing being weakly supported (0.92/0.91). Within the major non-Elasipodida clade, a Dendrochirotida/Dactylochirotida clade is formed basally to the other non-Elasipodida species (low support 0.63). Within this clade the coastal family Holothuriidae, and the deep-sea *Pseudostichopus* sp. A and B, fall basal to the remainder of the species (Figure 6.6). Minor, low supported clades are formed by *Molpadia* spp. (support 0.83), *Benthothuria funebris* and *Deima validum* (support 0.81), and *Gephyrothuria alcocki* and *Pseudostichopus villosus* (support 0.55). Very similar groupings occurred with *S. abyssorum* as outgroup, with the only exception, that *Pseudostichopus villosus* did not group together with *Gephyrothuria alcocki*, though still placed in the clade with the three sister clades.

6.4 Discussion

Species from the orders Dendrochirotida and Dactylochirotida were grouped strongly together. This grouping is interesting because both orders were considered Dendrochirotida until 1965, when Pawson & Fell split the order into the currently recognised orders Dendrochirotida and Dactylochirotida. Ossicle fossil evidence suggests a divergence of these two orders around the Carboniferous period (ca. 340 Ma). The taxonomic separation was carried out because the number of tentacles was not considered important enough in reflecting an evolutionary relationship. Instead, it was focussed on the difference in the calcareous ring, the shape of the tentacles and the differences in ossicle numbers and shapes in the body wall (Pawson and Fell, 1965). In this study no further conclusions can be drawn about this grouping, as there are too few representatives. However, further investigation into these orders and their relationships is encouraged.

The order Apodida is morphologically unique and some of its species are the largest echinoderms with up to 3 m body length (Kerr, 2001). Compared to other holothurians

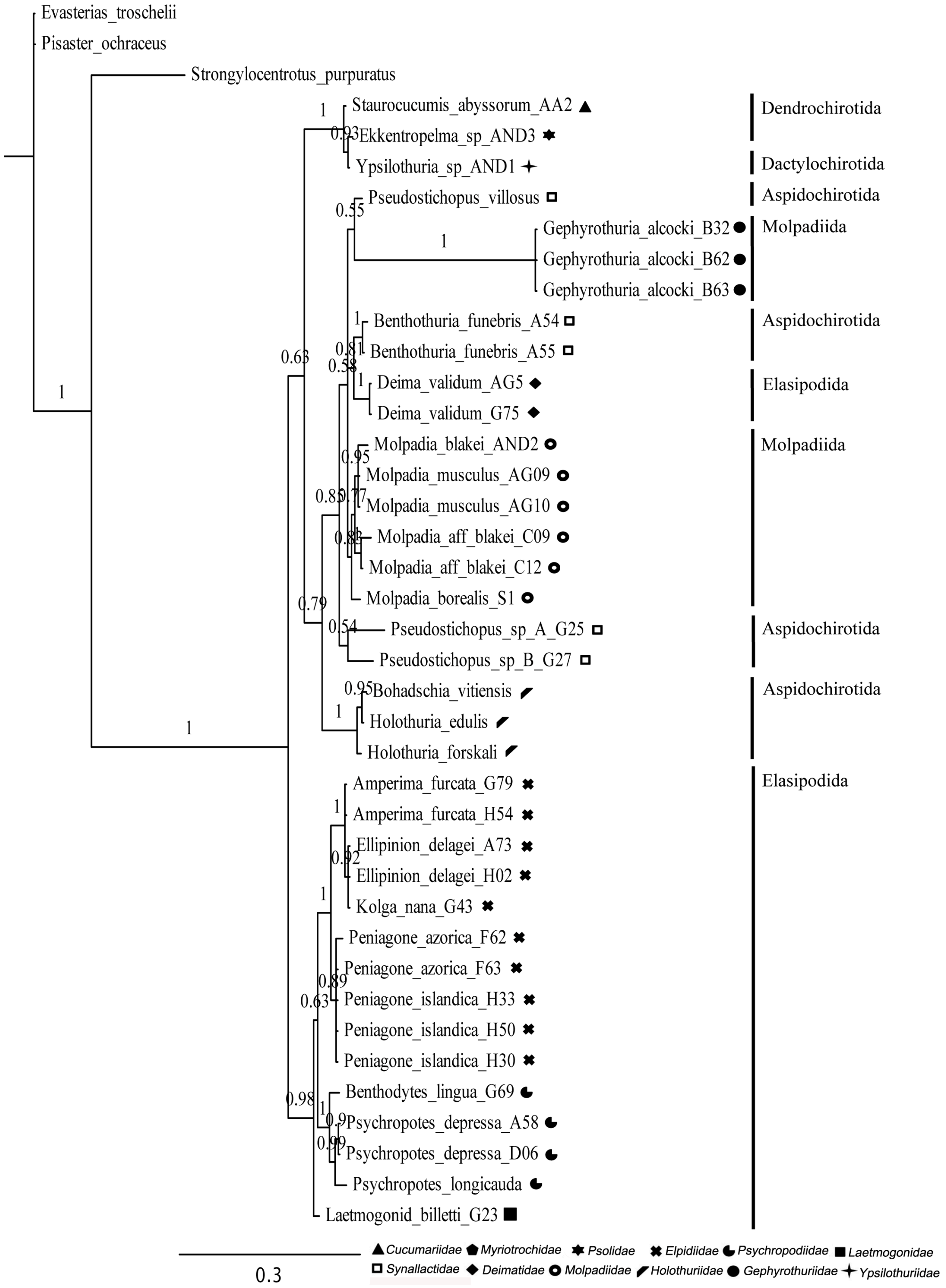


FIGURE 6.6: 18S Tree. Numbers after each species name refer to their individual sample code, and symbols show their families, which are listed below the table. Vertical bars on the right hand side highlight different orders.

they lack tubefeet, papillae and a radial water canal (Kerr, 2001). Yet, a clear separation of the order Apodida from other holothurian orders is not supported in the consensus tree (Figure 6.1), although more information and more species are needed for a detailed analysis into the relationship of its genera. The strong grouping of the Apodida representative with the Dendrochirotida/Dactylochirotida, suggest a historic relationship. However, as there are only very few representative species from these three orders, this remains speculative.

The deep-sea order Elasipodida groups strongly together, with the exception of *Deima validum*. Taxonomically, the Elasipodida has been very carefully studied and it is the only order that is ecologically restricted to the deep sea. Morphologically one of its main distinguishing features is the absence of a respiratory tree (Hansen, 1975). The Elasipodida order shows a strong molecular support in the grouping of its Elpidiidae family members, which are further subdivided into *Peniagone* spp. and the other Elpidiidae family members, *Amperima* sp. and *Ellipinion* sp. Taxonomically, one of the main features that distinguishes the Elpidiidae family from other Elasipodida families is its unique shape of the calcareous ring (Hansen, 1975). Within the *Peniagone* clade there is good support across all genes studied (apart for COI where amplification was not possible) for the erection of the new species *Peniagone coccinea* (Rogacheva & Gebruk (2012) in Rogacheva et al. (accepteda)). The other two *Peniagone* species analysed from the MAR, while appearing to be distinct morphologically, appear to be the same species. *Peniagone azorica* was originally described by Marenzeller (1893), and *Peniagone islandica* by Deichmann, 1930 (Hansen, 1975). Molecular data presented here, suggest that *P. azorica* and *P. islandica* are the same species. Specimens of *P. islandica* were collected south of the **C**harlie-**G**ibbs **F**racture **Z**one (CGFZ), while specimens of *Peniagone azorica* were collected from the north. This indicates that these two species are most likely two morpho-types of the same species. However, the genes used in this study are not the most suitable for picking up fine scale changes, especially as the COI gene of *Peniagone azorica* could not be amplified. While there is a strong case that this is one species, a recent divergence is possible and needs further investigation at population genetics level. Taxonomically, these species are distinguished by their ossicle characteristics. Otherwise they are very similar morphologically (Rogacheva et al., accepteda). Traditionally, the Elasipodida is divided into the suborders, Deimatina and Psychropotina (Hansen, 1975). The non-Elpidiidae clade of the order Elasipodida do not conform to this division in the consensus tree (Figure 6.1). This clade, including *Benthodytes* spp., *Psychropotes* spp., and *Laetmogone billetti* Rogacheva & Gebruk (2012), has a strong molecular support. However, while *Benthodytes* spp. and *Psychopotes* spp. are considered, together with the family Elpidiidae, members of the Psychropotina suborder, the *Laetmogone* genus is considered part of the Deimatina suborder, jointly with the genus *Deima*. *Deima validum* is consistently placed outside the order Elasipodida and grouped together with *Benthothuria funebris*, a species of the order Aspidochirotida. This grouping is remarkable, not only because they are members of different orders, they are also distinctly different from each other morphologically. This clade is supported by an independent study, conducted by Solís-Marín in 2003, where the same grouping occurred (Solís-Marín, 2003). Although they only studied one mitochondrial gene (16S), the grouping of *Deima validum* and *Benthothuria funebris* is consistent with the consensus tree presented here (Figure 6.1). This is an indication of convergent morphological evolution, where both species resemble morphological characteristics of different orders, despite being most closely related to one another at molecular level. Why these two species should cluster together is very difficult to determine morphologically, suggesting that characteristics other than the presence/absence of respiratory trees and spicules might play a significant role in distinguishing deep-sea holothurians. The data presented here strongly suggest *Deima validum* does not belong to the order Elasipodida. The relationship of other members of the order Aspidochirotida is mainly unresolved, although shallow water representatives of Holothuriidae family are grouped together, as are the deep-sea *Pseudostichopus* sp. from the Synallactidae family. The species that is used in this study called *Pseudostichopus villosus* has, since its publication in gen bank, been reclassified as *Molpadiodemas villosus*. Looking at the molecular data presented here, its position is unresolved. This indicates that more research is needed in resolving the relationships of the Synallactidae species.

Finally, one of the striking characteristics in the order Molpadiida, are the ossicles, which change with age (Billett, 1991). Their morphology appears very basic. They lack tube feet, have basic tentacles and a general ovoid body shape, which makes it difficult to distinguish the species (O'Loughlin et al., 2011). In the present study, this order has two represented genera, *Gephyrothuria* and *Molpadia*. *Gephyrothuria* has a long history of taxonomic uncertainty. It does not appear to have any clear taxonomic characteristics. This genus was grouped together with the *Pseudostichopus* genera into the family Gephyrothurriidae by Svend Heding (Heding, 1935), while Deichmann placed this genus into the family Molpadiidae (Deichmann, 1930). Currently, this genus is accepted as part of the order Molpadiida, within its own family. Owing to *Gephyrothuria* being a very obscure genus it is often excluded from analyses (Kerr and Kim, 2001) and only one species is currently accepted for this genus (O'Loughlin, 1998). Similar to its morphological taxonomy, the genetic relationship of *Gephyrothuria* appears unclear, based on presented data. However, it appears that its inclusion into the order Molpadiida, is not supported genetically. With *Evasterias troscheli*, *Pisaster ochracheus*, and *Strongylocentrotus purupatus* as outgroup *Gephyrothuria alcocki* was grouped together, though with low support, with the orders Dendrochirotida/Dactylochirotida and Apodida. When *Staurocucumis abyssorum* was used as outgroup this species formed its own small branch that was positioned basal to all species representing the order Molpadiida, Aspidochirotida, and Elasipodida.

Species of the genus *Molpadia* are strongly grouped together. Most noticeable in the *Molpadia* clade is the grouping of *Molpadia blakei* and *Molpadia musculus* in one, strongly supported clade. This is particularly interesting in light of the recent study by O'Loughlin *et al.* that found a number of species complexes, one of which included *Molpadia musculus* (O'Loughlin et al., 2011). In their study only *Molpadia musculus* was investigated from the genus *Molpadia*. It was suggested that this cosmopolitan species is a species complex of cryptic species. We suggest the possibility that the species complexes described by O'Loughlin *et al.* might also include other morphologically distinct species that have been, taxonomically, recognised as separate species e.g. *Molpadia blakei*, but which are genetically not distinct. This implies that the entire genus *Molpadia* needs considerable reworking. As ossicles change with age in *Molpadia musculus* might not be a suitable indicator for taxonomic species in the Molpadiida.

6.4.1 Implications for Holothurian Systematics

In the past, studies on holothurian systematics have either only concentrated on discrete morphological characteristics (Kerr and Kim, 2001), mitochondrial DNA(Arndt et al., 1996), or on a combination of individual mitochondrial genes and discrete morphological characters (Arndt et al., 1996; Solís-Marín, 2003). Owing to the long geological history of the class Holothuroidea is morphologically very complex. Character states that have been assigned are not always reliable, e.g. *Molpadia musculus/Molpadia blakei.* Consideration of mitochondrial DNA alone to clarify the relationship of this group can result in unreliable outcomes, because mitochondrial DNA has a much smaller effective population size than nuclear genes (Zhan et al., 2007), and is only pased on through the maternal line. Additionally, holothurian DNA is notoriously difficult to amplify and it is rare that more than a DNA fragment is successfully amplified. Hence, the use of several genes, which evolve at different rates is very beneficial, in order to understand the overarching relationships within this class. It shows that there is a varying selective pressure on individual genes, emphasising the need for a balanced selection of nuclear and mitochondrial; protein and non-protein coding genes. The combined information of different genes give a much stronger overall relationship. There is good support that *Molpadia* aff. *blakei* is a separate species, at least to those investigated in this study.

Taxonomically, it should be possible to select current taxonomic character states that are most suitable in reflecting molecular information, while identifying those that might be redundant. With such an approach it could be possible to reduce the number of current morphological characteristics that need to be investigated to distinguish between species to fewer, more meaningful, characteristics.

6.5 Conclusion

Based on the data presented here *Deima validum* and *Bentothuria funebris* do not belong to the respective orders Elasipodida and Aspidochirotida. They form their own group, although it is unclear at what level. The Elasipodida suborders need reworking. Two morphological species of *Peniagone azorica* and *Peniagone islandica* are not distinct genetically. The order Aspidochirotodita is unresolved and more samples are needed to decide on its higher taxonomic structure. The same is true for the orders Dendrochirotida and Dactylochirotida. The genus *Gephyrothuria* is distinct genetically from species in the order Molpadiida. *Molpadia musculus* and *Molpadia blakei* are genetically similar, suggesting that they might be one species. The H3 gene was amplified for holothurians the first time.

Chapter 7

Synthesis

In this study aspects of the MAR were investigated using three different methodologies. In total, over 300 molecular samples were taken between 2009 and 2010, which resulted in the successful amplification of 2,248 base pairs belonging to five genes, from 47 holothurian specimens (Chapter 6). To clarify the faunal distribution and local habitat complexity, 32,000 m^2 of HD quality footage were analysed, resulting in 55,192 specimen counts (Chapter 4). Finally, an area of 50 ha was trawled, resulting in 21,974 identified specimens that were measured and weighed (Chapter 3). Molecular science can only point-sample a habitat, while imaging and trawling gear can sample areas that range from m^2 in images to ha in trawls. Collectively these techniques provide ecologically-relevant information on species richness, diversity, density, and community composition.

While the geomorpholgy of the **M**id-**A**tlantic **R**idge (MAR) is well documented, and chemosynthetic systems have been studied extensively, relatively little was known about its non-chemosynthetic environment prior to the MAR-ECO and ECOMAR projects (Bergstad et al., 2008). The numerous benthic invertebrate megafauna discovered during these projects highlight the importance of species identification for ecological understanding (Gebruk et al., 2008; Martynov and Litvinova, 2008; Mironov, 2008; Mortensen et al., 2008; Tabachnick and Collins, 2008; Rogacheva et al., accepteda). Even in major deep-sea megafauna groups, such as holothurians (Billett, 1991), there remain many unresolved relationships. Each new species description must take into account previously established characteristics that define different orders and families. Therefore, choosing suitable morphological traits becomes critical. While research into species and genera relationships is ongoing, families and orders are rarely revised (Pawson and Fell, 1965; O'Loughlin, 1998; Solís-Marín, 2003). The phylogenetic approach adopted by this study highlighted the need for further investigation into relationships at higher taxonomic levels. Two species, *Deima validum* and *Benthothuria funebris*, that are morphologically very distinct and belong to different families proved to be genetically closely related. This implies that morphological characteristics that are used by taxonomists to group species into their specific orders and families might not reflect their evolutionary relationship. This is also highlighted by genera *Molpadia* and *Peniagone*, which include species that are currently separate but appear to be conspecific morphotypes (Figure 6.1, page 113). As species form the basis for ecological studies, it is important to resolve these taxonomic problems. It is clear from the present study that many relationships between holothurian families are still poorly understood (Figure 6.1, page 113), and it is assumed that this issue applies to many deep-sea taxa.

Through their physical structures, or by creating structures such as mounds and tubes, some species can enhance local habitat heterogeneity (Buhl-Mortensen et al., 2010). The MAR is a very complex deep-sea region (Priede et al., in prep) that incorporates a range of biologically-generated microhabitats, as well as geological structures, such as boulders. These microhabitats can influence the distribution of epibenthic fauna (Auster et al., 1991). A strong effect of slope as habitat characteristic was observed in diversity and community composition, although its effect differed between sites. At the southern sites the community composition between flat and sloped terrain was noticeably more pronounced (Figure 4.8, page 84), while diversity differences between slope habitats were much stronger at the SE and NW sites, compared to the SW and NE sites (Figure 4.6, page 81). More investigations are needed to understand this contrast. It might be caused by a combination of factors, yet to be identified and quantified, such as the distance to geological structures affecting the local hydrology. Observations of biogenic structures on soft sediment were made at all MAR sites and within both habitats. Although species forming these structures differed between sites, overall only slightly fewer were present at the NE site, while there were no apparent differences between the SE, SW and NW sites (Table 4.7, page 85).

In contrast to biogenic structures, the overall composition (Figure 3.6, page 53; Figure 4.7, page 82), density, size and biomass of megafaunal communities differed between the sites. These variations were likely driven by a combination of environmental forces, such as food availability and quality (Gage, 2003), sediment type (Bett et al., 2001; Ramirez Llodra et al., 2010), habitat heterogeneity (Buhl-Mortensen et al., 2010) and possibly by levels of disturbance (Glover et al., 2010). The differences in species composition between the two northern sites indicate that the Scotland-Iceland Overflow Water does not act as a dispersal route for fauna. Instead, the southern sites share more species, though the exchange mechanism remains unclear.

7.1 Are the MAR and Charlie-Gibbs Fracture Zone Barriers?

This study suggests that the Mid-Atlantic Ridge may only act as barrier to megafaunal dispersal between the northern sites, where it is higher. If the ridge forms a consistent barrier, significant differences between the southern sites would have been observed, similar to those observed at the northern sites (Section 4.3.6, page 81). Although unlikely to have influenced the final results, consideration must be given to the low sampling effort at the SW site, which was only sampled in 2010. As already discussed, in video surveys it can be difficult to distinguish different species and morpho-types that are counted as one species might encompass several. As no trawling was achieved at the SW site, species could not be examined in detail and identifications are solely based on the expertise of taxonomists who viewed video recordings.

It is more likely that the Charlie-Gibbs Fracture Zone is a barrier to dispersal, although other factors may also drive differences between north and south. Firstly, the current system through the Fracture Zone may create an obstacle to the exchange of megafauna between the northern and southern sites. Secondly, differences between the northern and southern communities suggest that the northern sites were more dynamic and, therefore, unsuitable for species that occurred at the southern sites. A further factor in support of the idea of the Fracture Zone as barrier, are the molecular result for *Peniagone azorica* and *Peniagone islandica* (Figure 6.1, page 113). *Peniagone azorica* was restricted to the northern sites, while *Peniagone islandica* was only observed at the southern sites. Despite very similar external morphologies, their morphology of calcareous ossicles is distinctly different. However, their genetic similarity suggests that these two species are currently undergoing divergence (Rogacheva et al., accepteda), possibly driven by a lack of substantial gene flow across the CGFZ. In a study investigating two study sites separated by the Wyville-Thomson Ridge significant differences in species composition could be observed also (Bett et al., 2001). However, in this case, differences to the north and south of the ridge were explained by different hydrographic regimes (Bett et al., 2001).

7.2 The ECOMAR Study Area in Context

The diversity from the video survey was consistently higher than reported from the Faroe-Shetland channel (Jones et al., 2007) and the HAUSGARTEN observatory (Soltwedel et al., 2009). However, this may be a product of the higher quality video footage. Diversity values based on trawl catches were fairly similar to those reported from the New

England slope (Haedrich et al., 1980) (Figure 3.8, page 62). Densities were also similar to those expected for benthic megafauna (Figure 3.7, page 60). Species that occurred at both, the MAR and on continental margins, do not appear to show any bathymetric displacement at the ridge, a theory that had been proposed for scavenging fish (King et al., 2006). The initial hypothesis that the ridge supports a pool of species from the continental margins is neither supported nor rejected, as data are limited. The fact that fauna from the ridge are rather more similar to that on the eastern, than western continental slope is likely a result of greater sampling effort devoted to benthic megafauna on the European margins. Similarly, it is unlikely that the ridge hosts many endemic species. Although many new species have been found throughout the ECOMAR study (see forthcoming special issue of Marine Biology Research issue edited by A. Gebruk), this likely reflects the limited sampling prior to MAR-ECO and ECOMAR.

The MAR in the ECOMAR region has been previously recognised as an important barrier in the northern Atlantic, dividing the pelagic realm into east and west Atlantic biomes (Longhurst, 2007). While a similar division could also be observed for the benthos at the northern sites, the view that the ridge divides the Atlantic into an eastern and western sector cannot fully be supported through the present study while the hypothesis that the Charlie-Gibbs Fracture Zone divides benthic fauna into southern and northern communities (Vinogradova, 1997) finds support in the results of this study. The recent GOODS report, which considers all benthic bathyal fauna between 800 and 3,000 m part of the northern North Atlantic Province (Agostini et al., 2009) does not recognise any faunal boundaries along the Ridge or the Fracture Zone, the present study reveals considerable species-level differences between the sites.

Finally, the present study highlights the complexity of the MAR, which represents one of the most extensive bathyal environments on Earth. It has been suggested that the pelagic biomass that is displaced by the presence of this bathymetric feature is replaced by benthic biomass (Priede et al., in prep). While most research on bathyal environments have been carried out on continental slopes, differences in environmental setting at mid-ocean ridges has to be remembered, such as different hydrographic regimes, increased anthropogenic pressures at the continental margins, and different inputs of organic matter. As human impacts on continental margins increase, the biological diversity of the margins is likely to suffer, leaving mid-ocean ridges and seamounts some of the few bathyal biodiversity oases. Non-chemosynthetic habitats dominate mid-ocean ridges in terms of spatial coverage and it is crucial to understand their ecology.

