Under pressure: macro-ecological patterns in the benthic macrofauna in the northwest Atlantic deep sea

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Table of Contents

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I declare that the work presented here is my own, performed under the supervision of Professor Alex D. Rogers. Chapter Two has been published as a scientific paper in Advances in Marine Biology, with contributions from my aforementioned supervisor. In the instances where others have contributed, such as the provision of some of the physical geography data in the NEREIDA study programme, the contributions have been specifically acknowledged in the acknowledgement section. I have clearly indicated and referenced where I have quoted and discussed others' work throughout the document. In addition, I can confirm this thesis has not been submitted for any other qualification at any institution.

I hereby confirm this thesis is submitted in fulfilment of the requirements for the degree of Doctor of Philosophy.

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Abstract

Deep-sea systems are understudied compared to any other ecological system on Earth, but they are important for ecosystem functioning and services. The deep sea is important in the climatic regulation of Earth, and it is a new frontier for resource provisioning for humanity. Impacts, such as increased carbon emissions and deep-sea fishing and mining will likely influence the system, but these effects are not well understood. To recognise these impacts, common patterns in community structure need to be understood. This study aims to assess community structure in the deep sea by looking at patterns in body size and biodiversity. It uses polychaetes (bristle worms) as a study group as they are the most abundant group in the benthic macrofauna in terms of density and play key roles in the food web.

Body size is an important component of the community structure, as body size is correlated with many other traits of the organism, from physiological rates (e.g. heart or breathing rates) to population dynamics (e.g. production rates or population abundances) and species richness. It is thought that body size of deep-sea (endo)benthic organisms declines with increasing depth, which is often related to food availability which itself declines with increasing depth. Many contradictory results on body-size change with increasing depth, however, have been reported, including no change, increasing, or a parabolic relationship. It is demonstrated here (Chapter 2) that there is much variety in body-size estimates between different geographic regions and taxonomic groups. These differences can ultimately influence the predictions of other traits, and might hint at what might happen in changing climatic conditions. It sets the basis to argue that there should be a focus on explaining why there are differences, instead of focusing on finding a general trend for organisms in all geographical regions. Furthermore, it is unlikely that food availability alone can explain a change in body size. An alternative explanation is offered (Chapter 3), where habitat complexity is shown to influence body size. Sponge density, in the form of habitat complexity, can have a structuring effect on the community potentially through the loss of spicules that add complexity to soft-sediments, and this in turn can influence body size of organisms.

Deep-sea community structure in terms of family richness has been studied at local spatial scale. Fewer studies have been performed on regional spatial scale and these studies lack extensive sampling coverage of environmental gradients. Here (Chapter 4), the first study is presented on the maintenance of deep-sea family composition on regional scale with high sampling coverage along a variety of environmental gradients. It is shown that energy (food) availability, habitat complexity, and long-term temperature are important in influencing the polychaete distribution in this region. It is shown that there is an unusual high proportion of an opportunistic group, the Capitellidae, present in the study area. Biodiversity is important for the maintenance of ecosystem functioning, but human impacts result in the restructuring of biodiversity. The first deep-sea biodiversity - ecosystem functioning relationship for macrofauna is presented (Chapter 5). It is shown that there is a positive and saturating relationship between biodiversity and ecosystem functioning. However, fishing intensity seems to influence this relationship by potentially affecting secondary biomass production, abundance and taxonomic and functional diversity measures. It is suggested that as the disturbance of fishing negatively impacts taxonomic and functional evenness, a system is created where opportunistic species are dominant, like communities found in disturbed areas such as under fish farms. This will have consequences for the state of the system and energy transfer to trophic levels higher up.

List of Figures and Tables

1. CHAPTER ONE:

Introduction

CHAPTER ONE

1.1 The deep sea

The deep sea is the largest biome on Earth because of its large surface area and volume. For example, 434 million km^2 of the Earth's surface is seafloor, of which 90% is present in the deep sea (Ramirez-Llodra et al. 2010; Danovaro et al. 2014). However, compared to any other natural system on Earth, it is understudied. This has partly historical reasons, partly technical reasons, and obviously the size of the biome itself brings its own difficulties.

The Azoic Theory, stating no life existed in the deep sea, was proposed in 1844 as a result of decreasing sampling success with increasing depth in the Aegean Sea (Forbes 1844). However, several expeditions, including *HMS Lightning* and *HMS Porcupine* in the Atlantic and Mediterranean in the late 1860s showed evidence that this theory was unlikely to be true. This resulted in the *HMS Challenger* global expedition from 1872 to 1876, which is often recognised as the start of modern oceanography and the start of the systematically exploration of the deep sea (Ramirez-Llodra et al. 2010).

The deep sea is a harsh environment; the expectation of no life being present here was not completely strange. However, many organisms have adapted to the unique conditions of this biome. The deep sea is characterised by darkness, low food availability, low temperatures (with the exception of hydrothermal vents), and high pressures (Gage and Tyler 1991). Photosynthesis is absent below a depth of roughly 200 m as light levels are not adequate for this process. There is no light present at depths deeper than 1000 m. The 200-m depth limit, which delimits the euphotic zone, is considered the boundary between shallow waters and deep waters. Below this zone, there are several systems, such as hydrothermal vents, cold seeps, and food falls, which have in-situ primary production. These are reducing environments, where chemosynthesis is used for the production of new organic material, and they will not be considered in this thesis as they are unique in biotic and abiotic conditions (Rogers 2015).

The deep sea is food limited as it depends on the euphotic zone for input of organic material. Food availability decreases with increasing depth as pelagic organisms and microorganisms consume the particulate organic carbon (POC) sinking down. A decrease in abundance and biomass of organisms with increasing depth can be observed, likely reflecting this change in food availability, with less food availability resulting in less abundance and biomass (Rex et al. 2006).

Coastal waters are more productive than the open seas and provide more resources for the deep sea. This means that food availability will also decrease with distance from land. Large riverine runoffs can have an impact on organic material delivery in the deep sea as their outflow can be traced up to 10s, even 100s kilometres from land (Rex and Etter 2010). This increased food availability closer to land is noted in higher abundances of deep-sea organisms closer to coastal areas (Rex and Etter 2010).

Processes occurring in surface waters, therefore, have cascading effects on deep-water populations through the sinking of organic carbon (Smith et al. 2008; Rogers 2015). The response of benthic communities, for example through changes in abundance or biomass to increased food influx, can be rapid (days to months) (Billet et al. 2010). There is indication that the stability in carbon flux can also play a large role in structuring deep-sea communities, where stable sinking rates lead to higher abundances in the benthic community, while highly variable sinking rates might result in lower abundances (Graf 1989; Ruhl and Smith Jr. 2004; Corliss et al. 2009).

Deep-sea benthic community abundance and biomass can be predicted relatively well on a large spatial scale from surface chlorophyll α, estimated downward flux and climatic variability indices of the region (Pace et al. 1987; Smith Jr et al. 2006; Johnson et al. 2007). Potentially, these benthic communities might be sensitive to large-scale climatic variability, such as El Niño and the North Atlantic Oscillation events, whereby the downward flux of organic carbon changes as a result of temperature changes at the sea surface. The sensitivity of the communities might be reflected in abundance or biomass or community structure (Ruhl and Smith Jr. 2004; Smith Jr et al. 2013; Kuhnz et al. 2014).

The deep oceans are cold. In most oceanic regions, the thermocline lies between 800 and 1,300 m depth, and deep waters usually do not vary much between 4°C and -1°C (Gage and Tyler 1991). The seafloor temperature, and salinity concentrations for similar reasons, are influenced by the flow of the water masses around Earth. These large water masses form either in the Arctic Ocean or in Antarctica. As a result, temperatures and salinity concentrations vary across oceans. Areas such as the Mediterranean and the Red Sea can have higher bottom temperatures (and increased salinities), as they are almost completely land-locked in a relatively dry climate, and this is reflected in the biological community (Gage and Tyler 1991).

One important aspect of the flow of the water masses around the world is the delivery of oxygen to deeper waters. At the sea surface, waters are well oxygenated and are in equilibrium with the atmosphere. When the water sinks, oxygen gets used by metabolic processes (Gage and Tyler 1991). Most of the deep oceans have high oxygen levels, but there are areas that have low levels (below 0.5 ml l^{-1}); these areas are called extreme Oxygen Minimum Zones (eOMZs), and they are common in the Bay of Bengal, the Arabian Sea, and the Eastern Pacific Ocean. These regions are characterised by high productivity, which supports a highly productive bacterial community in the water column. These bacterial communities reduce the oxygen content in the water as they breakdown organic material. Often, these oxygen-limited zones appear between 100 and 1000 m depth as a result of the bacteria, but they are spreading (both vertically and horizontally), potentially as a result of changing climatic conditions (Stramma et al. 2008; 2010). Organisms present in these eOMZs are usually less diverse and are smaller in body size (Woulds et al. 2007; Gooday et al. 2010b). eOMZs, however, might increase speciation in areas surrounding the low oxygen waters as a result of selective pressures and through acting as barriers to gene flow (i.e. allopatric speciation) (Rogers 2000).

1.2 Deep-sea sampling

The size and volume of the oceans make it logistically (and financially) difficult to take (many) samples. Compared to the sampling techniques used during, for example, the *HMS Challenger* Expedition, sampling efficiency and quality have improved. There are a variety of sampling techniques for deep-sea organisms. For example, remotely operated vehicles (ROVs) are robots that can sample targeted megafauna (larger than 1 cm) without much destruction to other organisms and can be used for qualitative sampling. Nets, sledges and dredges are used in an effort-search sampling format (i.e. time towed) and are a form of semi-quantitative/qualitative sampling, but do remain a destructive way of sampling for the physical habitat and fragile, gelatinous organisms. To sample smaller organisms (especially infaunal organisms) corers, such as box cores or mega- or multicores are used because they are quantitative sampling devices. They do influence the sampling of (epi)benthic organisms by creating bow waves when they hit the seafloor. Box cores create a larger bow wave than mega- or multicores do as box corers are large boxes, while mega- or multicores consist of many smaller corers together (Bett et al. 1994). Box cores are used as they can sample a larger area than multicores per sample, which is especially needed at deeper depths where the abundance of macrofaunal organisms becomes very low.

Sediment subsamples can be taken from core samples to do a variety of additional analyses (e.g. nutrient analyses, measurements of sediment physical parameters), which allows for the characterisation the local environment of the animals (Gage and Tyler 1991; Rex and Etter 2010).

1.3 Deep-sea macrofauna

The definition of macrofaunal organisms vary from author to author, but the sizes of these organisms usually range between 1 mm and 1 cm (Gage & Tyler 1991). They live in and on the sediment, often in the top 5 cm layer of the sediment. American programs usually use 300 µm sieve mesh sizes to sample macrofauna, while European studies more commonly use 250 µm as sieve size. Early studies, however, often used 500 µm studies. (Rex and Etter 2010). It is important to note that one standard size is not used by the deep-sea community consistently, however abundance and biomass estimates are roughly similar (Gage et al. 2002). Meiofauna are organisms that are smaller than 1 mm and sieve mesh sizes of 32 µm are used to collect these organisms, although in the past, 500 µm could have been used as well (see Chapter 2 for more detail).

In the soft-sediment macrofaunal community, polychaetes (bristle worms) are the most dominant organisms, followed by the peracarid crustaceans (isopods, amphipods, cumaceans, and tanaidaceans), and usually, in third place, are the molluscs (mainly bivalves and gastropods) (Gage and Tyler 1991). Polychaetes can constitute more than 50% of the community in terms of abundance. Polychaetes are segmented worms, and they are the most diverse and abundant class in the Phylum Annelida. They are strictly aquatic, and they move using bristles and hooks called chaetae. They are extremely variable in terms of form and lifestyle and they are ecologically important organisms in the community (Glasby et al. 2000; Brusca and Brusca 2003). For example, they play important roles in the food web, and they are a major group contributing to bioturbation. Most of the families are relatively well characterised, although evolutionary relationships not so, and there are still some groups that are of uncertain affinity (Polychaeta *incertae sedis*). Recently, the Siboglinidae, Echiura and Sipuncula where included in the Class Polychaeta after previously being considered separate phyla (Struck et al. 2007; Bourlat et al. 2008; Dunn et al. 2008; Struck et al. 2011). The Echiura and Sipuncula were excluded from this thesis, so that the results are more comparable to other studies looking at traditional polychaete samples.

A note must be made on the debate on what constitutes macro- and meiofauna. For example, juvenile polychaetes will be small enough to classify as meiofauna. Nematodes, normally included in meiofauna, can grow up to macrofaunal sizes. Furthermore, the two size classes used to overlap in their distinction, determined by sieve mesh sizes. In this thesis, polychaetes are considered to be macrofauna *sensu stricto,* where the organisms used are classified as macrofauna, even if they had fallen in the meiofaunal size range. In other words, the metazoan groups are defined based on taxonomy rather than size. This means that juvenile polychaetes that are often small enough small enough to be included in the meiofauna would have been included in the macrofauna. No juvenile organisms, however, were used in this thesis; the definition is added for clarity.

The biological samples used in this thesis were damaged and in most cases they did not constitute complete individuals. Most individuals were fragmented, with chaetae and segments missing or broken. This limits the identification to higher taxonomic resolution. It also means that biomass estimates are an underestimation. To ensure that individuals were not counted multiple times because of this fragmentation, only the heads were used in the identification process, unless only a butt was found. For Glyceridae, a different strategy had to be used; individuals were only counted when jaws could be discerned. All fragments were used in the biomass estimation.

1.4 Body size and deep sea

There is a maximum amount of energy that can be provided by and in a system (Gaston and Blackburn 2000). This ultimately depends on the sun (ignoring reducing systems). This maximum amount of energy also means that there is a limit to the number of organisms that can be supported in a system. The allocation of the energy into biomass and individuals will ultimately determine how many individuals and species can be supported in a system (Gaston and Blackburn 2000; Brown et al. 2004b). Energy availability is important in the species-richness distribution of deep-sea organisms, with different forms of energy determining patterns at different depths. For example, Woolley et al. (2016) demonstrate that thermal energy can be used to predict shallow-water ophiuroid richness in shallow-waters (shallower than 2000 m), while chemical energy determines richness patterns in waters deeper than 2000 m depth.

Individuals will differ in how much chemical energy they can convert to biomass, and this ability of energy allocation is determined by an organism's metabolic rate. Metabolic rates have often been shown to be proportional to body mass (Peters 1983). There is some debate on whether the power relationship found has an exponent of ¾ or ⅓, although there seems to be more support for the ¾ exponent (Brown et al. 2004a). More importantly, the power relationship means that larger-bodied organisms require more total energy compared to small-bodied organisms to survive and sustain their populations. This will influence where they can survive, and what functions they can provide in a system (Peters 1983; Gaston and Blackburn 2000).

Body size is an interesting feature in an organism as it can be used to predict many other traits of the organism (Peters 1983). For example, physiological rates, like heart rate and oxygen consumption, are strongly correlated with body size. Life-history characteristics can be predicted from body size. Larger organisms, for example, tend to reproduce less often, tend to reproduce later in life, and tend to produce less offspring per litter compared to smaller organisms. Ecological predictions can also be made from body size. Rates of nutrient cycling, species richness patterns, and other factors can all be influenced by the size of the organisms in a community (Brown et al. 2004b). The mechanism that influences the change in body size is not well understood (Gaston and Blackburn 2000). Many hypotheses have been proposed, all predicting a change in size under different conditions (Allen et al. 2006). Only one hypothesis, the energetic hypothesis, which states that body size should increase when energy availability increases, has been suggested and tested for the deep sea (McClain et al. 2012). McClain et al. (2012) tested the influence of chemical energy (organic carbon) and thermal energy on individual level, such as metabolic rate and body size, and community level, such as abundance and biomass. Specifically, they show that chemical energy, not thermal energy, can be used to predict body size, with greater fluxes leading to larger organismal sizes. However, other studies on body size with depth have shown contradictory results; correlations included positive, parabolic and no correlations (Rex et al. 1999; Vanhove et al. 2004; McClain et al. 2005), highlighting the need to explore other hypotheses as well.

1.5 Biodiversity in the deep sea

Quantitative sampling at local spatial scales has shown high species richness in the soft-sediment macrofaunal community. The samples are characterised by high evenness, with many rare species being present in the community as singletons (Gage and Tyler 1991; Rex and Etter 2010). For example, Grassle and Maciolek (1992) found that in more than 200 box core samples, no species was represented by more than 10% as a proportion of the whole fauna combined, and most species constituted less than 1% in the total faunal abundance. The high species richness is unexpected in an energy-limited and harsh ecosystem according to ecological theory. Furthermore, soft-sediments do not seem to have many different niches available, especially as most deep-sea soft-sediment macrofaunal species are deposit-feeders (Dayton and Hessler 1972). Although there is evidence of particle size selectivity in feeding behaviour in the community, it alone cannot explain the high richness in the benthic community.

A parabolic relationship between depth and species richness has been found for several taxonomic groups (for example, gastropods, protobranch bivalves, polychaetes, cumaceans, and fish), in different areas around the world (North Atlantic, Gulf of Mexico, Norwegian Seas), with the peak in bathyal (1000 – 4000 m depth) areas, and lower diversity in the abyssal (4000 – 6000 m) depths and on the continental slope (200 – 1000 m depth) (Rex and Etter 2010). It is unknown what causes this pattern, but it has been suggested that it could reflect energy (food) availability at deeper depths. Population densities and population growth are determined by the amount of energy that is available in the system, and in turn this can affect diversity trends at deeper depths (Brown et al. 2004b). At shallower depths, it is possible that ecological interactions result in lower diversity, if competition is very strong. For example, in the northeast Atlantic it seems that predation and current velocity have an effect on communities on the slope, while patch-dynamics structured communities deeper than 1800 m (Paterson and Lambshead 1995). It is possible that the parabolic relationship between depth and species richness in the deep sea is therefore a diversity-productivity relationship (at large spatial scales). In terrestrial systems, such as on mountain slopes, diversity-productivity relationships have been observed (Rex and Etter 2010; Cox et al. 2016b) .

It is unknown how many species there are on Earth. Current estimates vary from 300,000 to 2.2 million species. Perhaps more than 90% of marine species still wait discovery and description (Mora et al. 2011). What maintains species richness in the deep sea is not well understood, but there are several factors suggested. These include factors such as food availability, current speed, oxygen levels, and physical and biological disturbance (Levin et al. 2001). It is possible that spatial scale perceived by the organism itself (the ambit), will determine how habitat heterogeneity influences diversity (Tews et al. 2004). Disturbance events might open new patches for organisms to come into. It is thought that colonization of free patches occurs mainly by organisms in larval stages, and the settlement of larvae is influenced by the strength of disturbance events (Smith and Brumsickle 1989). Disturbance events, such as turbidity flows or benthic storms, can influence taxonomic evenness; in areas with frequent storms there may be less evenness in taxonomic groups (Thistle et al. 1985; Smith et al. 1986).

Habitat heterogeneity can be measured as habitat complexity in physical structures and in the complexity provided by other organisms. For example, the presence of seamounts increases biodiversity, with abundance, biomass, and biodiversity increasing at a seamount compared to background diversity. Furthermore, habitat complexity can be present at different scales. Seamounts present complexity at a large spatial scale, while particle size diversity represents habitat complexity at a very fine spatial scale. Particle size diversity has been shown to correlate positively with species richness in the deep sea (Etter and Grassle 1992). Together, factors acting at varying spatial scales structure the community and influence biodiversity patterns observed locally and regionally. Many studies in terrestrial and aquatic environments have also shown that there is a positive correlation between physical habitat heterogeneity and diversity (Baker et al. 2012; Cox et al. 2016a). Habitat complexity can be created by other organisms, often referred to as ecosystem engineers, as they modify the habitat they are in (Jones et al. 1994). Such organisms in marine systems include corals, sponges, and sea pens. The diversity of these ecosystem engineers might not influence associated richness, but biomass and/or density might (Heck Jr. and Wetstone 1977). Ecosystem engineers increase small-scale habitat complexity. Larger structures, such as seamounts and canyons, can influence the presence of structure-forming organisms, for example through the influence of these physical structures on current regimes, resulting in high numbers of filter-feeding species present in the area (Genin et al. 1986).

There are several ideas proposed of what may maintain species richness in the deep sea (e.g. Levin et al. 2001), but actual tests with adequate sampling coverage of many environmental gradients are missing. It is necessary to understand the natural processes that structure species richness, especially when anthropogenic stresses (such as fishing or mining) will have an unknown impact on the community (Rogers et al. 2015).

Biological diversity, or biodiversity, is an umbrella term for the variety of life. The term includes genetic diversity, species diversity and ecosystem diversity. Additionally, it can be measured over different spatial (indicated by, for example, alpha, beta, and gamma diversity) or temporal (for example, annual or decadal) scales. Studies often use a subset of these components to characterise diversity. To add to the confusion in the literature, taxonomic richness and biodiversity are often used interchangeably. This thesis will make the distinction between taxonomic richness and biodiversity, with richness meaning number of taxa (in this these: family richness), and biodiversity constituting taxonomic richness and the abundance of these taxa. It will be indicated as much as possible where each of these terms is used to avoid confusion. The samples have come from box core samples, and represent alpha (local) diversity at the place of sampling. Together, the samples represent patterns at regional scale. Several environmental variables have been taken from the box core samples itself, others are modelled over a larger spatial scale, with subsampling for the specific box core locations. Throughout the thesis, which of these environmental variables are used and how they were obtained will be clarified in the method sections.

1.6 Biodiversity and ecosystem functioning

The diversity of life is involved in the flow of material and energy through ecosystems. The flow of energy and material fall under the umbrella term of ecosystem functioning. Functions in the system that are important to human wellbeing are called ecosystem services. A healthy system will be able to sustain its ecosystem functioning as the variety of species present will contribute to the flow of energy and material in the system. Species will vary in their contribution to this flow, depending on what functions they provide and at what rate. This means that when species are lost, the functioning of the natural system might decrease in rate or disappear completely.

The loss in function of a natural system is often not noticed immediately. The most common relationship between biodiversity and ecosystem functioning is positive and saturating, as some species provide the same function(s) (Cardinale et al. 2006). When a species is lost, others might still provide the same function. This is called the insurance effect or redundancy, whereby a species can provide another species' role in the system when the other species is lost (Naeem and Li 1997). However, if too many species are lost, this will have a noticeable impact on ecosystem functioning. Species are not equal in their roles in providing ecosystem function; they are adapted to different niches (i.e. they have different sets of functions, and/or providing the functions at different rates). The loss of some species might have cascading effects on other species (secondary extinctions).

CHAPTER ONE

Humans depend on ecosystem services (for example, water purification, food provision, material production, and climate regulation) for their wellbeing (Armstrong et al. 2012). As such, there is an appreciation for the conservation of biodiversity and its functioning (Millennium Ecosystem Assessment 2005). In order to adequately conserve systems and their functions, there is a need to understand the relationship and the mechanisms behind it. There has been an increase in interest in biodiversity – ecosystem functioning (BEF) relationships in the last decades. Most studies performed to increase the understanding in the BEF relationship have been done in experimental settings of terrestrial or shallow-water environments. Two mechanisms behind the BEF relationship have been proposed based on these experiments: the selection effect and the complementarity effect (Loreau and Hector 2001). The selection effect suggests that a high-functioning (for example, productive) species is increasingly likely to be included in the species pool when there are more species present. It would also suggest that, for example, the highest productivity in a system depends on the inclusion of the most-productive species. That is, the total productivity of the community would be similar to the productivity of species in monoculture, with the most productive species producing the bulk of the material. The complementarity effect, on the other hand, suggests that the functioning of the system increases as resources in the system are used up more completely. As more energy enters the biological system (rather than being unused), more biological material is produced. This mechanism is characterised by niche complementarity, and positive species interactions are more likely to occur when many species are present in the species pool.

The biodiversity – ecosystem functioning relationship has been understudied in the deep sea, and indicates a need for further exploration in this area. One study, for example, that has been performed, focusing on nematodes, showed an exponential increase in functioning with increasing species richness, which contrasts with the general positive and saturating relationship often observed in terrestrial environments (Danovaro et al. 2008). Perhaps the deep sea is a unique system, and positive species interactions are more important here

(Danovaro et al. 2008). However, that there are very limited studies on the BEF relationships to date might also suggest that Danovaro et al.'s trend might not be representative for the rest of the deep-sea biome, and potentially might be a result of selected methods and limitations. The samples used by Danovaro et al. (2008) had low species numbers. It is possible that studies that look at richer systems will show a slowdown in the BEF relationship and a saturation point; in other words, the positive and saturating relationship often observed in other systems.

1.7 The deep sea and humanity

Oceans are important for humanity as they play important roles in climatic control through the exchange of relevant gases, the exchange of water, and the storage and transport capacity of heat content (Riebesell et al. 2009; Armstrong et al. 2012). The deep sea is important in resource provision, climate regulation, and it has been suggested as a place to dispose of waste (Ramirez-Llodra et al. 2011). However, the oceans are changing in response to the changing climate and human resource exploitation. The increase in carbon emissions has changed atmospheric CO_2 concentrations, with consequences for the CO_2 concentrations in the oceans, and air and water temperatures. Deep-sea fishing is increasing as shallow-water stocks are declining and collapsing in order to provide food for the world (Roberts 2002).

The uptake of atmospheric CO_2 by the oceans influences the balance of calcium carbonate as CO_2 reacts with water molecules to form carbonic acid. Carbonic acid (H_2CO_3), in turn, is in equilibrium with an intermediate form of bicarbonate (HCO_3^-) that then forms into carbonate ions (CO_3^{2-}), which can form calcium carbonate ($CaCO_3$). When CO_2 concentrations in the oceans increase, the balance is shifted, in that the availability of carbonate ions will be reduced and the availability of bicarbonate and hydrogen atoms are increased (Doney et al. 2009). The increase in hydrogen atoms decreases the pH of seawater. The pH of the oceans has dropped since the onset of the Industrial Revolution in the late 18th Century, with a greater reduction predicted in the future (Orr et al. 2005; Cao and Caldeira 2008; Doney et al. 2009). A change in pH will have an impact on organisms, such as molluscs, corals and crustaceans, who use calcium carbonate for the production of their skeleton (Fabry et al. 2008). The increase in CO_2 concentration also affects early development of many invertebrates, with complications occurring more often at higher CO_2 concentrations (Kurihara 2008). It is possible that under higher CO_2 levels there will be winners and losers in the oceans; for example, calcifying sponges that use aragonite or high-magnesium calcite for their skeleton might suffer under high carbon dioxide concentrations (Smith et al. 2013). Another example can be seen in phytoplankton: agglutinated and thecate foraminifera do not seem impacted in survival by experimentally elevated CO_2 levels, while calcareous foraminifera suffered higher mortality (Bernhard et al. 2009). A change in community composition of phytoplankton in response to changing carbon dioxide levels in the oceans is likely, and with that a change in transfer efficiency of carbon to deeper waters (Buesseler et al. 2007; 2008). Benthic organisms are likely to be impacted as well, but how is not well understood yet (Rogers 2015). For example, scleratinian corals and octocorals, important structure-forming organisms in the deep sea, are influenced by calcium carbonate concentrations, and a change in the availability of calcium carbonate will influence their distributions (Rogers 2015).

It is thought that the oceans are increasing in temperature. This is not an easy feat to demonstrate; for example, the method of measurement has shown to be influential on the estimates (Gouretski and Koltermann 2007; Barker et al. 2011). Newer models that have reduced the measurement bias still show an increase in temperature (Giese et al. 2011). Furthermore, not all oceanic areas have been sampled (the Southern Ocean, for example, has been under-sampled), which leads to different approaches of estimation in these areas (Domingues et al. 2008; Lyman and Johnson 2008; Levitus et al. 2012). These different approaches can have substantial outcomes in predictions (Gleckler et al. 2012). In better-sampled areas, however, estimates for temperature change agree (Xue et al. 2012). Overall, estimates seem to agree on the warming of waters at depths to 700 m. Depths deeper than this have been sparsely sampled, but here it seems that temperatures are increasing as well (Rhein et al. 2013).

Marine organisms, like those in other systems, either need to adapt to these changing environmental conditions, go (locally) extinct, or change distribution. Distribution shifts have been observed in response to temperature changes affecting physiology, reproduction and dispersal (Poloczanska et al. 2013); many fish species in the North Sea are following temperature changes northward. Species invasions at higher latitudes are predicted for fish and invertebrate species, while local extinctions might occur in the tropics and sub-polar regions (Beaugrand et al. 2002; Cheung et al. 2009). For example, Cheung et al. (2015) show that community structure of pelagic fish in the northeast Pacific at shelf depth are likely going to change. These species are expected to expand their ranges poleward, while there will be a range contraction at lower altitudes. With these changes, a dominance of warmer-water species is likely to establish in these higher-latitudinal regions, whereby the changes might have ecological and socio-economic consequences through trophic effects and shifts in fishing grounds (Cheung et al. 2015). There are signs that an increase in ocean temperatures affect global fisheries catches (Cheung et al. 2013). The fish species that change distribution often are smaller in size (with faster life cycles) compared to the species that stayed at their original distribution (Perry et al. 2005).

Temperature changes might affect the plankton community composition and size, with likely cascading consequences for organisms that depend on them. It has been shown that the picoplankton community is decreasing in size in response to increasing temperatures, with associated changes in primary production. The smaller the picoplankton, the lower their export primary production (Morán et al. 2010). Plankton communities have been shown to have changed in composition as a result of changes in oceanic temperatures (Beaugrand et al. 2002). Such changes can result in regime shifts across trophic levels (Beaugrand et al. 2008; Kirby and

Beaugrand 2009). Sinking rates of carbon to deeper waters may be impacted as well when temperatures rise by affecting the biological carbon pump (Wohlers et al. 2009).

Increased sea surface temperature can lead to increased stratification and thereby nutrient availability, resulting in changes in the flow of energy and material (Doney et al. 2012). In some areas, like the Peruvian upwelling system, upwelling may intensify as a result of wind-driven oceanic processes through changes in thermal low-pressure areas, thereby highlighting the complexity of prediction changes associated with temperature increase (Bakun et al. 2010). Warmer waters contain less oxygen and thus might have an influence on the development, stability, and expansion of eOMZs (Keeling et al. 2010). Whether primary production is going to increase or decrease as a result of all these effects is controversial, with studies showing contradictory results (Rogers 2015). It is likely that the ratio between primary production and community oxygen consumption, and the quality of the carbon sinking down, will change (Rogers 2015).

Deep-sea organisms are not resilient against anthropogenic resource exploitation practices such as fishing. Many organisms in the deep sea have adapted to the cold and stable environment at the seafloor. Two typical differences in this biome compared to shallow-waters is the metabolic rate, and likely as a consequence of that, the longevity of organisms. The metabolic rates in deep-sea organisms are much lower compared to shallow-water organisms; this is useful for life at these depths as it means that these organisms are using less energy per unit time. They live life at a slow pace. As a result, deep-sea organisms can become much older compared to shallow-water organisms. For example, orange roughy (*Hoplostethus atlanticus*) can live more than 100 years old, several coral taxa can reach more than 1000 years old, and a sponge has been found to be around 11,000 years old (Fenton et al. 1991; Jochum et al. 2012; Prouty et al. 2015). However, recruitment levels are also low. For example, fish lay fewer (but larger) eggs. Deep-sea fish may not mature before they are 25 years old. As a result of this low recovery potential, deep-sea fishing has been referred to as mining fish (Roberts 2002).

Furthermore, in some deep-sea fisheries a large proportion of the organisms caught in trawls are bycatch. These organisms are fish or other organisms such as corals that are not consumed by people. Animals caught as bycatch often suffer 100% mortality rates as a result of nets that cut into the organisms and rapid changes in environmental conditions when brought up to the surface (Roberts 2002). Furthermore, trawling impacts the physical area by increasing homogeneity in the soft-sediment environment. It has been suggested that recovery times of the system may be over 100 years (Koslow et al. 2000; Puig et al. 2012; Pusceddu et al. 2014).

1.8 Study area – Flemish Cap, Flemish Pass, the Grand Banks and the NEREIDA programme

The Flemish Cap, the Flemish Pass, and the Grand Banks are located east and southeast from Newfoundland, Canada (figure 1.1). The Flemish Cap, in the northeast of the study area, is a shallow seamount with a minimum depth of 126 m. To the west and southwest of it are the Grand Banks, a flat area with a long history of fishing (Durán Muñoz et al. 2012). The Flemish

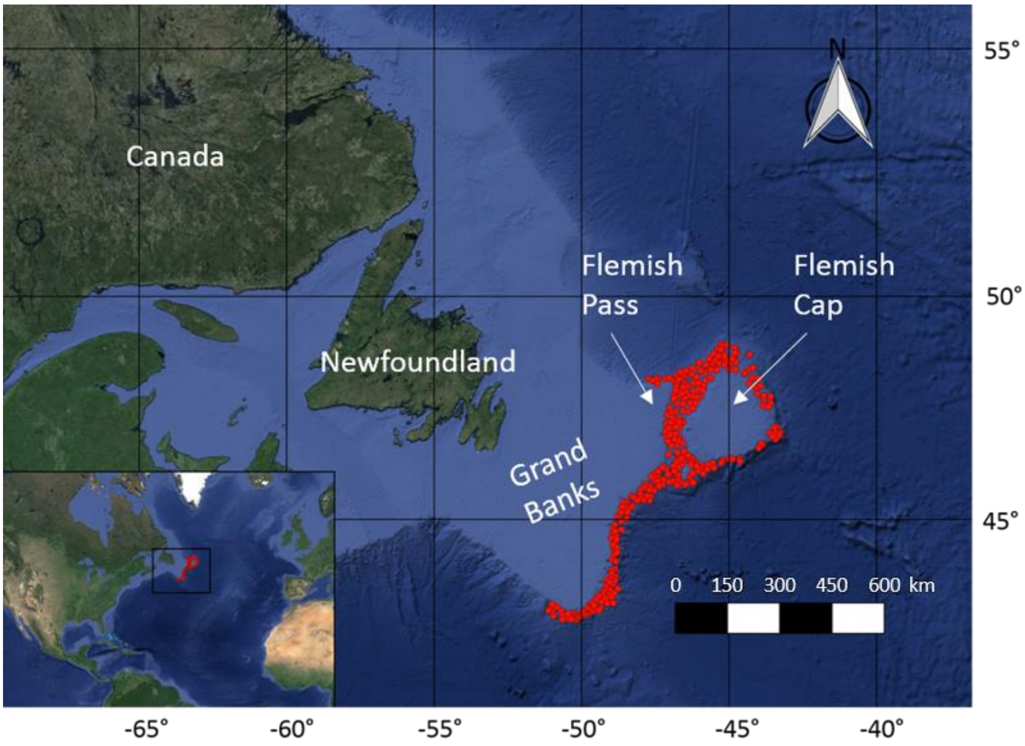

Figure 1.1 The Flemish Cap and Grand Banks, separated by the Flemish Pass, are located east, southeast from Newfoundland, Canada. The red circles indicate the sampling locations.