7.3 Working Hypotheses Revisited

- Biomass, as measure of energy input, does not differ between the south and north sites in benthic megafauna. **Hypothesis is supported.** *Data did not show any significant difference in biomass between the southern and northern sites, indicating that the energy availability is not significantly different on the benthos south and north of the Charlie-Gibbs Fractures Zone.*

- Biomass, as measure of energy input, does not differ between the east and west site in benthic megafauna. **Hypothesis is supported.** *Data did not show any significant difference in biomass between the eastern and western sites, indicating that the energy availability is not significantly different east and west of the Mid-Atlantic Ridge.*

- Body sizes of benthic megafauna do not differ between the south and the north. **Hypothesis rejected.** *Data show significant size differences between sites, with generally larger sizes observed at the northern sites.*

- Body sizes do not differ in benthic megafauna between east and west. **Hypothesis is supported.** *Although data showed significant differences in body size between sites, there was no clear pattern indicating that either the western or eastern sites of the ridge had larger specimens. Size differences are likely a result of environmental forcing and inter-specific resource competition.*

- No particular species dominate at any site, suggesting an even species distribution. **Hypothesis rejected.** *Although trawl samples showed a dominance at the NE site (by the holothurian Kolga nana), and an even distribution at the NW and SE site, all sites were dominated by few fauna that differed between sites in the video survey.*

- There is no difference in diversity in benthic megafauna between the southern and northern sites. **Hypothesis is supported.** *A significant difference in diversity was observed between sites in the trawl data, with the highest diversity observed at the SE site. However, the video survey did not show any significant difference in diversity and it is assumed that the more balanced sampling design in the ROV study reflects the differences in diversity more realistically.*

- There is no difference in diversity in benthic megafauna between the western and eastern sites. **Hypothesis is supported.** *A significant difference in diversity was observed between sites in the trawl data, with the highest diversity observed at the SE site, followed by the NW site. However, the video survey did not show any* *significant difference in diversity and it is assumed that the more balanced sampling design in the ROV study reflects the differences in diversity more realistically.*

- There is no difference in benthic megafauna community composition between the southern and northern sites. **Hypothesis rejected.** *There was a significant difference in the composition of benthic megafauna north and south of the Charlie-Gibbs Fracture Zone in datasets from both the trawl and video survey.*
- There is no difference in benthic megafauna community composition between the eastern and western sites. **Hypothesis rejected.** *There was a significant difference in the composition of benthic megafauna east and west of the Mid-Atlantic Ridge in datasets from both the trawl and video survey.*
- Small-scale habitat variations do not affect benthic megafauna assemblage structures at the MAR. **Hypothesis rejected.** *There was a significant difference in the community composition between flat and 10° slope habitats, suggesting that small-scale variations do affect the community composition in benthic megafauna.*
- Taxonomic relationships of benthic megafauna at the MAR are resolved. **Hypothesis rejected.** *Molecular analyses of holothurians showed that relationships between species, even as common as holothurians, are still unresolved for some species.*
- The new species *Peniagone coccinea*, *Laetmogone billetti*, *Molpadia* sp. nov. are not genetically distinct from close holothurian relatives found at the MAR. **Hypothesis rejected.** *While both morphological and molecular data on Peniagone coccinea and Laetmogone billetti clearly support their status as new species, Molpadia sp. nov. has morphologically not been accepted as new species and has been described as Molpadia aff. blakei. While molecular data supports the status of Molpadia sp. nov. as new species, this species does not appear to have enough distinguishable morphological characteristics to officially classify it as new. (Chapter 6 & Rogacheva et al. (accepteda))*
- *Gephyrothuria alcocki* does not belong to the order Molpadiida. **Hypothesis is supported.** *Although the position of Gephyrothuria alcocki has not been resolved within the order Holothuroidea, there is strong support that this species does not belong to the order Molpadiida.*

7.4 Future Perspectives

There remains a wealth of information to be acquired in addition to the interpretations presented in this study. The specimens from the trawl catches still hold much information regarding reproduction. Some species recorded from the MAR could be used for comparison between the sites and to similar species found at the continental margins. Individuals collected from the genus *Molpadia* could not only be compared reproductively, but also contribute to an overarching investigation that would clarify the systematics of this group through molecular and taxonomic studies. Molecular samples that were collected could be used to investigate the gene flow between the ECOMAR sites, while the phylogenetic data presented here could be further analysed to clarify possible divergence times of holothurian species. The ROV data collected represents the main opportunity for further study. Species and habitat patchiness may further be analysed, and visualised through habitat mapping. The sizes of the individual specimens counted in the videos could be obtained and compared between the sites. Based on information collected from trawl data, sizes from video footage could also be translated into biomass. These biomass and size measures would allow for a more comprehensive result, as problems associated with damage to individual specimens would no longer apply, and size would be unchanged through the fixation of specimens. The ROV and trawl data could also be further analysed by considering feeding guilds. Unfortunately, as a result of time constraint, none of these analyses were pursued, but it is hoped that in future time and money will be invested to carry on this study.

Appendix A

Species List - Trawling

A.1 Densities

TABLE A.1: Species collected with trawls and used for the analysis. Information on Class, the year the species were collected, and the average density at each site (individuals ha^{-1})

Class	Taxonomic Unit	Year	SE	SD	NE	SD	NW	SD
Holothuroidea	*Paelopatides grisea*	2007/2009	0.75		21.33	± 14.74	0.25	
Holothuroidea	*Amperima furcata*	2007/2009	52.50	± 21.21	0.00		0.00	
Holothuroidea	*Synallactes crucifera*	2007/2009	1.50		0.00		0.00	
Holothuroidea	*Psychropotes depressa*	2007/2009	4.75	± 5.50	1.67		4.00	± 4.51
Holothuroidea	*Deima validum*	2007/2009	0.50		0.00		0.00	
Holothuroidea	*Gephyrothuria alcocki*	2007/2009	61.00	± 51.85	4.67	± 3.21	15.50	± 12.50
Holothuroidea	*Psychropotes* sp. nov.	2007/2009	1.00		0.00		0.00	
Holothuroidea	*Pseudostichopus peripatus*	2007/2009	10.75	± 8.96	5.67	± 2.52	5.50	± 3.42
Holothuroidea	*Pseudostichopus* sp. 2	2007	0.00		0.00		4.25	
Holothuroidea	*Pseudostichopus* indet.	2009	0.75		0.25		0.00	
Holothuroidea	*Methothuria cathedralis*	2007/2009	21.00	± 13.49	0.33		1.75	± 0.71
Holothuroidea	*Mesothuria* indet.	2007/2009	0.00		0.00		1.00	
Holothuroidea	*Mesothuria maroccana*	2007/2009	3.50	± 2.31	0.00		3.25	± 2.08
Holothuroidea	*Benthodytes sanguinolenta*	2009	0.25		0.00		0.00	
Holothuroidea	*Benthodytes lingua*	2009	0.50		0.00		0.00	
Holothuroidea	*Benthodytes gosarsi*	2007/2009	34.00	± 12.73	0.33		30.75	± 16.86
Holothuroidea	*Bathyplotes natans*	2007	1.00	± 1.41	0.00		0.75	
Holothuroidea	*Benthothuria funebris*	2007/2009	25.50	± 19.77	2.00		0.50	
Holothuroidea	*Staurocucumis abyssorum*	2007/2009	112.00	± 20.51	0.00		0.00	
Holothuroidea	*Myriotrichus clarki*	2009	3.00	± 2.65	0.67		4.50	± 1.29
Holothuroidea	*Molpadia musculus*	2007	77.25	± 88.50	1.33	± 0.58	0.25	
Holothuroidea	*Molpadiodemas violaceus*	2007	0.00		0.00		0.25	
Holothuroidea	*Molpadia* sp. nov.	2007/2009	16.50	± 12.92	1.67	± 0.71	4.25	± 0.96
Holothuroidea	Elpidiidae mix	2007	0.00		3913.67	± 604.19	0.00	

table continues ...

Class	Taxonomic Unit	Year	SE	SD	NE	SD	NW	SD
Holothuroidea	*Peniagone islandica*	2007/2009	22.50	± 19.81	0.00		0.00	
Holothuroidea	*Peniagone ?islandica*	2007	25.75		0.33		0.00	
Holothuroidea	*Peniagone* sp. nov. ‘coccinea’	2009	9.75	± 2.65	0.00		0.00	
Holothuroidea	*Ellipinion delagei*	2009	5.25	± 13.44	0.00		0.00	
Holothuroidea	*Penillipidia midatlantica*	2009	0.25		0.00		0.00	
Holothuroidea	*Labidoplax* sp.	2007	0.00		0.00		0.25	
Asteroidea	*Dytaster grandis*	2007/2009	3.00	±3.00	0.00		0.00	
Asteroidea	*Dytaster* sp.	2009	0.75		0.00		0.00	
Asteroidea	Astropectinidae?famGoniasteridae	2007	0.25		0.00		0.00	
Asteroidea	fam. Astropectinidae	2009	1.00		0.00		0.00	
Asteroidea	*Hyphalaster inermis*	2007/2009	53.50	± 48.39	0.00		6.00	± 3.27
Asteroidea	*Porcellanaster* sp.	2007/2009	0.25		0.00		0.75	
Asteroidea	*Porcellanaster ceruleus*	2007/2009	153.00	± 76.37	6.33	± 1.15	149.75	± 45.09
Asteroidea	*Caulaster pedunculatus*	2007/2009	0.50		3.00	± 0.71	4.25	± 3.20
Asteroidea	*Plutonaster bifrons*	2009	2.75	± 4.95	0.00		0.00	
Asteroidea	*Plutonaster* cf. *bifrons*	2009	0.50		0.00		0.00	
Asteroidea	*Plutonaster agassizi*	2009	0.25		0.00		0.00	
Asteroidea	*Plutonaster* sp.	2007	1.50		0.00		0.00	
Asteroidea	*Freyella elegans*	2007/2009	18.00	± 14.09	5.00	± 3.46	16.25	± 6.55
Asteroidea	*Hymenaster membranaceus*	2007/2009	97.00	± 83.63	0.00		0.00	
Asteroidea	*Hymenaster ?membranaceus*	2007/2009	2.75	± 2.12	0.00		0.00	
Asteroidea	*Hymenaster reticulatus*	2007	0.25		0.00		0.00	
Asteroidea	*Hymenaster* cf. *coccinatus*	2007/2009	27.75	± 23.26	27.33	± 6.66	0.75	
Asteroidea	*Hymenaster* cf. *regalis*	2007/2009	0.25		0.67		0.00	
Asteroidea	*Hymenaster* cf. *rex*	2009	0.25		0.00		0.00	
Asteroidea	*Hymenaster pellucidus*	2007	0.00		3.33	± 2.08	0.00	
Asteroidea	*Hymenaster* cf. *gennaeus*	2007	0.00		1.33		0.00	
Asteroidea	*Hymenaster?latebrosus?gennaeus*	2007	0.00		0.67		0.00	
Asteroidea	*Bathybiaster vexillifer*	2007/2009	0.00		89.00	± 18.25	18.75	± 18.54

table continues ...

Class	Taxonomic Unit	Year	SE	SD	NE	SD	NW	SD
Asteroidea	*Eremicaster* sp.	2007	0.00		0.00		0.25	
Asteroidea	Asteroid misc A	2007	0.00		0.00		2.00	
Asteroidea	Asteroid misc B	2007	0.00		0.00		1.50	
Asteroidea	*Plinthaster* sp.	2007	0.00		3.33		2.50	
Asteroidea	Notomyotida*Cheiraster?planus*	2007	0.00		0.33		0.00	
Asteroidea	*Gaussaster antarcticus*	2007	0.00		0.33		0.00	
Asteroidea	*Pseudarchaster gracilis*	2009	0.50		0.00		0.00	
Asteroidea	*Petinaster filholi*	2009	1.25	± 1.15	0.00		0.00	
Asteroidea	*Hydrasterias sexradiata*	2009	21.75	± 16.52	0.00		6.25	± 7.51
Asteroidea	*Styracaster armatus*	2009	1.00		0.00		0.00	
Asteroidea	*Styracaster* sp.	2009	0.25		0.00		0.00	
Asteroidea	*Styracaster?armatus?chuni*	2009	0.25		0.00		0.00	
Asteroidea	juv Astropectinidae	2009	0.50		0.00		0.00	
Asteroidea	juv Goniasteridae	2009	0.25		0.00		0.00	
Asteroidea	?*Pectinaster* ?*Cheiraster*	2009	0.25		0.00		0.00	
Ophiuroidea	*Ophiocamax patersoni*	2007/2009	7.00	± 3.74	0.00		0.00	
Ophiuroidea	*Ophiomusium lymani*	2007	0.25		0.00		0.00	
Ophiuroidea	*Ophiura saurura*	2007/2009	11.50		0.00		15.50	± 5.45
Ophiuroidea	*Astrodia tenuispina*	2007/2009	4.50	± 1.00	0.00		0.00	
Ophiuroidea	*Amphilepis ingolfiana*	2007/2009	11.00	± 12.19	0.00		0.00	
Ophiuroidea	Ophiacantha aculeata	2007/2009	2.75	± 2.08	1.33	± 0.58	90.25	± 42.57
Ophiuroidea	*Ophiura ljungmani*	2007/2009	3.50		3.00	± 0.71	391.25	± 120.84
Ophiuroidea	*Ophiura irrorata*	2007/2009	0.75	± 0.71	1.67	± 0.71	40.50	± 15.93
Ophiuroidea	*Ophiacantha fraterna*	2007/2009	0.00		6.00	± 2.65	4.00	± 2.52
Ophiuroidea	*Ophiocten hastatum*	2007/2009	3.00	± 3.61	2.33	± 1.53	29.75	± 16.58
Ophiuroidea	*Ophiura* sp.	2007/2009	0.00		0.33		4.75	± 2.12
Ophiuroidea	*Ophiura nitida*	2007/2009	0.00		3.33	± 1.53	0.50	
Ophiuroidea	*Ophiolimna bairdi*	2009	0.00		0.00		9.00	± 7.55
Ophiuroidea	*Ophioplinthus tessellata*	2009	3.75	± 2.00	0.00		0.00	

table continues ...

Class	**Taxonomic Unit**	**Year**	**SE**	**SD**	**NE**	**SD**	**NW**	**SD**
Ophiuroidea	Ophiomyxidae gen. sp.	2009	1.00	± 0.58	0.00		0.25	
Echinoidea	*Salenia profundi*	2007/2009	4.75	± 5.86	0.00		0.00	
Echinoidea	*Aeropsis rostrata*	2007/2009	1.75	± 2.31	0.67		10.00	± 3.79
Echinoidea	*Tromikosoma koehleri*	2009	0.00		0.00		2.00	± 4.24
Echinoidea	*Tromikosoma* cf. *uranus*	2009	1.50		0.00		0.00	
Echinoidea	*Tromikosoma* aff. *uranus*	2007/2009	5.25	± 1.00	0.33		0.00	
Echinoidea	*Echinosigra phiale*	2007/2009	0.00		17.00	± 4.58	16.25	± 12.66
Echinoidea	*Tromikosoma koehleri*	2009	0.00		0.00		1.25	± 0.71
Echinoidea	*Tromikosoma* cf. *koehleri*	2009	0.25		0.00		0.00	
Echinoidea	*Tromikosoma* aff. *koehleri*	2007/2009	0.25		0.00		3.75	
Echinoidea	*Echinus alexandri*	2007/2009	0.00		0.00		1.00	
Echinoidea	*Hemiaster expergitus*	2007/2009	0.00		4.33	± 0.58	0.50	
Echinoidea	*Urechinus naresianus*	2007/2009	0.00		44.67	± 9.29	71.75	± 145.82
Echinoidea	Pourtalesidae sp. 2	2009	0.00		0.00		3.25	
Maxillopoda	Cirripedia sp.	2007/2009	3.75	± 2.22	0.67		0.25	
Maxillopoda	Lepadomorpha sp.	2009	0.00		0.00		0.50	
Ostracoda	*Azygocypridina imperialis*	2007/2009	1.50		2.00		64.00	± 33.79
Ostracoda	*Gigantocypris ?muelleri*	2007/2009	0.00		0.33		0.25	
Malacostraca	*Eurythenes obesus*	2007/2009	0.75	± 0.71	0.67		0.00	
Malacostraca	*Euandania gigantea*	2007	0.00		1.33	± 1.41	0.00	
Malacostraca	Amphipoda sp.	2007/2009	0.00		0.00		0.75	± 0.71
Malacostraca	Galatheid sp.	2007	2.00		1.33		0.00	
Malacostraca	*Stereomastis nanus*	2007/2009	1.00		43.67	± 8.62	15.00	± 3.74
Malacostraca	*Pentacheles validus*	2009	0.75	± 0.71	0.00		0.00	
Malacostraca	*Glyphocrangon sculpta*	2007/2009	27.50	± 14.22	1.33		0.25	
Malacostraca	Tanaidacea sp.	2007/2009	0.00		0.67		0.75	± 0.71
Malacostraca	*Munidopsis* sp.	2009	0.50		0.00		0.25	
Malacostraca	*Munidopsis rostrata*	2007/2009	24.25	± 9.03	0.00		0.25	
Malacostraca	Paguridae gen.	2007	0.25		0.00		0.00	

table continues ...

Class	**Taxonomic Unit**	**Year**	**SE**	**SD**	**NE**	**SD**	**NW**	**SD**
Malacostraca	Anomura sp.	2009	1.25	± 2.12	0.00		0.00	
Malacostraca	Isopoda sp.	2009	0.50		0.00		0.00	
Malacostraca	Isopoda Valvifera	2007	0.00		0.00		0.25	
Enopia	Reptantia sp. 1	2007/2009	0.25		0.00		2.25	± 1.26
Enopia	Reptantia sp. 2	2009	0.25		0.00		0.25	
Anthozoa	*Fungiacyathus marenzelleri*	2007/2009	4.75	± 7.57	0.00		0.00	
Anthozoa	*Kophobelemnon macrospinosum*	2007/2009	0.50		0.00		0.00	
Anthozoa	*Scleroptilum grandiflorum*	2007/2009	4.75	± 4.92	0.00		0.00	
Anthozoa	*Gorgonaria* sp.	2007/2009	0.50		0.00		0.00	
Anthozoa	*?Leiopathes* sp.	2007	0.00		0.00		0.25	
Anthozoa	*Paraphelliactis michaelsarsi*	2007	0.00		0.33		0.00	
Anthozoa	*Flabellum angulare*	2007/2009	31.50		0.33		0.00	
Anthozoa	*Heteropolypus* cf. *insolutus*	2007/2009	73.25	± 44.62	0.00		0.00	
Cephalopoda	*Grimpoteuthis discoveryi*	2007/2009	0.25		0.33		2.25	± 0.96
Cephalopoda	*Histioteuthis bonnellii*	2007/2009	0.25		1.67	± 2.12	0.25	
Cephalopoda	*Gonatus steenstrupi*	2009	1.25	± 0.58	0.00		0.75	± 0.71
Cephalopoda	Octopoda sp.	2007	0.00		0.33		0.00	
Cephalopoda	Teuthida sp.	2007	0.00		0.67		0.00	
Cephalopoda	Cephalopoda sp.	2007	0.00		0.33		0.00	
Scaphopoda	Scaphopoda sp.	2007/2009	0.75	± 0.71	1.00	± 0.71	2.25	
Bivalvia	Mollusca (Bivalvia) sp. A	2007/2009	0.75	± 0.71	0.00		4.00	
Bivalvia	Mollusca (Bivalvia) sp. B	2007	0.00		0.33		0.00	
Bivalvia	Bivalvia sp.	2009	0.00		0.00		0.50	
Gastropoda	Gastropoda sp. 2	2007/2009	3.00	± 2.65	0.00		0.75	
Gastropoda	Gastropoda sp. 1	2007/2009	2.00	± 2.08	0.67		0.00	
Gastropoda	Gastropoda sp. 3	2009	3.00	± 7.07	0.00		0.00	
Gastropoda	Gastropoda sp.	2009	0.25		0.00		0.00	
Gastropoa	Vestigastropoda sp.	2009	3.00	± 3.00	0.00		0.00	
Cephalocarida	Brachypoda sp.	2009	0.75		0.00		0.25	

Class	**Taxonomic Unit**	**Year**	**SE**	**SD**	**NE**	**SD**	**NW**	**SD**
Sipunculidea	*Sipuncula norvegicus*	2007/2009	30.25	± 36.94	38.33	± 19.55	5.00	± 1.41
Sipunculidea	Sipuncula sp. A	2007/2009	2.25	± 2.12	6.67	± 4.24	3.75	± 4.36
Sipunculidea	Sipuncula sp. B	2009	0.00		0.00		9.50	± 18.38
Pycnogonida	*Colossendeis colossea*	2007/2009	9.75	± 14.27	± 1.67	0.71	106.00	± 50.64

A.2 Mean Sizes

TABLE A.2: Mean sizes and weights of individual species collected with OTSB trawl in 2007 and 2009, with their respective standard deviation. The sizes are shown in mm and the weight in g.)

Taxonomic Group	**Species**	**SE Site**		**NE Site**		**NW Site**	
		Size (mm)	**Weight (g)**	**Size (mm)**	**Weight (g)**	**Size (mm)**	**Weight (g)**
Holothurian	*Molpadia musculus*	33 ± 13	5 ± 4	48 ± 7	< 1 ± 0	22 ± n.a.	1 ± n.a.
	Molpadia sp. nov.	25 ± 7	2 ± 2	41 ± 5	< 1 ± 0	25 ± 7	4 ± 4
	Gephyrothuria alcocki	38 ± 2	2 ± 2	36 ± 10	11 ± 8	44 ± 13	11 ± 11
	Staurocucumis abyssorum	56 ± 18	10 ± 7				
	Paelopatides grisea	126 ± 19	71 ± 32	141 ± 1	2 ± 0	96 ± n.a.	1 ± n.a.
	Amperima furcata	16 ± 4	1 ± 0				
	Ellipinion delagei	29 ± 8	2 ± 2				
	Synallactes crucifera	33 ± 7	2 ± 1				
	Peniagone sp.			32 ± 6	12 ± 9		
	Peniagone sp. nov. ”*coccinea*”	37 ± 9	3 ± 1				
	Peniagone islandica	36 ± 11	2 ± 2				
	Peniagone longipapillata			29 ± n.a.	11 ± n.a.		
	Psychropotes depressa	71 ± 28	13 ± 14	48 ± 13	< 1 ± 0	115 ± 33	1 ± 0
	Psychropotes sp. nov.	65 ± 17	11 ± 8				
	Benthodytes gosarsi	106 ± 29	39 ± 30	134 ± n.a.	95 ± n.a.	145 ± 24	90 ± 35
	Benthodytes lingua	225 ± 36	115 ± 21				
	Benthodystes sanguinolenta	158 ± n.a.	21 ± n.a.				
	Deima validum	53 ± 14	9 ± 9				
	Benthothuria funebris	90 ± 72	662 ± 579	155 ± 39	20 ± 12	210 ± n.a.	1 ± n.a.
	Pseudostichopus sp. 2					55 ± 15	1 ± 1
	Pseudostichopus peripatus	57 ± 15	5 ± 4	54 ± 16	3 ± 7	62 ± 21	2 ± 1
	Mesothuria maroccana	63 ± 5	6 ± 5				

table continues ...

Taxonomic Group	Species	SE Site Size (mm)	SE Site Weight (g)	NE Site Size (mm)	NE Site Weight (g)	NW Site Size (mm)	NW Site Weight (g)
Holothurian	*Mesothuria cathedralis*					16 ± 30	5 ± 6
	Mesothuria bifurcata	51 ± 19	3 ± 1			77 ± 16	2 ± 2
	Penillipidia midatlantica	16.7 ± n.a.	0.3 ± n.a.				
	fam. Astropectinidae	5 ± 1	1 ± 0				
	Styracaster armatus	8 ± 1	1 ± 0				
	Styracaster sp.	9 ± n.a.	1 ± n.a.				
	Myriotrichus clarki	27 ± 2	1 ± 0	25 ± 18	1 ± 0	36 ± 16	2 ± 1
Asteroids	*Hymenaster* cf. *coccinatus*	9 ± 2	1 ± 3	13 ± 2	3 ± 2	9 ± 1	1 ± 0
	Hymenaster cf. *gennaeus*			2 ± 1	< 1 ± 0		
	Freyella elegans	10 ± 2	4 ± 3	7 ± 1	< 1 ± 0	13 ± 6	10 ± 13
	Caulaster pedunculatus	3 ± 1	0 ± 0	3 ± 0	< 1 ±0	4 ± 1	< 1 ± 0
	Porcellanaster ceruleus	6 ± 2	1 ± 0	6 ± 1	1 ± 0	8 ± 2	2 ± 1
	Hymenaster pellucidus			12 ± 4	3 ± 2		
	Hymenaster ?latebrosus/gennaeus			10 ± n.a.	1.6 ± n.a.		
	Bathybiaster vexillifer			14 ± 6	54 ± 41	13 ± 6	37 ± 40
	Gaussaster antarcticus			3 ± n.a.	1 ± n.a.		
	?*Cheiraster planus*			9 ± n.a.	6 ± n.a.		
	juv. Goniasteridae sp.	3 ± n.a.	< 1 ± 0				
	Pectinaster ?Cheiraster	3 ± n.a.	< 1 ± 0				
	Pseudarchaster gracilis gracilis	10 ± 5	3 ± 4				
	Plutonaster agassizi	17 ± n.a.	11 ± n.a.				
	Plutonaster bifrons	19 ± 10	15 ± 14				
	Plutonaster cf. *bifrons*	9 ± 0	2 ± 0				
	Pectinaster filholi	11 ± 1	7 ± 2				
	Dytaster grandis grandis	14 ± 4	14 ± 11				
	Dytaster sp.	13 ± 5	9 ± 6				

table continues ...

Taxonomic Group	Species	SE Site		NE Site		NW Site	
		Size (mm)	Weight (g)	Size (mm)	Weight (g)	Size (mm)	Weight (g)
Asteroids	Goniasteridae indet.	17 ± n.a.	4 ± n.a.				
	Astropectinidae indet.	5 ± 0	< 1 ± 0				
	Hyphalaster inermis	10 ± 3	3 ± 3			13 ± 5	11 ± 10
	Hymenaster membranaceus	27 ± 10	12 ± 10				
	Hymenaster regalis	109 ± n.a.	718 ± n.a.				
	Hydrasteria sexradiata	3 ± 1	1 ± 9			4 ± 0	1 ± 0
	Hymenaster cf. *regalis*					8 ± n.a.	1 ± n.a.
Echinoids	*Hemiaster expergitus*			35 ± 2	5 ± 3	34 ± 5	4 ± 3
	Echinosigra phiale			52 ± 5	1 ± 0	56 ± 7	1 ± 0
	Aeropsis rostrata	25 ± 4	1 ± 0	33 ± n.a.	1 ± n.a.	44 ± 9	3 ± 1
	Urechinus naresianus			33 ± 5	2 ± 1	44 ± 4	3 ± 2
	Tromikosoma uranus			11 ± n.a.	1 ± n.a.	18 ± n.a.	1 ± n.a.
	Tromikosoma aff. *uranus*	24 ± 8	5 ± 3				
	Tromikosoma cf. *uranus*	16 ± 3	2 ± 1				
	Tromikosoma koehleri					85 ± 10	99 ± 26
	Tromikosoma aff. *koehleri*	79 ± n.a.	80 ± n.a.	62 ± 8	46 ± 16		
	Salenia profundi	12 ± 2	1 ± 0				
	Echinus alexandri					20 ± 0	17 ± 2
	Pourtalesiidae sp. 2					44 ± 8	2 ± 1
Ophiuroids	*Ophiura irrorata*	10 ± 4	< 1 ± 0	19 ± 3	2 ± 1	18 ± 4	1 ± 1
	Ophiura nitida			10 ± 1	< 1 ± 0		
	Ophiacantha fraterna			7 ± 1	< 1 ± 0	8 ± 1	< 1 ± 0
	Ophiura ljungmani	6 ± 1	< 1 ± 0	7 ± 1	< 1 ± 0	11 ± 27	< 1 ± 0
	Ophiocten hastatum	10 ± 1	< 1 ± 0	10 ± 3	< 1 ± 0	10 ± 2	< 1 ± 0
	Ophiocamax patersoni	14 ± 5	1 ± 1				
	Ophiomusium lymani	30 ± n.a.	6 ± n.a.				
	Ophiura saurura	11 ± 1	< 1 ± 0			13 ± 2	< 1 ± 0

table continues ...

Taxonomic Group	Species	SE Site		NE Site		NW Site	
		Size (mm)	Weight (g)	Size (mm)	Weight (g)	Size (mm)	Weight (g)
Ophiuroids	*Astrodia tenuispina*	8 ± 2	< 1 ± 0				
	Amphilepis ingolfiana			9 ± 1	< 1 ± 0		
	Ophiacantha aculeata			6 ± 1	< 1 ± 0	10 ± 3	< 1 ± 0
	Ophiolimna bairdi			5 ± 1	< 1 ± 0		
Crustaceans	Galatheidae indet. sp.			32 ± 0	13 ± 2		
	Polycheles sp.	28 ± 7	4 ± 3	22 ± 3	3 ± 1	19 ± 1	1 ± 0
	Pentacheles validus	25 ± 5	2 ± 0				
	Polycheles nanus					21 ± 3	2 ± 1
	Glyphocrangon sp.	22 ± 4	5 ± 3				
	Glyphocrangon sculpa	21 ± 5	6 ± 3				
	Munidopsis rostrata	24 ± 8	9 ± 10				
	Reptantia sp.					20 ± 8	4 ± 3
	Cirripedia indet.	27 ± 10	3 ± 4			42 ± 15	12 ± 9
Sipunculids	*Sipunculus norvegicus*	82 ± 14	8 ± 4	107 ± 82	13 ± 5	87 ± 29	10 ± 7
	Sipunculus sp. A	51 ± 27	2 ± 2	43 ± 18	1 ± 2	64 ± 44	2 ± 2
	Sipunculus sp. B					13 ± 2	< 1 ± 0

Appendix B

Species List - Video analysis

Table B.1: Total Density (number of individuals 8,000 m^2) of distinguished taxonomic units from the MAR.

Taxonomic Group	**Taxonomic Unit**	**NW**	**NE**	**SW**	**SE**
Asteroidea	Asteroidea (Class) indet.	3	4	40	24
Asteroidea	Asteroidea sp. 1	2	1	3	0
Asteroidea	Asteroidea sp. 7	6	0	3	1
Asteroidea	Asteroidea sp. 8	0	0	1	0
Asteroidea	Brisingida (Family) indet.	4	10	0	2
Asteroidea	*Freyella elegans*	50	86	2	0
Asteroidea	*Freyella* sp.	2	8	3	2
Asteroidea	Pterasteridae (Family) indet.	0	3	0	2
Asteroidea	*Hymenaster* sp. A	1	49	2	5
Asteroidea	*Hymenaster* sp. C	2	16	3	45
Asteroidea	*Hymenaster* sp. E	0	4	0	0
Asteroidea	*Bathybiaster vexillifer*	2	0	0	0
Asteroidea	*Plutonaster bifrons*	0	1	0	0
Asteroidea	*Porcellanaster ceruleus*	0	1	0	3
Asteroidea	*Hydraasterias sexradiata*	28	5	53	66
Asteroidea	Benthopectinidae sp. A	0	0	1	0
Holothuroidea	Holothurian (Class) indet.	23	48	59	21
Holothuroidea	Elasipodida (Order) indet.	1	58	66	20
Holothuroidea	Elpidiidae (Family) indet.	34	28	162	33
Holothuroidea	*Paelopatides grisea*	10	0	0	0
Holothuroidea	*Benthodytes gosarsi*	13	10	16	19

table continues ...

Taxonomic Group	**Taxonomic Unit**	**NW**	**NE**	**SW**	**SE**
Holothuroidea	*Amperima furcata*	2	0	118	14
Holothuroidea	*Benthodytes lingua*	0	1	9	1
Holothuroidea	*Psychropotes* sp. nov.	0	0	0	1
Holothuroidea	*Psychropotes depressa*	2	8	1	1
Holothuroidea	*Ellipinion* (Genus) indet.	1	0	23	0
Holothuroidea	*Ellipinion alani*	0	0	26	0
Holothuroidea	*Peniagone* (Genus) indet.	0	120	163	117
Holothuroidea	*Peniagone azorica/islandica*	1	36	15	11
Holothuroidea	*Peniagone coccinea*	0	18	33	13
Holothuroidea	*Kolga nana*	1	22,046	0	0
Holothuroidea	Deimatidae (Family) indet.	0	0	1	0
Holothuroidea	*Laetmogone billetti*	0	2	0	0
Holothuroidea	*Deima validum*	0	0	1	0
Holothuroidea	Aspidochirotida (Order) indet.	0	1	0	0
Holothuroidea	Synallactidae (Family) indet.	1	1	1	0
Holothuroidea	*Synallactes* sp. A	0	1	4	0
Holothuroidea	*Synallactes* sp. B	2	0	0	0
Holothuroidea	*Pseudostichopus* sp. A	65	3	5	1
Holothuroidea	*Pseudostichopus* sp. B	54	5	6	22
Holothuroidea	*Pseudostichopus* sp. C	14	9	1	3
Holothuroidea	*Mesothuria* (Genus) indet.	48	39	1	6
Holothuroidea	*Benthothuria funebris*	1	1	0	5
Holothuroidea	*Gephyrothuria* sp.	1	0	0	0
Holothuroidea	*Synallactes crucifera*	0	0	3	1
Holothuroidea	*Staurocucumis abyssorum*	1	4	4	28
Holothuroidea	Myriotrochus (Genus) sp.	1	0	0	0
Echinoidea	Echinoid (Class) indet.	0	1	0	0
Echinoidea	Echinothuriidae (Family) indet.	17	1	0	0
Echinoidea	*Tromokosoma* (Genus) indet.	0	0	1	3
Echinoidea	*Tromikosoma koehleri*	7	2	1	4
Echinoidea	Urechinidae/Hemiasteridae complex	996	689	2	0
Echinoidea	*Echinus* (Genus) indet. A	35	1	0	0
Echinoidea	Pourtalesia (Genus) indet.	0	476	0	3,360
Echinoidea	*Urechinus naresianus*	1,199	114	0	0
Ophiuroidea	Ophiuroidea (Class) indet.	708	451	19	33
Ophiuroidea	*Asteronix* (Genus) indet.	0	1	0	0
Ophiuroidea	Ophiuroid sp. C	22	0	0	0

table continues ...

Taxonomic Group	**Taxonomic Unit**	**NW**	**NE**	**SW**	**SE**
Ophiuroidea	Ophiuroid sp. E	387	3	0	0
Ophiuroidea	Ophiuroid sp. F	299	1	6	2
Crinoidea	*Anachalypsicrinus nefertini*	0	0	5	1
Crinoidea	*Bourgueticrinida* sp. A	0	1	1	0
Arthropoda	Arthropod (Phylum) indet.	0	1	2	0
Arthropoda	Amphipoda (Order) indet.	5	0	5	0
Arthropoda	Brachyura (Infraorder) indet.	0	0	7	0
Arthropoda	Lithodidae (Family) indet.	2	1	0	0
Arthropoda	*Munidopsis rostrata*	0	8	22	11
Arthropoda	*Munidopsis crassa*	3	5	1	2
Arthropoda	*Parapagurus pilosimanus*	0	0	2	0
Arthropoda	*Glyphocrangon sculpta*	1	6	12	31
Arthropoda	*Polycheles nanus*	0	0	1	1
Arthropoda	*Plesiopenaeus* sp.	20	3	16	10
Arthropoda	*Neoscalpellum debile*	1	3	3	0
Pycnogonida	Pycnogonida (Class) indet.	9	2	0	3
Pycnogonida	*Colossendeis colossea*	16	0	0	0
Mollusca	Octopoda (Order) indet.	0	1	0	0
Mollusca	*Grimpoteuthis discoveryi*	0	1	0	0
Mollusca	Scaphopod (Class) indet.	7	3	83	22
Annelida	Amphinomida (Order) indet.	2	0	3	6
Annelida	Maldanidae (Family) indet.	132	45	24	15
Annelida	Polynoidae (Family) indet. B	1	0	1	0
Annelida	Polynoidae (Family) indet. C	0	0	1	0
Nemertea	Nemertea (Phylum) indet.	352	6	4	6
Enteropneusta	Enteropneusta sp. A	32	48	6	16
Enteropneusta	Enteropneusta sp. B	1	12	105	195
Enteropneusta	Enteropneusta sp. C	0	0	9	10
Foraminifera	Xenophyophore (Class) indet.	0	8	0	0
Foraminifera	*Syringammina corbicuna*	6	0	24	0
Foraminifera	*Syringammina fragillissima*	586	7	170	62
Foraminifera	*Discospirina tenuissima*	2,353	1,055	3,565	2,081
Bryozoa	Bryozoa (Phylum) indet.	2	0	3	0
Cnidaria	Cnidaria (Phylum) indet.	7	31	25	46
Cnidaria	Hydroidolina (Subclass) indet.	302	64	258	175
Cnidaria	Hydroidolina sp. A	74	1	0	1
Cnidaria	Hydroidolina sp. B	7	0	0	1

table continues ...

Taxonomic Group	**Taxonomic Unit**	**NW**	**NE**	**SW**	**SE**
Cnidaria	Hydroidolina sp. C	15	2	26	15
Cnidaria	Anthozoa (Class) indet.	3	1	29	0
Cnidaria	Hexacorallia (Subclass) indet.	1	0	0	1
Cnidaria	Cerianthida (Family) indet.	2	1	1	2
Cnidaria	Ceriantharia sp. A	0	34	0	0
Cnidaria	Ceriantharia sp. B	6	1	0	0
Cnidaria	Ceriantharia sp. E	0	4	3	2
Cnidaria	Ceriantharia sp. F	3	0	0	0
Cnidaria	Ceriantharia sp. G	1	0	0	0
Cnidaria	Actiniaria (Order) indet.	1	4	6	0
Cnidaria	Actiniaria sp. C	1	0	4	2
Cnidaria	Actiniaria sp. E	0	1	1	0
Cnidaria	Actiniaria sp. H	3	0	1	0
Cnidaria	Actiniaria sp. I	1	0	0	0
Cnidaria	Actiniaria sp. J	0	14	11	5
Cnidaria	Actiniaria sp. K	1	0	0	0
Cnidaria	Actiniaria sp. L	1	0	6	0
Cnidaria	*Actinernus michaelsarsi*	1	0	2	0
Cnidaria	Scleractinia (Order) indet.	0	2	21	0
Cnidaria	*Flabellum angulare*	0	26	531	176
Cnidaria	Fungiacyathus fragilis	5	1	17	30
Cnidaria	Pennatulacea (Order) indet.	2	4	1	9
Cnidaria	Pennatulacea sp. A	1	0	0	1
Cnidaria	Alcyonacea (Order) indet.	5	11	10	11
Cnidaria	Alcyonacea sp. C	1	0	0	0
Cnidaria	Alcyonacea sp. I	0	0	1	0
Cnidaria	*Anthomastus* (Genus) indet.	1	0	0	0
Cnidaria	*Anthomastus agaricus*	0	52	4	55
Cnidaria	Antipatharia (Order) indet.	2	0	1	1
Porifera	Porifera (Phylum) indet.	6,015	695	1,210	634
Porifera	Demospongiae (Class) indet.	2	0	1	0
Porifera	Demospongiae sp. E	4	0	0	0
Porifera	Demospongiae sp. G	1	0	0	0
Porifera	Demospongiae sp. L	0	0	1	0
Porifera	Demospongiae sp. M	1	0	3	0
Porifera	Demospongiae sp. P	0	0	12	0

table continues ...

Taxonomic Group	**Taxonomic Unit**	**NW**	**NE**	**SW**	**SE**
Porifera	Hexactinellida (Class) indet.	562	468	165	122
Porifera	Hexactinellida sp. C	160	0	0	0
Porifera	Hexactinellida sp. D	2	0	3	0
Porifera	Hexactinellida sp. I	0	0	1	0
Porifera	Hexactinellida sp. M	1	0	0	0
Porifera	Hexactinellida sp. S	1	0	1	0
Porifera	Hexactinellida sp. T	1	0	0	0
Porifera	Hexactinellida sp. Z	1	0	0	0
Porifera	Hexactinellida sp. AB	0	0	4	0
Porifera	Hexactinellida sp. AH	0	0	5	0
Porifera	Hexactinellida sp. AI	8	1	0	1
Porifera	Hexactinellida sp. AM	3	0	1	0
Porifera	Hexactinellida sp. AO	120	5	0	0
Porifera	Hexactinellida sp. AT	0	0	4	6
Porifera	Hexactinellida sp. AV	0	0	3	0
Porifera	Hexactinellida sp. AX	1	0	1	0
Porifera	Hexactinellida sp. BE	1	0	1	0
Porifera	Hexactinellida sp. BF	0	0	1	0
Porifera	Hexactinellida sp. BJ	144	188	13	35
Porifera	Hexactinellida sp. BK	14	27	48	15
Porifera	Hexactinellida sp. BL	2	0	0	0
Porifera	*Regadrella phoenix*	0	0	2	1

Appendix C

ROV CTD Profiles

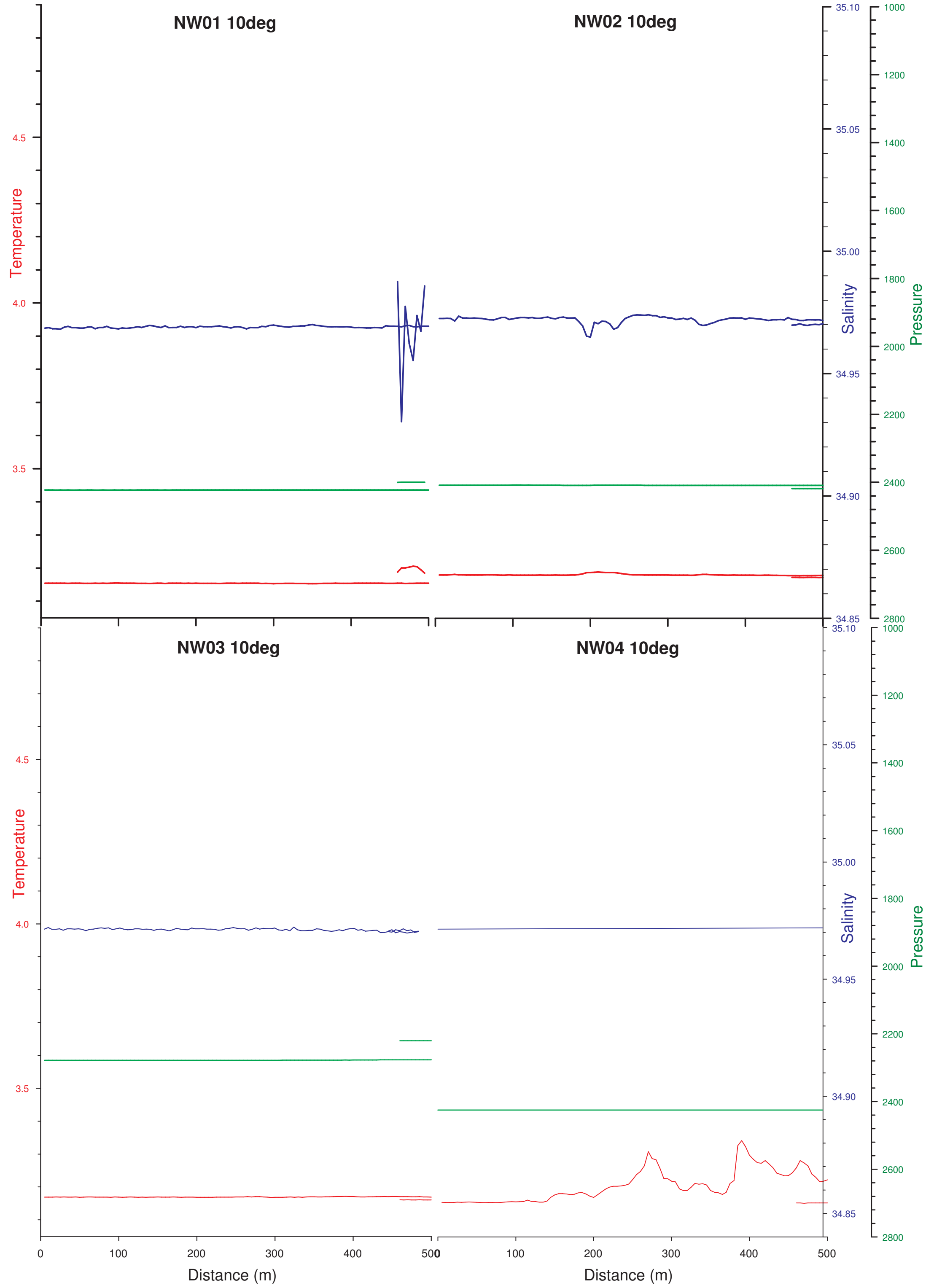


FIGURE C.1: CTD Profiles for individual transects run at the NW site in 10 degree slope habitats. Each transect represents 500 m along the x axis. Red lines show temperature profiles and are read off the left y axis. Blue lines show the salinity profile that can be read off the inner right y axis. Green show the pressure profile that can be read off the outer, right y axis.

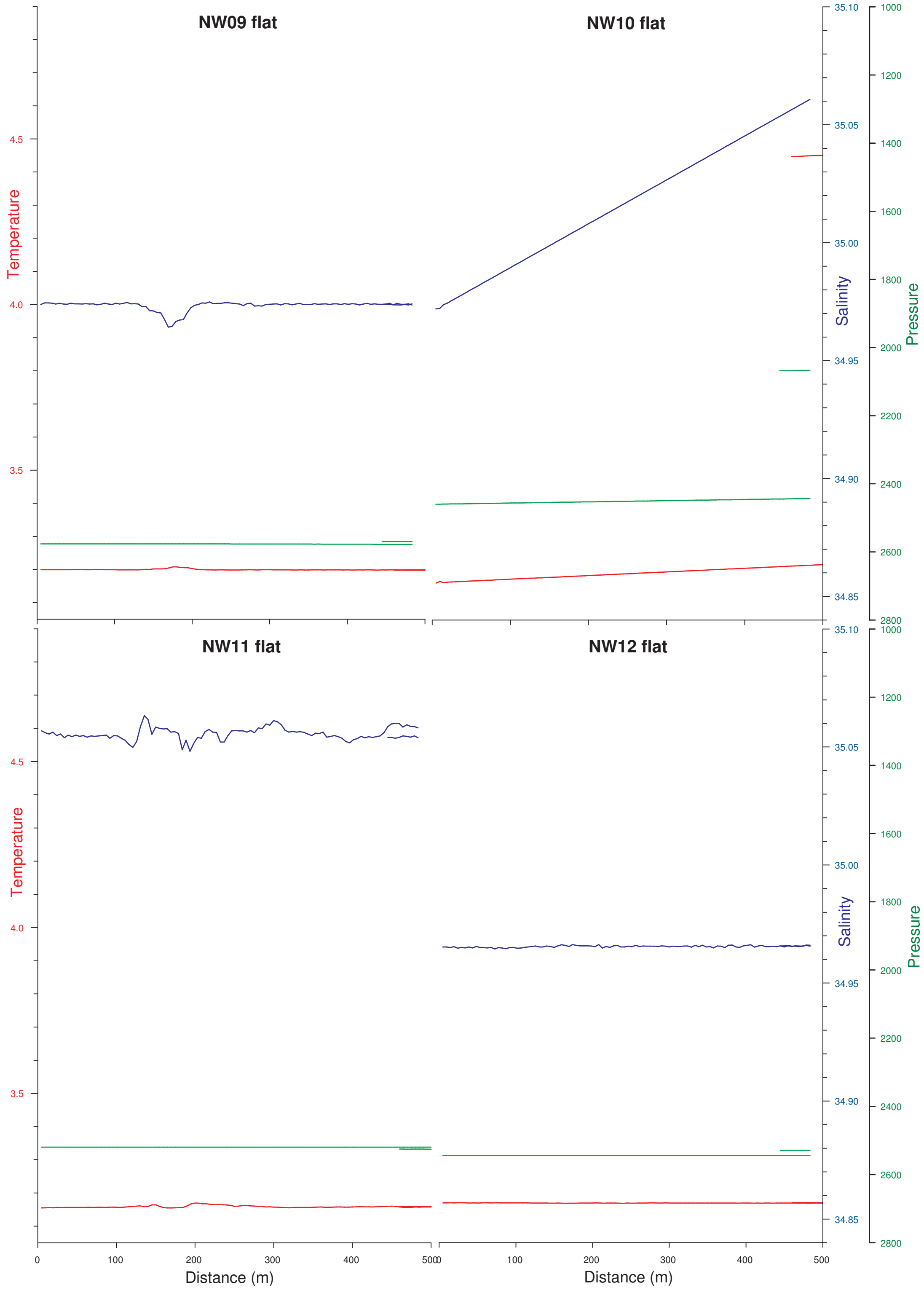


Figure C.2: CTD Profiles for individual transects run at the NW site in flat habitats. Each transect represents 500 m along the x axis. Red lines show temperature profiles and are read off the left y axis. Blue lines show the salinity profile that can be read off the inner right y axis. Green show the pressure profile that can be read off the outer, right y axis.