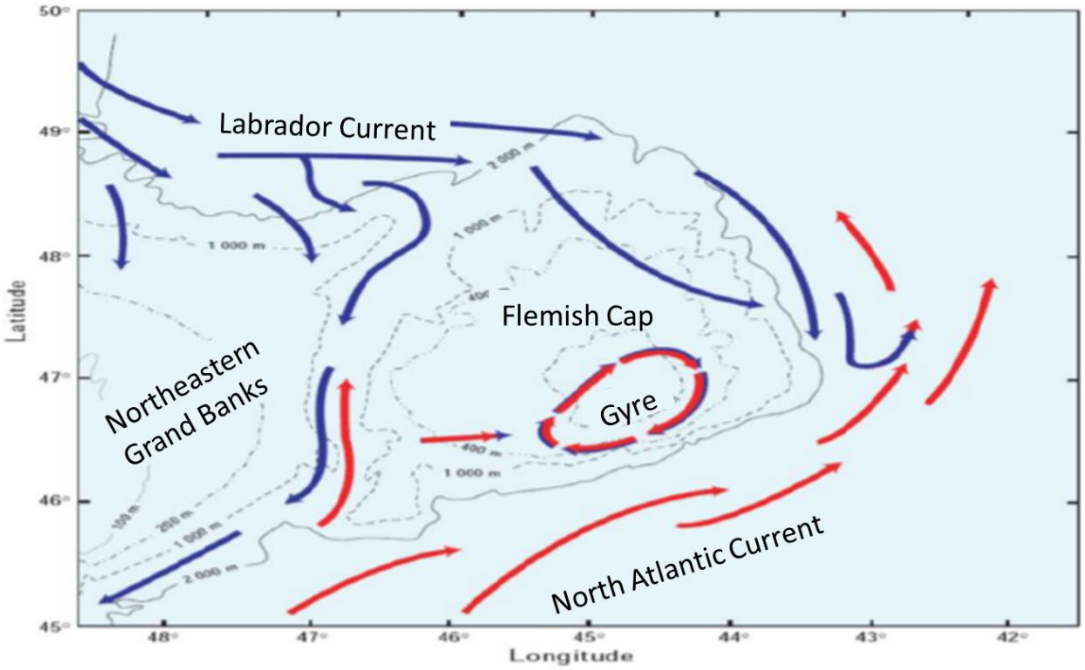

Figure 1.2 A map showing the Labrador Current (blue) coming in from the North, while the North Atlantic Current (red) comes up from the South. A gyre is formed over the Flemish Cap. Adapted from Colbourne and Perez-Rodriguez (2015).

Cap and the Grand Banks are separated from each other by the Flemish Pass (maximum depth 1100 m). The Labrador Current, coming from the North, brings cold water via side branches of the current into the Flemish Pass. The North Atlantic Current brings warmer water up from the South. There is a topographically induced anticyclonic gyre over the Flemish Cap in the summer, when strong wind forcing is reduced or absent (see figure 1.2) (Colbourne et al. 2014). Between the early 1990s and 2014, there has been an increasing trend in temperature around the Flemish Cap, with the exception of 2009 (Colbourne et al. 2009; 2014). The temperature trend was found at the sea surface and up to 100 m depth. The increase in temperature is possibly a result of the North Atlantic Oscillation, which has been higher than average at this time period compared to the years before (Colbourne et al. 2014).

The Flemish Cap and part of the Grand Banks are outside the Economic Exclusive Zone of Canada, the 200-mile boundary from land. As such, the regulation of the exploitation of this area is done by the North Atlantic Fisheries Organisation (NAFO). The history of fisheries in this area is one of inaccurate statistics; catches that were higher than national quotas set by NAFO, unreported catches, and unregulated catches (catches from non-member countries) (Vázquez et al. 2013). Since the 1950s, the Flemish Cap has been fished, resulting in changes in abundance and biomass of commercially- and non-commercially (i.e. bycatch) fished species (Pérez-Rodriguez et al. 2012).

Based on fish data, there seem to be two ecoregions in the Flemish cap region, with a distinct community in the central-south area (shallower area), and a northern (deeper) community (Pérez-Rodriguez et al. 2010). Furthermore, there are several distinct sponge communities present in the Flemish Pass and Flemish Cap, with at least 30 species of sponge in the whole area: on the continental slopes, there are mainly axinellid and polymastid sponges present, while in the Pass there are geodiids and *Asconema* sp. present (Murillo et al. 2012; Beazley et al. 2013). Sponges are vulnerable to trawling, and trawled areas have less sponge biomass present compared to non-trawled areas. Sponges break nets, as they contain sharp spicules, thus fisheries want to avoid them. Sponges are indicator species for Vulnerable Marine Ecosystems (VMEs), like corals and sea pens (Murillo et al. 2012). It is often not known where VMEs are present, and as part of the precautionary approach adopted in the UNGA 61/105 the move-on rule is implemented. This rule states that fishing boats in the NAFO area need to move two nautical miles when they catch more than 800 kg of sponge (Auster et al. 2011).

VMEs are characterised by diverse communities at the seafloor. They are often distributed in small patches, with a limited distribution. Species in these communities can be rare, endangered, and/or endemic, often with high associated diversity on and around them (FAO 2009). This might be caused by an increase in local food availability provided by the sponges or corals, they might provide living spaces, and offer protection against predation, they play important roles in carbon, nitrogen, and silicon cycling and thereby provide an important link for bentho-pelagic coupling (Maldonado et al. 2005; Bell 2008). Their presence has a significant impact on complexity in the surrounding area, especially in soft-sediment areas. It is thought that the importance of habitat-forming organisms increases with depth as physical environmental complexity decreases with depth (Buhl-Mortensen et al. 2010).

The NAFO NEREIDA (NAFO PotEntial VulneRable Marine Ecosystems-Impacts of Deep-sea Fisheries) programme was organised in response to the United Nations General Assembly (UNGA) 61/105 Resolutions on sustainable fisheries. It was a multidisciplinary programme, involving Canada, Spain, United Kingdom, and Russia. The presence of sponge grounds and other VME indicator species found during the expeditions of this programme resulted in the closure of several areas to bottom fishing practices (Rogers and Gianni 2009; Durán Muñoz et al. 2012; Murillo et al. 2012). Closure of areas to bottom-contact fishing practices have effect in shallow-waters: it has been shown that overfished areas can bounce back to their original state, but they need long periods of time (Worm et al. 2006; Frank et al. 2011). In the deep sea, this likely will take more time (if it happens at all) compared to shallow-water systems as a result of slow growth, extreme longevity and late maturation and low fecundity (Clark et al. 2016b). Many studies using the NEREIDA data have focused on fish and/or sponges data, and only one has looked at smaller (macrofaunal) organisms, and this with respect to the closed areas (Barrio Froján et al. 2012).

This thesis uses the NEREIDA samples to assess community structure of the polychaete community, an important benthic group. Two aspects of community structure were focused on: body size and biodiversity. Body-size patterns can be informative for organismal-environmental interactions, allowing indications of what potentially shapes community assembly and its persistence in a system. Other aspects of an organism or population can also be predicted from the organism's body size, such as individual biomass production, ontogenetic growth rates, survival and mortality rates, population density, population growth rates, diversity, species interactions, standing stock, energy flux or turnover, trophic dynamics, and the rates of nutrients cycling (Brown et al. 2004b; Allen et al. 2006). How and why body size, either of specific organisms or the community as a whole might change in the deep sea is not well understood. It is thought that organisms decrease in size with increasing depth, but whether this is the same everywhere is unknown. Chapter 2 addresses the variability of body-size variation between different geographic regions and taxonomic groups, and how this might influence community estimates of size. No slope analyses between different areas or taxonomic groups could be done because of limited data, but it does highlight the variability and thus opens the discussion of further research for winners or losers under changing climatic conditions. Furthermore, the work is presented with a critical discussion of sampling influences on body-size estimates, highlighting the need this needs to be standardised urgently in the deep sea.

Body-size change in the deep sea has only been discussed in terms of energetics (i.e. food availability), where body size decreases as a result of decreasing food availability. This explanation has been met with contradictory results, showing no relationship, positive relationships, or parabolic relationships (Rex et al. 1999; Vanhove et al. 2004; McClain et al. 2005). As such, it is likely that other factors play a role, which are in need to be studied. Chapter 3 offers a different mechanism not studied in the deep sea before that might explain changes in benthic macrofaunal sizes.

There is a high diversity observed in the deep sea, going against theoretical predictions. The deep sea, with is harsh living conditions, would be expected to have low taxonomic richness. It is important to know how community composition is structured in the deep sea, or, in other words, what influences macrofaunal community composition (richness and abundance distributions), to start understanding what and how communities change because of environmental disturbance or human disturbance. Chapter 4 tests the polychaete community composition in relation to well sampled environment gradients and thus will allow to elucidate environmental patterns that could potentially drive observed patterns in benthic organisms. The data presented is at family level, rather than species level. Family patterns are important on their own, as species within a family can behave relatively similar. For example, Capitellidae species are indicator species, and a change in this family is therefore informative. Patterns structuring family distribution can be important for directing research to studying particular areas or groups in more detail.

The biodiversity – ecosystem functioning relationship has gained much attention as an argument for conservation. This relationship has been understudied in the deep sea, with only meiofaunal nematodes used. Furthermore, the shape of the relationship contradicted each other, with one study showing no relationship (Leduc et al. 2013), while another showed an exponential increase (Danovaro et al. 2008). Both of these studies are very different to the more common one found in terrestrial and shallow-water experiments, namely positive and saturating (Cardinale et al. 2006). This thesis aims to address these contradictions. It is the first BEF study performed on deep-sea macrofaunal organisms. In natural systems, the diversity present is dependent on the environment. Anthropogenic actions, such as bottom trawling, can restructure the community and thus also has an influence on community structure. As such, any biodiversity – ecosystem functioning study in a natural system should incorporate these effects. In Chapter 5, a model is presented to incorporate these effects on and with the biodiversity – ecosystem functioning relationship. A structural equation model has been used to capture the network-like structure of the environment, the diversity components, and bottom trawling.

CHAPTER ONE

2. CHAPTER TWO:

Body size versus depth: regional and taxonomical variation in deep-sea meio- and macrofaunal organisms

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2.1 Abstract

Body size (weight per individual) is an important concept in ecology. It has been studied in the deep sea where a decrease in size with increasing depth has often been found. This has been explained as an adaptation to food limitation where size reduction results in a lowered metabolic rate and a decreased energetic requirement. However, observations vary, with some studies showing an increase in size with depth, and some finding no depth correlation at all. Here, we collected data from peer-reviewed studies on macro- and meiofaunal abundance and biomass, creating two datasets allowing statistical comparison of factors expected to influence body size in meio- and macrofaunal organisms. Our analyses examined the influence of region, taxonomic group and sampling method on the body size of meiofauna and macrofauna in the deep sea with increasing depth, and the resulting models are presented. At the global scale, meio- and macrofaunal communities show a decrease in body size with increasing depth as expected with the food limitation hypothesis. However, at the regional scale there were differences in trends of body size with depth, either showing a decrease (e.g. southwest Pacific Ocean; meio- and macrofauna), or increase (e.g. Gulf of Mexico; meiofauna only) compared to a global mean. Taxonomic groups also showed differences in body size trends compared to total community average (e.g. Crustacea and Bivalvia). Care must be taken when conducting these studies, as our analyses indicated that sampling method exerts a significant influence on research results. It is possible that differences in physiology, life-style and life-history characteristics result in different responses to an increase in depth and/or decrease in food availability. This will have implications in the future as food supply to the deep sea changes as a result of climate change (e.g. increased ocean stratification at low to mid latitudes and reduced sea ice duration at high latitudes).

2.2 Introduction

Body size (weight per individual) is one of the most important properties of an organism as it is related to, and can be used to predict, many other co-varying characteristics, such as physiology, life-history, and ecology (Peters 1983). The relationship between body size and abundance can link individual- and population-level species traits with the dynamics and structure of ecological communities (Woodward et al. 2005). Furthermore, body size is a determinant of resource use as it is related to metabolism, and thus can aid in predicting resource partitioning (Brown et al. 2004b). Body-size relationships have been extensively studied in terrestrial environments, but less so in the oceans and in particular the deep sea (depths greater than 200 m). The deep sea is the largest ecosystem on Earth and is increasingly recognized as important in global biogeochemical cycling (Dunne et al. 2007; Giering et al. 2014). Benthic ecosystems, especially those of ocean margins, are important in carbon burial (Dunne et al. 2007) and can have remarkably high levels of biodiversity, especially considering they are generally recognized as food-limited environments (Grassle and Maciolek 1992). Body size and temperature have been identified as having a significant influence on the metabolic rate of deep-sea organisms, as well as on aspects of life history such as longevity and population turnover (McClain and Barry 2010) supporting the Metabolic Theory of Ecology (Brown et al. 2004b).

Since the 1950s, quantitative sampling and ecological investigation in the deep sea have documented general patterns in community structure and functional ecology (Gage and Tyler 1991). One of the most widely recognized of these patterns is the decline in community biomass and abundance, and individual body size, with increasing depth and decreasing surface-derived particulate organic matter, in other words food (Rex et al. 2006; Wei et al. 2010b). Understanding how such patterns of community attributes and organismal traits vary both spatially and temporally is important to understanding how climate change effects, such as ocean warming, and other human impacts, like deep-sea trawling, may influence ecosystem function within these communities, ultimately with implications for predicting changes in the biological cycling of important nutrients within the Earth system.

Early work in deep-sea ecology resulted in the recognition of two trends of body size with increasing depth: dwarfism and gigantism (Jones 1969; Thiel 1979; Thurston 1979; Pfannkuche 1985; Schwinghamer 1985; Shirayama and Horikoshi 1989; Soetaert and Heip 1989; Pequegnat et al. 1990; Rowe et al. 1991; Rex and Etter 1998; Galéron et al. 2000; Danovaro et al. 2002; Berkenbush et al. 2011). Of these two, dwarfism is thought to be more common (Madsen 1961; Thiel 1975; Pfannkuche 1985; Soetaert and Heip 1989; Rex et al. 2006). Rowe & Menzel (1971) are often acknowledged as the first to have quantitatively demonstrated the trend of decreasing body size with increasing depth. Their results, however, showed no significant decrease in body size with increasing depth; rather, they accepted the hypothesis that the slope of decreasing abundance with increasing depth was different from the slope of decreasing biomass with increasing depth based on a non-significant p-value (P=0.13). The trend of no change in body size with increasing depth has been supported by some studies for macrofaunal and meiofaunal organisms (Polloni et al. 1979; Shirayama 1983; Vanhove et al. 2004), whilst other studies have found an increase in size (Alongi 1992; Rex et al. 1999). Alternatively, parabolic patterns of body size with depth have been observed as well (McClain et al. 2005). This variety of trends may indicate that there is no general rule; rather, we should look to explain the observed differences.

The conflicting results may reflect differences in oceanographic regions. Many studies present their data and trends as a universality, rather than as a local or regional phenomenon in ecology. However, when regions differ in food availability, for example if food is vertically transported or laterally advected or is subject to resuspension in different parts of the continental slope (Dell'Anno et al. 2013), then changes in body size may not correlate with depth. There are also potential regional variations in the efficiency of transfer of surface primary production to the deep sea (Buesseler et al. 2007).

If there is a taxonomic signal in body size, then changes in the taxonomic composition of communities as a result of changes in depth or other physical parameters (e.g. sediment grain size; (Rohal et al. 2014)), could also influence estimates of average community body size. Community composition is expected to differ in space and time, and this has been observed (Blake and Grassle 1994; Cosson-Sarradin et al. 1998; Flach and de Bruin 1999; Ruhl et al. 2008; Billett et al. 2010; Danovaro et al. 2010). Varying community composition can have contrasting influences on the nutrient recycling and carbon burial of a particular region, for example through differences in bioturbation potential (Dauwe et al. 1998; Braeckman et al. 2011).

Two size classes often studied in the benthic marine system are the meiofauna and the macrofauna. A rough distinction between the two is that macrofauna can be seen when they are lying in your hand, but are not visible in pictures of the environment; meiofauna require microscopes to see them. A more scientific distinction is the range of sieve mesh sizes that can be used to separate them. In older studies, sieve mesh sizes as small as 500 µm were used for macrofauna, but today 250 µm (Europe) or 300 µm (USA) are more often used (Rex and Etter 2010). A sieve mesh size used for deep-sea meiofauna is 32 µm (Soltwedel 2000). In earlier studies, however, sieve mesh sizes in meiofaunal studies have included 500 µm, showing that the two are not always well separated. Furthermore, juvenile macrofauna can be captured on meiofaunal sieve mesh sizes, while large meiofauna can be retained on 300 µm. For example, some agglutinated foraminiferans can grow up to 10 cm (Gooday et al. 2001; Rex and Etter 2010).

Many marine invertebrates have indeterminate growth and might be present in different size classes through different stages of their lives. Studies differ in their approach to this phenomenon: some include all organisms captured by a specific sieve size, while others look at the predetermined fauna *sensu stricto* meaning that they can potentially, for example, exclude nematodes from macrofauna and polychaetes from meiofauna. In other words, the metazoan groups are defined based on taxonomy rather than size.

When looking at the two size classes, a bimodal distribution in the frequency-size relationship is observed. There is much debate about whether this distribution shows biological adaptation to disruptive selection for two different lifestyles, resulting in the meio- and macrofaunal peak, or whether it is a result of sampling (Warwick et al. 2006; Bett 2013,2014; Warwick 2014). Many studies now confirm that the choice of sieve size can potentially influence estimates of abundance, biomass, body size, composition and biodiversity (Bett et al. 1994; Gage et al. 2002; Kaariainen and Bett 2006; Pavithran et al. 2009; Leduc et al. 2010b).

Here, available data on abundance, biomass and body size estimates are compiled for deep-sea meio- and macrofauna to test for the influence of depth, geographical region, taxonomic structure of communities, and sampling methods on body size. The results are discussed with respect to how the community-size structure changes at the regional scale, how size varies in taxonomic groups on a global scale, and the implications of this in the context of future climate change. Recommendations for sampling strategies are made based upon our findings.

2.3 Methods

2.3.1 Data collection

Data were assembled from peer-reviewed studies on macro- and meiofaunal abundance and biomass, creating two datasets. The oceanographic regions where the samples were taken in these individual studies were recorded. We note that the Polar Regions and southern Hemisphere are markedly under-sampled for both size classes. Few studies were available for the southern parts of the Pacific and Atlantic Oceans. The Indian Ocean is not represented in either data set. Carbon sequestration was calculated as the mean annual flux below 2000 m or the burial in sediment across time from the year 2003 to 2012 in arcGIS. The resulting data sets comprised a total of 96 published studies (3306 estimates from 46 published papers for macrofaunal data, and 5065 estimates from 66 published papers for meiofaunal data) (see Appendix A).

The abundance and biomass data were used to calculate average weight per individual in both datasets (as a proxy for body size). As not all studies reported both abundance and biomass, the data sets used in the models were reduced to 601 estimates for macrofauna and 740 estimates for meiofauna. This highlights the need to report these values in future studies.

Macrofaunal biomass was published as wet weight in all studies used in our analyses. For meiofauna, various measures of biomass were used among studies: wet weight, carbon wet weight, dry weight and carbon dry weight. Published conversion factors (Wieser 1960; Ankar and Elmgren 1976; Jensen 1984; Feller and Warwick 1988) have been used in this study to calculate the wet weight for meiofauna to ensure the biomass is on the same scale for all estimates. Most studies reported values of total community abundance and/or biomass, but many also reported values for separate taxonomic groups. The highest resolutions for taxonomic data available were included in our model to determine whether a taxonomic signal is present influencing body size change with increasing depth.

Published data on meiofaunal and macrofaunal abundance and biomass included a wide range of sampling methods, and these methods can potentially influence abundance and biomass estimates (Bett et al. 1994; Gage et al. 2002; Kaariainen and Bett 2006; Pavithran et al. 2009; Leduc et al. 2010b). Area sampled and sieve mesh sizes used were recorded in the current study. We found that no standard sieve mesh size was used, and, indeed, the sizes used overlapped for the two size classes. For macrofauna, sieve size ranged from 0.25 mm to 0.5 mm, and for meiofauna they ranged from 0.032 mm to 0.3 mm.

Published studies differed in the actual area sampled as a result of sub-sampling and/or sampling device. The actual areas sampled varied between the studies, with a range of 0.003 to 4 m^2 for macrofauna and a range of 0.0003 to 0.59 m^2 for meiofauna. The actual area sampled was, more often than not, different from the standardized measure presented in the studies:

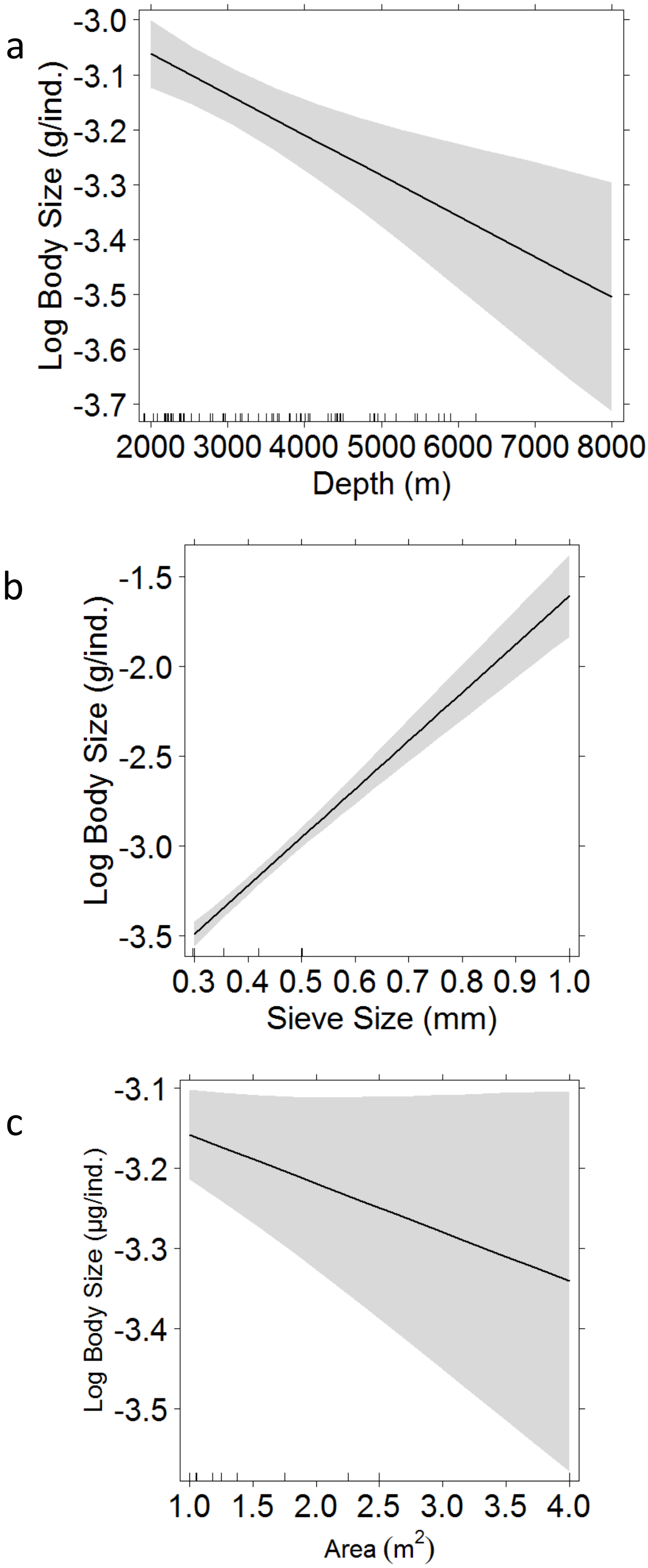
for macrofauna m^2 was used, and for meiofauna 10 cm^2 was used. The actual area sampled was used in this study to explore the effect of sampling area on body-size estimates. When the subsample dimension was not given in the original publication, the original core area was used for the purposes of the current work. Surface area was used as not all studies provided information about the depth of sampling.

Whether the organisms were juveniles or adults was not mentioned in the published studies used, but it was assumed data referred to adult organisms.

2.3.2. Statistical analyses

Two generalized least squares models were constructed from the two datasets we compiled based on 96 published studies, controlling for different variances in region, taxa, and sieve mesh size. Total community composition was used as a baseline comparison for taxonomic groups. A global average was derived from the dataset and used as a baseline for comparison of the regional effect. Standard errors (SE) and 99% confidence intervals (CI) are reported, as well as statistical significance values for analysis of variance. By using the 99% CI, a correction for multiple testing is applied. These two statistical values, SE and CI, provide the same qualitative information as t-tests and F-test, but they have the advantage that they stay closer to the biological data (Hector 2015). The SE and CI also provide more information than t- and F-values by showing statistical significance and the bounds of the estimated values.

All analyses were performed in the statistical program R, version 3.1.1 (R Core Team 2014), using the *nlme* package (Pinheiro et al. 2014). The graphs were produced with the *effect* package (Fox 2003).


a
Log Body Size (g/ind.)
-3.0
-3.1
-3.2
-3.3
-3.4
-3.5
-3.6
-3.7
2000 3000 4000 5000 6000 7000 8000
Depth (m)
b
Log Body Size (g/ind.)
-1.5
-2.0
-2.5
-3.0
-3.5
0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Sieve Size (mm)
c
Log Body Size (μg/ind.)
-3.1
-3.2
-3.3
-3.4
-3.5
1.0 1.5 2.0 2.5 3.0 3.5 4.0
Area (m2)

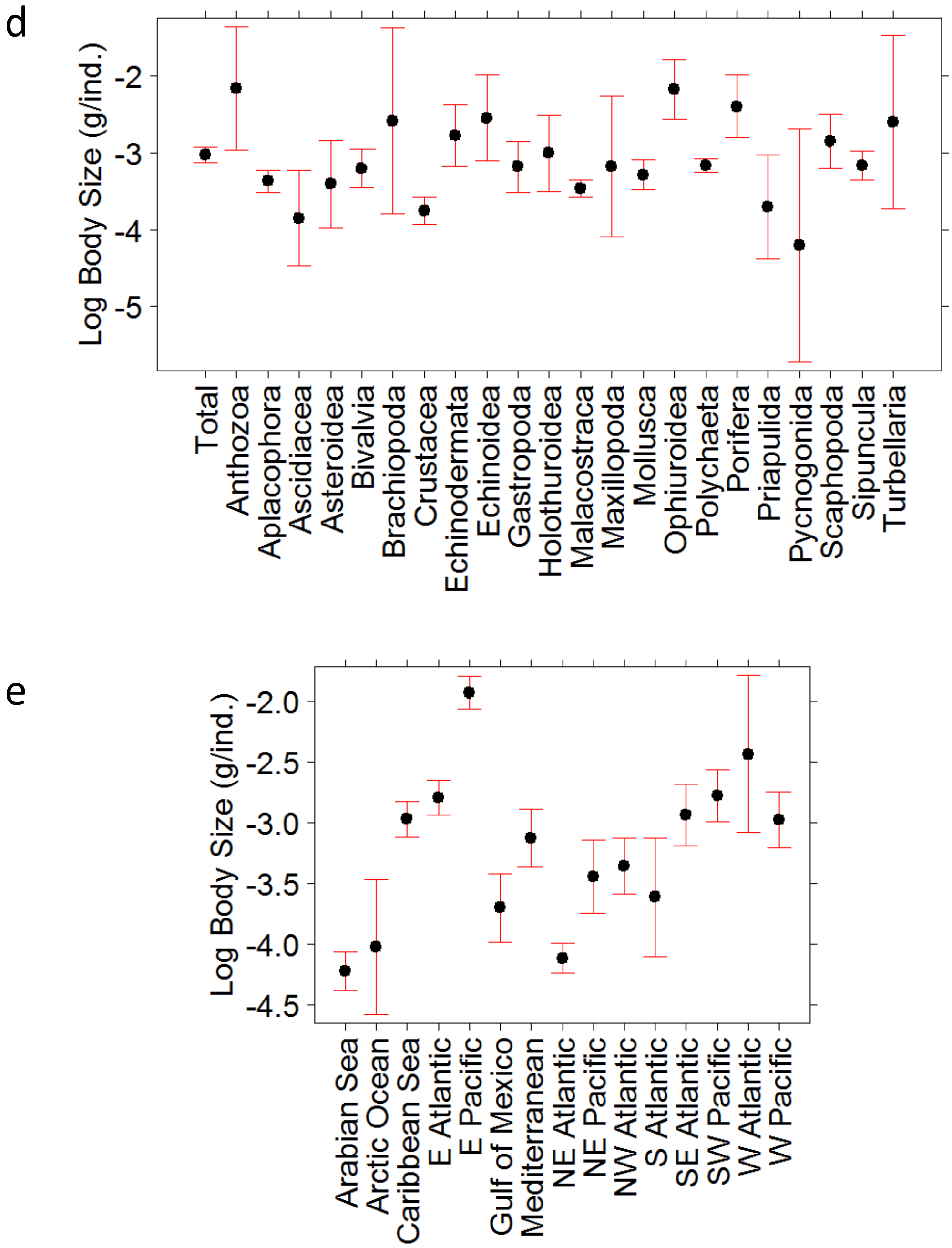


Figure 2.1 Deep-sea macrofaunal body size variation in relation to depth, sampling methods, geographical region or taxonomic groups: (a) log body size versus depth (in meters); (b) log body size versus sieve size (in millimetres); (c) log body size versus area sampled (in m^2); (d) log body size versus different geographical regions; and (e) log body size versus total community and different taxonomic groups. The grey bands in (a-c) present the 95% confidence intervals, and the red bars in (d) and (e) present the standard error.

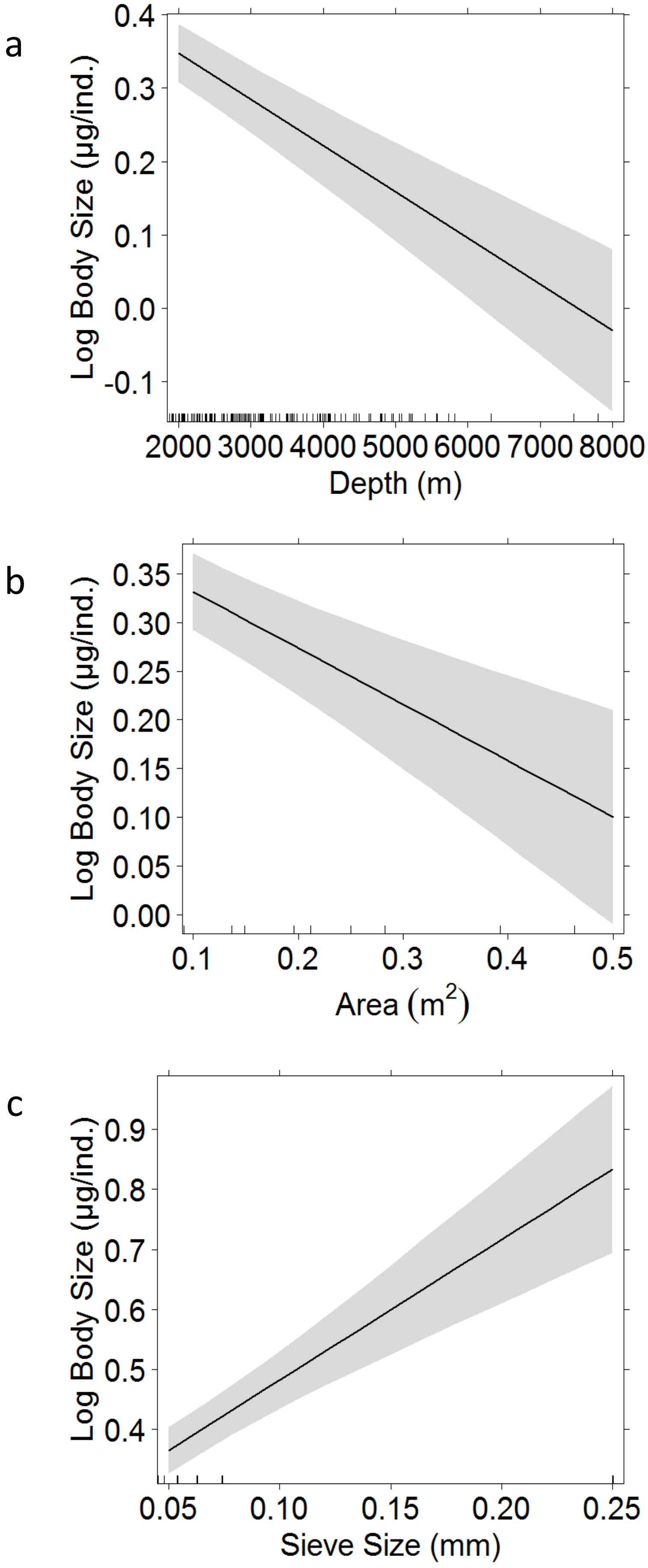
2.4 Results

2.4.1 Macrofauna

Average body size decreases with increasing depth. ($\bar{X}$ = -7.400×10^{-5} log gram, standard error of the mean = 2.040 × 10^{-5}, confidence interval = -1.266 × 10^{-4} to -2.125 × 10^{-5}, $P < 0.0001$; figure 2.1a). Sieve mesh size is positively correlated with average size of individual organisms collected ($\bar{X}$ = 2.690 log gram, standard error of the difference (SED) = 1.980 × 10^{-1}, confidence interval of the difference (CID) = 2.180 to 3.200, $P < 0.0001$; figure 2.1b). Area sampled was not significant (figure 2.1c). The carbon measure used in the model was non-significant, likely reflecting the limited use of a surface-derived carbon measure at depth.

There was a significant regional impact on the body size estimates ($P < 0.0001$). All oceanographic regions show a negative shift in body size with increasing depth, but the amount of decrease varies (figure 2.1d, Appendix B). For example, the Arabian Sea shows the largest shift in size ($\bar{X}$ = -5.024 log gram, SED = 1.467 × 10^{-1}, CID = -5.402 to -4.646, $P < 0.0001$), while the east Pacific shows the weakest ($\bar{X}$ = -2.726 log gram, SED = 1.628 × 10^{-1}, CID = -3.146 to -2.307, $P < 0.0001$).