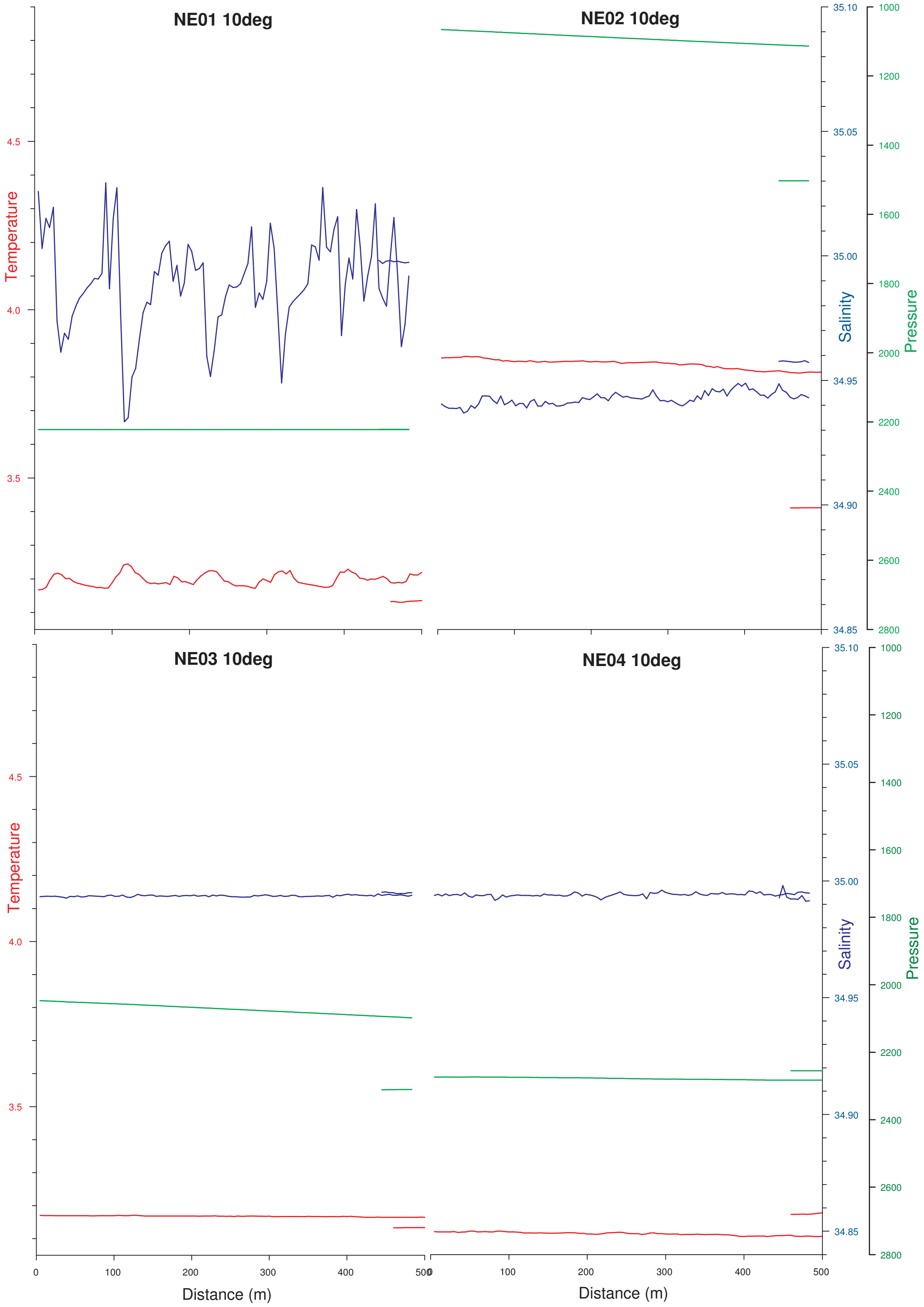


FIGURE C.3: CTD Profiles for individual transects run at the NE site in 10 degree slope habitats. Each transect represents 500 m along the x axis. Red lines show temperature profiles and are read off the left y axis. Blue lines show the salinity profile that can be read off the inner right y axis. Green show the pressure profile that can be read off the outer, right y axis.

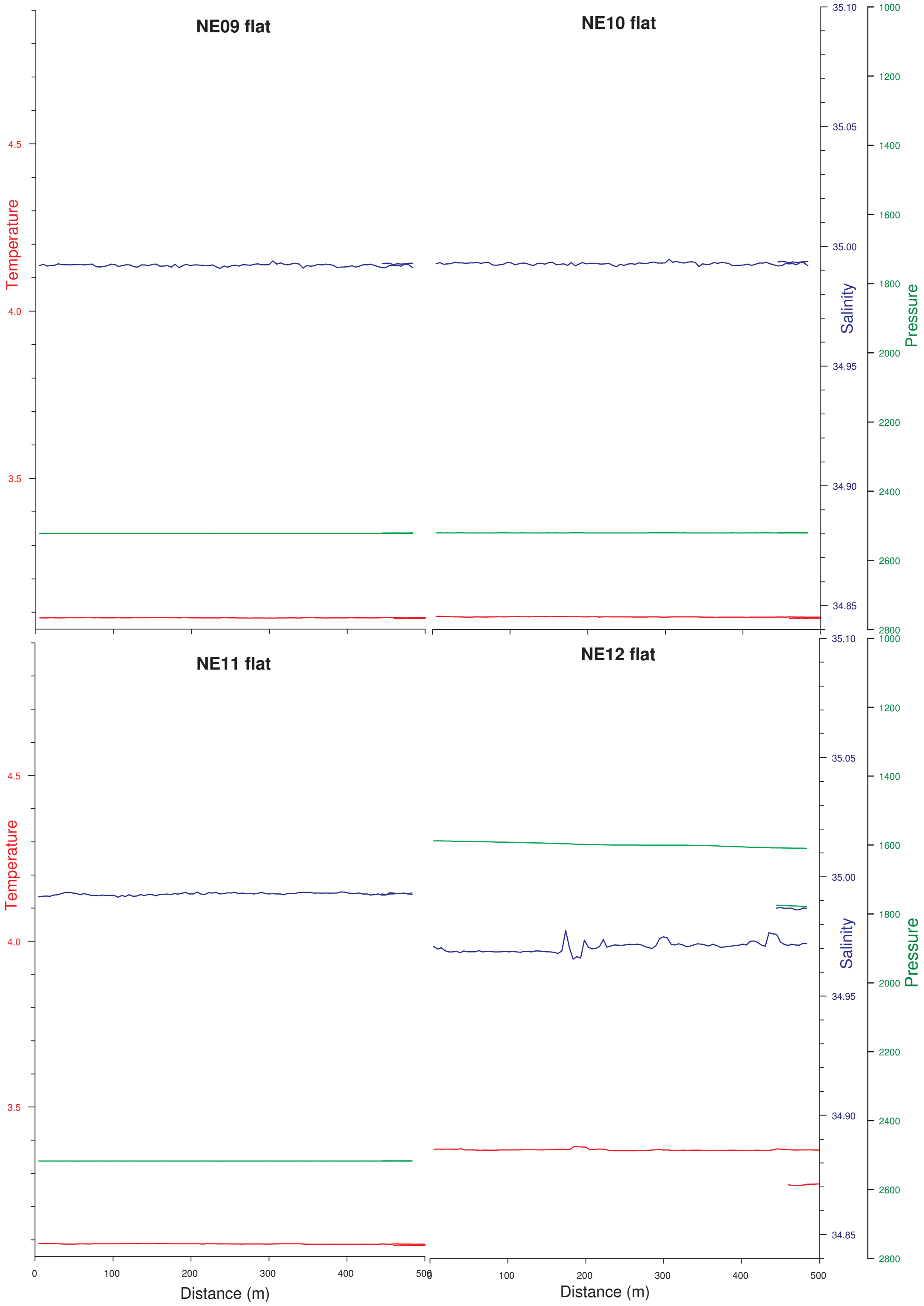


FIGURE C.4: CTD Profiles for individual transects run at the NE site in flat habitats. Each transect represents 500 m along the x axis. Red lines show temperature profiles and are read off the left y axis. Blue lines show the salinity profile that can be read off the inner right y axis. Green show the pressure profile that can be read off the outer, right y axis.

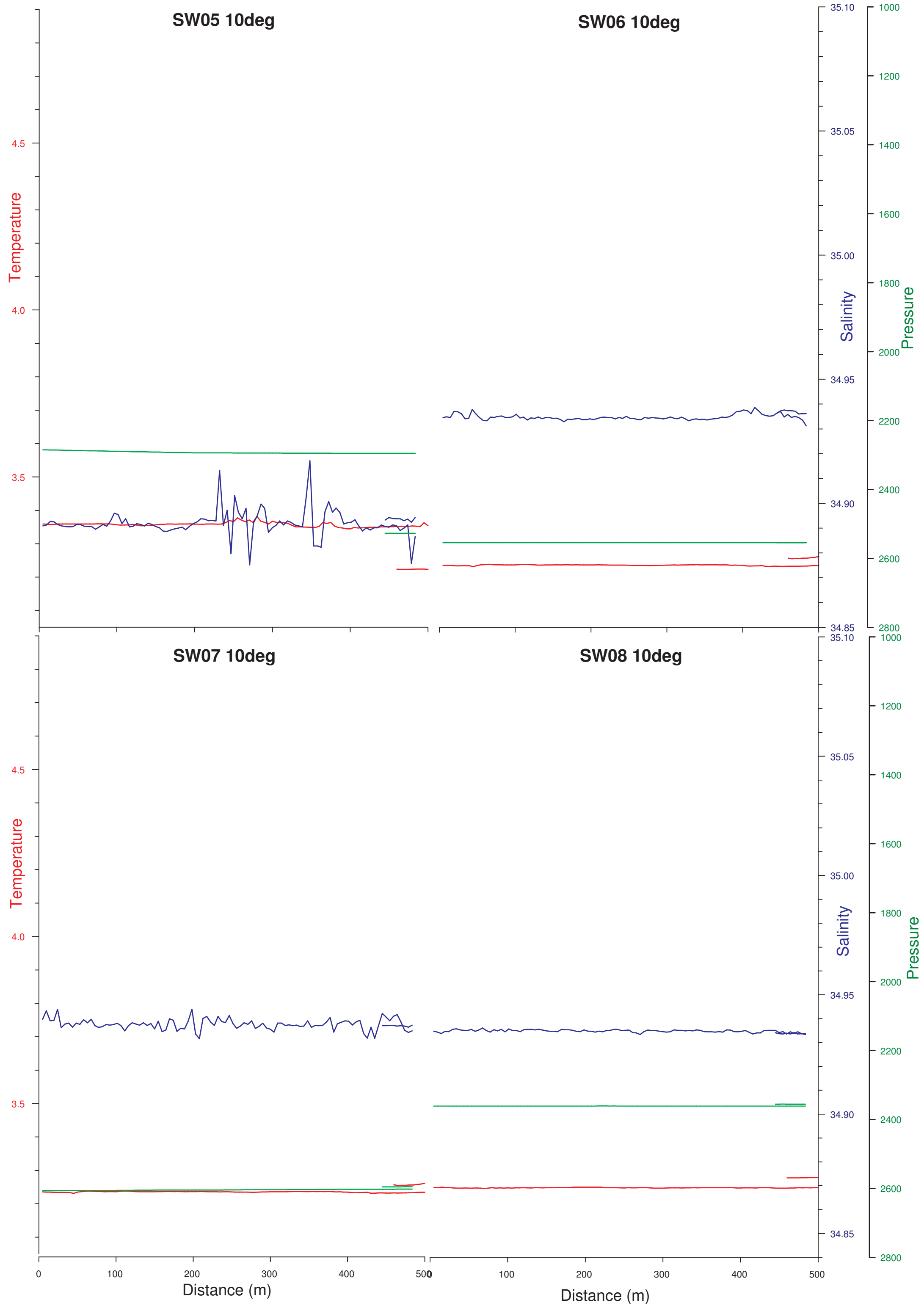


FIGURE C.5: CTD Profiles for individual transects run at the SW site in 10 degree slope habitats. Each transect represents 500 m along the x axis. Red lines show temperature profiles and are read off the left y axis. Blue lines show the salinity profile that can be read off the inner right y axis. Green show the pressure profile that can be read off the outer, right y axis.

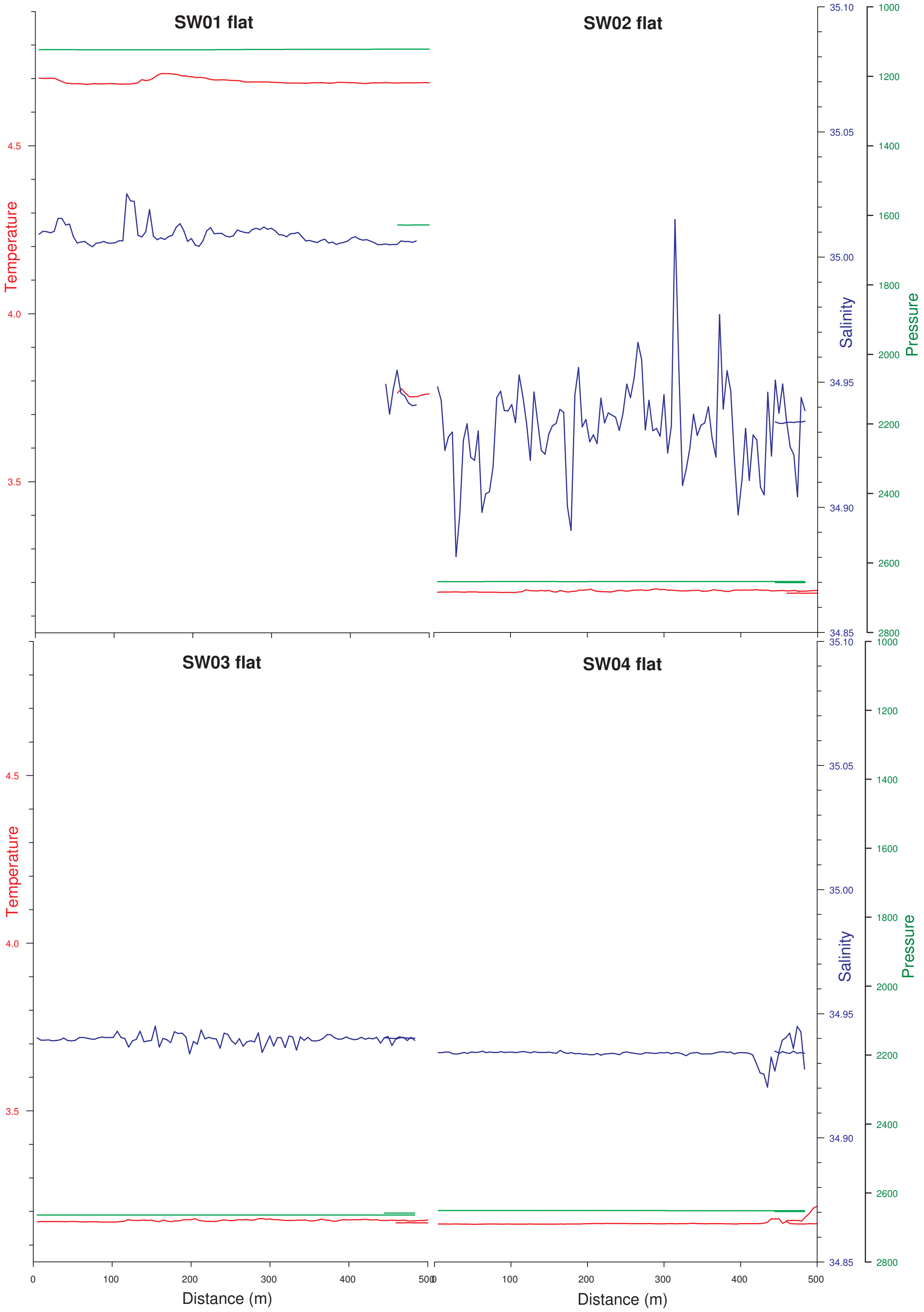


Figure C.6: CTD Profiles for individual transects run at the SW site in flat habitats. Each transect represents 500 m along the x axis. Red lines show temperature profiles and are read off the left y axis. Blue lines show the salinity profile that can be read off the inner right y axis. Green show the pressure profile that can be read off the outer, right y axis.

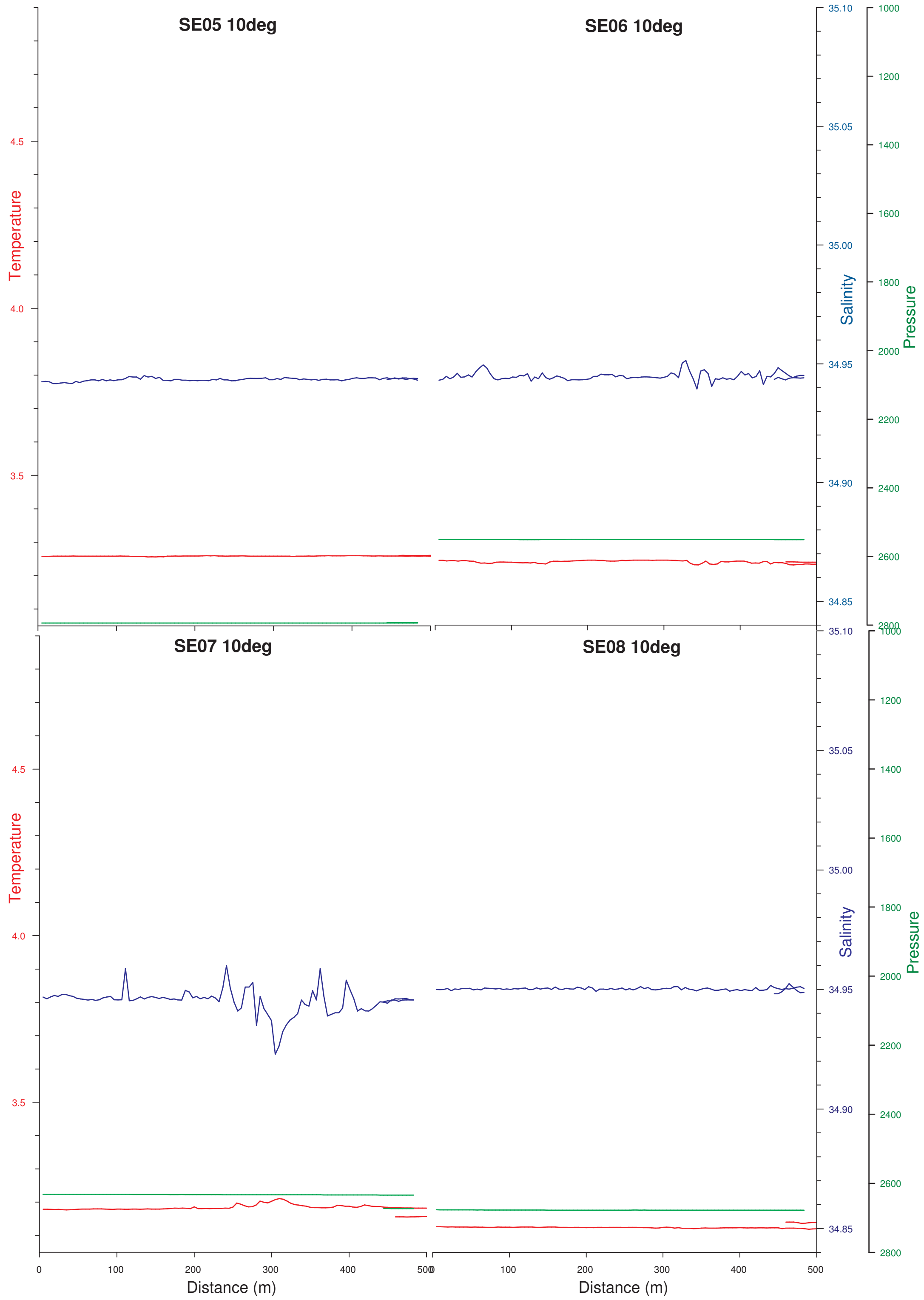


Figure C.7: CTD Profiles for individual transects run at the SE site in 10 degree slope habitats. Each transect represents 500 m along the x axis. Red lines show temperature profiles and are read off the left y axis. Blue lines show the salinity profile that can be read off the inner right y axis. Green show the pressure profile that can be read off the outer, right y axis.

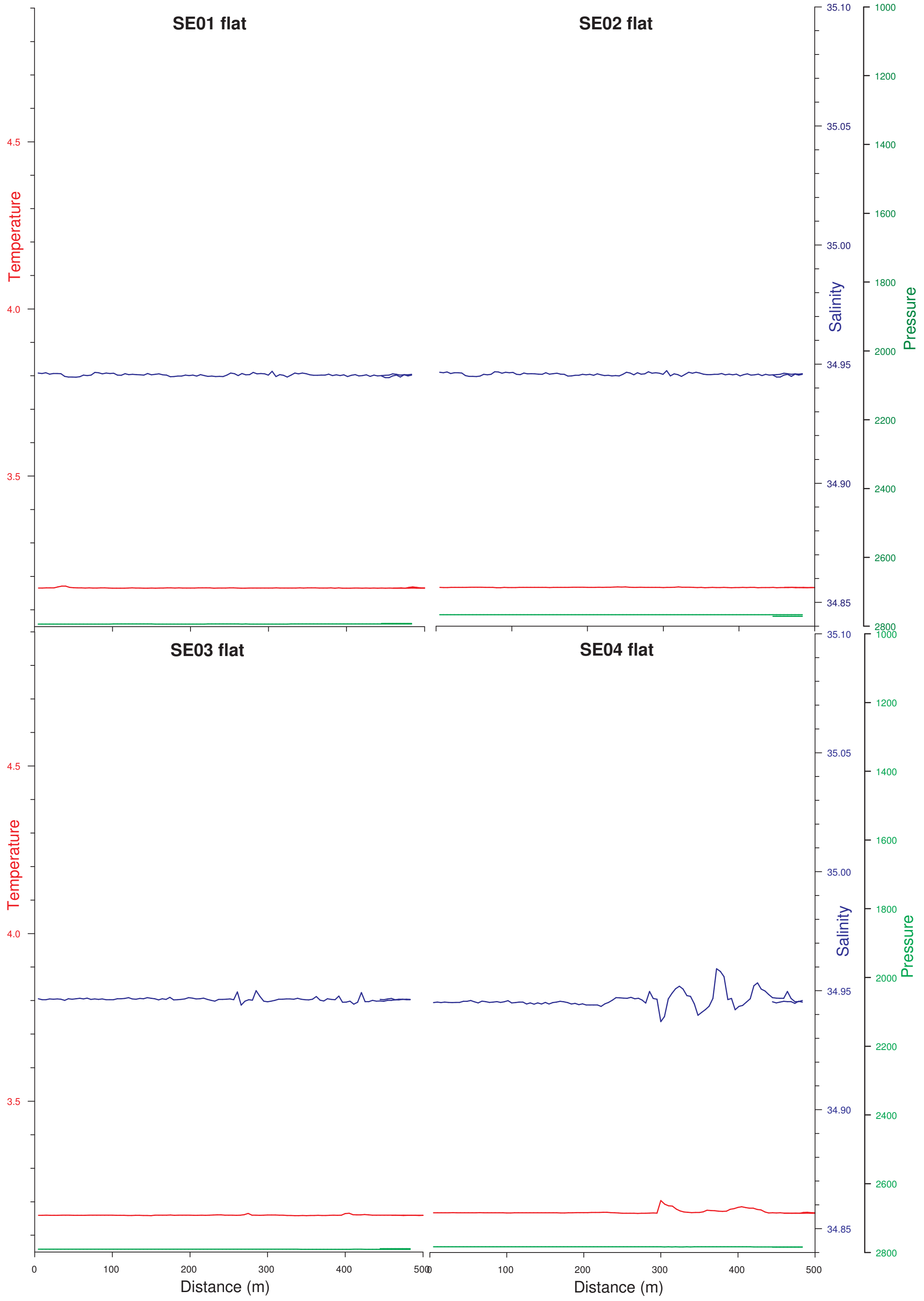


Figure C.8: CTD Profiles for individual transects run at the SE site in flat habitats. Each transect represents 500 m along the x axis. Red lines show temperature profiles and are read off the left y axis. Blue lines show the salinity profile that can be read off the inner right y axis. Green show the pressure profile that can be read off the outer, right y axis.

Appendix D

Specimens used for Phylogenetic Analysis

TABLE D.1: All species used for the molecular study, together with their taxonomic status. Individual species codes, together with the year and area of collection are listed. NCBI accession numbers for individual species are displayed for each gene, where available, X marks unsuccessful amplifications.

Order/ Family	**Species**	**Species Code/Year Collected/Location**	**16S**	**COI**	**18S**	**28S**	**H3**
Dendrochirotida/ Cucumariidae	*Staurocucumis abyssorum* (Théel, 1886)	AA2/2007 ECOMAR SE	Y	Y	Y	Y	Y
Dendrochirotida/ Psolidae	*Ekkentropelma* sp. (Pawson, 1971)	AND3/2002 Antarctica	X	Y	Y	Y	Y
Aspidochirotida/ Synallactidae	*Pseudostichopus* sp. (Théel, 1882)	G27/2009 ECOMAR NW	Y	Y	Y	Y	Y
Aspidochirotida/ Synallactidae	*Pseudostichopus* sp. (Théel, 1882)	G25/2009 ECOMAR NW	Y	Y	Y	Y	Y
Aspidochirotida/ Synallactidae	*Pseudostichopus villosus* (Théel, 1882)	NCBI	DQ777098	AF486436	DQ777086	DQ777088	X
Aspidochirotida/ Synallactidae	*Benthuthuria funebris* (Perrier, 1898)	A54/2009 ECOMAR SE	Y	Y	Y	Y	Y
Aspidochirotida/ Synallactidae	*Benthuthuria funebris* (Perrier, 1898)	A55/2009 ECOMAR SE	Y	Y	Y	Y	Y
Aspidochirotida/ Holothuriidae	*Bohadschia vitiensis* (Semper, 1868)	NCBI	FJ223868	EU848267	AY133477	X	X
Aspidochirotida/ Holothuriidae	*Holothuria edulis* (Lesson, 1830)	NCBI	EU220806	EU220830	AY133471	X	X
Aspidochirotida/ Holothuriidae	*Holothuria forskali* (Delle Chiaje, 1823)	NCBI	GQ214740	GQ214762	AY133470	X	X
Molpadiida/ Gephyrothuriidae	*Gephyrothuria alcocki* (Koehler & Vaney, 1905)	B32/2009 ECOMAR SE	Y	Y	Y	Y	Y
Molpadiida/ Gephyrothuriidae	*Gephyrothuria alcocki* (Koehler & Vaney, 1905)	B62/2009 ECOMAR SE	Y	Y	Y	Y	Y

table continues ...

Order/ Family	**Species**	**Species Code/Year Collected/Location**	**16S**	**COI**	**18S**	**28S**	**H3**
Molpadiida/ Gephyrothuriidae	*Gephyrothuria alcocki* (Koehler & Vaney, 1905)	B63/2009 ECOMAR SE	Y	Y	Y	Y	Y
Molpadiida/ Molpadiidae	*Molpadia musculus* (Risso, 1826)	AG09/2009 ECOMAR SE	Y	Y	Y	Y	Y
Molpadiida/ Molpadiidae	*Molpadia musculus* (Risso, 1826)	AG10/2009 ECOMAR SE	X	X	Y	Y	Y
Molpadiida/ Molpadiidae	*Molpadia* sp. nov. (Rogacheva & Gebruk 2012)	C12/2009 ECOMAR SE	Y	Y	Y	Y	X
Molpadiida/ Molpadiidae	*Molpadia* sp. nov. (Rogacheva & Gebruk 2012)	C09/2009 ECOMAR SE	Y	Y	Y	Y	Y
Molpadiida/ Molpadiidae	*Molpadia borealis* (Sars, 1859)	S1/2006 Kara Sea	Y	Y	Y	Y	Y
Molpadiida/ Molpadiidae	*Molpadia blakei* (Théel, 1882)	AND2/2002 Antarctica	Y	Y	Y	Y	Y
Elasipodida/ Elpidiidae	*Peniagone coccinea* (Rogacheva & Gebruck 2012)	D42/2009 ECOMAR SE	Y	Y	X	X	Y
Elasipodida/ Elpidiidae	*Peniagone coccinea* (Rogacheva & Gebruck 2012)	D40/2009 ECOMAR SE	Y	Y	X	Y	X
Elasipodida/ Elpidiidae	*Peniagone coccinea* (Rogacheva & Gebruck 2012)	B30/2009 ECOMAR SE	Y	Y	X	X	X
Elasipodida/ Elpidiidae	*Peniagone islandica* (Deichmann, 1930)	H33/2009 ECOMAR SE	Y	Y	Y	Y	Y
Elasipodida/ Elpidiidae	*Peniagone islandica* (Deichmann, 1930)	H50/2009 ECOMAR SE	Y	Y	Y	Y	Y
Elasipodida/ Elpidiidae	*Peniagone islandica* (Deichmann, 1930)	H30/2009 ECOMAR SE	Y	X	Y	Y	X
Elasipodida/ Elpidiidae	*Peniagone islandica* (Deichmann, 1930)	B04/2009 ECOMAR SE	Y	X	X	Y	X

table continues ...

Order/ Family	Species	Species Code/Year Collected/Location	16S	COI	18S	28S	H3
Elasipodida/ Elpidiidae	*Peniagone azorica* (von Marenzeller, 1893)	F62/2009 ECOMAR NE	Y	X	Y	X	X
Elasipodida/ Elpidiidae	*Peniagone azorica* (von Marenzeller, 1893)	F63/2009 ECOMAR NE	Y	X	Y	Y	Y
Elasipodida/ Elpidiidae	*Peniagone azorica* (von Marenzeller, 1893)	F65/2009 ECOMAR NE	Y	X	X	Y	Y
Elasipodida/ Elpidiidae	*Amperima furcata* (Hérouard, 1899)	F54/2010 ECOMAR SE	Y	Y	Y	Y	Y
Elasipodida/ Elpidiidae	*Amperima furcata* (Hérouard, 1899)	FG79/2010 ECOMAR SE	Y	Y	Y	Y	Y
Elasipodida/ Elpidiidae	*Amperima furcata* (Hérouard, 1899)	F81/2010 ECOMAR SE	Y	Y	Y	Y	Y
Elasipodida/ Elpidiidae	*Kolga nana*	G43/2010 ECOMAR NE	Y	Y	Y	Y	Y
Elasipodida/ Elpidiidae	*Ellipinion delagei* (Hérouard, 1899)	B01/2010 ECOMAR SE	Y	Y	X	Y	X
Elasipodida	*Ellipinion delagei* Elpidiidae	A73/2010 (Hérouard, 1899)	Y ECOMAR SE	X	Y	Y	Y
Elasipodida/	*Ellipinion delagei* Elpidiidae	H02/2010 (Hérouard, 1899)	Y ECOMAR SW	Y	Y	Y	Y
Elasipodida/ Laetmogonidae	*Laetmogone billetti* (Rogacheva & Gebruck 2012)	G23/2010 ECOMAR NW	Y	Y	Y	Y	Y
Elasipodida Psychropotidae	*Psychropotes depressa* (Théel, 1882)	A58/2009 ECOMAR SE	Y	Y	Y	Y	Y
Elasipodida/ Psychropotidae	*Psychropotes depressa* (Théel, 1882)	D06/2009 ECOMAR SE	Y	Y	Y	Y	Y
Elasipodida/ Psychropotidae	*Psychropotes longicauda* (Théel, 1882)	NCBI	DQ777099	X	Z80956	X	X
Elasipodida/ Psychropotidae	*Benthodytes lingua* (Perrier, 1896)	G69/2010 ECOMAR SW	Y	Y	Y	Y	X

table continues ...

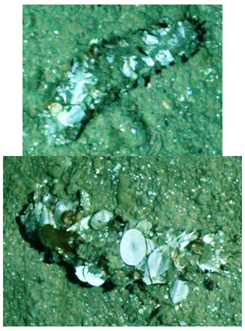
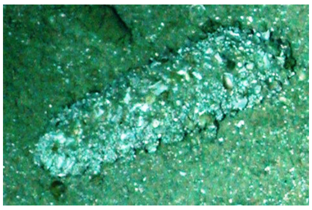
Order/ Family	**Species**	**Species Code/Year Collected/Location**	**16S**	**COI**	**18S**	**28S**	**H3**
Elasipodida/ Psychropotidae	*Benthodytes gosarsi* (Gebruk, 2008)	E08/2009 ECOMAR NW	Y	Y	X	Y	X
Elasipodida/ Psychropotidae	*Benthodytes gosarsi* (Gebruk, 2008)	E09/2009 ECOMAR NW	Y	Y	X	Y	Y
Elasipodida/ Deimatidae	*Deima validum* (Théel, 1879)	AG4/2007 ECOMAR SE	Y	Y	X	Y	Y
Elasipodida/ Deimatidae	*Deima validum* (Théel, 1879)	AG5/2007 ECOMAR SE	Y	Y	Y	X	Y
Elasipodida/ Deimatidae	*Deima validum* (Théel, 1879)	G75/2010 ECOMAR SW	Y	Y	Y	Y	Y
Apodida/ Chiridotidae	*Chiridota laevis* (Fabricius, 1780)	G1/2007 White Sea	Y	Y	Y	Y	Y
Apodida/ Myriotrochidae	*Myriotrochus longissimus* (Belyaev, 1972)	V2 Pacific	X	Y	Y	Y	Y
Apodida/ Myriotrochidae	*Acanthotrochus mirabilis* (Danielssen & Koren, 1879)	A1	Y	X	X	Y	Y
Dactylochirotida/ Ypsilothuriidae	*Ypsilothuria* sp. (Heding, 1942)	AND1/2002 Antarctica	X	Y	Y	Y	Y
Camarodonta/ Strongylocentrotidae	*Strongylocentrotus purpuratus* (Stimpson, 1857)	NCBI	X12631	HM542410	L28056	AF212171	NW001293040
Forcipulatida/ Asteriidae	*Evasterias troscheli* (Stimpson, 1862)	NCBI	DQ297090	GQ902422	DQ060788	DQ273706	DQ676909
Forcipulatida/ Asteriidae	*Pisaster ochraceus* (Brandt, 1835)	NCBI	DQ297110	HM542339	DQ060813	DQ273718	X07503

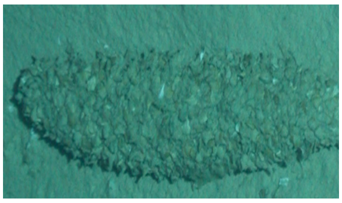
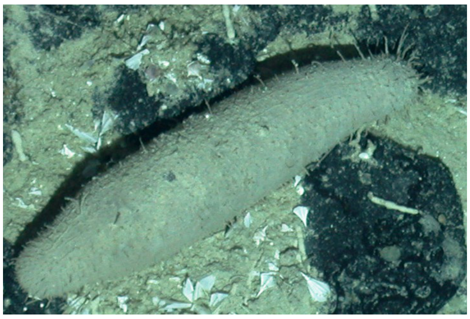
Appendix E

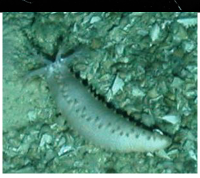
Species Catalogue

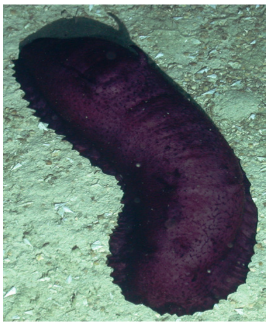
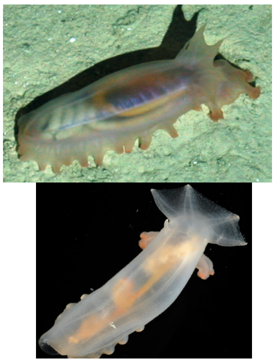
In this section all species from the trawl and video survey are compiled as a reference guide. Images were included where available, and their origin has been referenced. Information on the taxonomic status are given as well as the species names. Preliminary species names changed in some cases, after taxonomic experts were consulted. Because the species lists for the individual chapters refer to preliminary names, those are also given in the species catalog, below the verified species name. Names of the taxonomic experts identifying the species are given for each species. The method by which species were sampled is given in the gear section, together with the ECOMAR site, species were sampled from. These sites only refer to trawl samples and video transects described in this study. In cases were no further specification is given, general observations were made, outside the sampling designs (in ROV collection dives rather than observations from within transects).

It is intended to give as comprehensive a species list as possible. Therefore, species are included that are considered by-catches from trawl and video surveys, which are not considered megafauna i.e. polychaetes caught at trawl by-catches.

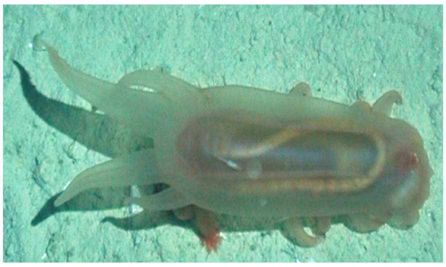
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Paelopatides grisea*	**Gear:** Rov, Trawl **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Hansenothuria* sp. A (Synnallactidae A & B)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NE, SW		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	Synallactidae (Family) sp. D (Synallactidae gen. sp.)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** observation		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	Synallactidae (Family) sp. B (Synallactidae sp. B)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Pseudostichopus peripatus* (Pseudostichopus sp. A)	**Gear:** Rov, Trawl **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Pseudostichopus* sp. B	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		

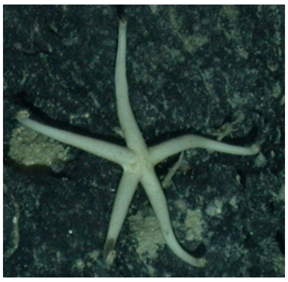
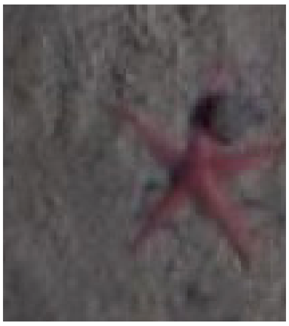
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Pseudostichopus* sp. C	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		 
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Pseudostichopus* sp. D (Pseudostichopus sp. 2)	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** NW		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Mesothuria* (Genus) sp. A (*Mesothuria* spp.)	**Gear:** Rov, Trawl **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Mesothuria marrocana*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Mesothuria cathedralis*	**Gear:** Trawl **Photo by:** *Isis* 2010, David Shale **Identified by:** A. Rogacheva **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Benthothuria funebris*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SE	lower image shows ventral side	 

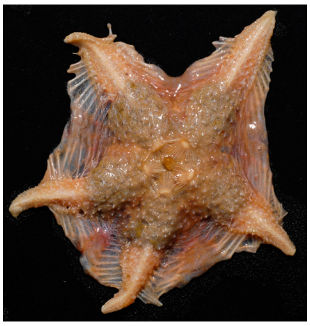
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Gephyrothuria alcocki*	**Gear:** Trawl **Photo by:** David Shale **Identified by:** A. Rogacheva **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Molpadiodemas violaceus*	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** NW		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Aspidochirotida **Family:** Synallactidae	*Bathyplotes natans*	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** NW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Molpadiida **Family:** Molpadiidae	*Molpadia musculus*	**Gear:** Trawl **Photo by:** David Shale **Identified by:** A. Rogacheva **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Molpadiida **Family:** Molpadiidae	*Molpadia* sp. A	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** NW, NE, SE	This species has been classified as *Molpadia blakei* by A. Rogacheva (Rogacheva et al, submitted), but appears to be genetically distinct. Because of it genetic distinction, it remains separated in this study	
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Dendrochirotida **Family:** Cucumariidae	*Staurocucumis abyssorum* *(Abycucumis abyssorum)*	**Gear:** Trawl, Rov **Photo by:** David Shale, *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		 

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Psychropotidae	*Benthodytes gosarsi*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010, David Shale **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Psychropotidae	*Benthodytes lingua*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NE, SW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Psychropotidae	*Benthodytes sanguinolenta*	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Psychropotidae	*Psychropotes depressa*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Psychropotidae	*Psychropotes* sp. nov.	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Amperima furcata*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010, David Shale **Identified by:** A. Rogacheva **Site:** NW, SW, SE		

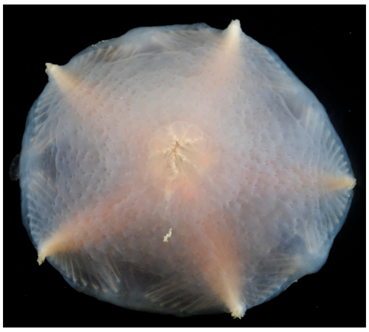
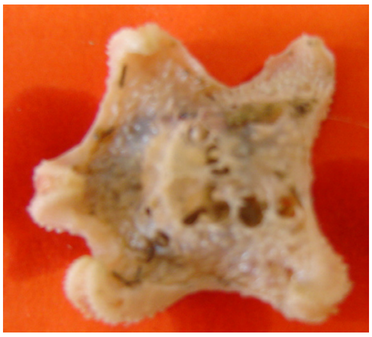
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Ellipinion* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Ellipinion delagei*	**Gear:** Trawl, Rov **Photo by:** David Shale, *Isis* 2010 **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Ellipinion alani*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Peniagone longipapillata*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Peniagone azorica*	**Gear:** Trawl, Rov **Photo by:** **Identified by:** A. Rogacheva **Site:** NW, NE	*Peniagone islandica* and *Peniagone azorica* have such similar morpho-types that it is not possible to distinguish them. *P. azorica* occurs at the northern sites, and *P. islandica* at the southern one. These two species are not clearly distinguished in the molecular study and might be the same species.	
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Peniagone islandica*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** SW, SE		

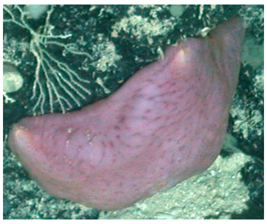
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Peniagone* sp. nov. “coccinea” Rogacheva & Gebruk 2012 in Rogacheva et al (submitted)	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NE, SW, SE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Laetmogone* sp. nov. “billetti” Rogacheva & Gebruk 2012 in Rogacheva et al (submitted)	**Gear:** Rov **Photo by:** David Shale, *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NE		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Elpidiidae	*Kolga nana*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010, David Shale **Identified by:** A. Rogacheva **Site:** NE	species found aggregating	
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Deimatidae	*Synallactes crucifera*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** SE, SW		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Elasipodida **Family:** Deimatidae	*Deima validum*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** SE, SW		
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Apodida **Family:** Myriotrochidae	*Myriotrichus clarki*	**Gear:** Trawl, ROV **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SE, SW		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Holothuroidea **Order:** Apodida **Family:** Synaptidae	*Labidoplax* sp.	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** NW		
Phylum: Echinodermata **Class:** Asteroidea **Order:** **Family:**	Asteroidea (Class) sp. A (Asteroidea sp. 1)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE, SW		
Phylum: Echinodermata **Class:** Asteroidea **Order:** **Family:**	Asteroidea (Class) sp. C (Asteroidea sp. 3)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** **Family:**	Asteroidea (Class) sp. D (Asteroidea sp. 4)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** **Family:**	Asteroidea (Class) sp. G (Asteroidea sp. 7)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, SE, SW		
Phylum: Echinodermata **Class:** Asteroidea **Order:** **Family:**	Asteroidea (Class) sp. H (Asteroidea sp. 8)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** SW		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:**	Paxillosida (Class) sp. A (Asteroidea sp. 5)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Gioniasteridae	*Plinthaster* sp. A (Plinthaster)	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** NW, NE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster membranaceus*	**Gear:** Trawl **Photo by:** David Shale **Identified by:** A. Dilman **Site:** NE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster reticulatus*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* cf. *coccinatus*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Dilman **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* cf. *regalis*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Dilman **Site:** SE, NE		

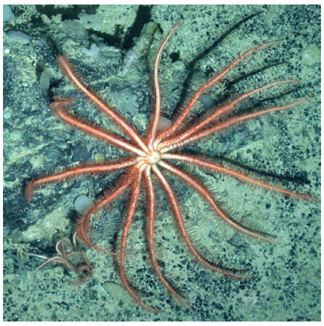
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* cf. *rex*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster pellucidus*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Dilman **Site:** NE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* cf. *gennaeus*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Dilman **Site:** NE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* sp. B	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* sp. C	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE, SW, SE		

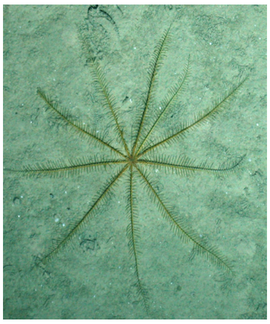
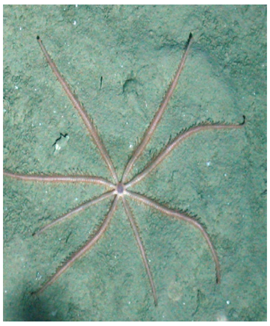
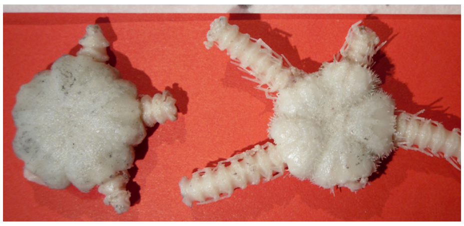
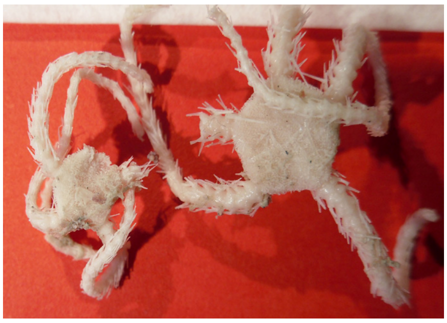
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* sp. E	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* sp. F	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* sp. G	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* sp. H	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster* sp. I	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Pterasteridae	*Hymenaster ?latebrosus ?gennaeus*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Dilman **Site:** NE		