A significant taxonomic signal was detected ($P < 0.0001$; figure 2.1e, Appendix B); negative shifts in body size compared to the total community average were observed in many taxonomic groups, although most were found to be non-significant. Some taxonomic groups, like the Ophiuroidea (brittle stars) and Porifera (sponges), showed a positive shift (Ophiuroidea: $\bar{X}$ = 8.518 × 10^{-1} log gram, SED = 2.069 × 10^{-1}, CID = 3.190 × 10^{-1} to 1.385, $P < 0.001$; Porifera: $\bar{X}$ = 6.283 × 10^{-1} log gram, SED = 2.174 × 10^{-1}, CID = 6.829 × 10^{-1} to 1.188, $P < 0.001$). Most taxonomic groups did not differ from the total community average; however, taxonomic resolution can change the significance of the relationship. For example, the Phylum Echinodermata was not found to differ significantly from the total community (2.439 × 10^{-1} log gram, SED = 2.083 × 10^{-1}, CID = -2.926 × 10^{-1} to 7.804 × 10^{-1}), while the Ophiuroidea seemed to be larger than the total average. It is possible that this pattern can hold for other groups as well when more data is


a
Log Body Size (µg/ind.)
0.4
0.3
0.2
0.1
0.0
-0.1
2000 3000 4000 5000 6000 7000 8000
Depth (m)
b
Log Body Size (µg/ind.)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0.1
0.2
0.3
0.4
0.5
Area (m^2)
c
Log Body Size (µg/ind.)
0.9
0.8
0.7
0.6
0.5
0.4
0.05
0.10
0.15
0.20
0.25
Sieve Size (mm)

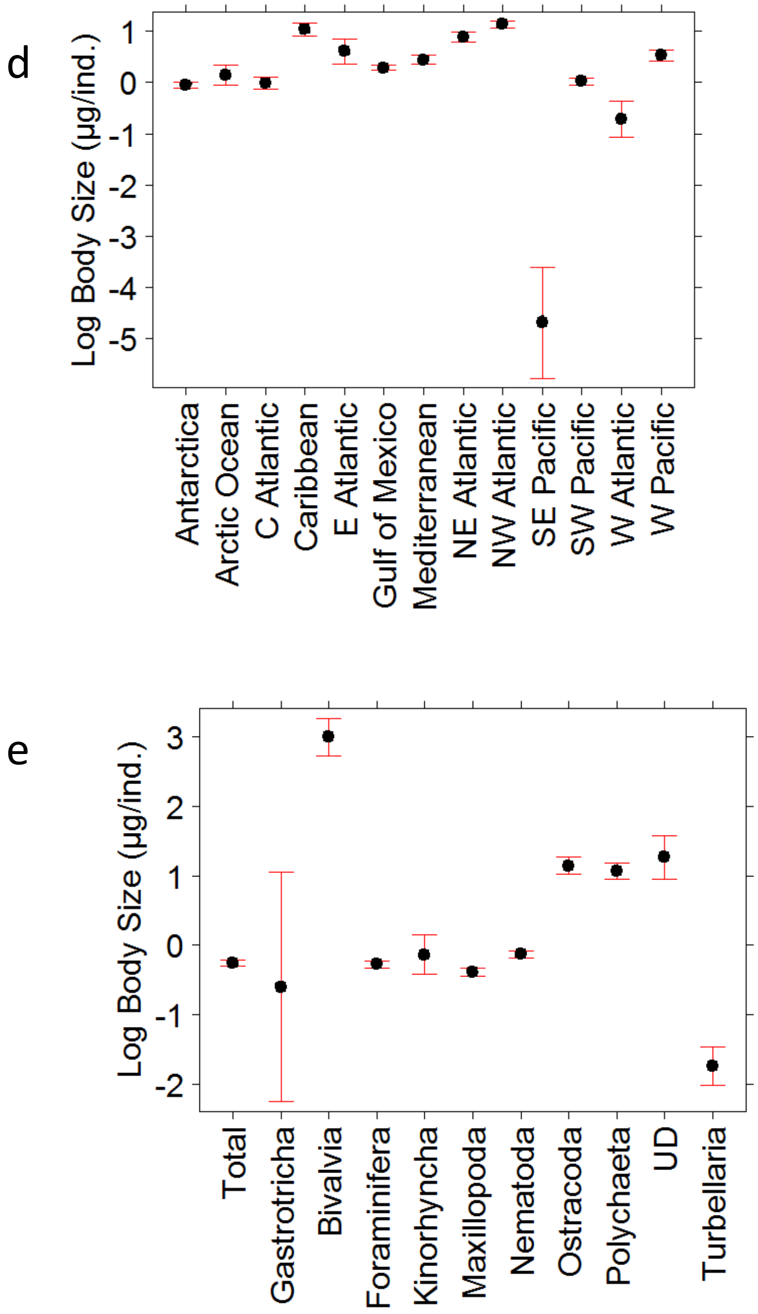


Figure 2.2 Deep-sea meiofaunal body size variation in relation to depth, sampling methods, geographical region or taxonomic groups: (a) log body size versus depth (in meters); (b) log body size versus sieve size (in millimetres); (c) log body size versus area sampled (in m^2); (d) log body size versus different geographical regions; and (e) log body size versus total community and different taxonomic groups. UD, undetermined. The grey bands in (a-c) present the 95% confidence intervals, and the red bars in (d) and (e) present the standard error.

collected on the taxonomic Class level rather than Phylum. Also, groups at the same taxonomic level can vary in their response: the Class Malacostraca (subphylum Crustacea) was found to show a negative shift in body size compared to the total community, while for the Class Maxillopoda (subphylum Crustacea) no significant shift was found (Malacostraca: 4.409 × 10^{-1} log gram, SED = 8.406 × 10^{-2}, CID = -6.574 × 10^{-1} to -2.244 × 10^{-1}, $P < 0.001$; Maxillopoda: -1.575 × 10^{-1} log gram, SED = 4.692 × 10^{-1}, CID = -1.366 to 1.051).

2.4.2 Meiofauna

Our analyses indicated that body size decreased with increasing depth, ($\bar{X}$ = -6.3 × 10^{-5}, SEM = 8.3 × 10^{-6}, CI = -8.449 × 10^{-5} to -4.164 × 10^{-5}; figure 2.2a). Both sieve mesh size (figure 2.2b) and area sampled (figure 2.2c) were found to have a significant impact on individual body size; increasing sieve size had a positive influence on mean individual body size, while area sampled had a negative influence on mean individual body size (Sieves: $\bar{X}$ = 2.342 log weight, SED = 3.598 × 10^{-1}, CID = 1.415 to 3.269, $P < 0.0001$; Area: $\bar{X}$ = -5.789 × 10^{-1} log weight, SED = 1.261 × 10^{-1}, CID = -9.036 × 10^{-1} to -2.539 × 10^{-1}, $P < 0.0001$). The carbon measure, again, was not significant.

Geographical region and taxonomic group had significant influence on body size patterns ($P < 0.001$; figure 2.2d-e, Appendix C). Interestingly, the shift in body size differed among different oceanographic regions. Most regions showed a negative shift in body size, and differed in the strength of the response. The largest strength of response was found in the southeast Pacific, while the weakest was in the southwest Pacific (southeast Pacific: $\bar{X}$ = -4.828, SED = 5.57 × 10^{-1}, CID = -6.263 to -3.393, $P < 0.0001$; southwest Pacific: $\bar{X}$ = -1.246 × 10^{-1}, SED = 3.976 × 10^{-2}, CID = -2.270 × 10^{-1} to -2.215 × 10^{-2}, $P < 0.0001$). Some regions, however, like the Caribbean and the northwest Atlantic, seemed to show a positive shift in body size compared to the global average (Caribbean: $\bar{X}$ = 8.917 × 10^{-1}, SED = 7.383 × 10^{-2}, CID = 7.015 × 10^{-1} – 1.082, $P < 0.0001$; northwest Atlantic: $\bar{X}$ = 9.908 × 10^{-1}, SED = 4.884 × 10^{-2}, CID = 8.65 × 10^{-1} – 1.117, $P < 0.0001$).

Meiofaunal taxonomic groups differed in the direction and strength of the relationship between body size and depth. For example, the Nematoda had a significant decrease in body size with depth ($\bar{X} = -1.487 \times 10^{-1}$, SED = 3.157×10^{-2}, CID = $-2.3 \times 10^{-1} - -6.739 \times 10^{-2}$, $P < 0.0001$), while the Polychaeta showed an increase in body size with depth ($\bar{X} = 1.344$, SED = 4.797×10^{-2}, CID = 1.221 – 1.468, $P < 0.0001$).

2.5 Discussion

Dwarfism was once suggested to be the main universal trend for body size with increasing depth in the deep sea (Madsen 1961). The models constructed here only allowed for the analyses of differences in intercepts - not for slopes - in the correlations for regional and taxonomic effects. This choice in analysis was made based on the availability of data in the published scientific literature. The models presented here appear to be consistent with the hypothesis of a total community decrease in body size with increasing depth for both meiofauna and macrofauna (Thiel 1975). The trend, however, can be a reflection of other depth-correlated factors that influence the change, with food availability as the proposed major factor.

2.5.1 Regional effects

2.5.1.1 Sea surface primary production

Our models indicate that there is a regional effect on the correlation of body size with increasing depth for both meio- and macrofaunal size classes, and that the responses of the two size classes can vary within the same region. The regional differences in body size could reflect variations in carbon flux. Carbon is a proxy for food resources and a form of chemical energy. It has been proposed that food availability is the main influencing factor on body size change in the deep sea (McClain et al. 2012). The current study did not find an association between body size and carbon flux. However, it is likely that the method used has limited the detection of a correlation. The carbon flux was calculated from surface-derived carbon measures to a specific depth (below

2000 m) or burial rate. Much of the data used in the current analyses were based on samples taken at differing depths. Samples at shallower depths will potentially have had higher carbon content than those from deeper depths. Another problem with this measure is the obvious time difference. Some samples were taken several decades ago, while the carbon-flux measure is a mean over the last decade. Carbon flux is known to vary temporally and thus the flux calculated for the last decade can vary from the flux several decades ago. It is likely that carbon measures taken contemporaneously with samples will have a stronger correlation.

Most of the deep sea - apart from chemosynthetic environments - is dependent on sea surface primary production for food; calcareous phytoplankton, like coccolithophores, can aggregate and sink as their calcite plates form ballast (Honjo et al. 2008). Likewise, silica can be used by diatoms in exoskeletons and acts as ballast and promote sinking. Together with living and dead cells, faecal pellets, dead organisms, polysaccharide flocculates (e.g. mucus) and other organismal associations (e.g. larvacean houses), this sinking organic material forms marine snow (Silver et al. 1978; Robison et al. 2005; Buesseler et al. 2007; Honjo et al. 2008). Food availability is negatively correlated with depth as it is remineralized in the water column, mainly by microorganisms but also by animals (Rex and Etter 1998; Rex et al. 1999). Most is recycled in the upper layers of the oceans, resulting in a small proportion reaching the benthic system. The amount that reaches the bottom of the oceans varies regionally, with seasonality playing a role in this too (Buesseler et al. 2007).

The variation observed in the models we have produced based upon the peer-reviewed studies listed in Appendix A, agrees with previous findings that carbon can play a role in body size (McClain et al. 2012). For example, the northwest Atlantic has a high primary production and shows that the mean meiofaunal community size is larger than the global average, while the central Atlantic, which has a lower surface primary production and has a smaller meiofaunal community size than the global mean. The Caribbean meiofaunal community may profit from the riverine runoff from the Orinoco River that increases primary production in this region

(López et al. 2013), resulting in an increase in carbon flux and larger meiofaunal-community size compared to the global mean. Other larger rivers, like the Amazon are known to have an impact on the deep sea (Rex and Etter 2010). It is also notable that the Caribbean is partially land-locked and organic material of terrestrial origin may also influence food availability in the deep sea.

Seasonality plays a role in the regional effects resulting from primary production with a change in flux during seasons at higher latitudes (Buesseler et al. 2007). It has been shown that the magnitude of the carbon flux does not determine remineralization rates, but the composition of the flux does. For example, the K2 and ALOHA time-series sites are both located in the Pacific, with K2 being present at a higher latitude with colder subarctic waters, higher nutrient concentrations and a larger seasonality flux in phytoplankton, while ALOHA is located at a lower latitude within warmer subtropical waters with low nutrient concentrations and less seasonal variation. Both sites differ in their phytoplankton composition, resulting in different ballast types that likely influence the remineralization rate of the carbon flux (Buesseler et al. 2007). In the analyses presented here, such differences were not clearly defined. Sampling coverage among the various studies included in our analyses was limited, making comparisons on a latitudinal scale difficult. Many samples have been taken in the northwest Atlantic, but fewer samples have been collected from the central West Atlantic and southwest Atlantic. The southern Hemisphere is characterized by under-sampling. It is to be expected that the benthic system in the Southern Ocean will benefit from the higher sea surface productivity that sinks in pulses linked to seasonality. Sea ice extent and duration in the Southern Ocean system is changing, and this is likely affecting sea surface primary production. Sampling of this system is necessary now to get a baseline and to track the changes at greater depths. A more focused effort on filling in these data gaps will allow for the detection of possible patterns of seasonality with latitude and future change.

Other environmental conditions that vary by region can also influence the observed body size-depth pattern and give contrasting results with the surface primary production patterns. For example, the Arabian Sea has high primary production, yet the community size is smaller compared to the global average. This region is characterized by an extreme oxygen minimum zone (OMZ) (Wyrtki 1966). Oxygen levels are maintained in the deep sea by ocean ventilation. Microbial activity mainly influences oxygen levels, with higher activity levels resulting in a larger decrease of oxygen concentration with depth. Microorganisms use the carbon flux as food source, and their activity is correlated with depth (i.e. corresponding decrease in carbon flux with depth). Larger organisms are apparently influenced the most by the dropping levels of oxygen, resulting in standing stock changes and smaller community sizes (Levin et al. 1991; 2000; Gooday et al. 2009). Often, the community below the OMZ is more abundant and possibly larger in size as a result of reduced rates of remineralization in hypoxic water (Levin et al. 2000; Rogers 2000). The present study found a decrease in community size for the Arabian Sea, which might well reflect the influence of oxygen. It might also reflect a hierarchy of controlling mechanisms on body size, with lower levels of oxygen resulting in smaller size even when there is a large influx of food. When oxygen levels are high, meio- and macrofauna standing stock and size likely correlate better with food availability (Levin et al. 1991).

Regional differences in meiofaunal abundance reflecting surface primary production have been observed (Lambshead and Gooday 1990; Soltwedel 2000; Sommer and Pfannkuche 2000). When comparing oligotrophic sites with eutrophic sites in the Northwest Pacific, Itoh et al. (2011) found that meiofaunal organisms were smaller in the oligotrophic regions compared to the eutrophic regions with increasing depth. However, when the trenches were considered separately, no size-depth relationship was found. In a global study, Udalov et al. (2005) observed that nematode body size did not change with increasing depth in eutrophic regions, but it did decrease significantly in oligotrophic regions. Brown et al. (2001) noted that nematode body size increased with increased food supply in the central Equatorial Pacific.

Future predictions for sea surface conditions show a change in primary production in both quantity and quality, which will influence the export of POC to the deep sea. In turn, this will affect remineralization and the sequestration of organic carbon by reducing benthic biomass, thereby influencing the global carbon cycle and the carbon budget (Wei et al. 2010a; Smith Jr et al. 2013; Jones et al. 2014). The predictions are that the community-size structure will be smaller because of a decrease in biomass, but not abundance. This, in turn, can reduce energy fluxes in the system (Wei et al. 2010a; Jones et al. 2014) and possibly impact biological processes such as bioturbation leading to other effects at the community level.

2.5.1.2 Food webs

Deep-sea food webs are poorly understood. There have been mixed reports for a correlation between meio- and macrofaunal abundance, biomass or body size with the availability of food, in the form of carbon flux, plant pigments or bacterial biomass. Meio- and macrofaunal abundance and biomass have been found to correlate with organic carbon or plant pigments (Pfannkuche 1985; Alongi and Pichon 1988; Tietjen et al. 1989; Soetaert et al. 1991; Alongi 1992; Schaff et al. 1992; Vanhove et al. 1995; Galéron et al. 2000; Sommer and Pfannkuche 2000; Johnson et al. 2007; Górska et al. 2014). McClain et al. (2012) is one of the few studies that tested whether carbon flux influences body size. They found that carbon flux positively predicts body size in deep sea communities. However, many studies also reported no correlation between meio- or macrofaunal standing stock and carbon flux measures (Sanders et al. 1965; Tietjen 1971; Polloni et al. 1979; Shirayama 1983; Danovaro et al. 1995; Clough et al. 1997; Shimanaga et al. 2007; Bianchelli et al. 2010). Furthermore, meiofauna might not be feeding on carbon itself, but on bacterial populations that feed on the organic carbon. de Bovée (1990) found a positive relation between the meiofaunal abundance and viable bacterial population size. Others have also noted strong correlations between bacterial activity and meiofaunal abundance (Danovaro et al. 2000; Flach et al. 2002; Hoste et al. 2007). Vanhove et al. (1995) did not find a correlation between meiofaunal abundance and bacteria, but they did for meiofaunal biomass. However interactions might be more complicated, with certain meiofaunal groups feeding off bacteria while others feed of the detritus (Hughes and Gage 2004). Danovaro et al. (2000) reported no correlation of meiofaunal abundance and bacteria for the East Mediterranean, but they found one in the Northeast Atlantic and West Mediterranean. It is likely that factors influencing bacterial populations differ on a regional scale; the bacterial populations might be driven by the carbon flux from the sea surface. It is possible that the bacteria respond to the carbon flux and the meiofauna to the bacteria.

The differences among correlations between carbon and body size, abundance or biomass can possibly be explained by another factor. Carbon is composed of labile and refractory components. It is the labile part that organisms use as food, while the refractory portion is a low-quality resource. The higher the proportion of labile carbon is present in the flux, the higher the quality of carbon. When organismal abundance and biomass are related to quality, rather than quantity, the relationships are positive, with higher quality resulting in larger numbers. This relationship is especially clear in oligotrophic regions (Probert and McKnight 1993; Danovaro et al. 1995; Probert et al. 1996; Dauwe et al. 1998; Grove et al. 2006; Hoste et al. 2007; Berkenbush et al. 2011).

The food-web structure has to be considered, because it could explain the absence of a pattern, as found in the present study. It is possible that the “wrong” measure has been taken in this study (and potentially others): carbon flux instead of bacterial populations, which might have shown a correlation, or that the focus has to shift from quantity (used here) to quality of carbon. Furthermore, if macrofauna and possibly meiofauna are not feeding directly on the carbon flux, there will be a lag between the influence of carbon flux on lower trophic levels and higher trophic levels as the energy is transferred through the system. A response (change in standing stock or body size) might be detected at a later stage, influenced by how quickly energy is moved through the system and how much energy is lost in this process. Thus, measures of carbon/bacteria taken at the same time as the samples can still be confounded by this lag. It is not known how quickly carbon is transferred between trophic levels in deep-sea systems.

Food is likely to be a fundamental factor affecting body size, but the question remains as to what constitutes the food source. This highlights the lack of understanding of food webs in the deep sea. With improved understanding of trophic structure in the deep sea, it will be possible to predict how communities might change when the community composition changes. This will be important in the future, for example for identifying and understanding the impacts of climate change, with changing sea surface production and increased ocean stratification.

2.5.2. Taxonomic signals

There are clear taxonomic signals in the current datasets. We found that that community structure can vary with depth and region, and that total community does not reflect how different taxonomic groups would respond. We found that different taxonomic groups have either a positive or negative shift in body size compared to the total community. It is possible that this could reflect differences in functional groups or life styles. It has been shown that scavenging and non-scavenging fish differ in their change of body size with increasing depth (Collins et al. 2005), with scavenging fish becoming relatively larger and non-scavenging fish smaller with depth. It has been proposed that the predictability of food resources for fish determines the direction of selection for body size: when food resources are unpredictable in time and/or space (e.g. food falls for scavengers), organisms benefit from being larger as they can survive between finding food falls and get to resources quicker once detected (Collins et al. 2005). Food resources for non-scavengers, like filter feeders and predators, are more predictable in time and/or space and these organisms benefit from smaller sizes that function better for lower levels of food, thereby conserving energy. It is possible that similar patterns can be found in invertebrates. For example, Tietjen (1971) found that feeding styles in nematodes changed with food availability and sediment characteristics. No information is available on whether the feeding guilds differ in size, but this is conceivable. Also, a change in community composition can often be observed, depending on whether organisms colonize the sinking phytodetritus, which in turn could influence a response to change in body size (Lambshead and Gooday 1990; Sommer and Pfannkuche 2000). A 10-year study in the Northeast Atlantic showed that macrofaunal community structure changed in response to variation in sea surface conditions (Ruhl et al. 2008). In the northeast Pacific, the megafaunal community composition has been observed to change from a sponge-dominated community (suspension-feeding) to a holothurian-dominated community (detritus-feeding) in two years (Kuhnz et al. 2014). This was accompanied by changes in densities of organisms and community diversity, showing that the deep sea is a dynamic place. Changes in community composition and densities over time have been observed elsewhere as well (Gooday et al. 2010a; Kalogeropoulou et al. 2010; Soto et al. 2010; Rogers 2015). In the present study, taxonomic groups that were found to be larger compared to the average community size often include filter feeders. Larger filter feeders will be able to capture more food particles suspended in the water column. Larger organisms require more energy in total, but they require less energy per unit biomass. Combined with the low metabolic rate in deep-sea organisms, it may prove advantageous to be larger for certain feeding styles. For example, the taxonomic groups that tend to be smaller than the community average seem to be associated with predatory lifestyles. It should be noted that these are generalizations across the taxonomic groups - there is still much unknown about lifestyles of deep-sea organisms, which makes comparative analyses difficult to make.

Two groups, the Bivalvia and Polychaeta seem to be larger than the community average in the meiofauna, but do not differ in size from the community average in macrofauna. This could reflect different life stages, where juveniles are present in the meiofaunal size class (and growing) and adults in the macrofaunal size class. Whether the organisms were juveniles or adults was not mentioned in the studies from which data were obtained. It is important to incorporate this information in analyses. When the juveniles are similar in their ecology as their adult forms, the body-size estimates, or any other related aspect, may be confounded by splitting them into meio- or macrofauna and treating them as two different entities, with potentially different lifestyles (Warwick 2014). However, some taxonomic groups do have different lifestyles at varying life stages. For example, shallow-water polychaetes can switch feeding guilds depending on life stage: juvenile polychaetes from larger-bodied adult species have a macrophagous lifestyle, while the adults switch to a microphagous lifestyle. In such an instance, it is reasonable to treat them differently and put them in different size classes. It is important to note that this lifestyle-switch does not happen in small-bodied adult polychaete species. It is not known whether this also occurs in the deep-sea, where polychaetes tend to be smaller in general (Jumars et al. 2015).

Larger organisms often have lower population sizes. A population has to be of a large enough size in order to maintain effective reproduction. If the population size is too low, organisms can suffer from Allee effects, especially in benthic invertebrates where free spawning may require sufficient concentrations of gametes to ensure effective fertilisation. This mechansim may contribute to source-sink populations, with the bathyal zone containing source populations, where individuals reproduce and larvae spread across bathyal and abyssal locations. However, populations on the abyssal plain are effectively sinks, where individuals occur but are non-reproductive. Many organisms with large depth ranges seem to agree with this pattern (bivalves, gastropods, and polychaetes), although there are organisms with narrow depth ranges that are capable of maintaining sufficient population densities at deeper depths for effective reproduction and recruitment (Porifera, Isopoda, Holothuria, Echiura, and Pogonophora). Perhaps organisms with narrower depth ranges are better adapted to the environmental conditions of these depths and can adopt larger sizes over evolutionary timescales. For example, the present study found that Porifera had larger body sizes than average community structure and this group of organisms can have restricted depth ranges (Rex and Etter 2010).

There is also evidence that sediment grain size or type may influence the presence of some taxonomic groups (Rohal et al. 2014), therefore it is conceivable that changes in availability of substrata with depth could influence the community structure, and as a result the size structure of the overall community or individual groups. In a similar way, biogeochemistry of sediments may influence changes in body size with depth, either amongst the community in general or differentially amongst taxonomic groups depending on their physiology. An example is the reponse to oxygen concentration that may influence body size across the entire community or within specific groups (e.g. the extreme oxycline in the Arabian Sea; (Levin et al. 1991; Gooday et al. 2009; Rohal et al. 2014).

Bianchelli et al. (2010) noted that habitat-specific and region-specific topographic characteristics were related to meiofaunal standing stock on a regional scale, rather than food availability. It is possible that factors on different spatial scales structure the community in different ways. Higher taxonomic resolution or functional information along with improved data on seabed composition/structure is needed to explore this further. If functional groups are found to respond differently to increasing depth (the proxy for food availability), it is possible that changes in food availability in the future (e.g. surface primary production changes through anthropogenic actions) will affect the components of the community differently, and cause a change in community structure. This in turn can affect ecosystem functions such as bioturbation that in turn impact on carbon burial rates.

2.5.3 Sampling artefacts

2.5.3.1. Sieve mesh size

The results of our analyses showed that sampling method has an influence on body size, indicating that more attention to sampling design is needed, especially in sieve size choice. Sieve size was found to have a significant positive influence on mean individual body size for both meiofaunal and macrofauna. Larger sieve mesh sizes result in larger body size estimates as larger sieve sizes - used as a lower limit of the selected size - will retain larger animals, while small animals will pass through to be retained on smaller sieve sizes corresponding to meiofaunal sizes or smaller and therefore excluded from the analyses with larger size classes. This finding of the influence of sieve size is supported by previous observations (Schwinghamer 1985; Shirayama and Horikoshi 1989; Gage et al. 2002; Kaariainen and Bett 2006; Pavithran et al. 2009; Leduc et al. 2010b). Furthermore, it has been shown that the influence of sieves might be taxonomically specific, meaning it does not affect the total community in the same way (Bachelet 1990; Gage et al. 2002). This should be another point of consideration when choosing sieves. The choice of sieve mesh size is therefore very important when studying the deep-sea benthic fauna.

The studies used in these analyses show a variety of sieve mesh sizes, especially for the meiofauna, which showed a 10-fold range. As a result, comparison of estimates across studies was confounded by the choice of sieve. Two measures might help to mitigate this problem: (1) a standardized sieve size for further studies, allowing for better comparison among studies, with one sieve size for each of these (arbitrary) size classes, or (2) the use of multiple sieves. For example, by using lower and upper sizes plus multiple sieves in between these limits would allow for better capture of the size distribution of body size and thus energy and carbon fluxes in the form of biomass. This would also allow for a better appreciation of the variation in body size and community structure and a distinction between size classes would not necessarily be needed.

2.5.3.2. Area and sediment-depth effects

We found that the influence of area sampled on meiofauna is of importance for the investigation of changes in meio- and macrofaunal body size with depth. There are many different sample devices that can be used to sample the soft-benthic community. Our analyses found that the choice of sample device did not influence estimates, supporting previous observations (Udalov et al. 2005), although not all studies agree (Bett et al. 1994). Usually, sub-samples of the cores or grabs are taken for meiofaunal analyses, thereby reducing the surface area (and volume) that is analyzed quantitatively. From this, the data are more often than not extrapolated, which increases error. Macrofauna, on the other hand, are rarely sub-sampled. Previous researchers have suggested that the decreasing abundance of animals with depth leads to issues with small sample size whereby larger members of the community are under-sampled, skewing the data towards individuals with a smaller body size (Polloni et al. 1979). The models presented here showed that a larger sampling area resulted in larger body sizes. Sampling a larger area would increase the chance of finding rarer larger individuals. However, larger, often older, individuals might be included in the larger size classes – rather than treating groups as meio- or macrofauna *sensu stricto* -, thereby skewing the relationship.

Some researchers have viewed the meio- and macrofaunal size classes as arbitrary, not reflecting any meaningful biological division (Thiel 1975; Bett 2013,2014), while others have suggested that the size divisions represent optimal sizes for different lifestyles (Warwick et al. 2006; Warwick 2014). Meiofauna predominantly live in interstitial habitats whilst macrofauna utilize sediment as a whole (Schwinghamer 1985). Given the results concerning the influence of sampling area of the present study, it is possible that the differences observed between the two size classes result from under-sampling of large meiofauna and small macrofauna. While larval stages might well show different lifestyles compared to adults, juveniles and adults will not show such large difference; they will show similar adaptations to similar environmental conditions, thus eliminating the need to categorize them into different size classes.

Depth in the sediment was excluded in the analyses presented here, as not all studies provided information on the sampling depth within the sediment. This is important, as depth penetration can vary as a result of food availability. For example, Sommer & Pfannkuche (2000) noticed that sediment penetration by nematodes in the Arabian sea was deeper when more carbon was available. Dauwe et al. (1998), however, showed that the deepest macrofaunal depth penetration in the North Sea was dependent on intermediate quality of organic carbon. When the organic carbon was of higher quality, the penetration depth was less. When the organic carbon consisted of mainly refractory carbon, the macrofauna penetrated deepest, but were also smaller. Further, Shirayama (1983) showed that size-depth trends can be restricted to certain layers in the sediment, thereby indicating again the importance of sampling at various layers in the sediment. Macrofauna may influence the depth penetration of meiofauna by bioturbating the sediments, which allows deeper oxygen and carbon penetration in the sediments, and thus creating niches that can be occupied by meiofauna (Braeckman et al. 2011). Importantly, Leduc et al. (2010a) showed that meiofaunal estimations of abundance and biomass are influenced by depth penetration. Core penetration can be affected by sediment characteristics as well, thereby potentially influencing estimates of standing stock.

The analyses presented here confirm the previously suggested trend that meio- and macrofaunal body size decreases with increasing depth at the global scale. When the data are partitioned at the regional scale, there is variation in the trend, likely reflecting the difference in food availability in different areas. Furthermore, at a global spatial scale, different taxonomic groups respond in different ways, with some groups showing a positive shift, negative shift or no difference from the community mean. These results could reflect differences in life-history characteristics, physiology and/or life styles. Understanding patterns of body size in deep-sea communities will allow for understanding and prediction of patterns in abundance, diversity, food web interactions, human impacts (Hildrew et al. 2007), and climate change effects. For example, there is often a right skew toward larger sizes in fished areas, thereby influencing body size estimates (Maurer et al. 1992; Brown et al. 1993). Climate change will likely lead to changes in global surface primary productivity as well as changes in the flux of particulate organic carbon to the seabed (Gregg et al. 2003; Tunnicliffe et al. 2003). Deep-sea organisms will respond differently to this change in food supply, depending on their life-history characteristics, resulting in changes in community structure. This, in turn, can influence remineralization and carbon burial in the deep-sea sediments. The deep sea is already showing signs of being affected by climate change (Touratier and Goyet 2011; Balmaseda et al. 2013; Llovel et al. 2014). To understand the future effects of climate change and to implement mitigating measures, it is important to know how community structure responds to varying regional factors.

3. CHAPTER THREE:

Habitat complexity as an alternative explanation for body-size patterns in the largest ecosystem on Earth

3.1 Abstract

Changes in body-size distributions can be an important indicator of the reorganisation of animal communities in response to human influences. To understand such changes and their consequences, it is necessary to understand what structures body-size distributions in natural communities. Two hypotheses concerning the mechanisms of the change in size have often been proposed, which are the energetic and textural discontinuity hypotheses. The energetic hypothesis states that body size should change with changes in energy availability, while the textural discontinuity hypothesis states that body size should change in response to changes in habitat complexity. The deep sea forms a unique system where these two hypotheses can be tested against each other as a result of food (energy) limitation and varying habitat complexity, with strong responses expected from the community. Here size distributions of benthic macrofauna on the continental slope and upper bathyal area of the northwest Atlantic Ocean are analysed with regard to these two hypotheses. There was limited to no support for the energetic hypothesis, contradicting previous suggestions that food availability influences body-size change in the deep sea. Habitat complexity had an unrecognised strong relationship with body size, thereby supporting the textural discontinuity hypothesis. The idea of habitat complexity as an influencing factor on body-size patterns in the deep sea has not been tested before. However, it is recognised that habitat complexity alone can not explain all the variety in body size in the deep sea. A link between habitat complexity and energy availability is likely necessary, in both deep-sea research and other systems.

3.2 Introduction

Human influences are altering natural communities by affecting interactions between organisms and their environment (Millennium Ecosystem Assessment 2005). It is important to understand the mechanisms between anthropogenic changes in the environment and the biological community response to fully appreciate changes in the community and resulting changes in ecosystem function. Body size patterns can be informative in understanding such changes as the body size of an organism is one of the most important features of a species: it correlates with and can be used to predict many other traits such as life-history (e.g. longevity), physiology (e.g. oxygen consumption rate), and ecology (e.g. population dynamics). Body-size patterns are also less likely to be influenced by taxonomic constraint than other aspects of community ecology (Peters 1983; Schmidt-Nielsen 1984; Damuth 1992; Enquist et al. 1999; Woodward et al. 2005).

Relationships associated with body size are referred to as allometric relationships, they are often well described with power laws, and they can behave as fractal or fractal-like associations, likely influenced by the distribution of material and/or energy in time or space (Mandelbrot 1982; West et al. 1997; Enquist et al. 1999; Brown et al. 2004b). However, the distribution of body sizes in a community often follows a log-normal distribution, suggesting that the most animals are not the very smallest ones, or indicating that these have not been sampled well (Hutchinson and MacArthur 1959; May 1978,1986; Maurer 1999; Gaston and Blackburn 2000). Several processes, including evolutionary and ecological processes, influence this log-normal distribution, thereby skewing it (Krummel et al. 1987; Brown and Nicoletto 1991; Holling 1992; Losos and Schluter 2000). For example, nomadic species, species that are declining in abundance, or invasive species influence body-size distributions (Allen et al. 1999; Allen and Saunders 2002). Several hypotheses have been proposed to explain the observed log-normal distribution in body-size distributions. Two promising hypotheses are the energetic hypothesis and the textural discontinuity hypothesis (Allen et al. 2006).

The energetic hypothesis states that an observed body-size pattern is a result of resource availability in the environment. Organisms will vary in how well they can take up the resources and use it for survival and reproduction (Brown et al. 1993; Enquist et al. 1999). For example, small organisms need less energy per individual than a large organism (Brown et al. 2004b). This means that if energy is finite, more small organisms can be supported on that amount of energy compared to large individuals. Therefore, there is a trade-off between density and body size, and this trade-off is called the energy-equivalence rule (Damuth 1987). The metabolic rate of an organism, the rate at which an organism uses energy, is correlated with size, with smaller organisms having a higher metabolic rate than larger organisms. This is the result of the change in energy consumption per unit of biomass. Although larger organisms need more absolute energy, per unit biomass they need less, so the relative energy usage goes down. As a result of these considerations, it can be predicted that there should be a higher density of smaller organisms compared to larger organisms in any area with finite energy (Damuth 1981). A change in habitat complexity should not influence body size estimates.