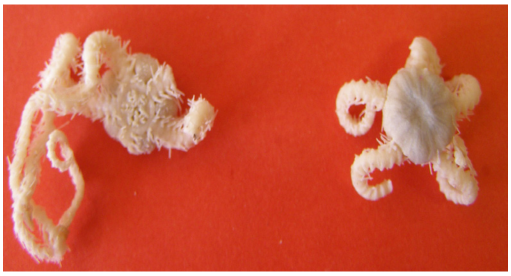
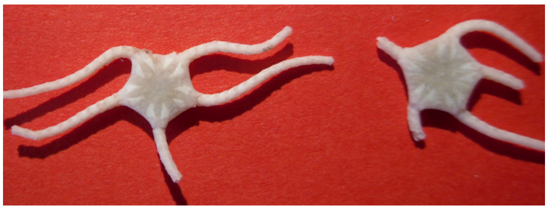
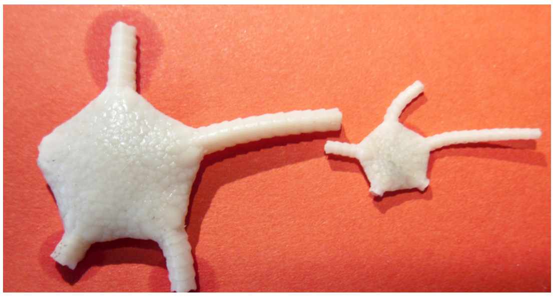
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Poraniidae	*Porania pulvillus*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Dilman **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Valvatida **Family:** Poraniida	*Porania* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Dilman **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Astropectinidae	*Bathybiaster vexillifer*	**Gear:** Trawl, Rov **Photo by:** C. Alt **Identified by:** A. Dilman **Site:** NW, NE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Astropectinidae	*Plutonaster bifrons*	**Gear:** Trawl **Photo by:** David Shale **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Astropectinidae	*Dytaster grandis*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Astropectinidae	*Dytaster* sp. A	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		

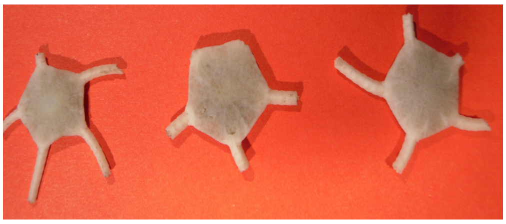
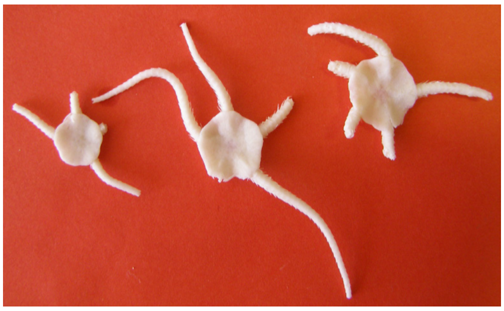
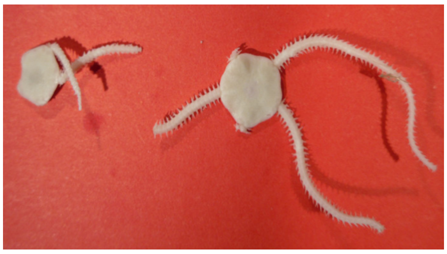
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Astropectinidae	?Astropectinidae (Astripectinidae ?Goniasteridae)	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Astropectinidae	Astropectinidae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Porcellanasteridae	*Hyphalaster inermis*	**Gear:** Trawl **Photo by:** David Shale **Identified by:** A. Dilman **Site:** NW, SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Porcellanasteridae	*Porcellanaster ceruleus*	**Gear:** Trawl, Rov **Photo by:** David Shale **Identified by:** A. Dilman **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Porcellanasteridae	*Caulaster pedunculatus*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Dilman **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Porcellanasteridae	*Porcellanaster* sp. A (Porcellanaster sp.)	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** NW, SE		

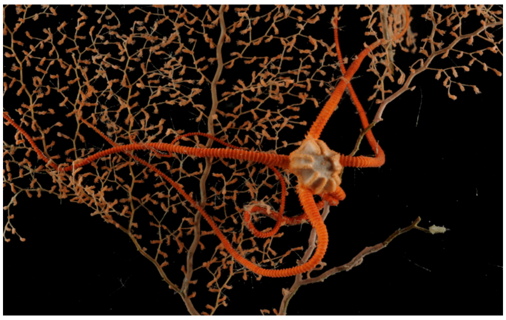
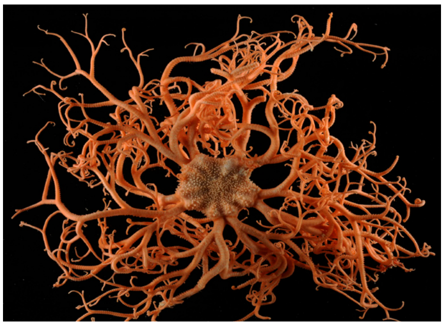
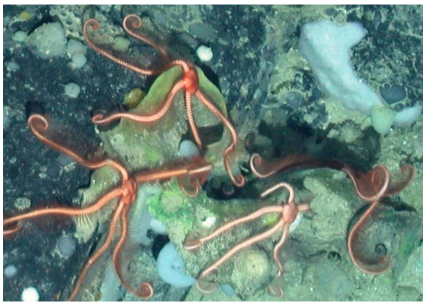
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Porcellanasteridae	*Styracaster* sp. A (Styracaster sp.)	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Porcellanasteridae	*Styracaster aramatus*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Porcellanasteridae	*Styracaster ?aramatus ?chuni*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Porcellanasteridae	*Eremicaster* sp. A (*Eremicaster* sp.)	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** NW		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Benthopectinidae	*Petinaster filholi*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Benthopectinidae	*?Pectinaster ?cheiraster*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		

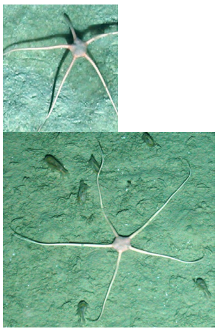
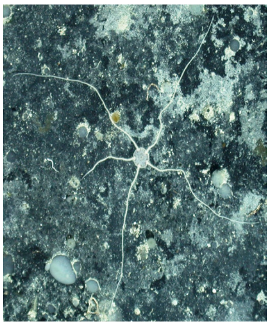
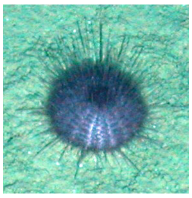
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Benthopectinidae	Benthopectinidae sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Dilman **Site:** SW		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Benthopectinidae	*Cheiraster ?planus*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** NE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Benthopectinidae	*?Gaussaster antarcticus*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** NE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Paxillosida **Family:** Pseudarchasteridae	*Pseudarchaster gracilis*	**Gear:** Trawl **Photo by:** **Identified by:** A. Dilman **Site:** SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Brisingida **Family:**	Brisingidae sp. A (Brisingidae sp. 1)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Brisingida **Family:**	Brisingidae sp. B (Brisingidae sp. 2)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		

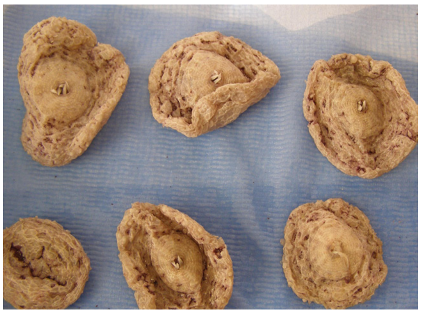
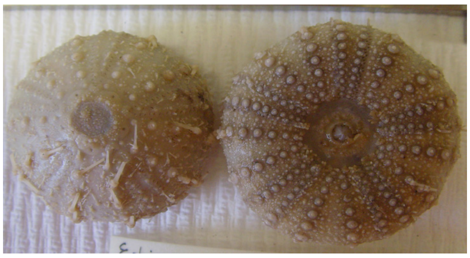
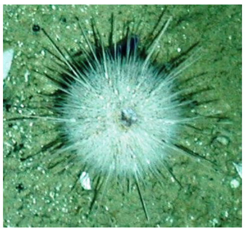
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Asteroidea **Order:** Brisingida **Family:**	Brisingidae sp. C (Brisingidae sp. 3)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Brisingida **Family:** Freyellidae	*Freyalla elegans*	**Gear:** Rov, Trawl **Photo by:** *Isis* 2010 **Identified by:** A. Dilman **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Brisingida **Family:** Freyellidae	*Freyalla* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Dilman **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Asteroidea **Order:** Forcipulatida **Family:** Pedicellasteridae	*Hydrasteria sexradiata*	**Gear:** Rov, Trawl **Photo by:** *Isis* 2010 **Identified by:** A. Dilman **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiacanthidae	*Ophiocamax patersoni*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiacanthidae	*Ophiacantha aculeata*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** NW, NE, SE		

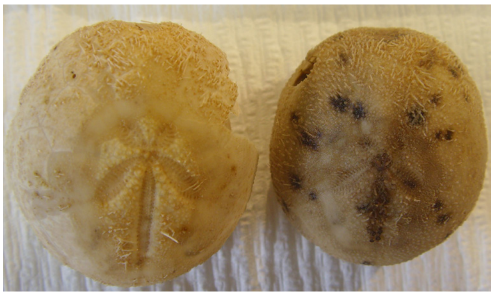
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiacanthidae	*Ophiacantha fraterna*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** NW, NE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiacanthidae	*Ophiolimna bairdi*	**Gear:** Trawl **Photo by:** **Identified by:** A. Martynov **Site:** NW		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiolepididae	*Ophiomusium lymani*	**Gear:** Trawl **Photo by:** **Identified by:** A. Martynov **Site:** SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiactidae	*Ophioactis* sp. A	**Gear:** Trawl **Photo by:** **Identified by:** A. Martynov **Site:** NW, NE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiuridae	*Ophiura ljungmani*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiuridae	*Ophiura irrorata*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** NW, NE, SE		

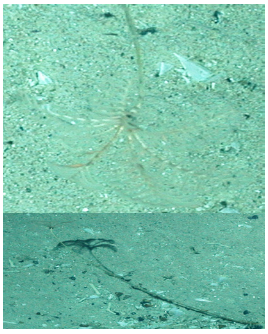
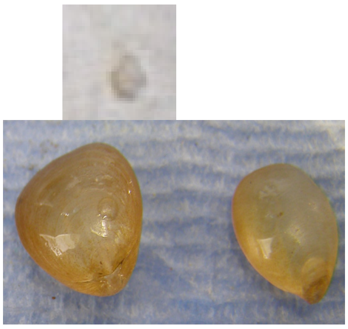
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiuridae	*Ophiura saurura*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** NW, SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiuridae	*Ophiocten hastatum*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiuridae	*Ophiura nitida*	**Gear:** Trawl **Photo by:** **Identified by:** A. Martynov **Site:** NW, NE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiuridae	*Ophioplinthus tessellata*	**Gear:** Trawl **Photo by:** **Identified by:** A. Martynov **Site:** SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Amphilepididae	*Amphilepis ingolfiana*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Ophiurida **Family:** Ophiomyxidae	Ophiomyxidae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** A. Martynov **Site:** NW, SE		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Euryalida **Family:** Asteronychidae	*Astrodia tenuispina*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Martynov **Site:** SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Euryalida **Family:** Asteronychidae	*Asteronyx* sp. A	**Gear:** Rov **Photo by:** David Shale **Identified by:** C. Alt **Site:** NE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** Euryalida **Family:** Gorgonocephalidae	*Gorgonacephalus* sp.	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:**		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** **Family:**	Ophiuroidea (Class) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** **Family:**	Ophiuroidea (Class) sp. C	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** **Family:**	Ophiuroidea (Class) sp. D	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** **Family:**	Ophiuroidea (Class) sp. E	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** **Family:**	Ophiuroidea (Class) sp. F	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE, SW, SE		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** **Family:**	Ophiuroidea (Class) sp. G	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** **Family:**	Ophiuroidea (Class) sp. H	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Ophiuroidea **Order:** **Family:**	Ophiuroidea (Class) sp. I	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Echinothurioida **Family:** Echinothuriidae	*Tromikosoma koehleri*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** K. Minin **Site:** NW, NE, SW, SE		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Echinoidea **Order:** Echinothurioida **Family:** Echinothuriidae	*Tromikosoma* cf. *uranus*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** K. Minin **Site:** NE, SE		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Holasteroida **Family:** Pourtalesiidae	Pourtalesiidae (Family) sp. B (Pourtalesidae sp. 2)	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** K. Minin **Site:** NW		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Holasteroida **Family:** Pourtalesiidae	*Echinosigra phiale*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** K. Minin **Site:** NW, NE		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Holasteroida **Family:** Urechinidae	*Urechinus narensianus*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** K. Minin **Site:** NW, NE		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Camarodonta **Family:** Echinidae	*Echinus alexandri*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** K. Minin **Site:** NW		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Camarodonta **Family:** Echinidae	*Echinus* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE		

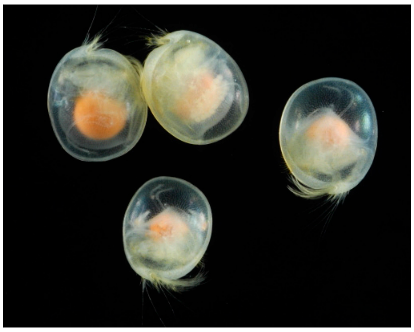
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Echinoidea **Order:** Camarodonta **Family:** Echinidae	*Echinus* sp. B	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Spatangoida **Family:** Hemiasteridae	*Hemiaster expergitus*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** K. Minin **Site:** NW, NE		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Spatangoida **Family:** Aeropsidae	*Aeropsis rostrata*	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** K. Minin **Site:** NW, NE, SE		
Phylum: Echinodermata **Class:** Echinoidea **Order:** Salenioida **Family:** Saleniidae	*Salenocidaris profundi*	**Gear:** Trawl **Photo by:** **Identified by:** K. Minin **Site:** SE		
Phylum: Echinodermata **Class:** Crinoidea **Order:** Millericrinida **Family:** Hyocrinidae	*Anachalypsicrinus nefertini*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gebruk/A. Rogacheva **Site:** SW, SE		
Phylum: Echinodermata **Class:** Crinoidea **Order:** Bourgueticrinida **Family:** Septocrinidae	*Roucicrinus vestitus* (Bourgueticrina sp.)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gebruk **Site:** NE, SW		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Echinodermata **Class:** Crinoidea **Order:** Comatulida **Family:** Bathycrinidae	Bathycrinidae (Family) sp. A *(Bathycrinidae sp.)*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gebruk **Site:**	This is a white/ translucent 5-arm crinoid and might be a new species.	
Phylum: Echinodermata **Class:** Crinoidea **Order:** Comatulida **Family:**	Comatulida (Order) sp. A (Comatulida sp.)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gebruk **Site:**		
Phylum: Echinodermata **Class:** Crinoidea **Order:** Comatulida **Family:**	Comatulida (Order) sp. A (Comatulida sp.)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gebruk **Site:**	These were only seen in the Charlie-Gibbs Fracture Zone	
Phylum: Arthropoda **Class:** Cephalocarida **Order:** Brachypoda **Family:**	Brachypoda (Order) sp. A (Brachipoda)	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010, C. Alt **Identified by:** A. Rogacheva **Site:** NW, SW, SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Amphipoda **Family:** Eurytheneidae	*Eurythenes gryllus* *(Eurythenes obesus)*	**Gear:** Rov **Photo by:** David Shale **Identified by:** T. Horton **Site:**		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Polystilifera **Family:**	Reptantia (Suborder) sp. A	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** NW, SE		

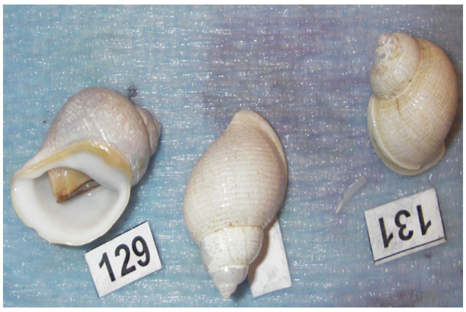
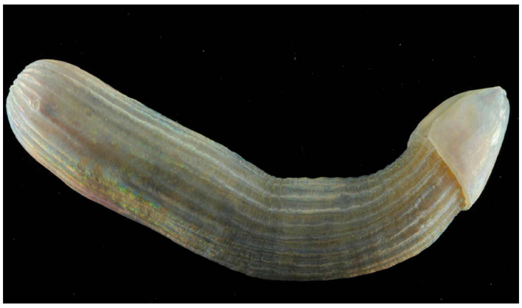
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Arthropoda **Class:** Malacostraca **Order:** Polystilifera **Family:**	Reptantia (Suborder) sp. B (Reptantia sp.2)	**Gear:** Trawl **Photo by:** **Identified by:** C. Alt **Site:** SE, NW		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:**	Anomura (Infraorder) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** C. Alt **Site:** SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Galatheidae	Galatheidae (Family) sp. A	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** C. Alt **Site:** NE, SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Galatheidae	*Munidopsis* sp. A	**Gear:** Trawl **Photo by:** **Identified by:** C. Alt **Site:** NW, SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Galatheidae	*Munidopsis rostrata*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** W. Reid/B. Wigham **Site:** NE, SW, SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Galatheidae	*Munidopsis crassa*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** W. Reid/B. Wigham **Site:** NW, NE, SW, SE		

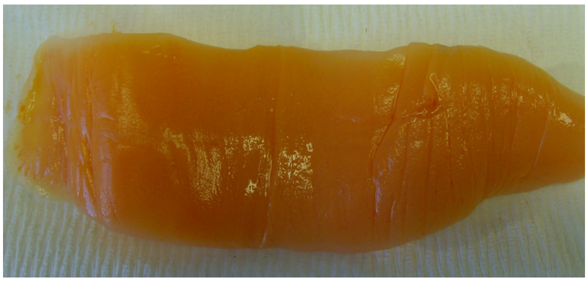
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Ploychelidae	*Stereomastis nanus*	**Gear:** Trawl **Photo by:** David Shale **Identified by:** W. Reid/B. Wigham **Site:** NW, NE, SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Ploychelidae	*Pentacheles validus*	**Gear:** Trawl **Photo by:** **Identified by:** W. Reid/B. Wigham **Site:** SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Paguridae	*Parapagurus pilosimanus*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** D. Jones **Site:** SW		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Paguridae	Paguridae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Lithodidae	Lithodidae (Family) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Aristeidae	Aristeidae (Family) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Letessier **Site:**		

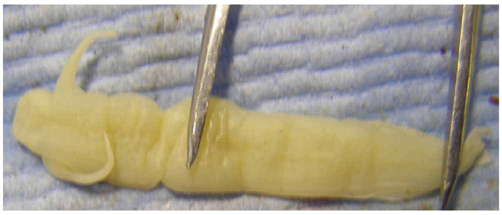
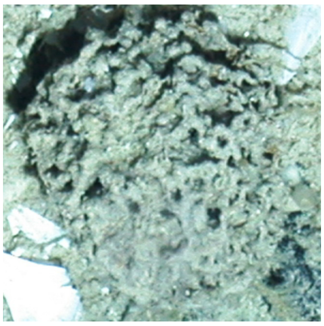
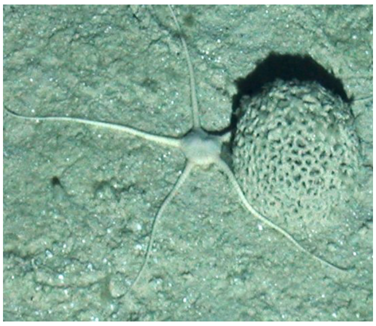
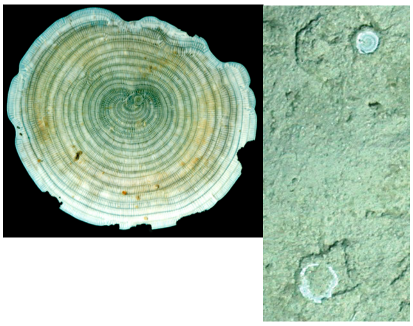
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Arthropoda **Class:** Malacostraca **Order:** Decapoda **Family:** Glyphocrangonidae	*Glyphocrangon sculpta*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010, David Shale **Identified by:** W. Reid/B. Wigham **Site:** NW, NE, SW, SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Tanaidacea **Family:**	Tanaidacea (Order) sp. A	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** NW, NE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Isopoda **Family:**	Isopoda (Order) sp. A	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Arthropoda **Class:** Malacostraca **Order:** Isopoda **Family:**	Valvifera (Suborder) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** NW		
Phylum: Arthropoda **Class:** Maxillopoda **Order:** **Family:**	Copepoda (Subclass) sp. A	**Gear:** Rov **Photo by:** David Shale **Identified by:** C. Alt **Site:**		
Phylum: Arthropoda **Class:** Maxillopoda **Order:** Lepadiformes **Family:**	Lepadiformes (Order) sp. A	**Gear:** Trawl **Photo by:** David Shale **Identified by:** A. Rogacheva **Site:** NW		

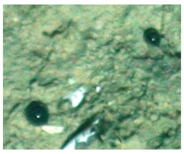
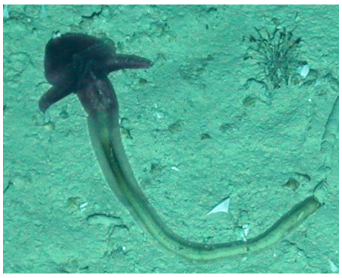
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Arthropoda **Class:** Maxillopoda **Order:** Scalpelliformes **Family:** Scalpellidae	*Neoscalpellum debile*	**Gear:** Rov **Photo by:** C. Alt **Identified by:** C. Alt **Site:** NW, NE, SW		
Phylum: Arthropoda **Class:** Ostracoda **Order:** Myodocopida **Family:** Cypridinidae	*Azygocypridina imperialis*	**Gear:** Trawl **Photo by:** David Shale **Identified by:** M. Angel **Site:** NW, NE, SE		
Phylum: Arthropoda **Class:** Ostracoda **Order:** Myodocopida **Family:** Cypridinidae	*Gigantocypris ?muelleri*	**Gear:** Trawl **Photo by:** **Identified by:** M. Angel **Site:** NW, NE		
Phylum: Arthropoda **Class:** Pycnogonida **Order:** Pantopoda **Family:** Colosseneidae	*Colossendeis colossea*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** A. Raiskyi **Site:** NW, NE, SE		
Phylum: Mollusca **Class:** Cephalopoda **Order:** Octopoda **Family:** Grimpoteuthidae	*Grimpoteuthis discoveryi*	**Gear:** Trawl, Rov **Photo by:** **Identified by:** M. Vecchione **Site:** NW, NE, SE		
Phylum: Mollusca **Class:** Cephalopoda **Order:** Oegopsida **Family:** Histioteuthidae	*Histioteuthis bonnellii*	**Gear:** Trawl **Photo by:** **Identified by:** M. Vecchione **Site:** NW, NE, SE		

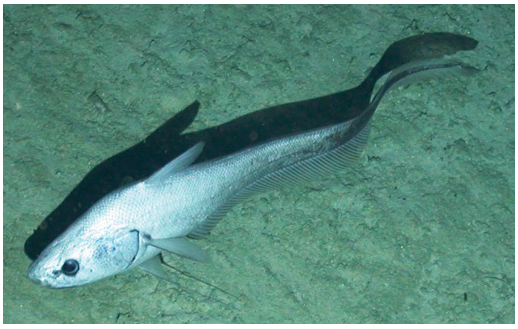
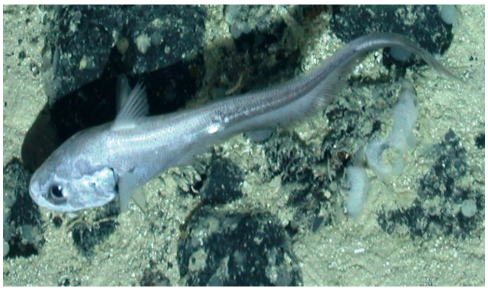
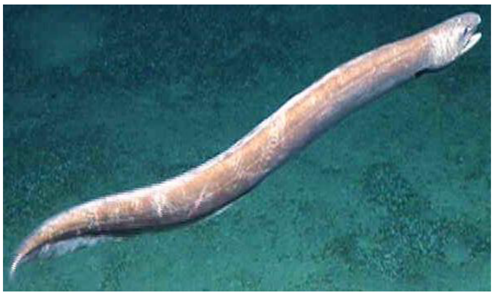
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Mollusca **Class:** Cephalopoda **Order:** Oegopsida **Family:** Gonatidae	*Gonatus steenstrupi*	**Gear:** Trawl **Photo by:** **Identified by:** M. Vecchione **Site:** NW, SE		
Phylum: Mollusca **Class:** Cephalopoda **Order:** Teuthida **Family:**	Teuthida (Order) sp. A	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** M. Vecchione **Site:** NE		
Phylum: Mollusca **Class:** Scaphopoda **Order:** **Family:**	Scaphopoda (Class) sp.A	**Gear:** Trawl, Rov **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		
Phylum: Mollusca **Class:** Mollusca **Order:** **Family:**	Mollusca (Class) sp. A (Mollusca A)	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** SE, NW		
Phylum: Mollusca **Class:** Mollusca **Order:** **Family:**	Mollusca (Class) sp. B (Mollusca B)	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** NE		
Phylum: Mollusca **Class:** Bivalvia **Order:** **Family:**	Bivalvia (Class) sp. A	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** NW		

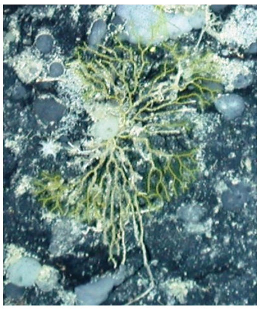
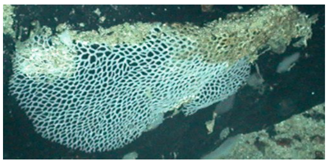
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Mollusca **Class:** Gastropoda **Order:** **Family:**	Gastropoda (Class) sp. B (Gastropoda 2)	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** C. Alt **Site:** NW, SE		
Phylum: Mollusca **Class:** Gastropoda **Order:** **Family:**	Gastropoda (Class) sp. A (Gastropoda 1)	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** C. Alt **Site:** NE, SE		
Phylum: Mollusca **Class:** Gastropoda **Order:** **Family:**	Gastropoda (Class) sp. D (Gastropoda sp.)	**Gear:** Trawl **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** SE		
Phylum: Mollusca **Class:** Gastropoda **Order:** **Family:**	Vestigastropoda (Superfamily) sp. A (Vestigastropoda)	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Sipuncula **Class:** Sipunculidea **Order:** Golfingiida **Family:** Sipunculidae	*Sipunculus norvegicus*	**Gear:** Trawl **Photo by:** David Shale **Identified by:** A. Rogacheva **Site:** NW, NE, SE		
Phylum: Sipuncula **Class:** **Order:** **Family:**	Sipuncula (Phylum) sp. A	Trawl **Photo by:** David Shale, C. Alt **Identified by:** C. Alt **Site:** NW, NE, SE		

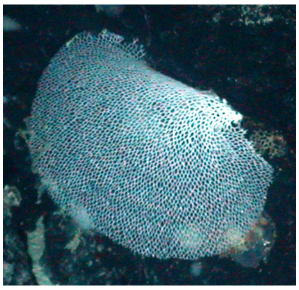
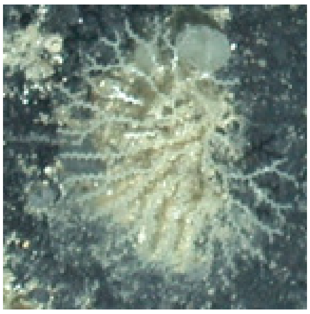
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Sipuncula **Class:** **Order:** **Family:**	Sipuncula (Phylum) sp. A	**Gear:** Trawl **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE, SE		
Phylum: Echiura **Class:** **Order:** **Family:**	Echiura (Phylum) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Echiura **Class:** **Order:** **Family:**	Echiura (Phylum) sp. B	**Gear:** Trawl **Photo by:** David Shale **Identified by:** A. Rogacheva **Site:** SE		
Phylum: Echiura **Class:** **Order:** **Family:**	Echiura (Phylum) sp. C	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** SE, NW		
Phylum: Echiura **Class:** **Order:** **Family:**	Echiura (Phylum) sp. D	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Rogacheva **Site:** NW, NE, SW, SE		
Phylum: Nemertea **Class:** **Order:** **Family:**	Nemertea (Phylum) sp. A	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** SE		

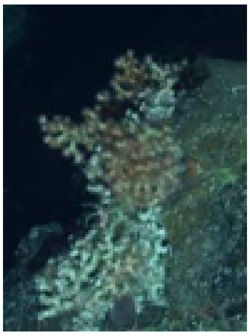
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Nemertea **Class:** **Order:** **Family:**	Nemertea (Phylum) sp. B	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** NW		
Phylum: Nemertea **Class:** **Order:** **Family:**	Nemertea (Phylum) sp. C	**Gear:** Rov **Photo by:** C. Alt **Identified by:** A. Rogacheva **Site:** NE		
Phylum: Foraminifera **Class:** Xenophyophorea **Order:** Psamminida **Family:** Syringamminidae	Xenophyophorea (Class) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gooday **Site:** NE		
Phylum: Foraminifera **Class:** Xenophyophorea **Order:** Psamminida **Family:** Syringamminidae	*Syringammina corbicula*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gooday **Site:** NW, SW		
Phylum: Foraminifera **Class:** Xenophyophorea **Order:** Psamminida **Family:** Syringamminidae	*Syringammina fragillissima*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gooday **Site:** NW, NE, SW, NE		
Phylum: Foraminifera **Class:** Polythalamea **Order:** Miliolida **Family:** Discospirinidae	*Discospirina tenuissima*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** A. Gooday **Site:** NW, NE, SW, NE		

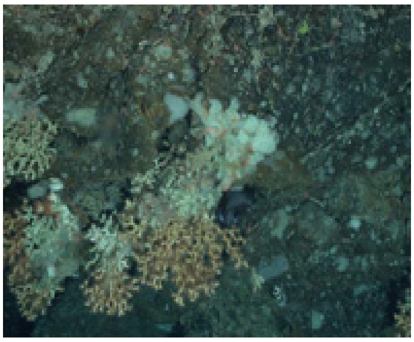
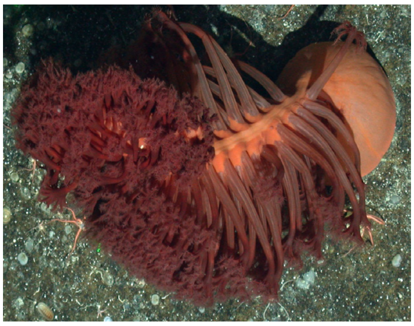
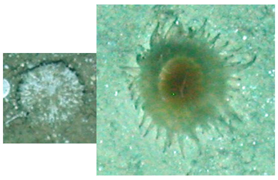
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cercozoa **Class:** Gromiidea **Order:** Gromiida **Family:** Gromiidae	*Gromia sphaerica*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Hemichordata **Class:** Enteropneusta **Order:** Enteropneusta **Family:**	*Tergivelum* sp. nov. *'cinnabarinus'* (Enterpneusta A) Holland 2012 in Priede et al (in prep)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE, SW, SE	white spots inside specimen are aggs	
Phylum: Hemichordata **Class:** Enteropneusta **Order:** Enteropneusta **Family:**	*'Yoda purpurata'* n. gen, n. sp. (Enterpneusta B) Holland 2012 in Priede et al (in prep)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** SW, SE		
Phylum: Hemichordata **Class:** Enteropneusta **Order:** Enteropneusta **Family:**	*Allapasus* sp. nov. *'isidis'* (Enterpneusta C) Holland 2012 in Priede et al (in prep)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** SW		
Phylum: Chordata **Class:** Actinopterygii **Order:** Notacanthiformes **Family:** Halosauridae	*Halosauropsis macrochir*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Linley **Site:** NW, NE, SW, SE		
Phylum: Chordata **Class:** Actinopterygii **Order:** Notacanthiformes **Family:** Notacanthidae	*Polyacanthonotus challengeri*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Linley **Site:** NE, SW		

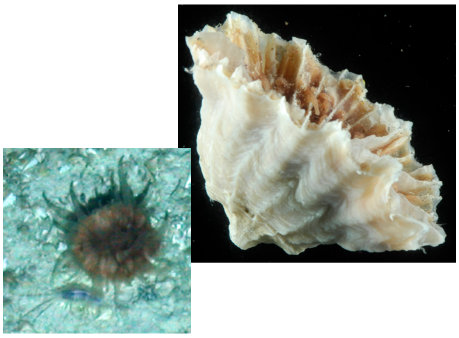
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Chordata **Class:** Actinopterygii **Order:** Aulopiformes **Family:** Synadontidae	*Bathysaurus ferox*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Linley **Site:** NW, NE, SE		
Phylum: Chordata **Class:** Actinopterygii **Order:** Gadiformes **Family:** Moridae	*Antimora rostrata*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Linley **Site:** NW, NE, SW, SE		
Phylum: Chordata **Class:** Actinopterygii **Order:** Gadiformes **Family:** Macrouridae	*Coryphaenoides armatus*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Linley **Site:** NW, NE, SW, SE		
Phylum: Chordata **Class:** Actinopterygii **Order:** Gadiformes **Family:** Macrouridae	*Coryphaenoides brevibarbis*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Linley **Site:** NW, NE, SW, SE		
Phylum: Chordata **Class:** Actinopterygii **Order:** Gadiformes **Family:** Synaphobranchidae	*Histiobranchus bathybius*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Linley **Site:**		
Phylum: Chordata **Class:** **Order:** **Family:**	Tunicata (Subphylum) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		

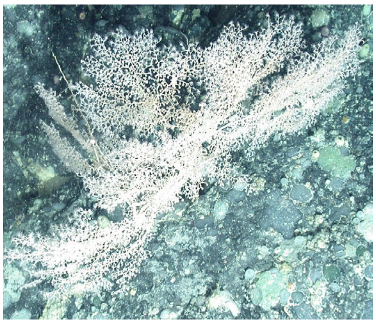
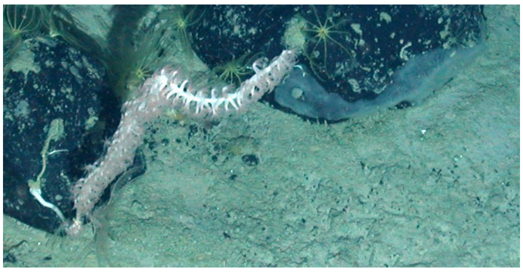
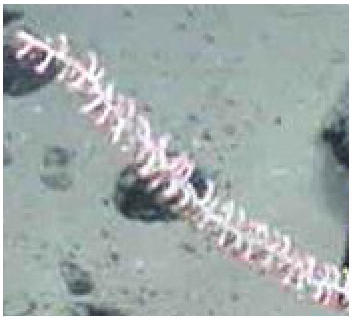
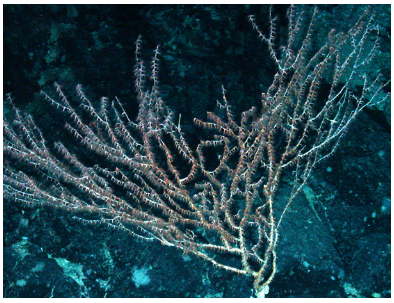
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Bryozoa **Class:** **Order:** **Family:**	Bryozoa (Phylum) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Bryozoa **Class:** **Order:** **Family:**	Bryozoa (Phylum) sp. B	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Bryozoa **Class:** **Order:** **Family:**	Bryozoa (Phylum) sp. C	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Bryozoa **Class:** **Order:** **Family:**	Bryozoa (Phylum) sp. D	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Bryozoa **Class:** **Order:** **Family:**	Bryozoa (Phylum) sp. H	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Bryozoa **Class:** **Order:** **Family:**	Bryozoa (Phylum) sp. I	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		

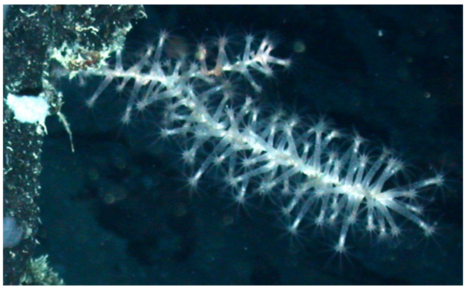
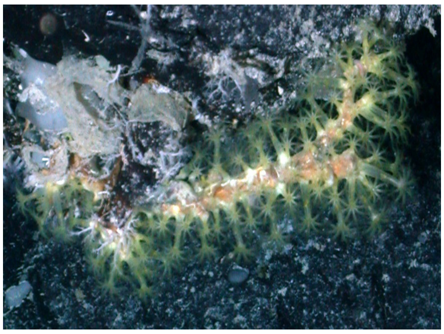
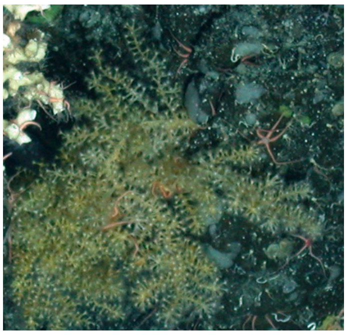
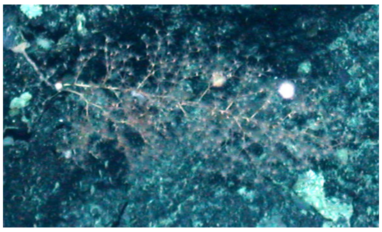
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Bryozoa **Class:** **Order:** **Family:**	Bryozoa (Phylum) sp. J	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Bryozoa **Class:** **Order:** **Family:**	Bryozoa (Phylum) sp. E	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Ctenophore **Class:** Ctenophora **Order:** **Family:**	Ctenophora (Class) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** M. Youngbluth **Site:**		
Phylum: Cnidaria **Class:** Hydrozoa **Order:** Trachymedusae **Family:** Rhopalonematidae	*Benthocodon* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** M. Youngbluth **Site:** NW, NE, SW, SE		
Phylum: Cnidaria **Class:** Hydrozoa **Order:** Trachymedusae **Family:** Rhopalonematidae	*Crossota* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** M. Youngbluth **Site:** NW, NE, SW, SE		
Phylum: Cnidaria **Class:** Hydrozoa **Order:** **Family:**	Hydroidolina (Subclass) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE, SE		

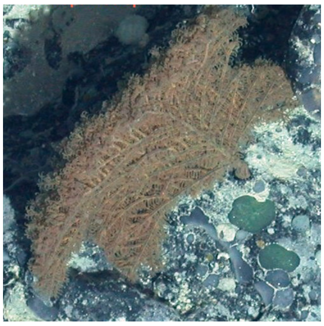
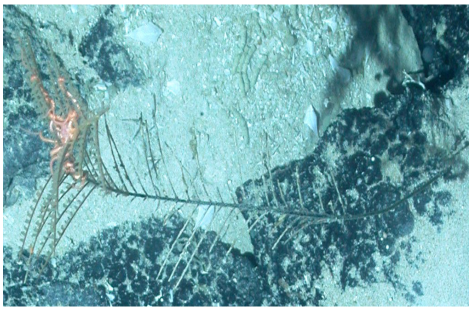
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Hydrozoa **Order:** **Family:**	Hydroidolina (Subclass) sp. B	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, SE		
Phylum: Cnidaria **Class:** Hydrozoa **Order:** **Family:**	Hydroidolina (Subclass) sp. C	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, NE, SW, SE		
Phylum: Cnidaria **Class:** Hydrozoa **Order:** **Family:**	Hydroidolina (Subclass) sp. D	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** NW, SW, SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Scleractinia **Family:**	Scleractinia (Order) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Scleractinia **Family:** Caryophylliidae	*Lophelia pertusa*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Scleractinia **Family:** Caryophylliidae	*?Solenosmilia* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		

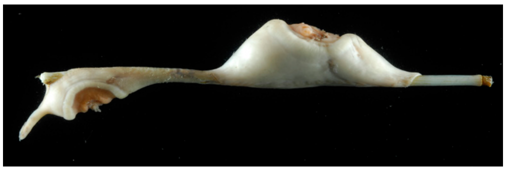
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Scleractinia **Family:** Caryophylliidae	*?Solenosmilia* sp. A (or *Acanthogorgia sp.*)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Pennatulacea **Family:** Pennatulidae	*Scleroptilum grandiflorum*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Pennatulacea **Family:** Pennatulidae	*Pennatuacea* (Order) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Pennatulacea **Family:** Umbellulidae	*Umbellula* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Pennatulacea **Family:** Kophobelemnidae	*Kophobelemnon macrospinosum*	**Gear:** Trawl **Photo by:** **Identified by:** T. Molodtsova **Site:** SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Scleractinia **Family:** Fungiacyathidae	*Fungiacyathus marenzelleri*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW, NE, SW, SE		

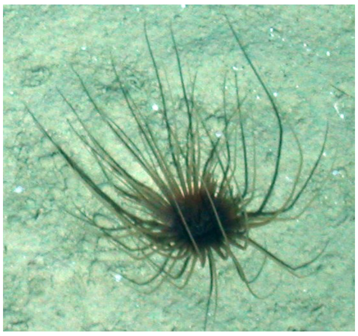
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Scleractinia **Family:** Flabellidae	*Flabellum angulare*	**Gear:** Trawl, Rov **Photo by:** *Isis* 2010, David2010 **Identified by:** T. Molodtsova **Site:** NW, NE, SW, SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Alcyoniidae	*Heteropolypus* cf. *insolitus*	**Gear:** Trawl **Photo by:** *C. Alt* **Identified by:** T. Molodtsova **Site:** SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Alcyoniidae	*Anthomastus* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Chrysogorgiidae	*Chrysogorgia* sp.	**Gear:** Trawl **Photo by:** David Shale **Identified by:** T. Molodtsova **Site:** SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Chrysogorgiidae	*Chrysogorgia* (Family) sp. B (Gorgonacea sp. B)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Chrysogorgiidae	*Chrysogorgia* (Family) sp. C (Gorgonacea sp. J)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		

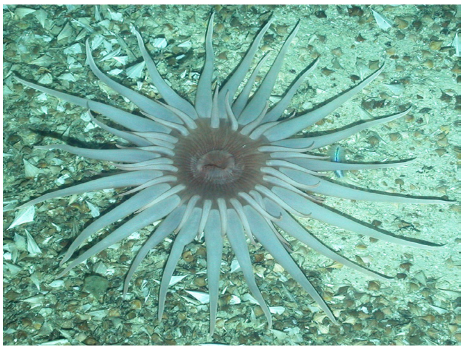
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Chrysogorgiidae	*Metallogorgia* (Family) sp. A (Metallogorgia sp.)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Chrysogorgiidae	*Metallogorgia* (Family) sp. B (Gorgonacea sp. H)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Isididae	*Isididae* (Family) sp. A (Gorgonacea sp. A)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Isididae	*Isididae* (Family) sp. B (Gorgonacea sp. C)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Isididae	*Isididae* (Family) sp. C (Gorgonacea sp. D)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Isididae	*Isididae* (Family) sp. D (Gorgonacea sp. E)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		

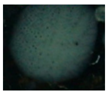
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:**	*Alcyonacea* (Order) sp. F (Gorgonacea sp. F)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:**	*Alcyonacea* (Order) sp. G (Gorgonacea sp. G)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:**	*Alcyonacea* (Order) sp. K (Gorgonacea sp. K)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:**	*Alcyonacea* (Order) sp. I (Gorgonacea sp. I)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:**	*Alcyonacea* (Order) sp. L (Gorgonacea sp.)	**Gear:** Trawl **Photo by:** **Identified by:** T. Molodtsova **Site:** SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Antipatharia **Family:** Leiopathidae	*?Leiopathes* sp. A	**Gear:** Rov **Photo by:** **Identified by:** T. Molodtsova **Site:** NW		

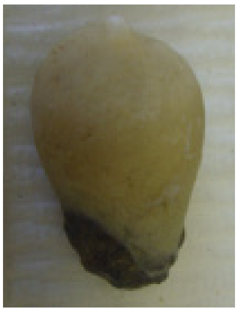
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Schizopathidae	*Stauropathes ?punctata*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Schizopathidae	*Stauropathes* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Schizopathidae	*Bathypathes* ?sp. nov.	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Schizopathidae	*Bathypathes* sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Schizopathidae	*Parantipathes* sp.	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Alcyonacea **Family:** Hormathiidae	*Paraphelliactis michaelsarsi*	**Gear:** Rov **Photo by:** *C. Alt* **Identified by:** T. Molodtsova **Site:**		

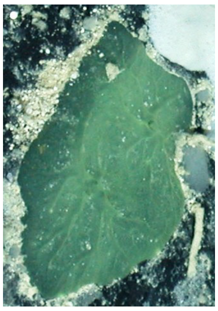
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:** Hormathiidae	*Stephanactis inornata* *(?Amphianthus inornata)*	**Gear:** Trawl **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:** SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:** Actinernidae	*Actinernus michaelsarsi*	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:**	Actiniaria (Order) sp. C (Anemone3)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW, SW, SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:**	Actiniaria (Order) sp. E (Anemone5)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NE, SW		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:**	Actiniaria (Order) sp. F (Anemone6)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:**	Actiniaria (Order) sp. H (Anemone8)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW, SW		

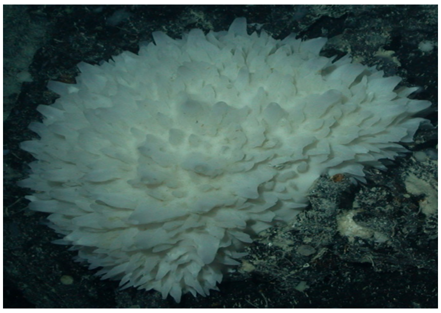
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:**	Actiniaria (Order) sp. I (Anemone9)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:**	Actiniaria (Order) sp. J (Anemone11)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NE, SW, SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:**	Actiniaria (Order) sp. L (Anemone13)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW, SW		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:**	Actiniaria (Order) sp. M (Anemone14)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Actinaria **Family:** Zoanthidae	Zoanthidae (Family) sp. A (Anemone12)	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Ceriantharia **Family:**	Ceriantharia (Order) sp. A	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NE		

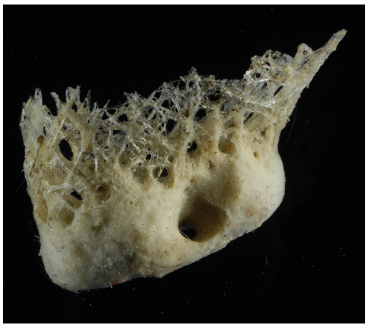
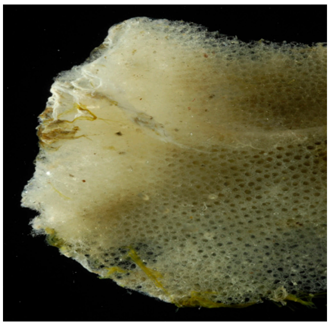
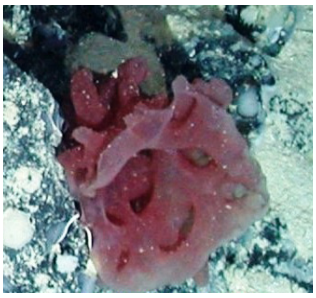
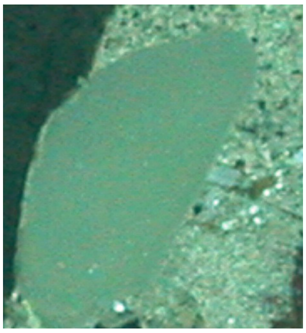
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Ceriantharia **Family:**	Ceriantharia (Order) sp. B	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW, NE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Ceriantharia **Family:**	Ceriantharia (Order) sp. C	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Ceriantharia **Family:**	Ceriantharia (Order) sp. E	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NE, SW, SE		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Ceriantharia **Family:**	Ceriantharia (Order) sp. F	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Ceriantharia **Family:**	Ceriantharia (Order) sp. G	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:** NW		
Phylum: Cnidaria **Class:** Anthozoa **Order:** Ceriantharia **Family:**	Ceriantharia (Order) sp. H	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		