The textural discontinuity hypothesis can be used to explain body-size patterns according to the complexity of the environment (Holling 1992). Small organisms are expected to be more numerous as a result of the availability of micro-niches in a more complex habitat (Hutchinson and MacArthur 1959; May 1978; Morse et al. 1985; Lawton 1986; May 1986; Williamson and Lawton 1991; Davenport et al. 1996; Rafaelli et al. 2000). The change in body size might depend on perceived spatial scale, meaning that smaller organisms potentially perceive a unit area differently compared to larger organisms (Shorrocks et al. 1991; Gee and Warwick 1994b,a). According to the textural discontinuity hypothesis, body-size patterns should not change when there is a change in energy availability (Allen et al. 2006).

A study system where these two competing hypotheses can be tested is the soft-sediment benthic community of the deep sea (>200 m depth), the largest biome on Earth. One of the recognised trends in this system is a decrease in body size with increasing depth (Thiel 1975; Sommer and Pfannkuche 2000; Brown et al. 2001; Udalov et al. 2005; Rex et al. 2006; Johnson et al. 2007; Itoh et al. 2011). This decrease in size has been suggested to result from a decrease in food availability, or chemical energy, with increasing depth and distance from land; or in other words (Rex and Etter 2010; McClain et al. 2012), supporting the energetic hypothesis. However, many contradictory results are reported for the change in body size, including no relationship, and positive and parabolic relationships (de Bovée et al. 1990; Alongi 1992; Vanhove et al. 1995; Rex et al. 1999; Hughes and Gage 2004; Vanhove et al. 2004; McClain et al. 2005; Hoste et al. 2007; Berkenbush et al. 2011), indicating a need to look for other explanations.

Most soft sediments have low habitat complexity at large spatial scale. This is offset by local-scale heterogeneity in sediment particle size and the presence of structure-forming species, such as many coral and sponge species (Baker et al. 2012; Demopoulos et al. 2014). Particle size diversity has been shown to correlated positively with species richness in the sediment (Etter and Grassle 1992; Leduc et al. 2012). This local increase in heterogeneity might also mean that more micro-niches are available, which could increase the abundance of small organisms. Another mechanism to increase habitat complexity in a soft-sediment area is the loss of body components from structure-forming organisms, for example the loss of spicules by sponges can form dense spicule mats in the sediment, which can persist long after the structure-forming organism has died (Bett and Rice 1992; Jones et al. 1994; Barrio Froján et al. 2012). Living structure-forming organisms provide living spaces for the smaller organisms by providing internal spaces and crevices to live in and on, and they often have a high associated biodiversity. Associates might feed on food particles not utilized by the host itself or feed on the host (Buhl-Mortensen et al. 2010). It has been suggested that higher habitat complexity could lead to increased food availability (Bologna and Heck 1999; Laegdsgaard and Johnson 2001), although this explanation is inferred (Warfe et al. 2008). It has been suggested that structure-forming organisms increase in importance with increasing depth as they provide local habitat complexity in an increasingly less complex background environment (Buhl-Mortensen et al. 2010). For example, grain size, current velocity at the seafloor, food availability and substrata variability decrease with increasing depth at continental margins that are well oxygenated (Levin et al. 2001; Carney 2006)

As both food availability and habitat complexity are limited in the deep sea, a strong response of the community to these variables is expected, allowing for comparison of these two hypotheses. Rapid changes in abundance have been observed with sudden impulses of food in the deep sea, which can affect the community's average body size (Billett et al. 2010; Smith Jr et al. 2013). The influence of habitat complexity on body size in the deep sea has had limited attention. Here, we compare whether the energetic hypothesis or the textural hypothesis can best explain the change in body size distribution in deep-sea benthic macrofaunal organisms present on the continental slope and upper bathyal depths. To our knowledge, no other hypothesis apart from the energetic hypothesis has been tested for body-size patterns in the deep sea.

3.3 Methods

3.3.1 Fauna

This study was undertaken on 30 box core samples (2844 individual organisms in total) taken as part of the NEREIDA (North Atlantic Fisheries Organisation PotEntial VulneRable Marine Ecosystems - Impacts of Deep-sea Fisheries) project. The samples were taken around the Flemish Cap, the Flemish Pass and Grand backs east and southeast of Newfoundland, Canada during cruises in 2009 (May to August) and 2010 (June to August) on board of the *Miguel Oliver* (figure 3.1). The box cores ranged between 580 m and 1890 m depth and they were selected using a random-stratified sampling method allowing for latitudinal coverage. Biological samples were taken from the top 5 cm sediment layers, sieved over 0.5 mm sieve, and stored in 4% formaldehyde. Samples were later sieved over 1 mm sieve mesh sizes and specimens were sorted into major taxonomic groups by the Institute of Estuarine and Coastal Studies (IECS), Hull, United Kingdom, and stored in 70% industrial methylated spirits (IMS). The polychaete data were sorted to family level under a Motic SMZ-140/143 Stereo microscope (50× magnification) and stored in 80% IMS after sorting.

Polychaetes are macrofaunal organisms that are numerically dominant in this size class in benthic deep sea soft sediment ecosystems. During the sampling and sorting process, most of the fragile worms had broken. This is a common problem in deep-sea research, and other methods have been developed to study polychaete body size. The width of the first chaetiger (segment) has been shown to correlate strongly with body length, and can therefore be used as a proxy (Paterson et al. 2006; Laguionie-Marchais et al. 2016). The width of the first chaetiger (mm) was measured from photos taken under the microscope using ImageJ V1.49. Each polychaete was measured three times and the average of the results were taken to minimise measurement bias. The polychaetes were identified to family level; it is assumed that body-size patterns are free from taxonomic constraint (Damuth 1992). The body-size mean per sample was calculated and used as a community value to study body-size change in the deep sea. There was no difference in body size between the northern, central or southern regions and the width of the first chaetiger was logged to meet the assumption of normality.

3.3.2 Habitat complexity

The latitude and longitude for each box core sample was recorded at the time of sampling. Depth (bathymetry) was recorded from the ship's multibeam surveys (Kongsberg EM 302 30 kHz system). The bathymetric data were gridded to 75 m and smoothed with a 5-cell neighbourhood filter in ArcGis10.1. These data were used to extract other bathymetric variables, such as slope angle, and rugosity (25-cell neighbourhood radius) using the Spatial Analyst extension and bathymetric position index (25-, 50-, 75-, 100-, 125-, and 150-cell neighbourhood radii) using the Benthic Terrain Modeller (Lundblad et al. 2006).

A subsample (2 cm depth) from each box core sample was taken using a PVC (10-cm diameter) tube for particle size analysis (PSA). The size fractions were calculated using a Beckman Coulter LS230 Counter (Weitzman et al. 2014). The following categories were used to determine percentage clay, silt and sand: 0.375 – 7.421 µm (clay), 8.147 – 57.77 µm (silt) and

63.41 – 2000 µm (sand). The size fractions used included 12 size classes on the Krumbein phi scale, ranging between -1 and >10 Φ. Φ is calculated as follows:

$$\Phi = -\log_2 D/D_0,$$

where D represent the diameter of the particle, and D_0 is a reference particle diameter (Krumbein and Aberdeen 1937). This reference is set to 1 mm for this scale to make the scale dimensionless (Krumbein and Aberdeen 1937). These size classes were used to calculate particle size diversity (Shannon-Weiner) using the vegan package in R (R Core Team 2015; Oksanen et al. 2016) following methods used in Etter & Grassle (1992) and Leduc et al. (2012). Particle size diversity and percentage silt was used in this study.

Sponge data, collected from research trawls, were modelled via the Kernel Density Tool in the Spatial Analyst extension in ArcGIS10.1 following Kenchington et al. (2014). Sponge density (kg km^{-2}) was obtained via the Extract Values (with local interpolation option selected) for each box core sample.

Fishing is known to influence sediment characteristics and homogenising sediments, or in other words, influence habitat complexity, and thus a measure of this is included in the analyses (Thrush and Dayton 2002). Fishing intensity was modelled in two ways: Vessel Monitoring System (VMS) location data from 2003-2012 and VMS time-reference locations from 2008-2012. The VMS location data were mapped in ArcGIS10.1 and the intensity of fishing was determined as the density of VMS records in a radius of 1, 3, or 5 km from each box core sample. The Point Sampling Tool in the Spatial Analyst extension was used to obtain the densities for each box core sample (local interpolation option selected). The time-reference locations that had boat speed between 0.5 and 5 knots were used to construct trawl paths (based on boat, boat speed, date, time and location). The speeds of 0.5 and 5 knots were used as trawling activities generally use such speeds (Lambert et al. 2012; Campbell and Federizon 2013; Mangano et al. 2014). The Line Density Tool from the Spatial Analyst extension was used to measure the trawl path lengths (km^2) within box core radii from 1, 3 or 5 km, and the corresponding values were extracted. Fishing intensity (3km radius) was used in this study.

3.3.3 Energy

Monthly average data on temperature (°C) and meridional velocity (m s^{-1}) from 1990 to 2010 at 1/12-degree resolution was available, along with temperature data measured at the time of sampling using a Sea-Bird Electronics 25 CTD. Annual averages for the year of sampling and the previous year were used to create two raster files in qGIS2.2 through interpolation using 3000 × 3000 pixels and inverse distance weighting, and the values for the box core samples (determined by collection year) were extracted. Long-term influences of mean and maximum bottom current speed (m s^{-1}) and mean and minimum bottom temperature using 10-year average were calculated via interpolation (75m grid) using the Empirical Bayesian Kriging function in ArcGIS10.1. Meridional and zonal velocities were used to calculate current speed using the Pythagorean Theorem. Current speed data was used rather than meridional and zonal velocities.

Particulate organic carbon (POC; mg m^{-3}) data at the surface were downloaded from the Giovanni ocean colour radiometry online data system from NASA Goddard Earth Sciences Data and Information Center (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month), using MODIS AQUA (4km resolution) for the years 2008 to 2010. These data were used to create two raster files for the year of sampling plus the previous year in qGIS2.2 through interpolation using 2500 × 2500 pixels and inverse distance weighting, and the data were extracted for the relevant box core samples (determined by collection year). Terrestrial data were filtered out prior to interpolation. POC at surface was used as it has been shown to influence benthic communities (Smith et al. 2008). As the sinking of carbon will have a time lag, it is possible that the influences of available carbon will not show later. Therefore, carbon measures from the box core samples were taken as well.

From the same subsample used to calculate the particle size diversity, carbon content in the sediment samples was calculated. A Leco TruSpec CHN analyser (model 630-100-400) was used to calculate total and organic carbon percentage. Prior to analysis, the samples were dried at 60°C and pulverised to a fine homogeneous powder. Intermittent measurements for total carbon were made and compared to analytical standards to ensure consistency. Inorganic carbon content was measured by subtracting the organic carbon content from the total carbon values (Weitzman et al. 2014). Inorganic carbon was excluded from this study.

3.3.4 Data analysis

Data were analysed in R (R Core Team 2015). A general linear model was constructed which included all explanatory variables: monthly and decadal temperature observations, monthly and decadal velocity observations, particulate organic carbon at sea surface, organic carbon and total carbon at the seafloor, slope angle, rugosity, benthic position index, particle size diversity, percent clay, percent silt, sponge density, and fishing intensity. Body size, sponge density and fishing intensity were logged to meet the assumption of normality. Backward selection of the full model using likelihood-ratio test was used to optimise the model, where the variable with the highest *P*-value was deselected and the model refitted. This was continued until all explanatory variables were significant.

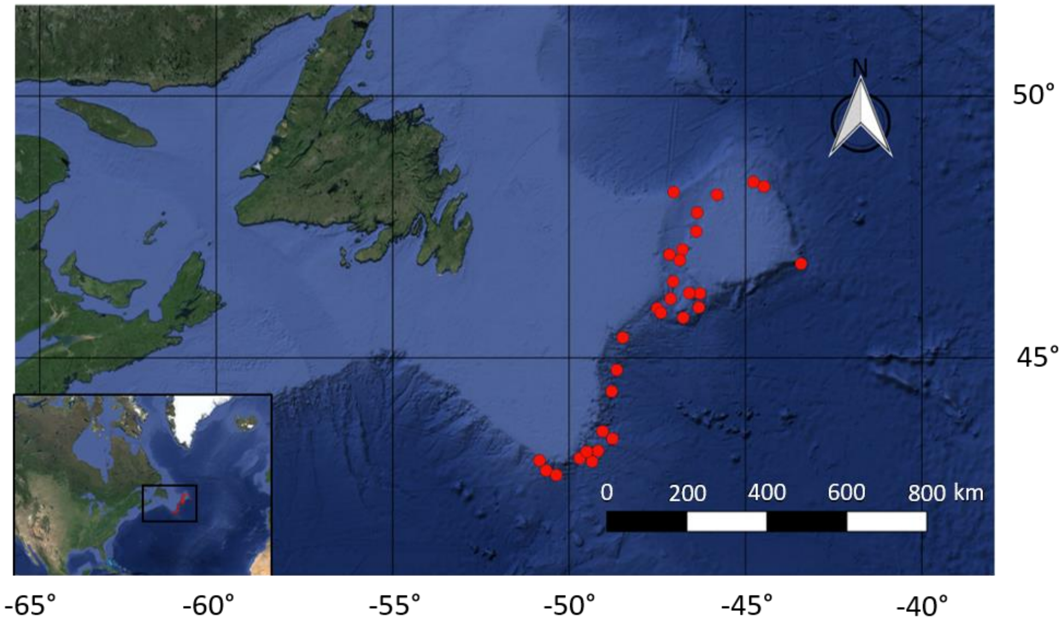


Figure 3.1 The sample locations of the 30 box core samples from the northwest Atlantic represented by the red circles.

3.4 Results

The variation in body size was best explained by two variables of habitat complexity: sponge density and slope angle, and one weak correlation with particulate organic carbon (POC), an energy variable. All other variables were selected against in a step-wise manner.

Sponge density was negatively related with body size (*r* = -0.131, confidence interval (CI) = -0.227 to -0.032, *P* = 0.0074; figure 3.2). There was an outlier present, however, the result did not vary with the removal of this outlier (*r* = -0.130, CI = -0.227 to -0.032, *P* = 0.009). An interaction was present between sponge density and slope angle, and between sponge density and POC. However, both were not included in the final model as model diagnostics were not acceptable with the interaction included.

Slope angle was weakly positively correlated with body size (*r* = 0.051, CI = 0.007 to 0.096, *P* = 0.02443; figure 3.3), and this did not change when the outlier in POC was removed from the model (*r* =0.053, CI = 0.007 to 0.098, *P* = 0.02384).

There was a negatively and weakly relationship between POC and body size (*r* = -0.007, CI = -0.016 to 0.005, *P* = 0.08; figure 3.4). This result was caused by an outlier at around 182.44

mg/m^3 POC. When this observation was removed, there was no significant relationship (*r* = -0.005, CI = -0.016 to 0.005, *P* = 0.3211) and the model diagnostics were similar. It is kept here for discussion purposes. There was an interaction present between POC and slope, but this was left out because model diagnostics were not acceptable with the interaction included. Other relationships that might confound the results were checked as well to facilitate interpretation. No significant relationship between POC and depth were found, no significant interaction between slope angle and sponge density were found. Furthermore, abundance of the polychaetes was not influenced by sponge density.

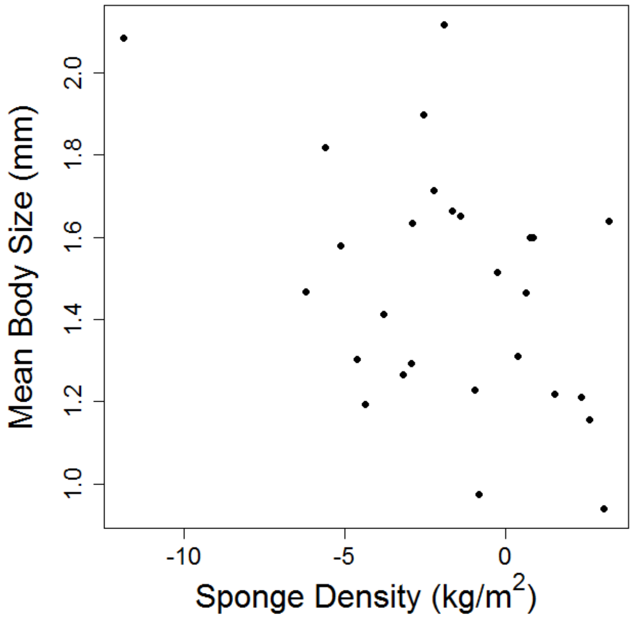


Figure 3.2 There is a negative relationship between log sponge density (kg/m^2) and mean body size (mm). Note that the outlier at low negative log sponge density did not influence the negative relationship.

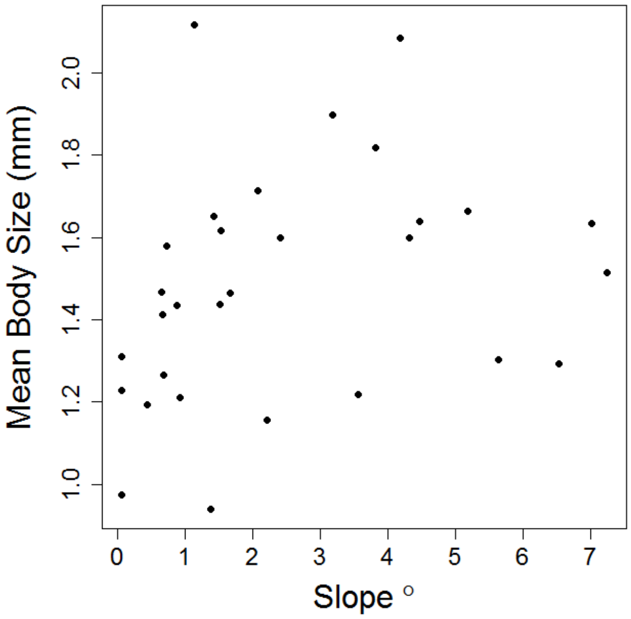


Figure 3.3 There was a positive relationship between slope aspect (°) and mean body size (mm).

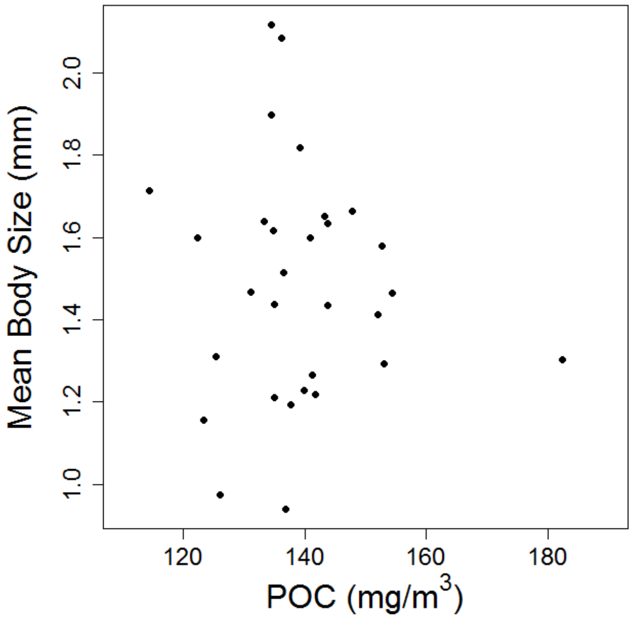


Figure 3.4 There was no relationship between particulate organic carbon (POC; mg/m^3*) availability and mean body size (mm). Note that the removal of the outlier at high POC values did not influence the relationship.*

3.5 Discussion

Two hypotheses, both predicting a change in body size as a result of different variables, were compared in a deep-sea system. The energetic hypothesis relates the change in body size to variation in energy availability. There was limited evidence of this in the data. The other hypothesis, the textural discontinuity hypothesis, associates change in body size with variation in habitat complexity. This hypothesis has not been tested before in the deep sea. It was found that body size changes are explained well by changes in two measures for habitat complexity in the form of sponge density and slope angle.

3.5.1 Habitat complexity

Sponge density and slope aspect are both forms of habitat complexity in the deep sea (Tissot et al. 2006; ICES 2009). Habitat complexity in the form of sponge density showed the strongest correlation for a decrease in body size in this study, with higher densities of sponges leading to smaller organisms in the sediment. This lends support to the textural discontinuity hypothesis. Whole sponges rarely featured in box core samples, however, their presence will have affected sediments around them in the creation of dense spicule mats. The presence of these dense mats have been recognised in this area before (Barrio Froján et al. 2012). Therefore, the presence of sponges might act indirectly by creating higher habitat complexity in the sediments around them, resulting in smaller organisms. As the presence of, for example, sponges, was not included in previous studies, it is possible that the smaller size of organisms might have been related to the effect of more complex habitat rather than food availability.

Sponges have been recognised as important factors in ecosystem functioning relationships in aquatic systems (Bell, 2008). They perform important roles in biogeochemical cycles (such as nitrogen, carbon, silicon cycles) and also in the provision of habitat, oxygen depletion, viral predation, protection, camouflage, settlement substrate, and the influence on near-boundary and reef-level flow regimes (Wulff 2006; Bell 2008). Sponges create a more complex habitat against a less-complex soft-sediment system (Tissot et al. 2006; ICES 2009). There is an increase in invertebrate biodiversity associated with sponges compared to the surrounding soft sediments (ICES 2009; Hogg et al. 2010). Sponge grounds are considered to be vulnerable marine ecosystems as they are easily destroyed by bottom-contact fishing gear and are likely to have a low capacity to recover over short (decadal) timescales (FAO 2009). Furthermore, their spicules provide an increased habitat complexity (Bett and Rice 1992; Buhl-Mortensen et al. 2010). This structuring effect can be noted even when the biological community is aggregated to phylum level (Barrio Froján et al. 2012). It is unknown whether the presence of sponges results in size selectivity by the exclusion of large individuals (Hacker and Steneck 1990), or whether the sponges are ecosystem engineers, providing living spaces for more smaller organisms (Bell 2008) or physically modify the abiotic habitat and facilitate the presence of other, smaller organisms in other ways (Hastings et al. 2007).

Habitat complexity will influence hydrographic phenomena, which in turn will influence the presence or absence of sponges. The physical environment, such as slope angle, can influence the formation of internal waves (Xing and Davies 2006; Garrett and Kunze 2007). Internal waves are important in global ocean mixing, such as the increased rate in transport of sediment to greater depths (Rudnick et al. 2003; Garrett and Kunze 2007). Deep-sea sponges often occur in areas where there are internal waves formed. Sediment transport is important for sponge reefs and gardens as they influence the availability of silicon, they prevent reef collapse, and it delivers food (Rice et al. 1990; Klitgaard and Tendal 2004; Whitney et al. 2005). Slope angle has been shown to be important in sponge distribution models in the Flemish Cap and Grand Banks area (Knudby et al. 2013). It is possible that slope angle influences the presence of sponges, and thereby indirectly the body size of macrofaunal organisms. No interaction was found between slope angle and sponge density, but it is possible that this is a result of using modelled sponge distribution data, rather than observed sponge data. It could potentially explain why there was a weakly significant correlation between slope angle and body size.

Other forms of local habitat complexity include sediment particle size. This factor has been shown to influence species diversity (Etter and Grassle 1992; Leduc et al. 2012). It did not influence body size significantly here, possibly indicating that different habitat complexity variables affect organisms in different ways. It must be noted as well that organisms might not respond to the diversity of sediments, but to the food availability distributed around them (Snelgrove and Butman 1994).

Fishing intensity was expected to be of importance as it affects the density of sponges. Trawling doors, sweep nets and ground ropes for nets are likely to disrupt sediments as well, thereby influencing the dense spicule mats (Thrush and Dayton 2002; Barrio Froján et al. 2012). No relationship between fishing intensity (in the form of trawling) and body size was found in this study. Likewise, sponges are filter feeders, and will be influenced in terms of their distribution by the presence of currents. No relationship between current speed and body size was found. Fishing intensity and sponge density, and current speed and sponge density were not co-linear in this study, which might also explain why there was no relationship found. There might be more complex relationships between the different environmental and human variables than included in this study.

3.5.2 Energy

POC is a food source in the deep sea and is a form of chemical energy. The deep sea is a food-limited system that mainly depends on food particles sinking down from the euphotic zone (upper 200m of the ocean) where photosynthesis takes place. Food availability varies through vertical transport, lateral advection, resuspension, transfer efficiency, and primary production (Buesseler et al. 2007; 2008; Honjo et al. 2008; Rex and Etter 2010; Dell'Anno et al. 2013). The POC values used here were measures at the sea surface from satellite data. It has been shown that such values can predict abundance and biomass in the deep sea very well (Behrenfeld et al. 2006; Smith Jr et al. 2006; Johnson et al. 2007).

As in several previous studies, this study did not find a body size-energy relationship in the benthic community (de Bovée et al. 1990; Alongi 1992; Vanhove et al. 1995; Rex et al. 1999; Hughes and Gage 2004; Vanhove et al. 2004; McClain et al. 2005; Hoste et al. 2007; Berkenbush et al. 2011). This limits the support for the energetic hypothesis. An outlier in the POC data was present. Before the removal of this outlier, there was a weak relationship between POC and body size. When this outlier was removed, no influence of POC on body-size patterns was found. It is possible, however, that the influence of chemical energy works over larger depth ranges compared to the depth range used here. The depth range of this study was between 580 and 1890 m depth, which is possibly too small for chemical energy to be of influence on body size. No relationship between POC and depth was observed in this study. Perhaps, to detect an effect of food availability, several kilometres should be investigated, so that the variation in POC is larger. Chemical energy has been shown to be of importance of species richness over large depth ranges (Woolley et al. 2016).

Alternatively, it has been shown that deep-sea organisms can rapidly response to sudden food impulses, for example through increased recruitment (Billett et al. 2010; Smith Jr et al. 2013; Rogers 2015). POC flux to the deep sea is not constant, but varies seasonally (Buesseler et al. 2007). To remove the influence of this seasonal variability, the monthly average was taken in this study. It is possible that this variability in the deep sea is more important than the absolute energy (Billett et al. 2010). It is possible that changes in body size become apparent with this sudden impulse, and that no relationship was found here as food influx might have been relatively constant. The energetic hypothesis does not make assumptions about the variability of energy in time (only in space) (Allen et al. 2006), and it is well worth exploring this extension. However, it must be noted that, if variability is of importance, then the energy availability in the cores (measured as total carbon and organic carbon content), potentially should have had a correlation with body size. The current food availability could have an impulse on the body size while an average over a longer time period might reduce the effect of such an impulse detection. In this study, that was not found, with no correlation between total or organic carbon between body size measures.

Temperature has an effect on metabolic rate and therefore should be linked to body size according to the Metabolic Theory of Ecology (Brown et al. 2004b). A higher metabolic rate is expected at higher temperatures, and a higher energy flux should be expected, meaning that more food should be consumed. No relationship between short-term or long-term temperature and body size was observed. According to the energetic equivalence rule the energy flux in a population at a given unit area should be the same (Damuth 1987). The data used here were standardised for unit surface area, which might explain why there was no relationship between temperature and body size. Alternatively, temperature and food supply were not co-linear in this study, and temperature might not have an effect on body size across the depth range used here. It has been shown that thermal energy is important for the diversity of marine organisms at shallow depths measured over large (latitudinal and bathymetric) spatial scale (Woolley et al. 2016).

3.5.3 Oxygen and biotic interactions

Habitat complexity and energy availability are not the only factors influencing body size in deep-sea organisms. It is well known that oxygen concentration affects body size, with lower levels of oxygen concentration favouring smaller body sizes (Levin et al. 1991; 2000; Gooday et al. 2009). This is especially the case in extreme Oxygen Minimum Zones (eOMZ) (Wyrtki 1966), where high surface primary production would predict higher biomass and sizes of benthic organisms. Microbial activity, however, reduces oxygen levels to a critical minimum in which larger organisms cannot survive. Benthic organisms that live below an eOMZ are often abundant as they profit from the higher carbon availability towards the benthic environment as a result of reduced recycling in the water column by larger organisms (Levin et al. 2000; Rogers 2000). Data on oxygen levels for this study were not available, thus could not be investigated to determine whether oxygen concentration varied in the region corresponding with higher or lower body sizes of the polychaetes. The area at and around the Flemish Cap, however, are known to be oxygenated waters (Colbourne et al. 2014), which would suggest no influence of this variable on body-size estimates provided here. Previous studies indicate that polychaetes can also be resistant to low oxygen levels, often being one of the dominating groups with nematodes and bivalves (Arntz et al. 1991; Levin et al. 1991), suggesting that even if oxygen levels could be potentially low at local places in the Flemish Cap area, it might not influence the polychaete community necessarily.

The deep-sea food web has been understudied, meaning that it is unsure what most organisms eat. For example, most polychaetes are considered deposit feeders, but whether that means they feed of sinking organic material directly, or potentially even from the bacteria that feed of the available carbon material, is unknown (Jumars et al. 2015). It is possible that carbon per se does not inform well on body-size relations, but rather the labile or refractory component of carbon should be used. Labile carbon is readily available as a food source for animals, while refractory carbon is inorganic carbon and can be assimilated by bacteria. A higher proportion of labile carbon is usually suggested to be a higher quality of carbon, and it relates well with body size, especially in oligotrophic regions (Probert and McKnight 1993; Danovaro et al. 1995; Probert et al. 1996; Dauwe et al. 1998; Grove et al. 2006; Hoste et al. 2007; Berkenbush et al. 2011). As the links in the food web are not resolved yet, it can make the use of carbon availability as energy source difficult; thus, when relationships are not present between carbon availability and body size it could be a result of these unresolved food webs.

Other biotic interactions in the food web are known to influence body size. For example, most predators will not ingest prey that are larger than the predator itself (ignoring parasites who do feed on prey larger then themselves), although the sizes of prey and predators are not proportionally related (i.e. when prey size increases the size of its predator might not increase the same amount) (Cohen et al. 1993; Leaper and Huxham 2002). It has been shown that body size has a structuring effect on food webs, with size influencing interaction strengths, as there is a connectedness between food web, density, and body size (Warren and Lawton 1987; Cohen et al. 2003; Emmerson and Raffaelli 2004). Predator-prey interactions have not been included in this study, as the trophic positions and relations of the polychaetes used in this study are not well understood. Furthermore, many predatory groups in the deep sea switch to scavenging life styles. It has been shown that omnivory is very important in food webs, especially for its stability and complexity (Williams and Martinez 2000), but how this plays out in the deep sea is again not well understood.

3.5.4 Sampling

Both the energetic hypothesis and the textural discontinuity hypothesis state that the most abundant organisms are the smallest ones (Morse et al. 1985; Williamson and Lawton 1991). However, in most studies, including this one, body-size distribution is log-normal, meaning that the most abundant individuals are not the smallest organisms. It has been noted before that the relationship between abundance and body size might not be linear, and can result from sampling bias (Mittelbach 1981; Armstrong and Nudds 1985; Gaston and Lawton 1988; Gunnarsson 1992; Gaston and Blackburn 2000; Stead et al. 2005). Abundance was not correlated with sponge density in this study, suggesting that the highest abundance is not necessarily present in the areas with the densest spicule mats. The sampling method used here has likely underestimated the number of small organisms as well as a result of sieve size. It is more conventional to use smaller sieve sizes, between 0.3 and 0.5 mm, rather than the 1 mm used here in deep-sea research for macrofaunal studies. As this trend between habitat complexity and body size was still found with the bias in the sampling, it is expected that the trend is valid and that with accurate sampling an even stronger trend might be found.

A step forward for deep sea research and the detangling of the body-size patterns in general would be to include a larger community. In the case presented here, the focus was on macrofauna, which limits the generalization of the hypothesis to this size class. There is an idea that there is bimodality in body size in small marine benthic organisms, corresponding to the meiofauna and macrofauna. It has been suggested that meiofauna and macrofauna sizes represent ecological adaptive peaks as a result of living at different spatial scales, although this idea is contested and it has been shown that sampling methods can result in the observed bimodal distribution (Warwick et al. 2006; Bett 2013,2014; Warwick 2014). Using a larger range of sieve sizes will give a more accurate representation of benthic marine organisms' sizes (Leaper et al. 2001). Studies often report extrapolated values for the density, biomass, and/or body size in terms of surface area sampled. For example, for macrofauna, standardised areas of 0.25 m^{-2} are often reported in the final estimates, while areas between 0.003 and 4 m^2 are actually sampled. Likewise, values for meiofauna are often reported as 10 cm^{-2}, while actual areas sampled include 0.0003 to 0.59 m^2. The actual size of the area sampled has an influence on body-size estimates as well, and should be standardized (van der Grient and Rogers 2015).

3.5.4 Concluding remarks

The textural hypothesis predicts that body size should not change with a change in energy availability, and should change with a change in habitat complexity. The results presented here suggest that the inclusion of habitat complexity in the energy availability debate can enhance our understanding of body-size changes in the deep sea. Habitat complexity influencing body size has had much attention in terrestrial and shallow-water systems, showing the wider application of this framework. In these studies, habitat complexity is measured by fractal dimensions. Fractals increase in structure when studied at finer scales. This change in detail which becomes apparent when zoomed in on the fractal can be quantified and represented as the fractal dimension. The dimension captures the complexity of the fractal and the space it occupies at high resolution. If deep-sea studies would include such observations of fractal dimensions in their habitat (for example, sponges or sediment grains could be represented by this dimension), it would make these studies comparable to other complexity studies (Halley et al. 2004). Furthermore, the use of fractal dimensions could suggest if and how energy is distributed in a certain way in a more or less complex habitat. Thus, fractal research could be a link between energy distributions in complex habitats. The deep sea would provide an alternative system with unique features that allow for the testing of competing hypotheses between energy availability and habitat complexity, formulated in terrestrial and shallow-water systems, as responses of the community can be very strong and therefore potentially easier to observe.

Sponge spicules present in the sediment add to habitat complexity. These are often found in box cores, but not included in terms of ecological influences. Potentially, the supposed trend with energy is a result of subsampling areas with decreased body sizes driven by habitat complexity. It is also possible that energy will have a larger influence at greater depths. With increasing depth, food supply (energy) will decrease further. It is possible that there might be a switch between major controlling factors at a certain depth. It has been shown before that several factors influence body-size dynamics (Gaston and Blackburn 2000; Stead et al. 2005). At this point, it is unknown whether the presence of sponges result in size selectivity by the exclusion of large individuals (Hacker and Steneck 1990) or whether the sponges are ecosystem engineers, thereby physically modifying the abiotic habitat and facilitating the presence of other organisms (Hastings et al. 2007). It has been proposed in other systems that energy and habitat complexity might act in a hierarchical manner (i.e. local scale versus regional scale), and this notion is well worth exploring (Gaston and Blackburn 2000; Stead et al. 2005).

4. CHAPTER FOUR:

The maintenance of macrofaunal diversity on deep-sea continental slopes and upper bathyal depths

CHAPTER FOUR

4.1 Abstract

The maintenance of biological diversity is not well understood, with several unexplained patterns observed. The most challenging examples of these are the high diversity of plants in the tropics, the high diversity of plankton in the upper layers of the oceans, and the high richness in deep-sea deposit-feeding species in soft-sediment communities. The deep sea is the largest biome on Earth; it is a cold and low-energy environment. Most of the theories aiming to explain high species richness in the deep-sea are based on local sampling studies. The study presented here focuses on family level, rather than species level, to understand how the environment might structure the community at such a taxonomic resolution. A regional approach was taken to analyse deep-sea family composition, the distribution of families in space. It is one of the first test on regional spatial scale with high sampling coverage. Factors that were found to significantly structure deep-sea community composition are: food availability (particulate organic carbon, total carbon), habitat heterogeneity (bathymetric position index), sediment characteristics (percentage clay and silt) and long-term temperature variability. Food availability and habitat heterogeneity have been proposed in the past to structure deep-sea communities, although it is not clear whether they present mutually exclusive effects. Sediment characteristics, as particle size diversity, have been suggested as important in the past, while in this study percentage clay and silt were found to be of influence, not particle size diversity. A modified conceptual model based on Levin et al. (2001) is proposed that aims to encompass the direct and indirect effects of different environmental factors at local and regional scale at which these effects potentially structure the community.

4.2 Introduction

The importance of biodiversity for Earth system and for human well-being has been recognised in the Convention on Biological Diversity (CBD) and in the Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005; Conventional on Biological Diversity 2010).

Biodiversity can encompass taxonomic richness, genetic richness, or even ecosystem richness. One aspect of the CBD, for example, is understanding how many and why there are so many species on Earth, and how to conserve these species. It is well known that most species have not been described yet, and there is a risk that these will be lost before being discovered (Appeltans et al. 2012; Caley et al. 2014; Fisher et al. 2015). The deep sea (>200 m depth) constitutes a special case in this framework. Owing to its sheer size in terms of surface area and volume, it is logistically difficult to estimate the taxonomic richness of this environment. It has, however, been recognised that local species richness can be extremely high (Grassle and Maciolek 1992). Whether that means that the deep sea is as species rich or richer than, for example, tropical terrestrial ecosystems remains to be seen. It is possible that local species richness reflects regional diversity in the deep sea (Lambshead and Boucher 2003; Buzas et al. 2014).

The deep sea is an interesting case to study the drivers of richness because of its special characteristics. Most of the deep sea, apart from reducing environments, is food-limited, with the system depending on food particles sinking down from the euphotic (upper 200 m layer) zone. Primary production, transfer efficiency, resuspension, vertical transport, and lateral advection influence food availability sinking down to the lower depths of the oceans (Buesseler et al. 2007; 2008; Honjo et al. 2008; Rex and Etter 2010; Dell'Anno et al. 2013). Combined with the low temperatures, high pressure and low to no light present, the deep-sea may be regarded as a harsh environment. It has therefore defied prediction of general ecological theory that diversity should be low in areas with extreme physical conditions.

Most benthic organisms are deposit feeders (Dayton and Hessler 1972), thereby making it difficult to understand what constitutes a niche in the deep sea and how this can lead to the observed diversity in soft-sediment communities. Such questions do not limit themselves to the deep ocean. For example, it is still not known why there are so many terrestrial plants in the Tropics, or why it is possible to have so many plankton species present in the upper layers of the oceans (the Plankton Paradox) (Hutchinson 1961). In all these cases, organisms seem to feed off similar resources, making it is difficult to determine how they all might occupy different niches.

Species identification in the deep sea is difficult, and many species still await description. As such, studies at species level can be very difficult because of the lack of information. Many hypotheses have been proposed for the maintenance of high taxonomic richness in the deep sea including: energy (McClain et al. 2012), habitat heterogeneity (Etter and Grassle 1992; McClain and Barry 2010), historical factors (Gage 2004), disturbance (Grassle 1989), stability (Sanders 1969), and biological and ecological interactions (Rex 1976). Many of these hypotheses are similar to those in terrestrial and shallow-water ecosystems (Whittaker et al. 2001; Cox et al. 2016a) suggesting that the systems are comparable in terms of determining what maintains taxonomic richness.

Levin et al. (2001) proposed a conceptual model (figure 4.1) of how deep-sea regional species richness may be maintained. They proposed that species richness is influenced by heterogeneity in the environment, food supply, oxygen concentration, current speed, sediment characteristics, and disturbance events. These variables can have links between each other as well. Proper tests of this model are rare as a result of low sample sizes with limited environmental gradient coverage. Most deep-sea taxonomic richness, composition or diversity patterns are based on local sampling records. These studies, therefore, are limited in what potentially drives community differences at different environmental conditions. Furthermore, the inclusion of human disturbance in such models, such as trawling, which have been shown to influence taxonomic composition, are lacking (Kaiser et al. 2006). The proposed factors could influence family composition and its distribution as well. Families are often readily recognised in the deep sea, and an understanding in the structuring of family composition could aid further development in species structuring by directing research to specific areas or families.

Sea surface particulate organic carbon (POC), constitutes food supply (figure 4.1), and has been suggested as the major influencing factor of community structure in the deep sea (Rex and Etter 2010; Tittensor et al. 2011; Woolley et al. 2016). The flux of POC decreases with increasing depth and distance from land, and it is influenced by seasonality and upwelling regions (Rex and Etter 2010). A unimodal parabolic pattern within phyla or classes has often been observed in species richness with increasing depth (for example, in polychaetes, molluscs, and fish), which has been shown to be non-random (Pineda and Caswell 1998; Rex and Etter 2010). This pattern might be attributed to nutrient availability at deeper depths, while ecological interactions and competition might reduce richness at shallower depths (Rex 1973,1981; Gage et al. 2000; Stuart et al. 2001). However, regional, taxonomic and environmental variation has been shown to influence the pattern (Levin and Gage 1998; Vetter and Dayton 1998; Wilson 1998; Rex and Etter 2010). Unimodal patterns in species (or higher taxonomic aggregations) richness in relation to productivity or nutrient availability have been observed in terrestrial systems as well (Tilman 1982; Rosenzweig and Abramsky 1993; Rosenzweig 1995; Cox et al. 2016b).

Many deep-sea organisms are deposit-feeders eating the organic material (detritus) sinking down from the surface waters (Dayton and Hessler 1972; Jumars and Eckman 1983) and occur in a relatively stable system with narrow temperature and salinity gradients (Sanders 1968; Gage and Tyler 1991). There are indications of size selectivity, for example between polychaete families, in terms of particle ingestion (niche partitioning) (Whitlatch 1980; Taghon 1982; Wheatcroft and Jumars 1987; Self and Jumars 1988; Wheatcroft 1992). However, this alone cannot explain the observed composition in the deep sea, as it does not explain the richness within such polychaete families (Dayton and Hessler 1972).

Habitat heterogeneity in the form of particle size diversity has been shown to correlate positively with species richness (Etter and Grassle 1992; Leduc et al. 2012). This is scale dependent, and might only be able to explain local-scale diversity patterns. It is not known whether particle size diversity could structure diversity at higher taxonomic aggregation. Furthermore, organisms might not respond to the particle size per se, but to the food associated with the particles (Snelgrove and Butman 1994).

At larger spatial scales, depth and large topographic features such as canyons, seamounts and slopes can also explain variation in the patterns of diversity and distribution. Other features, such as extreme Oxygen Minimum Zones (eOMZs) have been shown to have reduced taxonomic richness compared to well-oxygenated surrounding areas. eOMZs may form a barrier to dispersal, though, and over evolutionary time they could promote speciation through selective pressures (Rogers 2000). For example, certain families of polychaetes (such as Capitellidae) are more resistant to permanently reduced oxygen levels (Levin et al. 1991; Levin et al. 1994; Diaz and Rosenberg 1995).

Current speeds, disturbance, and patch dynamics with high local food resources have been suggested to influence composition, although the effect depends on the size of the organism (Thistle 1983; Gage et al. 1995). Current speeds can influence species, genera, or families directly and indirectly through larval settlement, stability of sediments, and creating conditions for certain groups to exist (e.g. presence of passive filter-feeders) (Levin et al. 2001). Food supply will be influenced by currents, which in turn has a potential cascading effect on richness. Likewise, sediment characteristics (e.g. percentage clay) or oxygen levels will be influenced by current speed and so indirectly current speed influences richness through these variables (Levin et al. 2001). Sediment instability will result in lower richness, while patch dynamics might increase richness when patches are different from one another and thus provide more habitat heterogeneity. Intermediate current speed is thought to result in the highest richness as a result of habitat heterogeneity that is created through patches and disturbance events that reduces the influence of dominant groups, but is stable enough to allow many groups to persist (Levin et al. 2001).

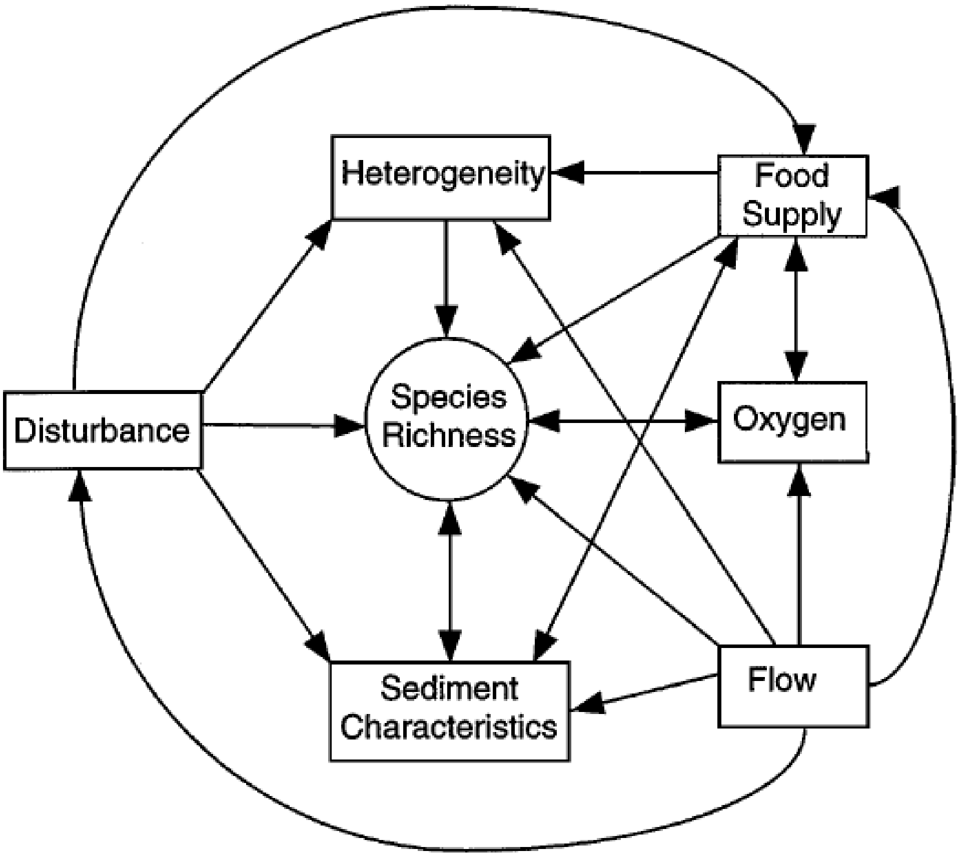


Figure 4.1 Levin et al. (2001) conceptual model of environmental influences on species richness maintenance in the deep sea.

The study presented here uses family data to understand structuring processes on family levels which will be used to modify Levin et al. (2001)'s model to construct an adjusted model for family level data. Family data is readily available in the deep sea as they are well characterised and thus can be easily determined in samples. Patterns observed at family level may direct focus to specific groups to study in more depth. Additionally, some families could potentially respond as a whole to specific events. For example, Capitellidae are known to be a family of indicator species to local organic enrichment (Gage and Tyler 1991). As such, there is much that can be learned from patterns on family level. Furthermore, this study focuses on family composition, rather than family richness. Taxonomic composition includes abundances and richness, and is concerned with its distribution in space. It is possible that areas do not differ in family richness, but the individual abundances in families can differ, and this can potentially be caused by the environment.

This study aims to fill in the gap of how environmental influences and human disturbance potentially relate to family composition on deep-sea continental slopes. In particular, it is hypothesized that the community composition at polychaete family level is influenced by habitat heterogeneity at regional scale, it is influenced by energy at regional scale, and the community is structured by disturbances from environmental conditions, such as current speed, and anthropogenic influences, such as bottom trawling.

4.3 Methods

Box core samples (ULSNER Iron Hot Dip Mega Box Corer 50 × 50 × 50 cm) were taken east and southeast of Newfoundland, Canada, around the Flemish Cap, on the continental slopes of the Flemish Pass, and down south to the continental slopes of the Grand Banks during cruises in 2009 (May to August) and 2010 (June to August) on board of the *Miguel Oliver*. The collection was part of the international NEREIDA (North Atlantic Fisheries Organisation potential vulnerable marine ecosystems – impacts of deep-sea fisheries) study programme. The biological samples were taken from the top 5 cm sediments, sieved over 0.5 mm sieve, and stored in 4% formaldehyde (see figure 4.2). Samples were sieved through 1 mm sieves at a later stage and specimens were sorted into major taxonomic groups by the Institute of Estuarine and Coastal Studies (IECS), Hull, United Kingdom, and stored in 70% industrial methylated spirits (IMS). The polychaete data were sorted to family level under a Motic SMZ-140/143 Stereo microscope (50× magnification) and stored in 80% IMS after sorting.

304 box core samples that had polychaete data were used. In total, 51,595 polychaete individuals were identified to 42 families. Identification to finer taxonomic scale was tried, but the individuals were damaged and missed characteristics important in genus identification.

The latitude and longitude for each box core sample was recorded at the time of sampling. Depth (bathymetry) was recorded from the ship's multibeam surveys (Kongsberg EM 302 30 kHz system). The bathymetric data were gridded to 75 m and smoothed with a 5-cell neighbourhood filter in ArcGis10.1. These data were used to extract other bathymetric variables, such as slope angle, rugosity (5- and 25-cell neighbourhood radii), roughness (3-cell neighbourhood radius), northness and eastness, and standard deviation of bathymetry (3-cell neighbourhood radius) using the Spatial Analyst extension and bathymetric position index (25-, 50-, 75-, 100-, 125-, and 150-cell neighbourhood radii) using the Benthic Terrain Modeller (Lundblad et al. 2006).

Monthly average data on temperature (°C), salinity (PSU), zonal velocity (m s^{-1}) and meridional velocity (m s^{-1}) from 1990 to 2010 at 1/12-degree resolution were available, along with temperature and salinity data measured at the time of sampling using a Sea-Bird Electronics 25 CTD. Annual averages for the year of sampling and the previous year were used to create two raster files in qGIS2.2 through interpolation using 3000 × 3000 pixels and inverse distance weighting, and the values for the box core samples (determined by collection year) were extracted. Long-term influences of mean and maximum bottom current speed (m s^{-1}) and mean and minimum bottom temperature using 10-year average were calculated via interpolation (75m grid) using Empirical Bayesian Kriging function in ArcGIS10.1. Meridional and zonal velocities were used to calculate current speed using the Pythagorean Theorem.

Particulate organic carbon (POC; mg m^{-3}) and chlorophyll data (mg m^{-3}) at the surface were downloaded from the Giovanni ocean colour radiometry online data system from NASA Goddard Earth Sciences Data and Information Center (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month), using MODIS AQUA (4km resolution) for the years 2008 to 2010. These data were used to create two raster files for the year of sampling plus the previous year in qGIS2.2 through interpolation using 2500 × 2500 pixels and inverse distance weighting, and the data were extracted for the relevant box core samples (determined by collection year). Terrestrial data were filtered out prior to interpolation.

A subsample (2 cm depth) from each box core sample was taken using a PVC (10-cm diameter) tube for particle size analysis (PSA). The size fractions were calculated using a Beckman Coulter LS230 Counter (Weitzman et al. 2014). The following categories were used to determine percentage clay, silt and sand: 0.375 – 7.421 µm (clay), 8.147 – 57.77 µm (silt) and 63.41 – 2000 µm (sand). The percent dry weight data from the 12 size classes (ranging between -1 and >10 Φ) were used to calculate particle size diversity (Shannon-Weiner) using the vegan package in R (R Core Team 2015; Oksanen et al. 2016) following Etter & Grassle (1992) and Leduc et al. (2012).

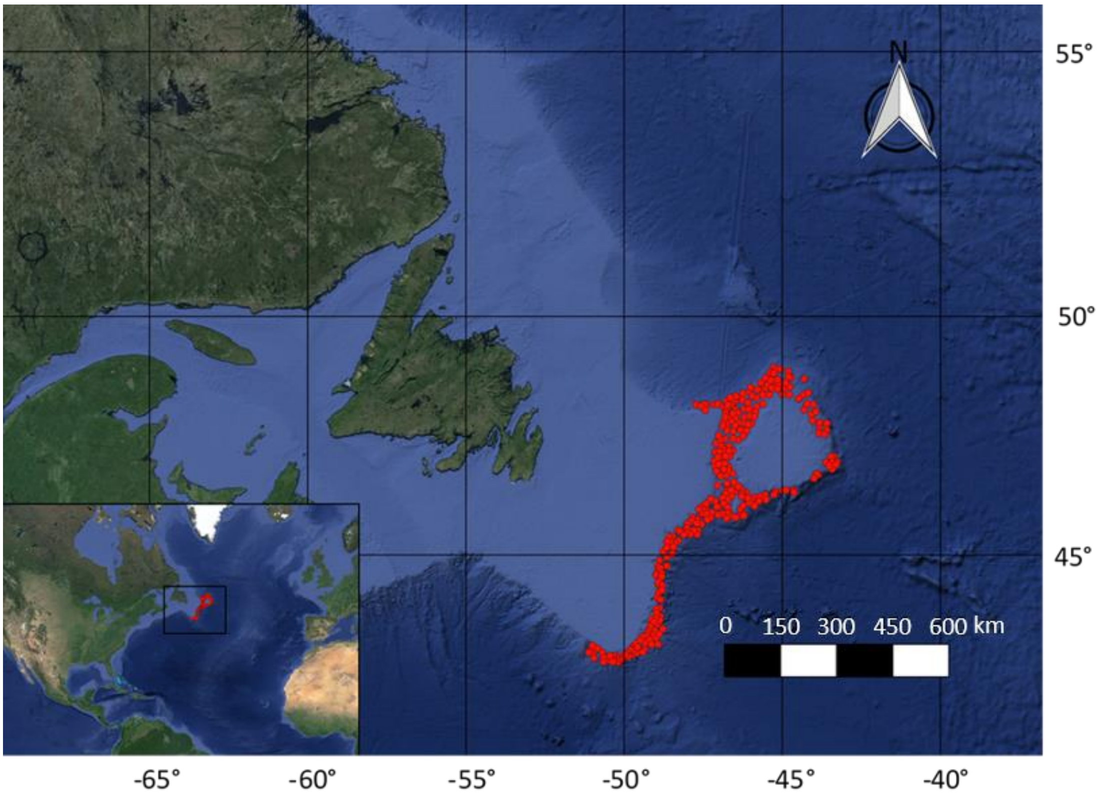


Figure 4.2 Sample locations east and southeast of Newfoundland, Canada, around the Flemish Cap, on the continental slopes of the Flemish Pass, and down south the continental slopes of the Grand Banks.

From the same subsample, carbon content in the sediment samples was calculated. A Leco TruSpec CHN analyser (model 630-100-400) was used to calculate total and organic carbon percentage. Prior to analysis, the samples were dried at 60°C and pulverised to a fine homogeneous powder. Intermittent measurements for total carbon were made and compared to analytical standards to ensure consistency. Inorganic carbon content was measured by subtracting the organic carbon content from the total carbon values (Weitzman et al. 2014).

Fishing intensity was modelled in two ways: Vessel Monitoring System (VMS) location data from 2003-2012 and VMS time-reference locations from 2008-2012. The VMS location data were mapped in ArcGIS10.1 and the intensity of fishing was determined as the density of VMS records in a radius of 1, 3, or 5 km from each box core sample. The Point Sampling Tool in the Spatial Analyst extension was used to obtain the densities for each box core sample (local interpolation option selected). The time-reference locations that had boat speed between 0.5 and 5 knots were used to construct trawl paths (based on boat, boat speed, date, time and location). The speeds of 0.5 and 5 knots were used as trawling activities generally use such speeds (Lambert et al. 2012; Campbell and Federizon 2013; Mangano et al. 2014). The Line Density Tool from the Spatial Analyst extension was used to measure the trawl path lengths (km^2) within box core radii from 1, 3 or 5 km, and the corresponding values were extracted.

Sponge data, collected from research trawls, were modelled via the Kernel Density Tool in the Spatial Analyst extension in ArcGIS10.1 following Kenchington et al. (2014). Sponge density (kg km^{-2}) was obtained via the Extract Values (with local interpolation option selected) for each box core sample.

Collinear explanatory factors will inflate the variance of the regression coefficients. Variance inflation factor (VIF) analysis is a method to test for this multicollinearity and to select variables that are not correlated. The formula is as follows: $VIF_k = \frac{1}{1-R_k^2}$, where R_k^2 is the R^2 value by adding the kth predictor to the model. When VIF equal 1, there is no correlation among the predictor variables, while if it is higher there might be, with values of 10 indicating high levels of multicollinearity. Recommendations vary on the acceptable levels the analysis, with values of 4, 5 or 10 being suggested. For this study, a value of 5 has been used (Hair et al. 1995; Rogerson 2001).

The uncorrelated variables that were selected using VIF were temperature (short-term), POC, chlorophyll, zonal velocity, meridional velocity, total carbon (TC), organic carbon (OC), day, silt, particle size diversity, vessel monitoring system (VMS; 3 km radius), mean velocity (long-term), mean temperature (long-term), rugosity (25-cell neighbourhood radius), benthic position index (BPI; 125-cell neighbourhood radius), roughness, and sponge density. Environmental variables were normalised for the analysis.

The community composition data and the environmental data were analysed with the Vegan package in R (R Core Team 2015; Oksanen et al. 2016). A family accumulation curve was constructed to determine sampling adequacy, using a random permutation function (999 permutations). The highest Spearman-rank correlated environmental variables with the community dissimilarities were selected via a BIO-ENV analysis (Clarke and Ainsworth 1993). A resemblance matrix for the community data was made using Bray-Curtis index. Euclidean distances were used to construct a similarity matrix for standardised environmental data. The same community data and environmental data (used in the BIO-ENV analysis) was used in PRIMER (v7) to construct a nMDS plot (50 iterations used) and tested with a RELATE (999 permutations) test. All environmental variables were used for the RELATE analysis, following recommendations of Clarke & Gorley (2015). The environmental variables that had come out of the BIO-ENV analysis were used in the nMDS plot. These analyses were used as they are relaxed in the assumptions thereby reducing the risk of violation, they do not assume any type of response function (for example, many redundancy analyses assume linear relationships), and they are one of the better methods in representing true relationships found in multivariate space on 2D space (Clarke and Gorley 2015).

4.4 Results

Family richness was adequately sampled in this study, with the accumulation curve reaching saturation (figure 4.3), and only few families are expected to have been missed. Family contribution in terms of percentage (figure 4.4) shows that the family Capitellidae was the most numerous: 25.6% of all individuals were capitellids, which was more than twice as much as the next largest group, the Cirratulidae (11.7%). This is followed by Glyceridae (8.3%), Onuphidae (8.1%), Orbiniidae (7.7%), Paraonidae (7.3%), and Lumbrineridae (7.1%). After these families, the contribution per family drops to less than 5%. Some families (Sternapsidae, Oenonidae, both 2.0×10^{-3} %) are represented by only one individual.

The BIO-ENV analysis showed that the highest correlation (36%) of the community composition was with the environmental variables clay, bathymetric position index (BPI), particulate organic carbon (POC), silt, total carbon (TC), and long-term temperature. These variables (figure 4.5) have complicated patterns in the family composition data, indicated by the variety across the figures. Furthermore, a large part of the samples is relatively similar, indicated by the clustering of the samples.

The variables from the BIO-ENV analysis constitute food availability, in terms of POC and TC; heterogeneity in the form of BPI; and sediment characteristics in the form percent of clay and silt. Temperature, together with food availability, can be grouped as energy in the system. The RELATE test showed that the correlation between community composition and the environmental variables was a significant pattern ($\rho = 0.268$, $P = 0.001$).

Current speed (zonal, meridional, long-term velocity), temperature (short-term), chlorophyll concentration, organic carbon, particle size diversity, vessel monitoring system, rugosity, roughness of the seafloor and sponge density were not selected in the BIO-ENV analysis in the highest correlation combination.

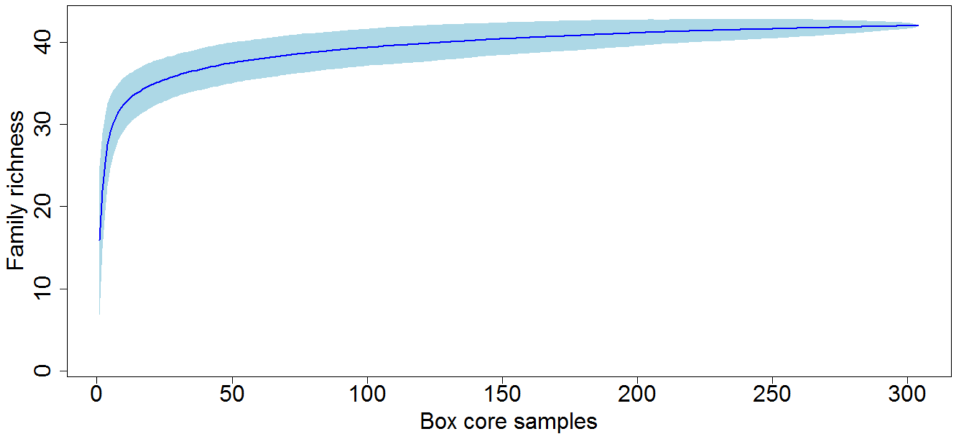


Figure 4.3 The family accumulation curve for the 304 box core samples used from the continental slopes in the Northwest Atlantic. The dark blue line represents the actual data, and the light blue shading represents the 95% confidence interval for the data.

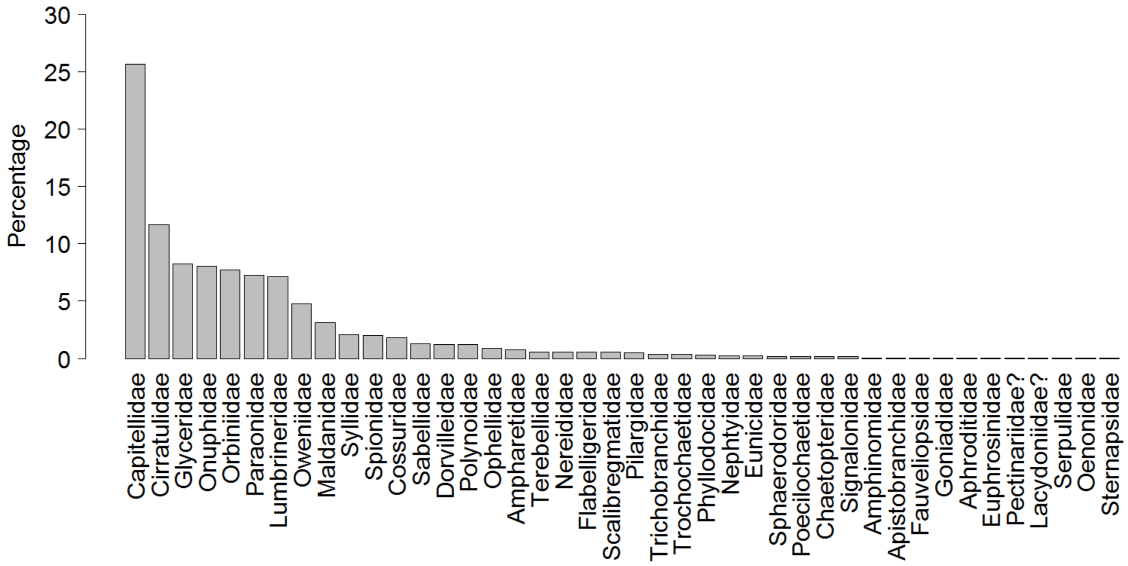


Figure 4.4 The polychaete families are ordered from highest percentage occurring to the lowest percentage of occurring.

4.5 Discussion

The data presented here aim to fill in a gap in how deep-sea macrofaunal family composition is structured by the environment at regional scale. It is one of the first studies to look at this variation in deep-sea community composition using well-sampled environmental gradients. Variables that were found to be important were energy availability, in the form of food availability (POC, TC) and long-term temperature, habitat heterogeneity, in the form of BPI and sediment characteristics in the form of percent clay and silt. Understanding how community composition at family level is structured is important, as, for example, anthropogenic disturbance events will not affect groups similarly. It is thought that some groups are more resistant than others to such perturbations (Diaz and Rosenberg 1995; Rijnsdorp and Vingerhoed 2001). These changes in community composition can affect ecosystem functioning and services, thereby impacting human wellbeing (Kaiser et al. 2006).

Food availability has been shown to be important in many deep sea studies: the decrease in abundance and biomass with increasing depth of many groups are likely linked to food availability (Rex et al. 2006). Some have suggested that body size is also influenced by food availability, but the results are varied (Alongi 1992; Vanhove et al. 2004; McClain et al. 2005), and the pattern in size might well be explained by habitat complexity or a combination of habitat complexity and food availability (Chapter 3). Here, both total carbon and organic carbon influence patterns in community structure, supporting the hypothesis that chemical energy has a structuring effect on community composition, although it is not clear through what mechanisms. According to the Metabolic Theory of Ecology (Brown et al. 2004b), metabolic rates are influenced by energy availability, and this in turn can be used to make predictions about biodiversity. Energy can constitute thermal energy (temperature) or chemical energy (food availability). Here, both chemical and thermal energy are shown to have a structuring effect in the family composition. It is thought that terrestrial tropical systems might have more species as a result of more energy availability, which is related to the species-energy hypothesis (Whittaker et al. 2001). Similar findings have been reported in the deep sea, where higher chemical or thermal energy results in higher species richness (McClain et al. 2012; Woolley et al. 2016). These studies described species richness, while the data presented here considers family richness and family abundance. It is possible that chemical or thermal energy might affect families differently, as suggested in this analysis of family composition.

Temperature (thermal energy) on a decadal scale was found to be important in the structuring of community composition. Long-term temperature is not stable. Temperatures at and around the Flemish Cap area have been shown to increase over the last decades, and this trend might influence the distribution of the polychaetes observed in this area (Colbourne and Perez-Rodriguez 2015). Temperature change will influence the environmental conditions of the oceans, and thereby influencing survival and persistence of organisms. Long-term changes in temperature might affect food production in the upper waters or might influence migration of organisms out of the area, or migration of new groups coming in from the South (Rogers 2015).

It has been shown that climate change has resulted in higher sea water temperatures, which in turn affect other chemical properties (e.g. oxygen levels, primary production) (Rogers 2015). Temperature changes will affect metabolic rate of organisms, which will have consequences for organismal life-histories, with a cascading effect to ecosystem functioning (Danovaro et al. 2001). The deep sea is warming up (Abraham et al. 2013; Balmaseda et al. 2013; Rhein et al. 2013), and it is not known how this will influence biogeochemical cycles in the future. It has been shown that there are distribution shifts in invertebrate and fish species in response to warmer oceanic temperatures (Cheung et al. 2009; Cheung et al. 2015). It is possible that the influence of long-term temperature observed here might be corresponding to a shift in distribution of the community, with potential emigration going further north and immigration coming in from the south.

It was expected that particle size diversity would correlate with the family composition pattern, as most deep-sea polychaetes are deposit feeders and therefore might be influenced by the heterogeneity in sediment grain sizes (Jumars et al. 2015). Etter & Grassle (1992) measured particle size diversity for silt and clay, the two sediment characteristics that were important in this study. Particle size diversity is a form of habitat heterogeneity, and could be have a structuring effect on deposit-feeders. For example, it could influence bioturbation through the stabilisation of sediments, and thus oxygenation of the sediments. Size-selectivity

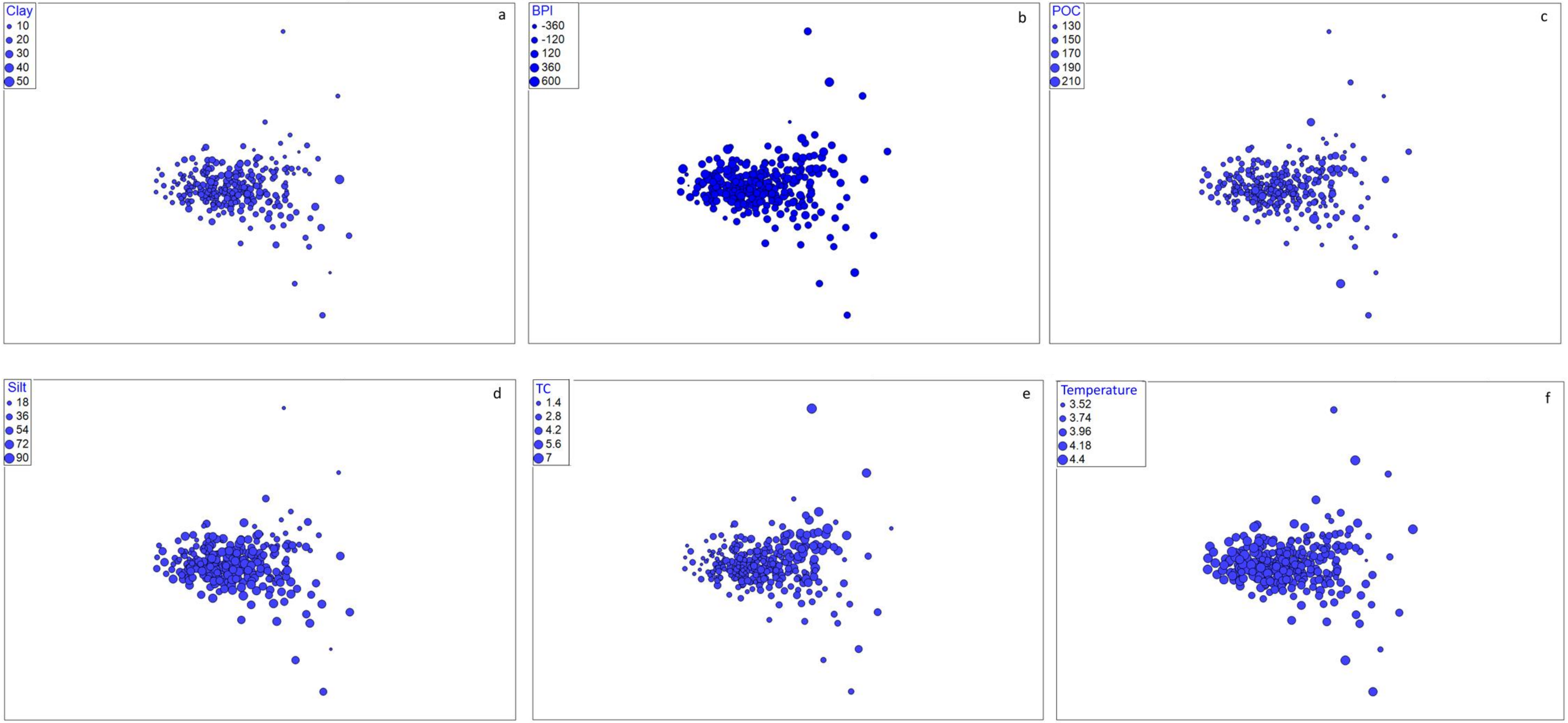


Figure 4.5 nMDS results on the biological community with different environmental factors influencing the community composition: (a) clay (%), (b) bathymetric position index (BPI), (c) particulate organic carbon (POC; mg m^{-3}), (d) silt (%), (e) total carbon (TC; %), and (f) long-term temperature (°C). Temperature was averaged over 10 years. nMDS stress was 0.16.

might allow for niche partitioning and thus should result in higher richness. There does appear to be some size selectivity for particle size at family level for polychaetes (Jumars et al. 2015), although it is unlikely to explain all the richness observed. Furthermore, sediment heterogeneity characteristics and food availability have been proposed to be interlinked, and potentially the particle size diversity could represent a proxy for local food availability (Snelgrove and Butman 1994). However, the food availability measures and particles size diversity used in this analysis were not correlated. It is possible that particle size, however, influences the local distribution of food particles, and thus indirectly particle size diversity might influence richness. Furthermore, the size selectivity might be influenced by ontogenic stage of the organisms, with small, juvenile worms being microphagous, and the larger, adult worms having a microphagous feeding habit. As such, there is not a clear distinction between micro- and microphagous feeding styles within polychaete families (Jumars et al. 2015). In this analysis, particle size diversity did not come up as correlating with the community composition. It is possible that particle size diversity acts at a local scale, while percentage clay and silt acts at larger spatial scales. This indicates that different spatial scale should be incorporated in any conceptual model to fully understand and explain and potentially predict the maintenance of taxonomic richness (species or otherwise).