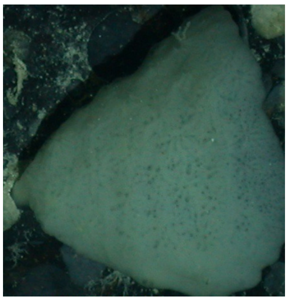
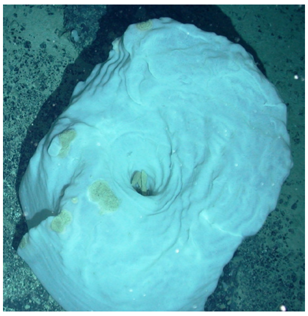
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Cnidaria **Class:** Anthozoa **Order:** Ceriantharia **Family:**	Ceriantharia (Order) sp. I	**Gear:** Rov **Photo by:** *Isis* 2010 **Identified by:** T. Molodtsova **Site:**		
Phylum: Porifera **Class:** **Order:** **Family:**	Porifera (Phylum) sp. A (Hexacteinellid AD)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** **Order:** **Family:**	Porifera (Phylum) sp. B (Hexacteinellid AM)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** **Order:** **Family:**	Porifera (Phylum) sp. C (Hexacteinellid K)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** **Order:** **Family:**	Porifera (Phylum) sp. D (Hexacteinellid AC)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** **Order:** **Family:**	Porifera (Phylum) sp. E (Hexacteinellid AE)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		

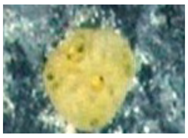
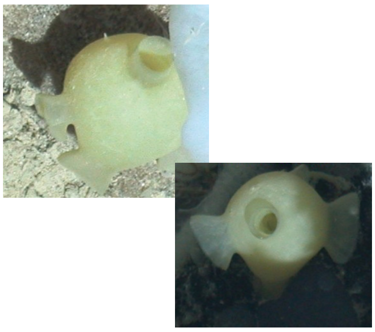
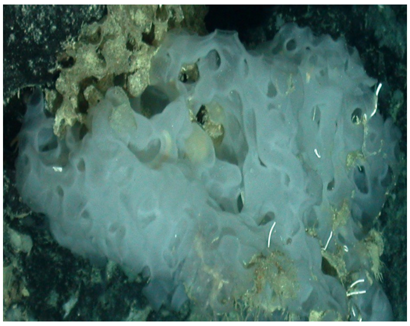
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** **Order:** **Family:**	Porifera (Phylum) sp. F (Hexacteinellid Z)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. A (Demospongia A)	**Gear:** Trawl **Photo by:** C. Alt **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. E (Demospongia E)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. F (Demospongia F)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. G (Demospongia G)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. J (Demospongia J)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		

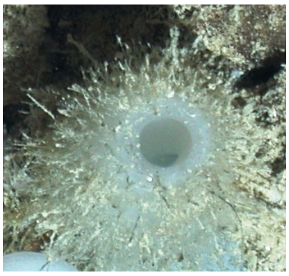
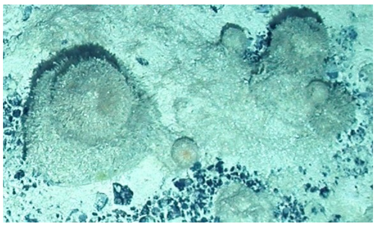
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. L (Demospongia L)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** SW		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. N (Demospongia N)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. P (Demospongia P)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** SW		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. Q (Hexacteinellid AL)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Demospongiae **Order:** **Family:**	Demospongiae (Class) sp. R (Hexacteinellid T)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW		
Phylum: Porifera **Class:** Demospongiae **Order:** Hadromerida **Family:** Polymastiidae	Polymastiidae (Family) sp. A (Demospongia C)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		

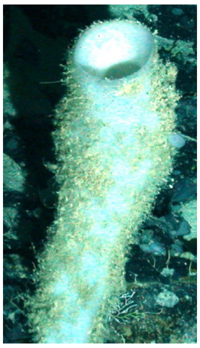
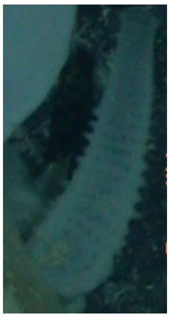
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Demospongiae **Order:** Hadromerida **Family:** Polymastiidae	Polymastiidae (Family) sp. B (Demospongia M)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW, SW		
Phylum: Porifera **Class:** Demospongiae **Order:** Hadromerida **Family:** Polymastiidae	Polymastiidae (Family) sp. C (Demospongia O)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Demospongiae **Order:** Hadromerida **Family:** Tethyidae	*?Tethya* sp. (Hexacteinellid AF)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Demospongiae **Order:** Astrophorida **Family:** Geodiidae	Geodiidae (Family) sp. A (Demospongae G)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Demospongiae **Order:** Astrophorida **Family:** Geodiidae	Geodiidae (Family) sp. A (Demospongae H)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Demospongiae **Order:** Astrophorida **Family:** Geodiidae	Geodiidae (Family) sp. A (Demospongae I)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		

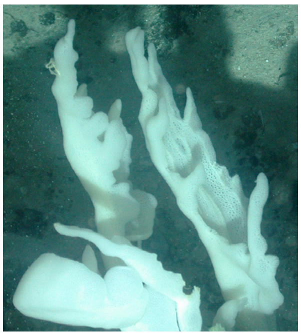
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Demospongiae **Order:** Astrophorida **Family:** Geodiidae	Geodiidae (Family) sp. A (Demospongae K)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. A	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. G	**Gear:** Trawl **Photo by:** David Shale **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. H	**Gear:** Trawl **Photo by:** David Shale **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. J	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. M	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW		

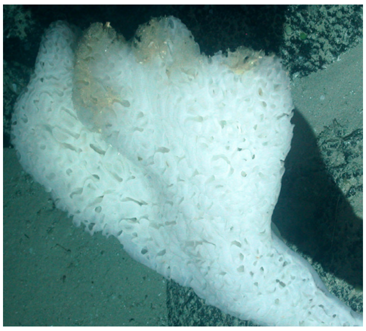
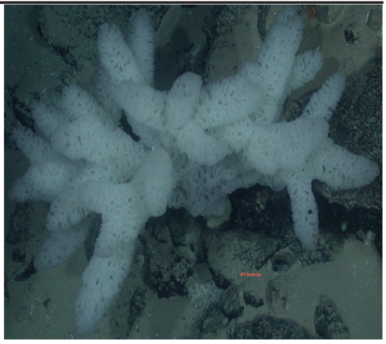
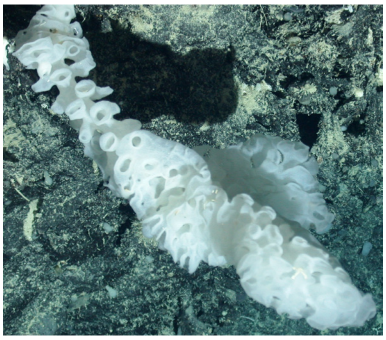
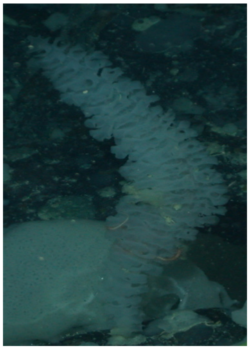
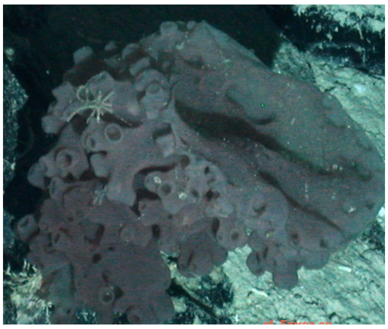
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. N	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. O	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. P	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. S	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW, SW		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. W	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. AB	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** SW		

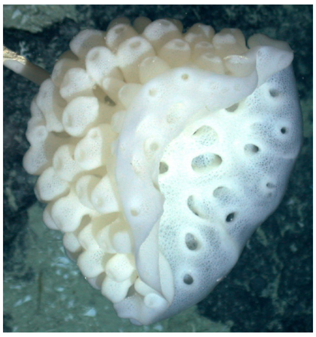
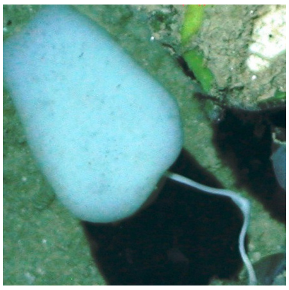
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. AK	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. AN	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. AO	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW, NE		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. AP	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. AU	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. AX	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		

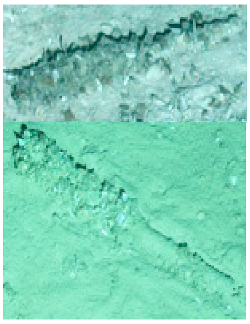
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. AY	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. BH	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. BJ	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW, NE, SW, SE		
Phylum: Porifera **Class:** Hexactinellida **Order:** **Family:**	Hexactinellida (Class) sp. BL	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW		
Phylum: Porifera **Class:** Hexactinellida **Order:** Amphidiscosida **Family:** Pheronematidae	*Pheronema* sp. A (Hexacteinellid C)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. A (Hexacteinellid D)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW, SW		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. B (Hexacteinellid BE)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. C (Hexacteinellid AQ)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. D (Hexacteinellid E)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. E (Hexacteinellid AR)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. F (Hexacteinellid AS)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. G (Hexacteinellid AT)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		

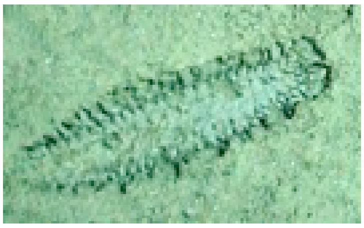
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. H (Hexacteinellid Q)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. I (Hexacteinellid BK)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW, NE, SW, SE		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. J (Hexacteinellid R)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. M (Hexacteinellid AV)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Rossellidae	Rossellidae sp. O (Hexacteinellid BC)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Euplectellidae	*Regadrella phoenix*	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** SW, SE		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Hexactinellida **Order:** Hexactinosida **Family:** Farreidae	Farreidae (Family) sp. A (Hexacteinellid I)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** SW		
Phylum: Porifera **Class:** Hexactinellida **Order:** Hexactinosida **Family:** Farreidae	Farreidae (Family) sp. B (Hexacteinellid BD)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Hexactinosida **Family:** Farreidae	Farreidae (Family) sp. C (Hexacteinellid BF)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Hexactinosida **Family:** Farreidae	Farreidae (Family) sp. D (Hexacteinellid B)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Hexactinosida **Family:** Farreidae	Farreidae (Family) sp. E (Hexacteinellid AA)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Hexactinosida **Family:** Farreidae	Farreidae (Family) sp. F (Hexacteinellid BG)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Euplectellidae	*Saccocalyx* sp. A (Hexacteinellid AH)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** SW		
Phylum: Porifera **Class:** Hexactinellida **Order:** Lyssacinosida **Family:** Euplectellidae	*Saccocalyx* sp. B (Hexacteinellid AW)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Porifera **Class:** Hexactinellida **Order:** Amphidiscosida **Family:** Hyalonematidae	*Hyalonema* sp. A (Hexacteinellid AI)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:** NW, NE, SE		
Phylum: Porifera **Class:** Hexactinellida **Order:** Amphidiscosida **Family:** Hyalonematidae	*Hyalonema* sp. B (Hexacteinellid AJ)	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** K. Tabachnick, **Site:**		
Phylum: Annelida **Class:** Polychaeta **Order:** Eunicida **Family:** Eunicidae	*Eunice* cf. *pennata*	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Eunicida **Family:** Lumbrineridae	*Lumbrineris* (Genus) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		

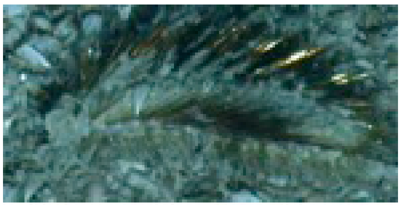
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Annelida **Class:** Polychaeta **Order:** Eunicida **Family:** Lumbrineridae	*Leptoecia* (Genus) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, NE, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Eunicida **Family:** Onuphidae	*Lumbrietymene* (Genus) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Eunicida **Family:** Onuphidae	*Paradiopatra ehlersi*	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Solecida **Family:** Maldanidae	*Abyssoclymene* (Genus) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Solecida **Family:** Maldanidae	Maldanidae (Family) indet.	**Gear:** Trawl, ROV **Photo by:** *Isis* 2010 **Identified by:** N. Budaeva, M. Shields **Site:** NW, NE, SW, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Terebellida **Family:** Terebellidae	Terebellidae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		

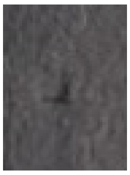
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Annelida **Class:** Polychaeta **Order:** Terebellida **Family:** Terebellidae	Terebellidae (Family) sp. B	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Terebellida **Family:** Ampharetidae	Ampharetidae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Terebellida **Family:** Ampharetidae	Ampharetidae (Family) sp. B	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Sigalionidae	*Leanira hystricis*	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, NE, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Asphroditidae	*Laetmonice* (Genus) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Asphroditidae	*Aphrodita* (Genus) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** SE		

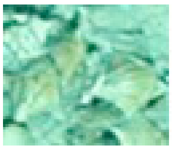
TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Asphroditidae	*Aphrodita* cf. *aculeata*	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Polynoidae	Polynoidae (Family) indet. A	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** M. Shields **Site:**		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Polynoidae	Polynoidae (Family) indet. B	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** M. Shields **Site:** NW, SW		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Polynoidae	Polynoidae (Family) indet. C	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** M. Shields **Site:** SW, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Polynoidae	Polynoidae (Family) indet. D	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, NE, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Polynoidae	Polynoidae (Family) indet. E	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, SE		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Polynoidae	Polynoidae (Family) indet. F	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Polynoidae	Polynoidae (Family) indet. G	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Glyceridae	Glyceridae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Phyllodocidea	Phyllodocidae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Nereididae	Nereididae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Oweniidae	Oweniidae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, NE		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Annelida **Class:** Polychaeta **Order:** Canalipalpata **Family:** Oweniidae	*Oweniid* (Genus) sp. A	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** M. Shields **Site:** NW, NE, SW, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Canalipalpata **Family:** Sabellidae	Sabellidae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Sabellida **Family:** Sabellidae	*Sabellida* (Genus) sp. A	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** M. Shields **Site:** NW, NE, SW, SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Sabellida **Family:** Opheliidae	Ophelliidae (Family) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, NE		
Phylum: Annelida **Class:** Polychaeta **Order:** Scolecida **Family:** Capitellidae	*?Decamastus* (Genus) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** SE		
Phylum: Annelida **Class:** Polychaeta **Order:** Tetraodontiformes **Family:** Monacanthidae	*Chaetoderma (Genus)* *sp. A*	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW, SE		

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: Annelida **Class:** Polychaeta **Order:** Phyllodocida **Family:** Nephtyidae	*Nephtys* (Genus) sp. A	**Gear:** Trawl **Photo by:** **Identified by:** N. Budaeva **Site:** NW		
Phylum: Annelida **Class:** Polychaeta **Order:** Amphinomida **Family:**	Amphinomida (Order) sp. A	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** M. Shields **Site:** NW, SW, SE		
Phylum: **Class:** **Order:** **Family:**	Bra	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	this might be a brachipod, but the resolution is not good enough to be sure	
Phylum: **Class:** **Order:** **Family:**	GT	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	a green thing, which is only visible in video. It might not be biological. The distribution is very sparse and it is therefore not likely to be phytodetritus.	
Phylum: **Class:** **Order:** **Family:**	Od	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	this a a faint red shape that appeared often to have a centre with, maybe tentacles moving out	
Phylum: **Class:** **Order:** **Family:**	Drt	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	dark red, irregular shape. This might be a small pebble, although the red colour ration suggest the possibility that it might be biologycal	

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: **Class:** **Order:** **Family:**	BrD	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	small brown dot, which could be a structure formed by mega- or macrofauna	
Phylum: **Class:** **Order:** **Family:**	SPp	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	small spike-like structure coming off the sediment. This could be either infaunal, or a Sabellid tube.	
Phylum: **Class:** **Order:** **Family:**	Sthg	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	green, irregular shape that appears to come out of the sediment, and moves in a wave-like manner on the video	
Phylum: **Class:** **Order:** **Family:**	Ten	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	Difficult to see on the image, but tentacles coming out of the sediment.	
Phylum: **Class:** **Order:** **Family:**	Pt	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	white/grey shaded elongated structure, without the conical shape associated with scaphopods	
Phylum: **Class:** **Order:** **Family:**	Bspider	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	structure with small black centre and tentacle/ leg- like structures surrounding it.	

TAXONOMY	NAME	HABITAT	NOTES	IMAGE
Phylum: **Class:** **Order:** **Family:**	Disc	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	small disc-like structure	
Phylum: **Class:** **Order:** **Family:**	Sta	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	very small half-moon shaped structure, which might be a very small *Staurocucumis abyssorum*	
Phylum: **Class:** **Order:** **Family:**	HoA	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** C. Alt **Site:**	This is either an old holothurian cast, or a holothurian from the Family Synallactidae, or Gephyrothuriidae	
Phylum: Mollusca **Class:** Gastropoda **Order:** Thecosomata **Family:** Cavoliniidae	*Diacria trispinosa*	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** M. Youngbluth **Site:** SW, SE	these shells were very abundant at the southern sites	
Phylum: Mollusca **Class:** Gastropoda **Order:** Thecosomata **Family:** Cavoliniidae	*Clio pyromidata*	**Gear:** ROV **Photo by:** *Isis* 2010 **Identified by:** M. Youngbluth **Site:** SW, SE	these shells were very abundant at the southern sites	
Phylum: **Class:** **Order:** **Family:**		**Gear:** **Photo by:** **Identified by:** **Site:**		

Appendix F

Publication List

F.1 Publications

C. H. S. Alt, D. O. B. Jones. **2012.** Litter Distribution identified along various ROV dive-transects at the Mid-Atlantic Ridge during the James Cook expedition JC048. National Oceanography Centre, Southampton,
http://doi.pangaea.de/10.1594/PANGAEA.778187
Note: Data submitted to this database were collected during ROV video analysis, but are not included in this thesis.

A. J. Gooday, **C. H. S. Alt**, D. O. B. Jones, D. Shale, K. Marsden, M. D. Brasier. **in press.** The Ecology and Biogeography of *Discospirina tenuissima* (Foraminifera) in the Atlantic and Indian Ocean, Deep-Sea Research II (special issue).
http://dx.doi.org/10.1016/j.dsr2.2012.05.001
Note: I provided data on *Discospirina* density and distribution, and still frames of each observation for reference; this data is included in Chapter 4 as part of the video survey.

J. B. Bell, D. O. B. Jones, **C. H. S. Alt. in press.** Lebensspuren of the Bathyal Mid-Atlantic Ridge. Deep-Sea Research II (special issue).
http://dx.doi.org/10.1016/j.dsr2.2012.09.004
Note: Data on Lebensspuren were quantified by James Bell, during his Master Project. I provided the still frames of the flat transects, which had been extracted as reference for the ROV video survey presented in this thesis, and assisted in the analyses and write-up.

A. Rogacheva, A. Gebruk, **C. H. S. Alt. accepted.** Holothuroidea of the Charlie-Gibbs Fracture Zone area, northern Mid-Atlantic Ridge. Marine Biology Research.

Note: Data provided by me were collected during the trawl survey and included information on species distribution, abundance and size ranges, all of which have been discussed.

A. Rogacheva, A. Gebruk, **C. H. S. Alt. accepted.** Swimming deep-sea holothurians on the northern Mid-Atlantic Ridge. Proceedings of the 7th European Conference on Echinoderms/ Lecture Notes Proceedings.
Note: Data provided by me were collected during the ROV video survey and included details on observations of swimming holothurians during video analysis.

F.2 Manuscripts Submitted for Peer-Review

C. H. S. Alt, A. Rogacheva, B. Boorman, J. A. Hughes, D. S.M. Billett, D. O. B. Jones. Trawled megafaunal invertebrate assemblages of the Mid-Atlantic Ridge (48 ° - 54 ° N). submitted to Deep-Sea Research II (special issue).
Note: This publication is in largly based on Chapter 3 of this thesis.

D. O. B. Jones, **C. H. S. Alt**, I. G. Priede, W. D. K. Reid, D. S. M. Billett, A. V. Gebruk, A. Rogacheva, A. J. Gooday. The ecology of deep-sea surface-dwelling enteropneusts from the Mid-Atlantic Ridge. submitted to Deep-Sea Research II (special issue).
Note: I provided data on enteropneust density and distribution, and still frames of each observation for subsequent analyses; this data is included in Chapter 4 as part of the video survey.

F.3 Manuscripts in Preparation to be Submitted for Peer-Review

T. D. Linley, **C. H. S. Alt**, D. O. B. Jones, I. G. Priede. Bathyal Demersal Fishes of Charlie Gibbs Fracture Zone region of the Mid-Atlantic Ridge: III. Reasults from remotely operated vehicle (ROV) video transects. will be submitted to Deep-Sea Research II (special issue).
Note: I provided data on fish density and distribution, and still frames of each observation for subsequent analysis; this data is not included in this thesis.

I. G. Priede, O. A. Bergstad, P. I. Miller, M. Veccione, A. Gebruk, T. Falkenhaug, D. S. M. Billett, J. Graig, A. C. Dale, M. A. Shields, T. T. Sutton, A. J. Gooday, M. E. Innal, D. O. B. Jones, V. Martinez-Vicente, G. M. Menezes, T. Niedzielski, G. H. Tilstone, N. Rothe, A. Rogacheva, **C. H. S. Alt**, T. Brand, R. Abell, A. S. Brierley, N. J. Cousins,

D. Crockard, A. R. Hoelzel, . Hines, T. B. Letessier, J. F. Read, T. Shimmield, M. J. Cox, J. K. Galbraith, J. D. M. Gordon, T. Horton, F. Neat, P. Lorance. The significance of the northern Mid Atlantic Ridge in basin-scale oceanic ecology. will be submitted to PLoS ONE
Note: I provided biomass and abundance data for benthic megafauna, which were combined with fish data from the same region. I further provided data to determine the unique benthic megafauna at the MAR. All data provided for this paper have been included in this thesis, Chapter 3.

C. H. S. Alt, A. Rogacheva, H. Fortherby, L. Corrigan, H. Wiklund, C. Gubili, T.White, D. S. M. Billett, A. Gebruk, R. Hoelzel. Adaptive radiation of holothurians and clarification on their systematic relationships. to be submitted to Ecology.
Note: This paper is based on Chapter 6 of this thesis, but will contain additional information on morphological traits. Such traits are compared and analysed with the molecular data to identify morphological traits that reflect the evolutionary relationships of holothurians to one another most effectively.

C. H. S. Alt, A. Rogacheva, A. Gooday, D. O. B. Jones. Effects of habitat variability and patch dynamics on community composition in the deep sea. to be submitted to PNAS
Note: This paper will be based largely on Chapter 4, but substantially more analyses will be carried out before this paper is ready.

Finally, Chapter 5 is also intended for publication, highlighting the pros and cons of trawling and video analyses, but this will only be pursued after the other publications have been submitted.

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