At a larger spatial scale, BPI seems to be correlated with family composition. BPI relates to local elevation, either in the form of depressions, flat areas, crests, or slopes, compared to the overall landscape. It is a form of habitat complexity whereby higher BPI measures relate to higher complexity in the landscape. This form of habitat mapping might show that there is more complexity in the soft-sediment areas than previous recognised in terms of slopes or crests. Increased variety in the habitat has been recognised for a long time to increase richness in terrestrial environments (Cox et al. 2016a).

Current speed was not selected in the BIO-ENV analysis results. Current speed has been suggested to influence taxonomic richness, with stronger current speeds resulting in lower richness (Thistle 1983; Gage et al. 1995). The current data used here was collected over the years 2008 to 2010. In the last year of sampling, the current speeds were a magnitude higher than the previous years (see Appendix F). This is possibly related to the cold winter of 2009/2010 (Seager et al. 2010; Fereday et al. 2012), which resulted in stronger wind forcing on the surface waters, which may have an effect on deep-sea bottom currents if the forcing of the surface waters extends its influence to deeper waters. It is possible that bottom-currents have a variable impact on taxonomic richness and composition, and that the variability of the current speed is of more influence on the community composition. For example, the variability of current speed might represent different forms of disturbance. When the current speed is stable, the community will adapt to it, but when it is variable, new spaces for organisms to come into the local community might open up. If variability in current speed is consistently variable over time, then organisms might well have adapted to this and the effect of the winter 2009/2010 might not be observed. Alternatively, it is possible that the effects of current speed change have a time lag if it affects dispersal and/or recruitment for example, and that the effect of the winter of 2009/2010 might have been observed if sampling had occurred at a later period. The change in current speeds might affect the distribution of food and so influence abundance and biomass of the community. If, however, this long-term variability was an important structuring effect, it would have been expected that long-term mean bottom current had come out of the BIO-ENV analysis, which it did not. This would suggest that current speeds in this area might have a minimum structuring effect. In other areas, however, there have been indications that it influences species richness directly (Gage 1997); perhaps the influence of current speed depends on region, or acts more locally than expected, or has an effect at both local and regional scales.

Bottom trawling did not come out of the BIO-ENV analysis to influence community structure. However, that is not to say that there might not be a structuring effect. High numbers of Capitellidae, constituting 25.6% of all individuals collected, were found in this area. This is a group of opportunistic species that tend to occur in high numbers in areas with local organic enrichment, and they have been used as indicators of disturbance (Grassle and Grassle 1974; Grassle 1977). It is possible that the distribution of the polychaetes in this region are uniformly influenced by fishing intensity, thereby limiting the power of detecting a correlation in this data set.

Taxonomic richness has been associated with habitat complexity in the form of organisms before; structure-forming organisms like sponges and corals often have a high associated biodiversity (Buhl-Mortensen et al. 2010). Sediments around these organisms can also show increased diversity compared to background levels, possibly through local enhancement of food availability and/or structuring from (broken) fragments from the structuring organisms (Bett and Rice 1992; Bongiorni et al. 2010; Demopoulos et al. 2014). It is possible that food availability and complexity are linked at different spatial scales (Gaston and Blackburn 2000). Sponges, for example, enhance local food availability, but also provide settling places for smaller organisms (Bell 2008). Sponge density was not selected in highest correlation in the BIO-ENV analysis, and this would suggest that there was limited influence on family richness from these structure-forming organisms. It is possible that structure-forming organisms provide increased diversity at species level, but not at family level. Their presence might still enhance other aspects of the community, such as biomass and abundance (see Chapter 5).

Considering the results presented above, and building on the model presented in Levin et al. (2001), a modified conceptual model is proposed for the maintenance of family composition in the deep sea (figure 4.5). It aims to incorporate spatial scale, recognising that certain factors, such as current speed and sediment characteristics might work at regional scale (100s meters to kilometres), while others like particle size diversity and structure-forming organisms act at local (<1 to 10s of meters) spatial scale. Certain factors, like disturbance effects and energy availability could potentially work at both local and regional scale. Furthermore, like in the conceptual model of Levin et al. (2001), interactions between these environmental variables are recognised. For example, it is expected that the amount of clay or silt will influence the particle size diversity. Particle size diversity, in turn, could influence (local) food availability. Large-scale physical structure, like seamounts, will influence current speeds, while increasing the habitat heterogeneity at regional scale.

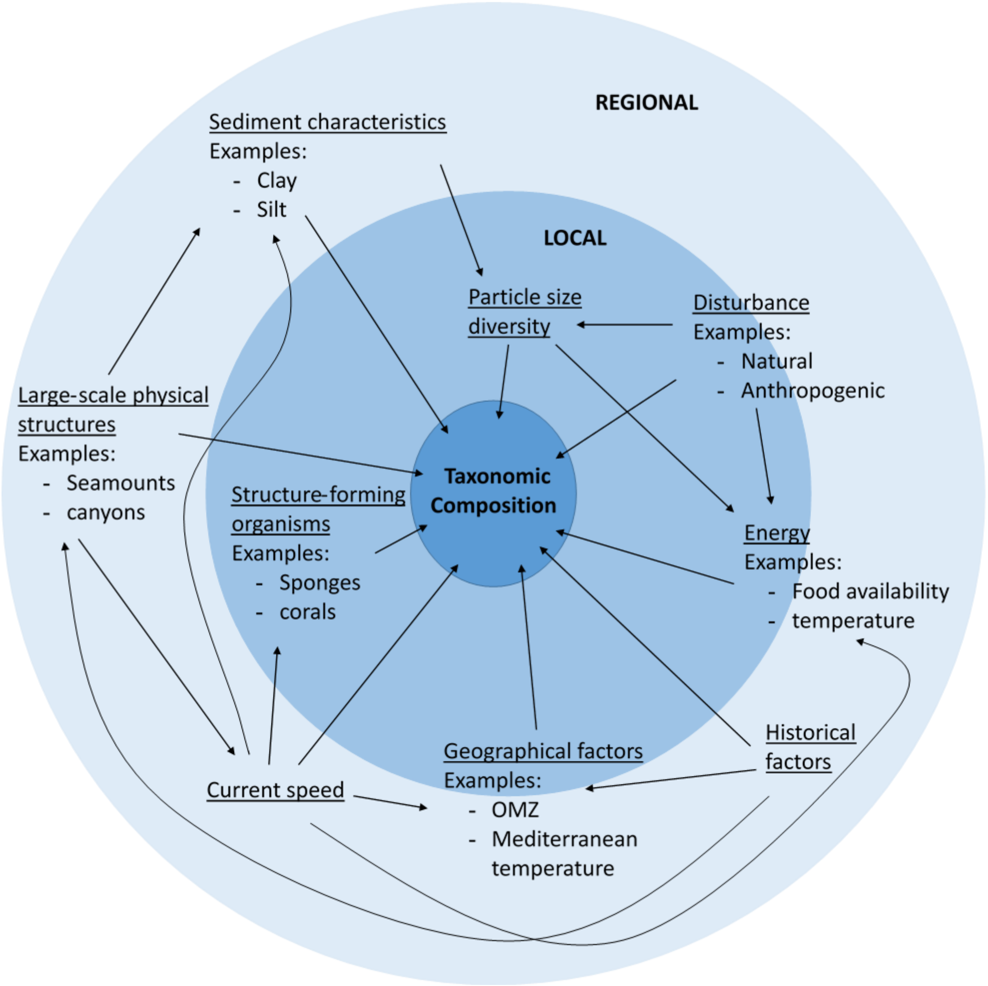


Figure 4.6 A modified conceptual model of how local and regional factor directly and indirectly influence taxonomic composition. Some factors are expected to act locally (e.g. particle diversity size), while others regionally (e.g. sediment characteristics), and some might act both locally and regionally (e.g. disturbance). Local scale could represent 10s of meters and smaller distances, while regional could represent 100s meters to larger distances.

This study has looked at the northwest Atlantic, but recognises that there will be geographical and historical differences between areas, and therefore these are also included in the conceptual model to aid in hypothesis formation of why there might be different biodiversity levels between areas. For example, the Arabian Sea has an eOMZ present that will exert influence on the diversity of the animals living there, with a reduced diversity compared to well-oxygenated areas as few organisms can survive in the low oxygen areas (Levin et al. 1991). Community compositions under eOMZs are often also different, as they have an increased food availability compared to background communities as food particles were not taken up by organisms in the water column above it (Levin et al. 1991). The eOMZ in the Arabian Sea is permanent, thereby allowing opportunistic groups to thrive (Levin et al. 1994; Diaz and Rosenberg 1995). Oxygen concentration levels influence richness in a selective manner. Larger organisms have a larger absolute oxygen-consumption rate (Peters 1983) and require waters that are well oxygenated. In eOMZs, larger animals are usually absent and species richness is reduced compared to areas surrounding these eOMZs where there are high levels of oxygen in the waters. It is possible that eOMZs form physical barriers and increase speciation opportunities, and thus might result in higher taxonomic richness (Rogers 2000).

This area will have a different structure compared to, for example, the Mediterranean, where bottom temperatures are much higher compared to most other deep-sea systems, and where historical factors (i.e. its age) means that the community is relatively young compared to the Atlantic, thereby influencing the community structure (Gage and Tyler 1991; Levin et al. 1991). The formation of the Mediterranean in the last 5 million years as a result of the fracture in the Gibraltar Strait, and the limited connectivity to the Atlantic Ocean onwards, will have influenced the community composition in the Mediterranean deep sea (Rohling et al. 2014). The limited inflow of the Atlantic Ocean into the Mediterranean will influence dispersal opportunities of Atlantic species to the Mediterranean, thereby reducing the diversity. The Mediterranean is land-locked, and it warmer and saltier than most other oceans. There is limited circulation present compared to other oceans. All these factors influence biodiversity in the deep sea. Such effects need to be considered when comparing areas containing eOMZs, or the Mediterranean, to other oceans.

This study was performed on adult individuals identified to family level. From Levin et al. (2001)'s model, it is expected that the environment potentially structures species richness or composition through similar effects as was observed for family composition here. As the proposed conceptual model is a modified version from Levin et al.'s, it would suggest there is a degree of flexibility to this concept for different taxonomic levels. As genera and species in families will share common characteristics, it is possible that they might be structured in similar ways. As such, patterns at family level can direct focus to higher taxonomic resolutions when certain patterns are observed, or when time or money is constrained. For example, indicator groups can be picked out quicker and studied in more detail when their distribution are observed to change, especially in respect to other groups.

Ideally, both Levin and al and this study's model also included phylogenetic diversity measures. Samples can be rich in species (Levin et al.) or families (this study), but a sample would be less diverse if these groups are very closely related compared to samples that are further removed in evolutionary history. Phylogenetic diversity can be represented by the average distance of one pair of individuals within a sample. This measure is influenced by abundance, with more abundant groups having a larger influence on the average. Taxonomic distinctness can be used instead as it removes this dependence. For this, phylogenetic trees are necessary. Several papers in the last years were published, and slowly a consensus is being reached (Struck et al. 2007; Bourlat et al. 2008; Dunn et al. 2008; Struck et al. 2011; Weigert and Bleidorn 2016). Ideally, in the next few years, taxonomic diversity measures will be included in studies studying what structures communities. Functional diversity should also be included to understand potential selection pressures on different functional groups, thereby potentially predicting which groups might be winners or losers under changing environmental conditions or increased human influence.

What the specific relationships are between the different environmental factors and the community structure needs further work. Certain factors might be linear and positive or negative, while more complex patterns, such as unimodal relationships, are also expected. For example, it is possible that disturbance events (biological and environmental), energy availability, and current speed might be unimodal (Cox et al. 2016a). Particle size diversity at local scale, or large-physical structures at regional scale might increase habitat heterogeneity, and this could have a positive relationship on family richness and composition, or it is possible that there will be a limit (a saturation effect) on richness when all niches are filled. The different relationships are expected to be complex and interlinked. Different models might aid in the understanding of these interconnected relationships; for example, generalised additive models (GAMs) or structural equation models (SEMs) can be used to study the relationship shape between different variables with multiple explanatory variables (Hodapp et al. 2015). GAMs are useful as they can be used to determine the shape with highly complex relationships. They are influenced by the level of smoothing, and can be difficult to interpret sometimes. Furthermore, they would require each variable of interest (each response variable) to be tested individually. SEMs, are not always the easiest models to study complex relationships, they do allow for the test of multiple relationships at the same time that are interlinked (Grace 2006), thereby reducing the likelihood of committing Type I errors. There are programmes available these days, for example WarpPLS (Kock 2015), that allows for the inspection of complex relationships between different variables as well. As such, SEMs are promising tools for the study of interlinked relationships often observed in ecology.

Many factors have been proposed to influence taxonomic composition in the deep sea. There is an appreciation for factors that are dependent on spatial-scale. How these separate and interact is still not well understood. Here, food availability, sediment characteristics, habitat heterogeneity and long-term temperature are proposed as influential factors acting on regional family community composition. A conceptual model based on the results presented here and previous studies has been proposed to split factors on spatial scale, with potential interactions between them. As ecological systems are complex and interconnected, new methods of analysis are necessary. A promising area might be structural equation models, which are a tool for modelling direct and indirect effects. Structural equation models allow for theory testing and theory development and they are becoming more common in terrestrial and shallow-water ecological studies, but have been absent from deep-sea ecology.

CHAPTER FOUR

5. CHAPTER FIVE:

A structural equation model of the environmental and anthropogenic influences on a polychaete community and ecosystem functioning

5.1 Abstract

Biological communities are changing as a result of anthropogenic impacts, likely with cascading consequences for ecosystem functioning and the provision of ecosystem services. There has been much experimental work considering the link between biodiversity and ecosystem functioning (BEF), generally demonstrating a positive and saturating relationship. In natural systems, BEF relationships have been shown to be more variable as a result of environmental feedbacks and anthropogenic stressors. The BEF relationship has been understudied in the deep sea, as have the impacts of fishing on this relationship, limiting the development of adequate strategies to mitigate this stressor. Here, the deep-sea BEF relationship is studied in a key group of the seabed infauna; the polychaete worms. These macrofaunal organisms play a key role in ecosystem functioning, including nutrient cycling and bioturbation, and are food sources for (commercially-caught) fish. We show that bottom-trawling influences the deep-sea BEF relationship through a potential selection effect. Bottom trawling reduces functional and taxonomic evenness, and positively influences the biomass and abundance of certain macrofaunal taxa. In particular, capitellids, a family of polychaetes that are known as opportunists and represent indicators of local carbon enrichment show elevated relative abundance with increasing trawling. This suggests a heavily impacted macrofaunal community, comparable in structure to those reported under fish farms where there is higher organic carbon available compared to background levels. Much policy work on creating sustainable fisheries focuses on megafauna (fish, corals, or sponges), but here we emphasise that there should also be a focus on smaller organisms to ensure a healthy-functioning system.

5.2 Introduction

It is widely recognised that human-made habitat modifications and increased CO_2 emissions have severe impacts on biological communities, resulting in changes in abundance, biomass, composition and taxonomic richness (Millennium Ecosystem Assessment 2005). The biological community plays an important role in the biogeochemical flow of energy and material within and between ecosystems. There is a well-established relationship between biodiversity and ecosystem functioning (BEF), which is generally thought to be positive and saturating (Cardinale et al. 2006; 2012). There is still much debate on the slope and magnitude of this relationship, and what the mechanisms are behind the relationship. Two mechanisms have been proposed: the selection effect, in which ecosystem functioning increases as taxonomic richness increases as a result of the increased probability that a species with important traits (e.g. productivity) is included in the species pool. The other effect is the complementarity effect, in which resources are used more completely when more species are present as a result of niche partitioning, resulting in higher functioning in the system (Loreau and Hector 2001).

Most studies on BEF relationships have been performed in terrestrial (field plots) and shallow-water (mesocosm) experimental systems, where species addition or elimination is artificial and environmental conditions are held constant. These studies have a limited ability to predict what will happen in natural systems (Díaz and Cabido 2001). There are few BEF studies performed in natural systems, and these have shown that there is more noise in BEF relationship in natural systems compared to the experimental systems, likely as a result of environmental feedback (Ptacnik et al. 2008; Cardinale et al. 2009; Hodapp et al. 2015). To get a better understanding of BEF relationships, how they might change as a result of environmental changes, and to understand how to conserve such functions, it is necessary to focus more attention on BEF relationships in natural systems.

There is a lack of BEF studies in the deep sea (>200 m depth), the largest biome on Earth. Two studies that have been published on this topic showed contradictory results in their nematode data. Danovaro et al. (2008) showed a positive exponential BEF relationship, while Leduc et al. (2013) showed no relationship. Danovaro et al. included geographical regions from all over the world (Mediterranean, Arctic, Atlantic and central and South Pacific) in their study than did Leduc et al. (New Zealand), but the biggest difference between the two studies is the number of species in the studies. Danovaro et al.'s study used samples with low species richness (less than 25 species), while Leduc et al. had higher species richness in its samples (30 to 42 species), but they had a lack of samples with low species richness. It is possible that the difference in the relationships found is caused by the different regions studied. However, it is also possible that the two studies captured different aspects of the BEF relationship, and the inclusion of a wider variation in taxonomic richness might elucidate the relationship in deep-sea systems.

The deep sea (excluding reducing environments), with its low temperatures and low-energy conditions, is a biome that has lower resilience and higher vulnerability to anthropogenic disturbance, such as trawling, compared to shallow-water systems (Rex and Etter 2010). Impacts from practices like deep-sea trawling are likely to influence the BEF relationship as a result of changes in community composition (Kaiser et al. 2006; Pusceddu et al. 2014). Trawling may alter biodiversity, increase bottom-water turbidity, create changes in seafloor morphology, cause variable sediment resuspension, result in stock impoverishment, increases (epi)benthos mortality, and alter nutrient cycles (Thrush and Dayton 2002). There is a high need to incorporate such practices in BEF analyses.

There is an increased interest in functional diversity in the BEF debate. The traits of species and the abundance of these traits (i.e. functional dispersion) should influence the functions and the rate of these functions that an ecosystem can possess and perform. There is evidence that functional richness is a better predictor of ecosystem functioning than taxonomic richness (Gagic et al. 2015). Very few BEF study performed in the deep sea have included functional diversity measures in relation, although it was not discussed in relation to the BEF relationship shape (Pape et al. 2013). Measuring functional richness for many other organisms (both in the deep sea and elsewhere) remains difficult and it is not always clear what traits should be included. The deep sea has been poorly studied, and not all functions are well characterised. However, if productivity (secondary biomass production) is used as a proxy for ecosystem functioning, traits characterising feeding guilds can be useful. It is possible that through the partitioning of feeding guilds more niches are created, resulting in higher taxonomic richness. It must be noted that taxonomic and functional diversity are not mutually exclusive, and there are no clear relationship between them either (Díaz and Cabido 2001).

This study intends to determine the BEF relationship in a deep-sea continental slope system using both taxonomic and functional diversity measures, while incorporating environmental and human influences on these measures. The hypotheses are: *i*) there is a positive saturating relationship between ecosystem functioning and taxonomic richness; *ii*) environmental conditions influence taxonomic and functional diversity measures in the deep sea on a regional scale, and; *iii*) human disturbance in the form of fishing has direct and indirect impacts on ecosystem functioning in the deep sea.

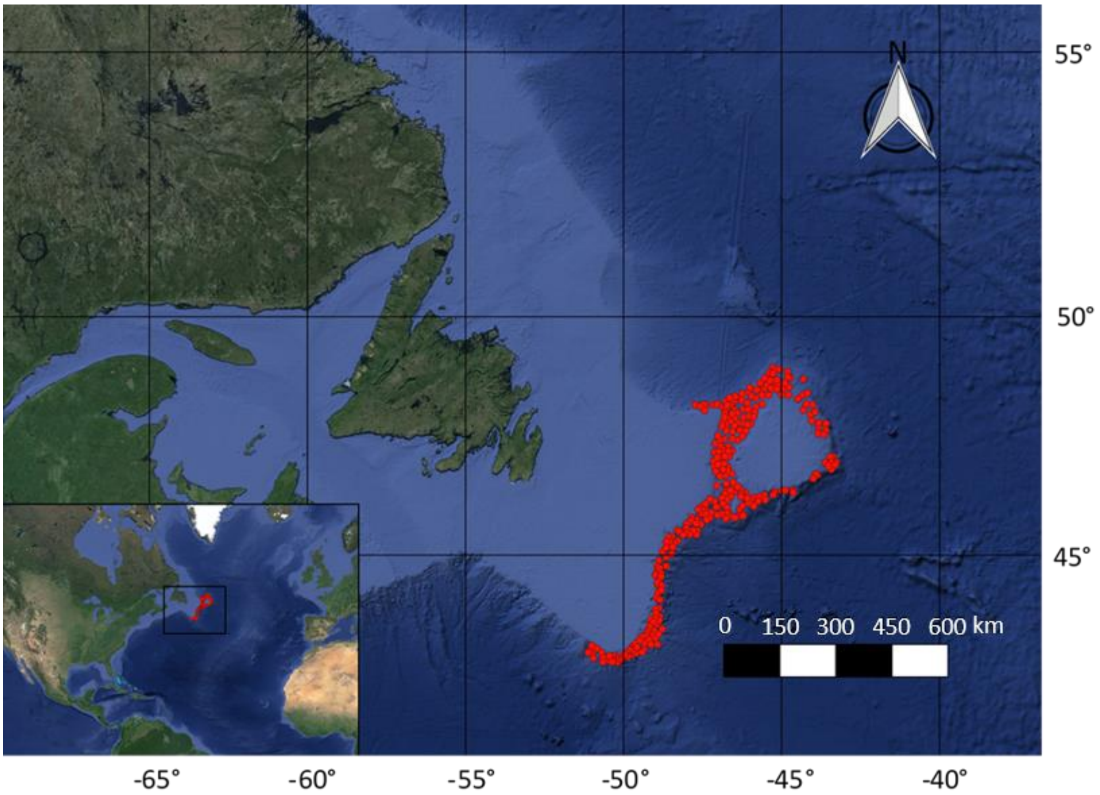


Figure 5.1 Sample locations east and southeast of Newfoundland, Canada, around the Flemish Cap, on the continental slopes of the Flemish Pass, and down south the continental slopes of the Grand Banks.

5.3 Methods

5.3.1 Location

337 box core samples were collected east and southeast of Newfoundland, Canada, around the Flemish Cap, on the continental slopes of the Flemish Pass, and down south to the continental slopes of the Grand Banks during cruises in 2009 (May to August) and 2010 (June to August) on board of the *Miguel Oliver* (figure 5.1). The samples were taken with a ULSNER iron hot dip Mega Box Corer (50 × 50 cm). The collection was part of the international NEREIDA (NAFO potential vulnerable marine ecosystems – impacts of deep-sea fisheries) study programme. The biological samples were taken from the top 5 cm sediment depth, sieved over 0.5 mm sieve, and stored in 4% formaldehyde until further processing.

5.3.2 Biological processing

Samples were sieved through 1 mm sieves and specimens were sorted in major taxonomic groups by the Institute of Estuarine and Coastal Studies (IECS), Hull, United Kingdom, and stored in 70% industrial methylated spirits (IMS). Wet weight of the samples was measured to 0.0001 precision. Excess IMS was first removed by placing samples on dry tissue paper. The polychaete data (304 box core samples) were sorted to family level under a Motic SMZ-140/143 Stereo microscope (50× magnification) and stored in 80% IMS after sorting. Sorting to finer taxonomic resolution was not possible as important characteristics for genus identification were missing.

5.3.3 Environmental variables

5.3.3.1 Latitude, longitude, bathymetry and related variables

The latitude and longitude for each box-core sample was recorded at the time of sampling. Depth (bathymetry) was recorded from the ship's multibeam surveys (Kongsberg EM 302 30 kHz system). The data were gridded to 75 m and smoothed with a 5-cell neighbourhood filter in ArcGis10.1. These data were used to extract other bathymetric variables, such as slope angle, rugosity (25-cell neighbourhood radius), roughness (3-cell neighbourhood radius) using the

Spatial Analyst extension, and bathymetric position index (125-cell neighbourhood radius) using the Benthic Terrain Modeller (Lundblad et al. 2006).

5.3.3.2 Temperature, salinity and velocity measures

Monthly average data on temperature (°C), salinity (PSU), zonal velocity (m s^{-1}) and meridional velocity (m s^{-1}) from 1990 to 2010 at 1/12-degree resolution was available, along with temperature and salinity data measured at the time of sampling using a Sea-Bird Electronics 25 CTD.

5.3.3.2.1 Short-term data

Annual averages for the year of sampling and the previous year were used to create raster files in qGIS2.2 through interpolation using 3000 × 3000 pixels and inverse distance weighting. Using Point Sampling Tool, the values for the relevant box core samples (determined by collection year) were extracted from the data layer. Velocity was calculated from zonal and meridional velocity measures using the Pythagorean Theorem.

5.3.3.2.2 Long-term data

Mean and maximum bottom current speed (m s^{-1}) and mean and minimum bottom temperature using 10-year average as a long-term influence. Meridional and zonal velocities were used to calculate current speed using Pythagorean Theorem. The values were interpolated to 75m grid using Empirical Bayesian Kriging function in ArcGIS10.1 Geostatistical Analyst.

5.3.3.3 Sea surface particulate organic carbon and chlorophyll

Particulate organic carbon (POC; mg m^{-3}) and chlorophyll data (mg m^{-3}) at the surface were downloaded from the Giovanni ocean colour radiometry online data system from NASA Goddard Earth Sciences Data and Information Center (http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month), using MODIS AQUA (4km resolution) for the years 2008 to 2010. These data were used to create raster files for the year of sampling plus the previous year in qGIS2.2 through interpolation using 2500 × 2500 pixels and inverse distance weighting. The Point Sampling Tool was used to extract data for the relevant box core samples (determined by collection year). Terrestrial data were filtered out prior of interpolation.

5.3.3.4 Sediment characteristics and carbon measures

A subsample (2 cm depth) from each box core sample was taken using a PVC (10 cm diameter) tube for particle size analysis (PSA). The size fractions were calculated using a Beckman Coulter LS230 Counter (Weitzman et al. 2014). The following categories were used to determine percentage clay, silt and sand: 0.375 – 7.421 µm (clay), 8.147 – 57.77 µm (silt) and 63.41 – 2000 µm (sand). The percent dry weight data from the 12 size classes (ranging between -1 and >10 Φ) were used to calculate particle size diversity (Shannon-Weiner) using the vegan package in R (R Core Team 2015; Oksanen et al. 2016) following Etter & Grassle (1992) and Leduc et al. (2012).

From the same subsample, carbon content in the sediment samples was calculated. A Leco TruSpec CHN analyser (model 630-100-400) was used to calculate total and organic carbon. Prior to analysis, the samples were dried at 60°C and pulverised to a fine homogeneous powder. Intermittent measurements from total carbon were made and compared to analytical standards to ensure consistency. Inorganic carbon content was measured by subtracting the organic carbon content from the total carbon values (Weitzman et al. 2014).

5.3.3.5 Sponge density

Sponge data, collected from research trawl, were modelled via the Kernel Density Tool in the Spatial Analyst extension in ArcGIS10.1 following Kenchington et al. (2014). Sponge density (kg km^{-2}) was obtained via the Extract Values (with local interpolation option selected) for each box core sample.

5.3.4 Fishing measures

Fishing intensity was modelled in two ways: Vessel Monitoring System (VMS) location data from 2003-2012 and VMS time-reference locations from 2008-2012. The VMS location data were mapped in ArcGIS10.1 and the intensity of fishing was determined as the density of VMS records in a radius of 1, 3, or 5 km from each box core sample. The Point Sampling Tool in the Spatial Analyst extension was used to obtain the densities for each box core sample (local interpolation option selected). The time-reference locations that had boat speed between 0.5 and 5 knots were used to construct trawl paths (based on boat, boat speed, date, time and location). The speeds of 0.5 and 5 knots were used as trawling activities generally use such speeds (Lambert et al. 2012; Campbell and Federizon 2013; Mangano et al. 2014). The Line Density Tool from the Spatial Analyst extension was used to measure the trawl path lengths (km^2) within box core radii from 1, 3 or 5 km, and the corresponding values were extracted.

5.3.5 Diversity measures, ecosystem functioning and ecosystem efficiency

Taxonomic diversity measures and functional diversity measures were calculated using the FD package in R (Laliberté et al. 2014; R Core Team 2015). Family richness and family evenness (Pielou's evenness index, *J*) were calculated for taxonomic diversity measures. These two measures rather than biological diversity (combined abundance and richness) were chosen to make comparisons with other studies possible. Evenness, rather than richness, has been shown to have a potential larger influence on ecosystem functioning (Hodapp et al. 2015). Functional dispersion and functional evenness were determined for the functional data. Functional dispersion was used as it is shown to be one of the better predictors for ecosystem functioning (Gagic et al. 2015). It is measured as the distance of individual groups, in this case families, to their weighted centroids. The centroid refers to average position of the groups in a plane or shape dependent on the multivariate relationship of the functional. The measure is weighted based on the relative abundance of each family within the sample (Laliberté et al. 2010). Functional data were based on polychaete family feeding guilds (Jumars et al. 2015). Ecosystem functioning is calculated as the secondary productivity measured as polychaete biomass. Ecosystem efficiency is a measure of nutrient cycling and is calculated as the ratio between total carbon at the seafloor and surface particulate organic carbon, and the ratio between secondary productivity and organic carbon. This measure was used to make it comparable to Danovaro et al. (2008).

5.3.6 Model

In order to incorporate the multivariate influences of the variables, a structural equation model (SEM) was constructed (Grace 2006). There are two types of SEMs, covariance-based SEMs and partial least square SEM (PLS-SEM). Here, PLS-SEM was used as PLS-SEM is more robust against violations of assumptions (e.g. non-normality in multivariate data, small sample sizes), and the aim of the study is exploratory rather than confirmative (Reinartz et al. 2009; Hair et al. 2011).

In a SEM, latent variables are constructed to reflect theoretical entities that are not necessarily measurable in reality or by one proxy variable; they are hypothesized to exist as concepts (Grace 2006). Indicator variables are the observed variables and they are used to characterise the latent variables. However, indicator variables do not capture the full extent of a latent variable; they inform about the latent variable as they are correlated. One or more indicator variables were used to reflect the latent variables used in this study (Appendix D).

Six latent variables (Habitat Heterogeneity, Current Speed, Food Availability, Sediment Characteristics, Biogenic Habitats, and Temperature) were constructed to capture the environment, one latent variable was erected for anthropogenic influences (Fishing Intensity), five latent variables (Family Evenness, Functional Evenness, Family Richness, Functional Dispersion, and Density) were formed to depict biological facets of the community, and two latent variables (Ecosystem Functioning, and Ecosystem Efficiency) were created to indicate functioning in the ecosystem. Relationships between each diversity (all biological latent variables except Density) variable and both functioning latent variables are hypothesized based on previous studies (Díaz and Cabido 2001; Gamfeldt et al. 2015; Strong et al. 2015) (figure 5.2). No correlation between Density and Ecosystem Functioning was specified as the two indicator

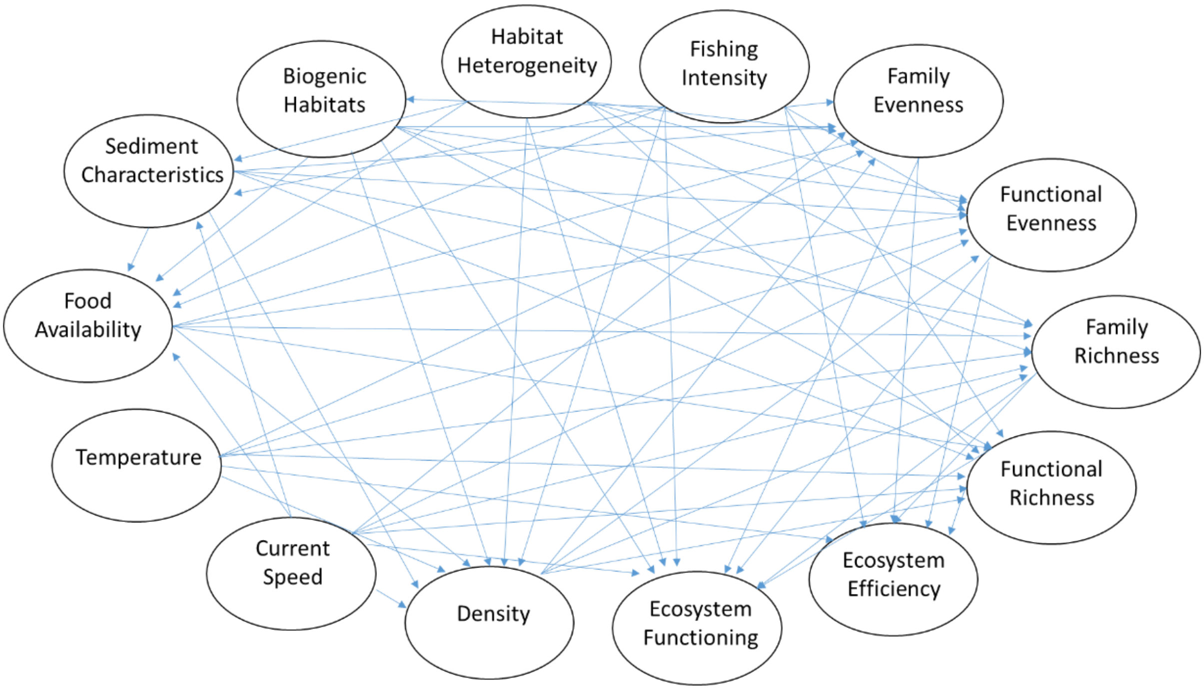


Figure 5.2 The initial model specification after the assumptions made. Note that only latent variables are displayed to increase readability.

variables used for these latent variables are highly correlated. As such, it would be difficult to distinguish between the effects of this correlation and the influence of other BEF pathways, which would make interpretation difficult. Relationships between the environmental latent variables and taxonomic richness were based on Levin et al.'s (2001) model for environmental effects on deep-sea regional taxonomic richness. As environmental conditions will influence what taxonomic groups can be present, so too will it influence the functions present in the biological community (Díaz and Marcelo 1997; Vandewalle et al. 2010). Temperature changes might influence the number of individuals present by affecting nutrient concentrations and/or metabolic rates (Danovaro et al. 2004; Hoegh-Guldberg and Bruno 2010). Temperature could affect ecosystem efficiency directly as a result of physical changes, indicated by a direct arrow, or indirectly by influencing other variables (such as diversity aspects), which is indicated by arrows from temperature to, for example, family richness, and then to ecosystem efficiency (Jones et al. 2014; Levin and Le Bris 2015). Fishing has drastic impacts on the environment by disturbing the sediments, through removing megafauna (e.g. sponges, corals) that could provide a living space for others, and causing physical damage to organisms that potentially result in death (Jennings et al. 2001; Bell 2008). Pathways between density and diversity measures are specified. Density is thought to influence taxonomic richness (sampling effect), but more individuals might also lead to less variation if it means that there is a dominance effect. More individuals should be able to survive in an area when there is more food available and/or habitat complexity that should provide more living space. When more individuals are present, it is expected that biomass increases, and thus these pathways are specified.

The data were analysed using warpPLS (v5.0), using PLS Mode M, Warp3, and Stable3 for nonlinear relationships (Kock 2015). This SEM programme offers the advantage of checking for and incorporating nonlinear relationships in a SEM. SEM analyses were based on standardized values of the indicator variables. Variation explained is presented for latent variables with direct arrows towards it. Significant regression coefficients (*β)* and associated *P*-values of these slopes are given.

5.3.7 Model fit

The measures of model fit are presented in table 5.1. Overall, all measures of model fit and quality indices are indicating that the model is fitting the data well, and thus the data can be discussed (Kock 2015). Average block variance inflation factor (AVIF) and average full co-linearity VIF (AFVIF) results show that multi-co-linearity is well below the thresholds, meaning that there is no influence of co-linearity (Kock and Lynn 2012). Both AVIF and AFVIF are reported here as AVIF is sensitive to the use of nonlinear algorithms, while AFVIF is not. The Tenenhaus GoF (Tenenhaus et al. 2005) index calculates explanatory power; the model here has high explanatory power as it is above the high threshold (>0.36) (Wetzels et al. 2009). The Simpson's paradox ratio (SPR) index is a measure to indicate whether causality is a problem; i.e. whether path coefficient and the associated correlation between a pair of linked variables have different signs (positive or negative) (Wagner 1982; Pearl 2009). As the value of our model is 1, it can be interpreted that the model is free from Simpson's paradox. A Simpson's paradox can be found together with negative R-squared contributions. The R-squared contribution ratio (RSCR) is a measure to show the extent of negative R-squared contributions. Here, there are no such contributions (RSCR = 1). The Simpson's suppression ratio (SSR) is an index to show whether path coefficients might be greater (in absolute terms) than the associated correlation between two linked variables (MacKinnon et al. 2000). Furthermore, it is an indication whether the hypothesized causality (direction of the arrow) is supported (Spirtes et al. 1993). A value of 0.7 would indicate that at least 70 percent of the paths in the model are free of statistical suppression. Here, almost 90% is free of statistical suppression, which is deemed acceptable, and it indicates that the pathway-directions specified are supported for causality. The last index concerns non-linear bivariate relationships (NLBCDR). Bivariate nonlinear coefficients vary, depending on the hypothesized causality direction. This can give partial evidence in support of the hypothesized links. The measure that is shown is the percentage of path-related instances in which the reverse causality direction is supported. Here, over 80% of the path-related instances are supported in the direction of causality specified, which is acceptable for model interpretation.

Table 5.1 Measurement and quality indices for the SEM-PLS. Results for each index are reported along with a measure of acceptability or higher. Small, medium, and large refer to explanatory power. AVIF = average block variance inflation factor; AFVIF = average full co-linearity; GoF = Tenenhaus GoF; SPR = Simpson's paradox ratio; RSCR = R-squared contribution ratio; SSR = statistical suppression ratio; NLBCDR = nonlinear bivariate causality direction ratio.

Measure	Result	Acceptable Level	Ideal Level	Small	Medium	Large
AVIF	1.119	< 5	< 3.3			
AFVIF	2.069	< 5	< 3.3			
GoF	0.47			0.1	0.25	0.36
SPR	1	> 0.7	1			
RSCR	1	> 0.9	1			
SSR	0.879	> 0.7				
NLBCDR	0.848	> 0.7				

5.4 Results

5.4.1 Ecosystem Functioning & Ecosystem Efficiency

33% and 15% of the variation in Ecosystem Functioning and Ecosystem Efficiency (figure 5.3) respectively were explained in the model presented here. Ecosystem Functioning (secondary production) is positively influenced by Family Richness ($\beta = 0.136$, $P = 0.008$), Fishing Intensity ($\beta = 0.208$, $P < 0.001$), Habitat Heterogeneity ($\beta = 0.185$, $P < 0.001$) and Biogenic Habitats ($\beta = 0.243$, $P < 0.001$). Ecosystem Functioning is negatively impacted by Functional Evenness ($\beta = -0.292$, $P < 0.001$). Ecosystem Efficiency (nutrient cycling) was positively influenced by Functional Richness ($\beta = 0.102$, $P = 0.035$). Functional Evenness ($\beta = -0.292$, $P = 0.003$) and Temperature ($\beta = -0.325$, $P < 0.001$) had a negative impact on Ecosystem Efficiency.

5.4.2 Family Richness & Family Evenness

57% and 45% of the variation in Family Richness and Family Evenness (figure 5.3) respectively were explained in the model presented here. Family Richness was positively influenced by Habitat Heterogeneity ($\beta = 0.158$, $P = 0.002$), Sediment Characteristics ($\beta = 0.128$, $P = 0.012$), Food Availability ($\beta = 0.12$, $P = 0.017$), and Density ($\beta = 0.713$, $P < 0.001$). Fishing Intensity had a negative impact on Family Evenness ($\beta = -0.112$, $P = 0.024$), as did Density ($\beta = -0.613$, $P < 0.001$) and Current Speed ($\beta = -0.096$, $P = 0.044$).

5.4.3 Functional Dispersion & Functional Evenness

14% and 58% of the variation in Functional Dispersion and Functional Evenness (figure 5.3) respectively were explained in the model presented here. Functional Dispersion was positively correlated with Habitat Heterogeneity ($\beta = 0.253$, $P < 0.001$). Functional Dispersion was negatively impacted by Density ($\beta = -0.189$, $P < 0.001$), Biogenic Habitats ($\beta = -0.105$, $P = 0.032$), and Sediment Characteristics ($\beta = -0.127$, $P = 0.012$). No positive correlations with Functional

Evenness were found in this model. Density (β = -0.693, $P < 0.001$) and Fishing Intensity (β = -0.14, $P = 0.006$) negatively influenced Functional Evenness.

5.4.4 Fishing Intensity and Density

Fishing Intensity (figure 5.3) has a positive impact on Ecosystem Functioning and Density (β = 0.234, $P < 0.001$). Fishing Intensity has a negative impact on Family Evenness, Functional Evenness, and Biogenic Habitats (β = -0.153, $P = 0.003$). 31% of variation in Density was explained in this model. Positive correlations between Density and Temperature (β = 0.26, $P < 0.001$), Biogenic Habitats (β = 0.315, $P < 0.001$), Habitat Heterogeneity (β = 0.209, $P < 0.001$), and Fishing Intensity (β = 0.234, $P < 0.001$) were found. Density was negatively correlated with Food Availability (β = -0.186, $P < 0.001$).

5.4.5 Food Availability and Sediment Characteristics

The relationships between these variables were specified to capture direct and indirect influences through these latent variables on latent variables of interest (figure 5.3). Habitat Heterogeneity and Sediment Characteristics had positive influences on Food Availability (β = 0.123, $P = 0.015$, and β = 0.165, $P = 0.002$, respectively). Current Speed and Sponge Density correlated negatively with Food Availability (β = -0.268, $P < 0.001$, and β = -0.177, $P < 0.001$, respectively). Sediment Characteristics were positively influenced by Current Speed (β = 0.26, $P < 0.001$), while negatively by Habitat Heterogeneity (β = -0.111, $P = 0.025$).

5.4.6 Non-linear relationships between latent variables of interest

There was a positive and saturating relationship between Family Richness and Ecosystem Functioning (figure 5.4a), with increasing variation in ecosystem functioning at higher family richness. Saturation is around 22 families (see unstandardized relationship in Appendix E). There was an exponential decay between Functional Evenness and Ecosystem Functioning (figure

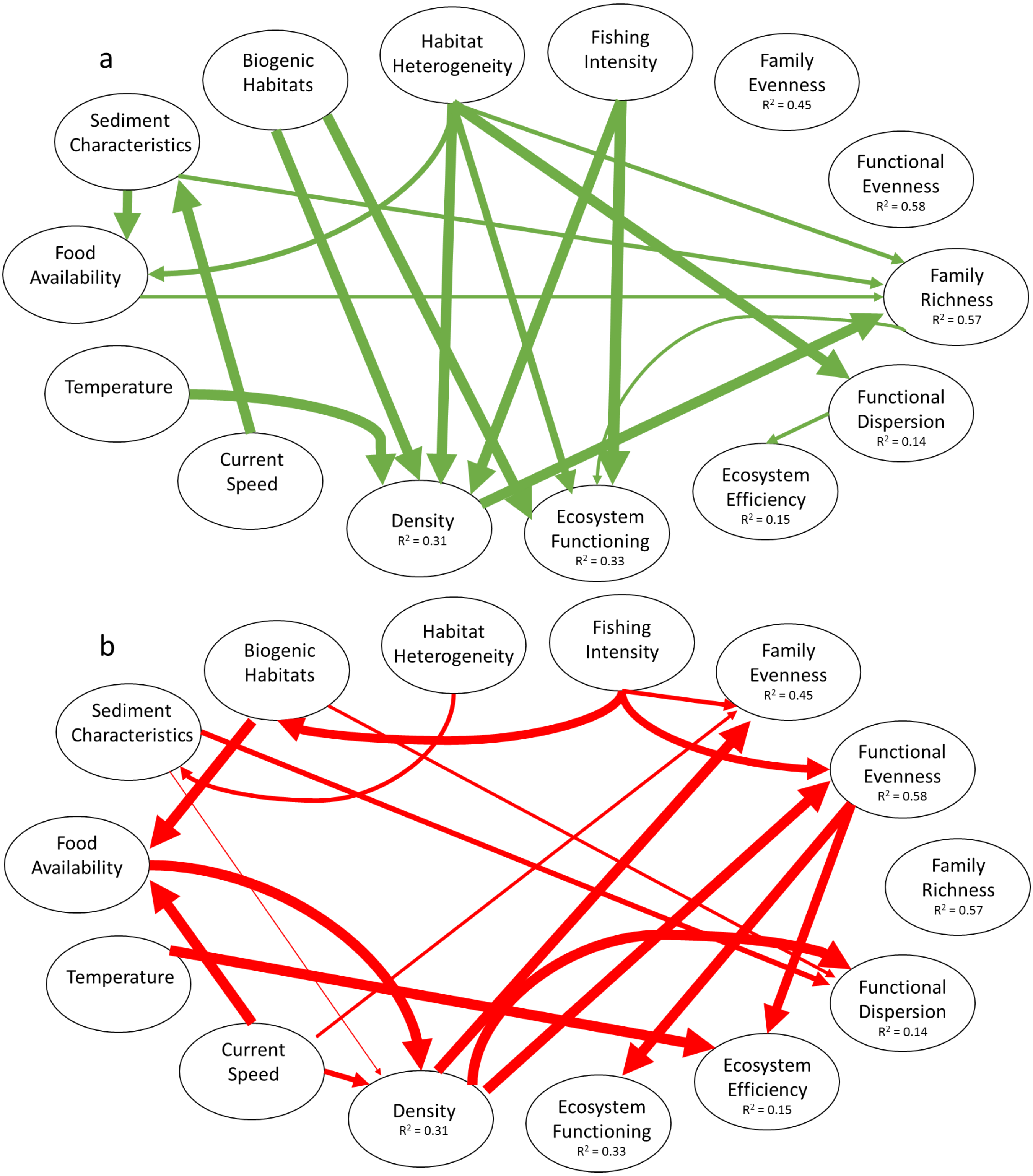


Figure 5.3 The significant relationships between the latent variables constructed in the structural equation model, showing (a) the positive relationships, and (b) the negative relationships. The thickness of the arrows is proportional to significance levels. For the latent variables of interest, the R^2 values are reported.

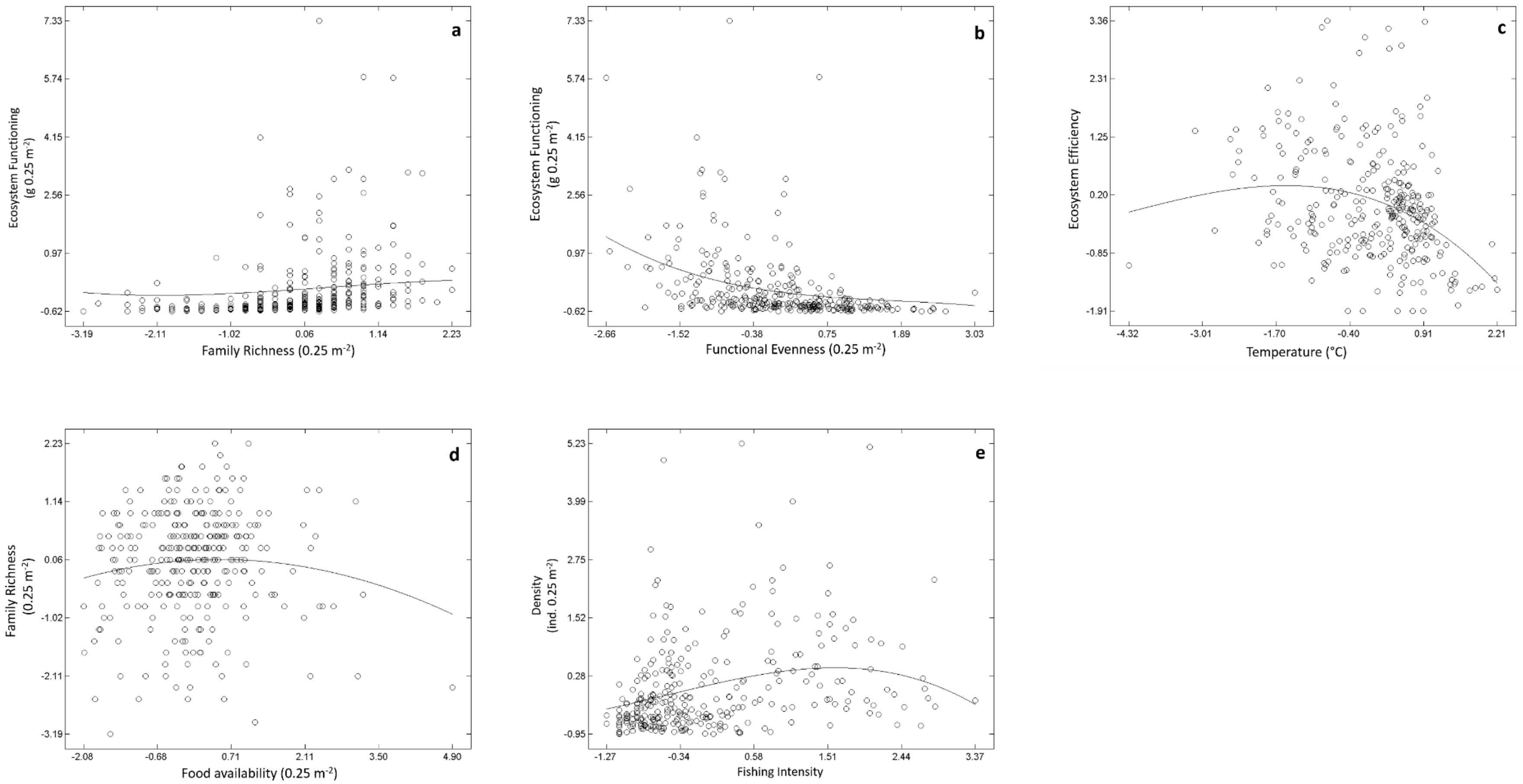


Figure 5.4 The standardised relationships between (a) Family Richness and Ecosystem Functioning, (b) Functional Evenness and Ecosystem Functioning, (c) Temperature and Ecosystem Efficiency, (d) Food Availability and Family Richness, and (e) Fishing Intensity and Density.

5.4b), showing that there is less secondary production at places with higher functional evenness. Ecosystem Efficiency had a unimodal relationship with Temperature (figure 5.4c), indicating that the transfer of carbon to deeper waters might increase a little when the ocean is warming, but with increasing temperatures, it is likely going to decrease. Respiration rates will likely increase with increasing temperatures, thereby resulting in less net carbon assimilation (Rogers 2015). Family Richness shows a unimodal pattern with Food Availability (figure 5.4d). Density and Fishing Intensity also show a unimodal pattern (figure 5.4e).

5.5 Discussion

This study looks at the influence of diversity measures on ecosystem functioning and efficiency, and how these relationships are affected indirectly and directly by the environment and anthropogenic disturbance in a deep-sea continental slope system.

5.5.1 Hypothesis 1

A positive saturating relationship between Family Richness and Ecosystem Functioning was found, supporting the large body of terrestrial and shallow-water research on BEF relationships. This is contradictory to previous studies based on nematodes. Such differences could be attributed to the different levels of taxonomic resolution: family level for this study and species level for both Danovaro et al. (2008) and Leduc et al. (2013). It is possible that, since all studies were concerned with an increase in taxonomic richness, an increase in one level (family) could perhaps also see an increase at other taxonomic levels. As such, a positive and saturating relationship observed here at family level, could mean that similar patterns could be found at genus level. In its simplest form, if there is only one genus or one species for each family, it would be the same relationship as observed here.

It is possible that the two BEF studies published on nematode data have captured different aspects of the BEF relationship. It is possible that Leduc et al. (2013) results showed the relationship after the saturation point of the BEF relationships, and Danovaro et al. (2008)

might have captured the beginning of the BEF relationship. The difference between the two studies is the richness observed in their samples. Danovaro et al. had low richness in their samples, while Leduc had much higher richness; neither overlapped in richness in their samples.

This study adds to BEF studies conducted in natural systems, and like other such studies, this relationship has much noise in the data. Abiotic factors influencing the BEF relationship are not well characterised. The environmental conditions vary per local sample compared to experimental studies where these are kept close to constant. Variation in environmental conditions can influence diversity locally as well as ecosystem processes (Díaz and Cabido 2001). This could potentially mask effects of diversity on the functioning of the ecosystem. The slope in the BEF relationship presented here is not strong, and this might well be the result of environmental conditions. To understand how changing environmental conditions influence ecosystem functioning, and how to incorporate such effects in management and conservation practices, there is a need to untangle these effects. BEF studies should focus on both biotic and abiotic factors.

The deep sea is characterised by the presence of many rare species and high taxonomic evenness, rather than a dominant species, which could influence the slope and saturation point of the BEF relationship (Gage and Tyler 1991). As this study focused on family level, such comparisons cannot be made. Some aspects in the data, however, are worth noting. There is dominance of a single family, the Capitellidae (see Chapter 4), which could potentially influence family diversity (see discussion below). Some of the individuals of this family had enough of the chaetae and segments present so that they could be identified to genus level (*personal observation*), and there was some indication that richness levels at genus level should be higher. However, for some other families (Onuphidae, Paraonidae), this did not seem to be the case, with very few genera, or just one appearing to be present (*personal observation*). Such conclusions are difficult, though, as the quality of the specimens was poor, making identification very difficult.

It is possible that in this area, a different relationship (saturating) has been found compared to Danovaro et al.'s study (exponential increasing), as a result of anthropogenic disturbance (see discussion below). Leduc et al.'s study in New Zealand was performed in areas that are or have been trawled, and they might not have found a relationship if trawling results in dominance of resistant species such resulting in a positive, saturating BEF relationship. As deep-sea animals are adapted to a slow-pace of life as a result of the low energy influxes and cold temperatures affecting metabolic rate and life-history characteristics, even at low trawling intensities there might be a strong selection effect on certain resistant taxa.

It is possible that the relationship for meiofauna (Danovaro et al. 2008; Leduc et al. 2013) and macrofauna (this study) are different. There are assumptions that the two size classes show different adaptation peaks to environmental conditions at different spatial scales (Warwick et al. 2006). However, whether these size classes are indeed separate entities remains to be seen. There is good indication that the peaks are a result of sampling strategies (Bett 2013). Other work on body size would suggest that there is an allometric relationship in body size, suggesting that there should be a continuous decline or increase in size rather than the separation of these two classes (Gaston and Blackburn 2000). If that is true, then the BEF relationship in deep-sea soft-sediment communities should be positive and saturating for both meio- and macrofauna, as shown in this study. If positive and saturating BEF relationships are observed in these groups in the deep sea, it would also indicate that this relationship holds in most systems on Earth, showing a generality in and perhaps importance of this relationship.

5.2.2 Hypothesis 2

Several environmental features influence the different diversity measures used in this study, including habitat heterogeneity, sediment characteristics, food availability, current speed, and biogenic habitats. Not all diversity measures were correlated with the same combination of variables, and some did not include environmental aspects at all. For example, functional evenness was found to correlate negatively with fishing and density, but it was not found to be correlated with any environmental conditions. Functional dispersion, however, was positively correlated with habitat heterogeneity. There were no negative relationships found for family richness, but there were for all the other three diversity measures, often with fishing intensity and density of the polychaetes themselves. As such, different diversity measures are potentially influenced by the environment, although they might be in different ways, indicating the need to focus on multiple measures within each study.

Family Richness is for a large proportion explained by the relationships specified in this model (almost 60%). Many latent variables (Habitat Heterogeneity, Sediment Characteristics, and Food Availability) specified here had a positive influence on taxonomic richness. These latent variables also influence each other, thereby indirectly influencing taxonomic richness. For example, many indicators were taken together for Habitat Heterogeneity. One of the indicators in Habitat Heterogeneity was depth, which has been shown to influence species richness in the deep sea. However, this might be a reflection of availability of food, which is also correlated with depth (with decreasing food availability with increasing depths and distance from land) (Rex and Etter 2010). Food availability has been proposed as a major structuring agent for taxonomic richness in the deep sea (Tittensor et al. 2011; McClain et al. 2012; Woolley et al. 2016). It is often found to be a very good correlative, especially on large spatial scales. Similar results have been shown in terrestrial systems as well (Whittaker et al. 2001). However, food availability had not the strongest correlation in this model. It is possible that, by not incorporating indirect effects, other models found strong support for food availability as they measured a variety of indirect influences as well as the direct influence of food. The latent variable Food Availability was influenced positively by Habitat Heterogeneity, suggesting that more heterogeneous sites had more food available, which in turn might increase taxonomic richness. Other variables, such as slope, seafloor rugosity, and bathymetric position index, all measure a form of heterogeneity. These variables increase the complexity of the landscape, which has been shown to influence many aspects of an organism's biology (e.g. body size). The relationship between habitat complexity and food is a complex one; it is possible that the two work in concert (e.g. more complexity leads to a different spatial distribution in food), although it is also possible that both work at different spatial scales (Gaston and Blackburn 2000). Food might be more patchy distributed, where there might be larger sources if the food is distributed unevenly in the area. For example, it is not too difficult to imagine that a very flat area might have most if not all food flushed away if the currents are too strong, while areas that contain more varied physical structures could have food holing up in crevices, behind small crests, etc. It is unknown how large such physical structures should be, but it is possible they do not have to be too large. A small mound might have already an effect on the unequal distribution of food. It is possible that more heterogeneous sites offer more hiding places, so there is an increased area to live in, and therefore there might be more food for higher trophic levels.

Sediment Characteristics had a positive influence on Family Richness. The indicator variables for this latent variable included percent silt, clay, and sand, and particle size diversity. Particle size diversity seems to have a smaller correlation with family richness than does either percentage clay or silt (*personal observation*). It is possible that at a large spatial scale, the fine-scale heterogeneity represented by particle size diversity has no measurable effect compared to large variations in percent clay, silt or sand, which was also suggested in Chapter 4. In other words, the number of sources of the sediments, which could be determined by inspecting distribution mode, peak and skewness, could be more informative at such spatial scales. Two studies that showed positive correlation between particle size diversity and species richness (Etter and Grassle 1992; Leduc et al. 2012), were performed on a smaller spatial scale than this study, which could explain the different results. Alternatively, the differences might be explained by using different taxonomic resolution; at species level, the diversity in particle size might be an important structuring agent, while not at family level. Food Availability and Sediment Characteristics are correlated in this model, with sediment positively influencing food. It has been suggested that the increase of taxonomic richness in increased sediment heterogeneity is not a direct response of the taxonomic groups to the heterogeneity, but to the food associated with that heterogeneity (Snelgrove and Butman 1994). It is possible that this relationship is another example of habitat complexity and food availability.

5.2.3 Hypothesis 3

Generally, it is thought that the diversity and identity of species influence the functioning of an ecosystem together (Cardinale et al. 2012). In this study, evenness (both functional and taxonomical) is negatively correlated with fishing practices, potentially suggesting that bottom trawling has a complex interaction with diversity, meaning that richness per se might not be harshly affected, but evenness is. Ecosystem functioning (secondary biomass production) can potentially increase under fishing intensity up to a certain level, where pressure of fishing will result in decrease again as a result of disturbance (van Denderen et al. 2013). This might be a result of selection effect, with the disturbance effects resulting in an increase of a dominant taxon. The sample locations with the highest numbers of individuals (and biomass) had unusually high numbers of Capitellidae (Chapter 3). Members of the Capitellidae family are considered opportunistic species and they can be used as indicators for disturbance resulting from local organic enrichment (Gage and Tyler 1991). This could indicate that there is local enrichment in the areas with more fishing; deep-sea fishing practices use trawling methods that are destructive to the sediment and sessile megafauna (Jennings et al. 2001; Hiddink et al. 2011). The bycatch mortality rates are high in the deep sea (Jennings et al. 2001), providing food for other organisms that survive the nets. van Denderen et al. (2013) have shown in their model that trawling intensity could have a positive effect on benthic abundance when the benthos is resistant to trawling impacts. It has been thought that at least some annelids are unaffected by trawling (Jennings et al. 2001; Rijnsdorp and Vingerhoed 2001; Kaiser et al. 2006). Similar findings of increased presence of opportunistic species have been reported for meiofauna in trawled areas as well (Pusceddu et al. 2014). It is unclear whether the changes in community composition, abundance and biomass are a direct result of trawling, or whether it is indirect via the influence of changes in fish communities (Thrush and Dayton 2002; van Denderen et al. 2013).

The community response to trawling observed here is similar to benthic community responses close to and under fish farms, where organic carbon fluxes are higher compared to background fluxes (Kutti et al. 2008). High densities of capitellids were also found in deep-sea colonization experiments in treatments with high organic enrichment, where capitellids have been shown to be pioneering species and early colonisers of a newly available patch of habitat (Grassle and Morse-Porteous 1987). Similar findings of increased presence of opportunistic species have been reported for meiofauna in trawled areas, suggesting this is a wider impact of trawling on benthic community structure than has been recognised (Pusceddu et al. 2014). Another possibility is that the change in community structure is a response to predator removal as a result of fishing, as predators have important structuring effects on lower-trophic communities (Rex 1981; Shepherd and Myers 2005).

Trawling is thought to decrease habitat heterogeneity (Pusceddu et al. 2014), while habitat heterogeneity should lead to higher taxonomic richness (Levin and Dayton 2009). Habitat heterogeneity could be the physical aspects of the environment (e.g. sediment characteristics), and biotic components (e.g. sponges and corals). No significant pathways were found between Fishing Intensity and Sediment Characteristics, although a reworking of the sediments, and thus a correlation, was expected (Thrush and Dayton 2002). It is possible that the sediments have already been reworked and that the change is not detectable anymore. Sponge and coral gardens have been shown to increase local species richness in the deep sea (Bell 2008). Trawling reduces the densities of sponges in this area, thereby potentially influencing taxonomic richness (NAFO 2009). No direct relationship, however, was found in this model. It is possible that as the modelled data of bottom trawling and sponge density are at a different spatial resolution and as a result the correlation was not detected. It is, however, expected that the influence of trawling is not limited to the area directly in contact with the trawl, but influences a much larger area because of sediments being resuspended in the area (Puig et al. 2012; Pusceddu et al. 2014). Filter feeding organisms, such as sponges, could be negatively impacted by this.

The density of sponges did influence abundance and biomass of the polychaetes (indicated by the positive pathways between Biogenic Habitats and Density and Ecosystem Functioning). It is possible that sponge presence is influenced by similar environmental variables as are polychaetes, such as habitat heterogeneity, food availability, etc. (see previous chapter), but whether their composition and distribution would be similar is not necessarily expected. These organisms perceive their environment at different scale because of their own sizes (sponges are megafauna, while polychaetes are macrofauna). There are filter feeding groups in the polychaetes, along with other feeding guilds, while most sponges are filter feeders (there might be carnivorous sponges present, but in low abundance). As such, caution is required to assume that sponge and polychaete abundances are distributed in the same way. They might, for example, be structured through the influence of habitat heterogeneity, but what the habitat heterogeneity represents can differ for both groups. For the polychaetes, sponges could be argued to create habitat heterogeneity. As such, the two should overlap a bit, but it will not explain the polychaete distribution completely.

5.2.4 Nonlinear patterns of the model

The positive correlation between Temperature and Density and the unimodal relationship between Temperature and Ecosystem Efficiency confirm other studies and highlight the need to understand climate change in the deep sea (Danovaro et al. 2004; Hoegh-Guldberg and Bruno 2010; Jones et al. 2014; Levin and Le Bris 2015). It is possible that temperatures affect transfer efficiencies of the carbon flux from the sea surface to benthic consumers, possibly as a result in a faster increasing rate of respiration compared to carbon assimilation in body tissues (Rogers, 2015). Whether temperature directly influences the relationship, or whether temperature influences the pelagic community that influences the transfer efficiency (Buesseler et al. 2007; 2008) is not known. Another possibility might be that certain species might be able to cope with the temperature change, while others cannot. This could result in resources not being used completely, with an associated reduction in efficiency. As deeper waters are warming in response to the warming of the oceans, this could indicate that the carbon cycle in the deep sea will potentially be impacted (Balmaseda et al. 2013). It must be noted that the R^2 value for Ecosystem Efficiency is low, showing that there are other factors influencing the efficiency that have not been included. Many studies have indicated the difficulty of measuring carbon availability (e.g. via particulate organic carbon or chlorophyll concentration) at the surface and relating it to carbon availability at the ocean floor. There is a time lag present as well as the influence of lateral transport through currents, and these factors will influence how quick food will sink to the ocean floor. It is well appreciated that transfer efficiency from the surface to deeper waters varies per region (Buesseler et al. 2007; 2008).

The patterns shown in figures 5.4d and 5.4e suggests a pattern predicted by the intermediate disturbance hypothesis (IDH) (Hutchinson 1961; Grime 1973; Connell 1978). The IDH was originally proposed by Connell (1978), who stated that the high diversity observed in tropical forests and coral reefs was possible as a result of disequilibrium caused by disturbance events. If these disturbance events should stop, the diversity of the systems should reduce as a result of competitive exclusion. In other words, the highest diversity (or richness) is expected at intermediate levels of disturbance, which includes frequency of disturbance, intensity of disturbance, predictability of disturbance, timing of disturbance, resource availability, environmental heterogeneity, and trophic interactions. Such effects might influence family richness observed in this study, where intermediate levels of resources correlate with the highest family richness values (figure 5.4d). Furthermore, although not directly related to richness, figure 5.4e shows a similar pattern; intermediate levels of fishing intensity might lead to the highest polychaete abundances. It is well known that more individuals lead to higher richness (known as the species – accumulation curve) (Fisher et al. 1943; Chao and Shen 2004). Figures 5.4d and 5.4e have much noise in the results, and the peaks potentially are skewed, indicating that other factors are involved. There continues to be a large debate on whether the IDH is supported (Mackey and Currie 2001; Shea et al. 2004; Hughes et al. 2007; Fox 2013a,b; Sheil and Burslem 2013). It is likely that in a complex system such as any natural system, multiple factors are at play, but that any type of disturbance can definitely have a major influence on the community and thus should be considered (Huston 2014).

The low R^2 values for both Functional Dispersion and Ecosystem Efficiency indicate that these factors are not well explained by the relationships specified in this model. It is possible that other factors, not included here, influence functional dispersion. SEMs have a limitation that only *a priori* determined relationships can be analysed. Another explanation why Functional Dispersion R^2 might be low is because of the functions chosen for this study. Most deep-sea benthic polychaetes are deposit feeders, with evidence of macrophagy and microphagy (i.e. particle size selectivity) (Jumars et al. 2015). The dichotomy between micro- and macrophagy is, however, not very clear, as juveniles might exhibit other feeding strategies to adult worms. This study incorporated only adult worms, reducing this blurred dichotomy. Jumars et al. (2015)'s feeding guilds are based on shallow-water organisms. Although a difference in functionality in deep- and shallow-water organisms is not necessarily expected within the same family, it is possible that the guild characteristics are slightly different as a result of food availability differences. Furthermore, even in shallow-water data there is still character information missing, which might affect the distances calculated for the functional diversity measures. It is also possible that, as functional dispersion is weighted by abundance, the Capitellidae family is such a dominant factor in the data that these results show no correlations.

Overall, it seems that a positive, saturating BEF relationship can be found the deep sea, as in many systems shown before. As in any other study in a natural system, there is environmental influence that can affect the relationship of interest. Here, it is also shown how anthropogenic influences, in the form of trawling, affects secondary productivity. It seems likely that diversity and ecosystem functioning studies in the deep sea should incorporate such effects in order to increase understanding and interpretation of how biodiversity is maintained and studies related to these aspects. This study has been performed on family-level data, and it is possible that similar patterns might be found at genus- or species-level data. The deep sea is poorly understood and many species still wait description, which will make species identification for studies as these difficult. By studying patterns at family level, the data could inform where the focus might be. In this way, information can be provided more quickly which could be very important given that deep-sea trawling is an ongoing disturbance and that other industrial activities in the deep sea, such as mining are about to start, with little knowledge of what impacts may be generated in this system (Rogers et al. 2015).

6. CHAPTER SIX:

Concluding Remarks

6.1 Key findings and implications

The deep sea is understudied, and as such, many observed trends are not well understood or explained. However, the deep sea is under threat as a result of anthropogenic impacts such as fishing, chemical pollution from oil and gas production as well as from terrestrial sources, pollution in the form of light for industrial and research activities, munitions (including chemical weapons), radioactive waste, local enrichment through sewage dumping, bycatch or offal release, and organic cargo on sunken ships, and the introduction of hard substrata to soft-sediments in the form of pipelines, garbage, cables and shipwrecks (Rogers 2015). Resource exploitation will continue to change deep-sea ecosystems, with little understanding of the repercussions of this process. Deep-sea trawling bans in the EU have been discussed since 2013, with a ban in place now for waters deeper than 800 m (http://eu.savethehighseas.org/eu-issue/). There is scientific support that this ban should decrease to 600 m depth (Clarke et al. 2015). Mangi et al. (2016) show that a ban with a 400 m depth-limit would be economically more viable than a 600 or 800 m ban. Several areas have been closed for bottom trawling in the Flemish Cap region (Durán Muñoz et al. 2012). Deep-sea mining is about to start, with the first explorative licenses granted (http://www.bbc.co.uk/news/science-environment-28442640) (Rogers 2015). The impacts of many of these activities are unknown.

There is a recognition that the protection of the seafloor is lagging behind developing exploitation (Wedding et al. 2015; Mangi et al. 2016). In the pursuit of deep-sea resources, accidents will likely happen, with potential horrible natural and social consequences. The Deepwater Horizon oil spill demonstrated in 2010 the social effects a deep-sea oil spill can have (https://www.theguardian.com/environment/2015/apr/18/lousiana-bp-oil-spill-five-years-not-going-back-to-normal). Deep-sea communities suffered from this unprecedented spill in terms of magnitude, amount of oil that was released, with corals showing, for example, tissue loss and increased mucous production, and coral-associates showing signs of bleaching (White et al. 2012). Working at greater depths goes along with increased risk, and more often than not there are no rescue preparedness agreements in place (Rogers et al. 2015).The ability of the scientific community to predict how biotic systems might respond to such perturbations, how resilient they are, and how long a recovery period might be and what the associated feedback will be like, is still very limited. Such predictions are dependent on the understanding of mechanisms that structure deep-sea communities. This thesis has contributed to the understanding of community structure in two main areas: body-size change in the deep sea, and the relationship between biodiversity and ecosystem functioning relationship, and how anthropogenic impacts might influence these relationships.

6.1.1 Body size

There has been an under appreciation of variability in deep-sea body-size research, whereby it is assumed that organisms decrease in size with increasing depth (Thiel 1975). Rather than trying to find a “one to rule them all” kind of trend, this area of research would benefit from understanding differences in body-size changes. Are there particular life-styles that might benefit from an increase or decrease of size? For example, although not studied in Chapter 2, there was some indication that filter feeders might increase in size with depth. It has been shown in fish that scavengers increase in body size with depth (Collins et al. 2005). Such considerations would aid in predictions of what might constitute “winners or losers” when sea surface primary productivity changes as a result of climate change and drives changes in community composition (Behrenfeld et al. 2006; Morán et al. 2010). Oxygen Minimum Zones are increasing in size and longevity (Stramma et al. 2010; Rogers 2015). Oxygen has a stronger selective pressure on body size than does food availability (Levin et al. 1991), and thus such areas will be affected differently. By trying to find a common “law”, we may not realise the loss of information we might obtain by studying and comparing differences between regions with different communities.

There has been a major focus on energy availability as structuring body size in the deep sea (McClain et al. 2012), but there might be other factors that are influential as well. Oxygen levels (Levin et al. 1991) have been mentioned in the previous section, but these will be very region-specific. Chapter 3 offers another perspective to explain body-size change in the deep sea: habitat complexity. Body-size change in the deep sea has not been studied in respect to habitat complexity before, although it has been recognised that structure-forming organisms such as corals and sponges host many small organisms (Jones et al. 1994). Disregarding this fact, but still sampling in the vicinity of structure-forming organisms, may have resulted in a bias towards smaller organisms, without realising why.

The debate as to whether energy availability or habitat complexity is a better predictor of body-size change has taken place in other biomes as well (Allen et al. 2006; Cox et al. 2016a). The deep sea offers a potentially very exciting place to study these rival hypotheses as the community can respond strongly to, for example, food impulses (Smith Jr et al. 2013). This could allow for a clearer separation of the different effects that food impulses and habitat complexity create. These findings can be tested through experimental manipulation in the deep sea. For example, it is possible to set up experimental plots in the deep sea with either increased food availability for the fauna, increased sediment complexity (mimicking, for example, sponge spicules), a combination of the two effects, and of course, a control where nothing is manipulated to understand the different effects.

6.1.2 Community structure

The deep sea is under threat from human activities; fisheries impact communities, plastic fibres can be found in the sediments, and oceans are increasing in temperature and undergoing acidification (Rogers 2015). In order to protect the deep sea, it is necessary to understand what lives there and what structures the diversity of communities. Less than 1% of the seafloor has been sampled, indicating that we are unlikely to know exactly what lives in any particular place.

There have been several studies looking at local-scale variation influencing richness (Rex and Etter 2010). The data presented in Chapter 4 aid in the understanding of what structures deep-sea richness at the regional scale. It advances our knowledge in deep-sea biogeography: it indicates what influences the distribution of animals in this region. Furthermore, the results show that, like with body-size relationships, energy and habitat are important and a link between these two mechanistic topics is discussed below in the section *broader implications and future research*. By starting to look at structuring processes at different spatial scales, it will become possible to start explaining why there might be so many species in the deep sea, what functions these communities perform, and potentially might aid formulating conservation strategies to conserve these functions.

6.1.3 Fishing

Most studies focusing on deep-sea fisheries have demonstrated an effect on megafauna. Mention of impacts on smaller organisms are limited, and often turn out to be smaller megafauna rather than macrofauna when the methods are inspected (e.g. the organisms can be observed with underwater cameras and do not require sieving) (Clark and Rowden 2009). A change in this component of the food web, however, can have effect on consumers at higher trophic levels as they might not be of the same food quality. It is possible that fish species might have to switch prey, and that can potentially affect population growth rate.

The study system in this thesis shows signs of a disturbed system in that an opportunistic group is dominant. The abundances of Capitellidae are very high, comparable to or potentially higher than early-colonization experiments which used local organic enrichment techniques (Grassle 1977; Grassle and Morse-Porteous 1987). Potentially other fished areas may show similar changes in community structure. It is possible that the meiofauna might show signs of disturbance in community structure as well. How long this opportunistic community in the Flemish Cap and Grand Banks area has been present, is not known. The area has been fished for many decades. It is also not known how long it will take to recover. It is not even known whether this community structure was there before fishing, as we do not have baseline information. Some areas in the study area have been closed for bottom trawling now (Durán Muñoz et al. 2012) and a comparison between areas that are still trawled and areas that have been closed might illuminate whether there is recovery potential or not. Such a study would provide potential information on resilience of the macrofaunal community against trawling. It is very likely that it is still too early to see an effect in large megafauna, such as corals (Huvenne et al. 2016), but potentially recovery might be seen in the smaller organisms.

To assess how the deep sea has been impacted by, for example, fishing, baseline studies are necessary. Currently, there is a lack of reliable data to establish baselines (Rogers 2015). This study demonstrates, however, that the system might already have changed – assuming that an opportunist-dominated system was not present before fishing commenced. It is possible that the baseline has already shifted as a result of fishing, and such information is critical for the evaluation of the system as other areas have shown (Baum and Myers 2004). Fishing organisations, such as NAFO, are funding research and monitoring of their areas of interest, and working towards a programme of sustainable fisheries management, in compliance with UNGA Resolution 61/105. To gain an understanding of the deep-sea system, large sampling programmes are necessary, but such programmes are very expensive. Such money might come more industry or fisheries management organisations, which may direct what areas should be sampled. Does this mean that there are areas that will never be sampled? Areas that might still be impacted, for example, by the storage of human waste (Rogers 2015). How will we be able to determine what represents a pristine state in the deep ocean, and how it has changed as a result of human activities and/or climate change or might change in the future?

6.1.4 Temperature

Temperature, especially long-term temperature, might be important in structuring family richness in the northwest Atlantic. This area has been shown to have an increasing trend in temperature (Colbourne et al. 2014), although there are some temporary changes in weather which might have their own effect (Seager et al. 2010; Fereday et al. 2012). Oceans worldwide have been shown to take up the excess heat of the atmosphere (Rhein et al. 2013). No significant relationship between temperature and family richness was found in the structural equation model presented in Chapter 5. However, Chapter 4 demonstrated that family distribution was influenced by long-term temperature. Geological records show that warm waters have lower oxygen levels and are more saline, which will influence deep-sea biodiversity - major deep-sea extinction events are linked to the changes from cool, well-oxygenated deep waters to warm, saline and hypoxic deep waters (Rogers 2000; Winguth et al. 2012; Dickson et al. 2014; Rogers 2015). Many deep-sea taxa are younger than expected, which could be linked to climate-driven extinction events in the deep (Rogers 2015). Some taxa are suspected to be more tolerant to hypoxic and anoxic conditions and have survived these events (Ullmann et al. 2014), while a few might have survived in refugia (Thuy et al. 2014). The response of the current deep-sea communities might be predicted from the geological observations. Temperature potentially also influences ecosystem efficiency (Chapter 5), meaning the transport of carbon from sea surface to benthic communities. The change in efficiency starts at the sea surface, where increased sea surface temperatures can lead to increased ocean stratification. This stratification affects nutrient availability for phyto- and zooplankton, and thus primary production and the amount and quality of carbon that will sink into the deep sea (Hoegh-Guldberg and Bruno 2010; Rogers 2015). As environmental conditions change, a change in the plankton community is expected, and is already observed (Nehring 1998; Johnson et al. 2011; Polovina and Woodworth 2012). Furthermore, the ratio between oxygen production and community respiration can shift as a result of the altered phytoplankton composition. As the community composition of plankton affects transfer efficiency and quality of organic matter to the deep sea (Buesseler et al. 2007), and benthic communities respond strongly to such changes (Ruhl and Smith Jr. 2004; Smith et al. 2008; Smith Jr et al. 2013), it is likely that deep-sea communities will alter in composition as oceanic waters warm up.

6.2 Broader implications and future research

6.2.1 Fractals

The metabolic theory of ecology (MTE) is very interesting as it offers the potential to make predictions from the growth rates of a single organism to community population dynamics to the biodiversity patterns of whole ecosystems (Brown et al. 2004b). However, as authors indicate (Brown et al. 2004a), it is far from complete. It is possible that when habitat complexity is incorporated in the theory, better predictions can be made. Energy is not freely available, and the structure of the habitat will influence its distribution. Over large spatial scales, physical structures show less variety. For example, when you look out of an aeroplane, forests, fields, and other small structures will look flat (2D). Mountains, however, are still obviously 3 dimensional. When you are on the ground, however, forests, houses, etc. have more structure, and suddenly, the 2D view has turned into a 3D view. The ocean floor is very similar: depending on the frequencies used in multibeam surveys, more or less structure will be visible on the ocean floor. Over a large spatial scale, thus, energy can have very good correlations with, for example, species richness as habitat complexity might look more 2D and so becomes a negligible effect. At finer scales, however, suddenly 3D structures will become visible (think about small mounds or knolls). The coupling theme between energy distribution and habitat complexity is fractals. The concept is represented in figure 6.1, where, to incorporate environmental conditions as well, two hypothetical current regimes are used as well. Differences in the distribution of food are created at different resolutions, with the first level showing a low resolution, while the third

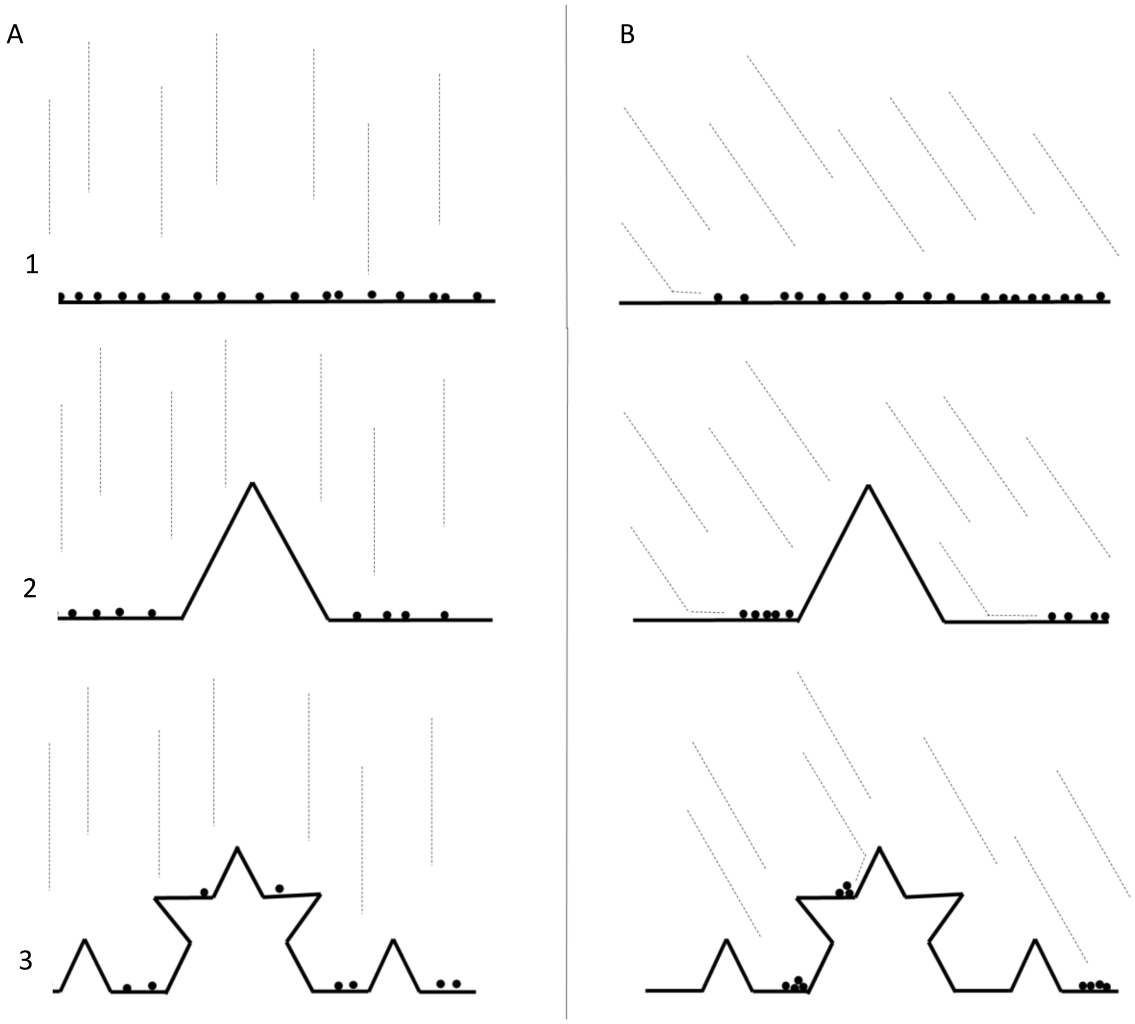


Figure 6.1 The influence of fractal-like structures on food distribution in space under two current regimes. Three different fractal dimensions, level 1, 2, and 3, are represented. In level 1, there is no structure. There is self-similarity in the physical structure in 2 and 3, with the structure of 2 repeated in level 3 at each line segment that was present in level 2. The three different levels of resolution are shown in both current regimes. At the first level (1), the resolution is very low, comparable to observing the seafloor from a large height; it looks flat. At the second level (2), there might be some structure present, comparable to a mound or knoll. At the third level (3), a more detailed on the fine-scale structure becomes apparent, influencing food availability. In A, it is hypothesised that food sinks vertically (no current), while in B the food is pushed sideways through the forcing of currents. The fine-scale physical structure that becomes apparent with higher resolution and the different current regimes show how hypothetically food may be distributed in space. The thick black lines represent the seafloor. The fine grey lines represent the path of food falling, or current speed for that matter. The black circles represent packets of food. In B, food packets may be more packed together as a result of current forcing, while in A the food falls in a direct vertical line, and no packing happens.

level showing a high resolution at which fine-scale structuring is apparent. Furthermore, as a result of other factors, here current regime, food can be distributed differently in the physical environment, here represented by food packaging when there is a current present. The fractal-like environment will create places where food is more likely to pile up than in other places.

Fractals are self-similar, size-dependent on scale (the finer the spatial scale, the larger the object), classical methods (geometry and mathematics) do not apply to fractals, they are recursive, and they have a natural appearance (Falconer 2013). The finer the scale of measurement, the larger the length of the fractal will be. This is comparable to the size of coastlines, which also increase in size when studied at a higher resolution. Physical structures in the world can be measured by fractals, which give a relatively good approximation of the size and shape of the structure. more often such structures are fractal-like rather than true fractals, and the approximations work well. Similarly, structure-forming organisms, such as trees, algae, and sponges, can be described as fractal-like (Falconer 2013). An understanding in fractal-like structures in the deep sea will allow for prediction in energy distributions at finer spatial scales, and thus explanations in family (and species) richness distributions and body size relationships.

6.2.2 Structural equation modelling - BEF in a natural system

Structural equation models (SEMs) provide an exciting opportunity to analyse complex systems, like communities and ecosystems. Much has been published on a variety of deep-sea patterns, but there has been a limitation of pooling these relations together; in other words, there has often been only one dependent variable studied and indirect effects might not be well characterised. As such relationships have been found, they can therefore be specified *a priori* in a SEM. This, in turn, can allow for the advancement of theory development in the deep sea when relationships are supported and confirmed in the SEM, together with direct and indirect effects. In the case of deep-sea research, it can accelerate our understanding of the system, which is very necessary in light of the increased anthropogenic exploitation. It will potentially help prioritise hypotheses to develop and test. In general, SEMs are useful for biodiversity – ecosystem functioning relationships in any natural system, where the community provides the functions, but where diversity is influenced by the environment itself as well, which creates noise in the system (Strong et al. 2015). Modelling these relationships together will elucidate specific influential factors.

6.2.3 Food webs

Food webs in the deep sea are understudied, with limited knowledge available of what organisms might eat. This is likely to explain in part why support for certain relationships is contradictory (van der Grient and Rogers 2015). It is likely that deep-sea communities will be impacted by changes (in pH, heat, and primary production) at sea surface through trophic links, which have implications for the biological carbon pump and carbon burial (Rogers 2015). Under changing conditions, there might be shifts in the benthic community structure. For example, organisms that use aragonite for the construction of their skeleton are likely to suffer from acidification. Other organisms that are dependent on these might suffer through oscillations in the food web. Trophic links can have impacts on the structuring of communities, as shown in exclusion experiments in the deep sea (Eckman et al. 2001; Thistle et al. 2008). Thistle et al (2008) showed that densities of copepods and polychaetes were lower when motile epifauna was excluded from the area. It would suggest that larger fauna are important in the stimulation of population growth in smaller fauna. This can either by reworking the sediment, which might be beneficial for smaller fauna, or potentially by top-down control that could stimulate faster turn-over rates. It has been suggested that predator interactions can be important in the deep sea by controlling populations at lower trophic levels, and this in turn could lead to increased biodiversity (Rex 1976; Gage and Tyler 1991).

6.2.4 Taxonomic limitations

Chapter 2 till 5 represent trends at family level. Ideally, we would understand this at species level. This is going to be difficult for deep-sea data, as many species have not been described yet, and proper identification keys are often missing for genera- and species-level data. Furthermore, we might well miss out on the opportunity to describe them when samples are sieved in a destructive way (see below for further discussion). Taxonomic experts are still needed (Kim and Byrne 2006). There is a lot of enthusiasm for genetic research, but if species are never properly described using genetic and morphological characteristics, it will stay known to humanity as a sequence of base-pairs and nothing about the ecology can be learned; an integrative approach is necessary (Vogler and Monghan 2006; Padial et al. 2010; Ross et al. 2010). There should be more appreciation for taxonomy and the description of new species (other than, for example, mammals or dinosaurs).

Even though it can be difficult to determine species or genera in the deep sea, family-level patterns are informative and valuable on their own. Patterns found at family level could direct research to specific, relevant genera. For example, in the work presented here it could be asked: why specifically are there capitellids so abundant? Are they all of the same genus (or species), and what would structure their distribution if they are not the same ? Are capitellids for more resistant to trawling impacts than other polychaete families, or do they respond to the release of biotic interactions or do they profit from potentially more food availability?

6.2.5 Sampling

One way for more effective research, especially in the deep sea, would be more attention to sampling design and processing. When there is a lot of money going into research, which is especially the case in deep-sea biology, it seems strange how lightly processing is treated sometimes. For example, in the data presented here, the sieving of the sediments was too fast, which has resulted in the fragmentation of fragile organisms; in other words, most organisms in the case of macrofauna. For example, in my - more than 50,000-individuals - dataset, perhaps less than 100 are still complete (*personal observation*). These complete organisms are often in families that occur rarely (for example, the Sternapsidae, which was only found once). Organisms that could have provided a wealth of information, like the Cirratulidae have been damaged to such a point that genus identification on them was given up (note made in lab book stated: “questioning sanity right now”). With more time, the Capitellidae might be able to be identified to genus level, but this was beyond the scope of this thesis. It is a real shame to think about how much information could have been lost by saving a relatively small proportion of money on an already expensive project. Information that has been lost could come in the form of new species description to finer identification of species-richness maintenance processes and selective pressures of human impacts.

The data presented in Chapter 2 was insufficient to properly test for differences in slopes between all different regions and/or taxonomic groups. However, as some authors have published on just biomass or abundance, it could mean these missing data is still somewhere. In a “hunt” for these data, which was not possible in the scope and time-frame of this thesis, a check could be carried out on the biomass estimates. In this thesis, the biomass data of polychaetes is underestimated as a result of the sieving method. Most worms were fragmented and were in a poor state. Whether the published data also represent fragile, fragmented organisms, is not known. If this is true, it could mean that biomass estimates are underestimated; in other words, potentially, body size has been underestimated and is decreasing at a slower rate – or not at all – than assumed. Fragmentation is rarely reported, but likely common in fragile organisms. As polychaetes make up the majority of the macrofaunal community, there should be more attention to this sampling artefact.

Sampling design needs more attention in the deep sea. As Chapter 2 demonstrates, results are biased by the sampling methods used. There have been studies published showing this, although not everyone agrees (Warwick et al. 2006; Bett 2014; Warwick 2014). It is positive to see a new book on sampling methods, just published in the last month of writing this thesis (Clark et al. 2016a), and hopefully this will be an encouragement to standardise sampling protocols. Standardised protocols will allow for better comparison between studies. One area that really needs to be considered is the choice of sieve sizes. It is very possible that the bimodality in meio- and macrofauna is a simple artefact of under-sampling the trough in the bimodal distribution. When sieve sizes are used to capture this size section as well, it is possible that a continuous decline in body size will be found, with the all implications of this in terms of ecology, oxygen consumption, nutrient cycling, etc. A stacked design, using multiple sieves on the same sample, could really capture the distribution of the community (see Chapter 2 for more details). It might be optional, one day, to not talk about meio- or macrofauna, but just small benthic organisms that form the basis of the food chain. Rather than choosing a system to study based on size, the organisms will be selected for biological aspects; for example, their involvement as food source for particular organisms, their life style, their bioturbation potential, etc. It will be the biology, not an arbitrary size class that will determine the choice.

During this thesis, several things became apparent in other sampling aspects that should be considered. For example, there is a tradition in deep-sea science to use expected numbers ($E(S_n)$). This makes sense when epibenthic sleds or nets are used to standardize sampling sizes. The sampling efficiency of these can depend on many factors, from area sampled to time towed. It allows for a more quantitative comparison. This tradition is still seen often in box core studies, which is unnecessary and loses information. Box core samples are quantitative; they have a standardized area and volume, (although it depends on the success of the core), and thus can be compared directly to other cores. There might be abiotic or biotic factors that influence abundances, and therefore richness, and it is this difference that should be of interest.

Furthermore, a consideration of data treatment needs to be made. Multivariate analysis programmes often state that the biological data needs to be transformed. The most commonly used transformation is a square root transformation. The effect of this is to remove influence of common and rare species (Clarke and Gorley 2015). It makes sense to do this in systems that commonly have high dominance, but in the deep sea, high rareness and high evenness is standard. Patterns that are caused by this will potentially be masked. A simple exercise of constructing, for example, nMDS plots with no transformation, square root transformation, or fourth-root transformation (even stronger one), shows that the pattern observed is, at least visually, lost (*personal observation*). The observation was a simple exercise, but has highlighted that this needs to be explored in more depth. Furthermore, such considerations in statistical treatment, not everyone's favourite area of work, should however be encouraged.

Another area of consideration of sampling design comes in the form of particle size diversity. Particle size diversity is calculated with the Shannon-Wiener index. The Shannon-Wiener index is based on discrete classes (as much as species are such a thing) and the abundance of each class. These are nominal classes. Sediment size classes (calculated in phi), however, are ordinal, which means that when one class has a high abundance, it is likely that the classes next to it are relatively high. This could influence the diversity measurements. Geographers studying sediment particle size instead look at the distribution, the mode, and skewness. As the correlation between particle size diversity and species richness is varied, it is possible that this is caused by not measuring it in an appropriate way, or it might hint at other factors that really influence the change and the sediment particle size diversity might represent an (unestablished) proxy for these factors.

6.3 Concluding remarks

Research presented here has advanced our knowledge in body-size research in the deep sea. It highlights where a focus on one universal trend might be limited, and it has offered a new perspective on structuring body size in the deep sea. Furthermore, it is one of the first studies to test what environmental drivers there might be behind family richness in the deep sea at a regional scale. It is also the first study on biodiversity – ecosystem functioning to use deep-sea macrofauna, and it is the first study to show a positive saturating relationship in the deep sea. Additionally, it has demonstrated how fishing intensity affects the community, potentially allowing for the dominance of an opportunistic group. Research using fractal dimensions is likely to push forward theory development of what structures body size and diversity by, for example, advancing the Metabolic Theory of Ecology. Furthermore, structural equation modelling provides an exciting opportunity to study complex relationships in complex systems and will allow the improvement of our understanding of natural systems, where interconnected relationships are the norm. However, no improvement in knowledge will reach its true potential if there is not more attention to sampling design and sample processing. These factors, which influence estimates of abundance, biomass, body size, etc., and thereby potentially confound relationships, need to be considered more carefully in future research.

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8. Appendix

8.1 Appendix A. Source references for meio- and macrofaunal abundance and biomass

Meiofauna:
Aller et al (2002), Alongi and Pichon (1988), Alongi (1992), Baguley et al (2008), Berkenbush et al (2011), Bianchelli et al (2010), Coull et al (1977), Danovaro et al (1995; 2000; 2002), de Bovée et al (1990), Escobar et al (1997), Fabiano and Danovaro (1999), Flach et al (2002), Gage, (1977), Galéron et al (2000; 2001), Gambi and Danovaro (2006), Garcia et al (2007), Gooday et al (1996), Grove et al (2006), Heip et al (2001), Herman & Dahm (1992), Hessler and Jumars (1974), Hoste et al (2007), Hughes and Gage (2004), Ingels et al (2011), Itoh et al (2011), Jensen (1988), Jensen et al (1992), Kröncke et al (2000), Lampadariou and Tselepides (2006), Levin and Thomas (1989), Newton and Rowe (1995), Pequegnat et al (1990), Pfannkuche and Thiel (1987), Pfannkuche (1985), Relexans et al (1996), Richardson et al (1985), Richardson et al (1995), Rowe et al (1997), Rowe et al (2008), Shimanaga et al (2007), Shirayama (1983), Sibuet et al (1989), Snider et al (1984), Soetaert et al (1991), Soltwedel and Thiel (1995), Soltwedel et al (2000), Sommer and Pfannkuche (2000), Tahey et al (1994), Thiel (1979), Tietjen (1971), Tietjen (1984), Tietjen et al (1989), van Gaever et al (2009), Vanaverbeke et al (1997), Vanhove et al (1995), Vanhove et al (2004), Vanreusel et al (1992), Vanreusel et al (1995b), Vanreusel et al(1995a), Vanreusel et al (2000), Wigley & McIntyre (1964), Yingst & Rhoads (1985).

Macrofauna:
Aller et al, 2002; Alongi, 1992; Blake & Grassle (1994), Blake and Hilbig (1994), Carey (1981), Clough et al (1997), Duineveld et al (2000), Flach and Heip (1996), Flach et al (2002), Frankenberg and Menzies (1968), Gage (1977) Galéron et al (2000), Gerdes et al (1992), Grassle and Morse-Porteous (1987), Hecker and Paul (1979), Hessler and Jumars (1974), Hughes and Gage (2004), Hyland et al (1991), Jażdżewski et al (1986), Jensen et al (1992), Jumars and Hessler (1976), Kaariainen and Bett (2006), Kröncke et al (2000), Kröncke et al (2013), Kröncke and Turkay (2003), Kröncke (1998), Laubier and Sibuet (1979), Levin and Thomas (1989), Levin et al (2000), Polloni et al (1979), Richardson et al (1985), Richardson et al (1995), Rowe and Menzel (1971), Rowe (1971), Rowe et al (1974), Rowe et al (1982), Sanders et al (1965), Schaff et al (1992), Shirayama (1983), Sibuet et al (1989), Smith (1978), Smith (1987), Wigley and McIntyre (1964), Witte (2000), 2000; Yingst & Rhoads (1985).

8.2 Appendix B. Parameter estimates with variability measures explaining macrofaunal body size

	Mean Body Size*	**Standard Error**	**Confidence Interval 0.5% - 99.5%**
Depth	-7.400×10^{-5}†	2.040×10^{-5}‡	-1.266×10^{-4} to -2.125×10^{-5}††
Sieve Size	2.690	1.980×10^{-1}	2.180 to 3.200
Area Sampled	-6.094×10^{-2}	3.462×10^{-2}	-1.501×10-01 to 2.8239×10^{-2}
Arabian Sea	-5.024	1.467×10^{-1}	-5.402 to -4.646
Arctic Ocean	-4.822	2.890×10^{-1}	-5.566 to -4.077
Caribbean Sea	-3.771	1.340×10^{-1}	-4.117 to -3.426
East Atlantic	-3.593	1.382×10^{-1}	-3.949 to -3.237
East Pacific	-2.726	1.628×10^{-1}	-3.146 to -2.307
Gulf of Mexico	-4.500	1.504×10^{-1}	-4.888 to -4.113
Mediterranean	-3.929	1.407×10^{-1}	-4.291 to -3.566
Northeast Atlantic	-4.915	1.110×10^{-1}	-5.201 to -4.629
Northeast Pacific	-4.243	1.832×10^{-1}	-4.715 to -3.771
Northwest Atlantic	-4.159	1.723×10^{-1}	-4.603 to -3.716
South Atlantic	-4.414	2.680×10^{-1}	-5.104 to -3.724
Southeast Atlantic	-3.738	1.996×10^{-1}	-4.252 to -3.224
Southwest Pacific	-3.579	1.511×10^{-1}	-3.968 to -3.190
West Atlantic	-3.234	3.662×10^{-1}	-4.178 to -2.291
West Pacific	-3.776	1.638×10^{-1}	-4.198 to -3.354
Anthozoa	8.616×10^{-1}	4.152×10^{-1}	-2.079×10^{-1} to 1.931
Aplacophora	-3.484×10^{-1}	9.497×10^{-2}	-5.931×10^{-1} to -1.038×10^{-1}
Ascidiacea	-8.310×10^{-1}	3.248×10^{-1}	-1.668 to 5.773×10^{-3}
Asteroidea	-3.867×10^{-1}	2.977×10^{-1}	-1.154 to 3.802×10^{-1}
Bivalvia	-1.759×10^{-1}	1.420×10^{-1}	$-5.417*10^{-1}$ to 1.900×10^{-1}
Brachiopoda	4.413×10^{-1}	6.205×10^{-1}	-1.157 to 2.040
Crustacea	-7.289×10^{-1}	9.506×10^{-2}	-9.738×10^{-1} to -4.841×10^{-1}
Echinodermata	2.439×10^{-1}	2.083×10^{-1}	-2.926×10^{-1} to 7.804×10^{-1}
Echinoidea	4.755×10^{-1}	2.921×10^{-1}	-2.769×10^{-1} to 1.228
Gastropoda	-1.577×10^{-1}	1.794×10^{-1}	-6.199×10^{-1} to 3.045^{-1}
Holothuroidea	1.608×10^{-2}	2.605×10^{-1}	-6.548×10^{-1} to 6.870×10^{-1}
Malacostraca	-4.409×10^{-1}	8.406×10^{-2}	-6.574×10^{-1} to -2.244×10^{-1}
Maxillopoda	-1.575×10^{-1}	4.692×10^{-1}	-1.366 to 1.051
Mollusca	-2.638×10^{-1}	1.037×10^{-1}	-5.310×10^{-1} to 3.426×10^{-3}
Ophiuroidea	8.518×10^{-1}	2.069×10^{-1}	3.190×10^{-1} to 1.385
Polychaeta	-1.383×10^{-1}	6.305×10^{-2}	-3.007×10^{-1} to 2.409×10^{-2}
Porifera	6.283×10^{-1}	2.174×10^{-1}	6.829×10^{-2} to 1.188
Priapulida	-6.838×10^{-1}	3.507×10^{-1}	-1.587 to 2.195×10^{-1}
Pycnogonida	-1.185	7.778×10^{-1}	-3.188 to 8.189×10^{-1}
Scaphopoda	1.733×10^{-1}	1.892×10^{-1}	-3.139×10^{-1} to 6.606×10^{-1}
Sipuncula	-1.375×10^{-1}	1.153×10^{-1}	-4.346×10^{-1} to 1.596×10^{-1}
Turbellaria	4.240×10^{-1}	5.777×10^{-1}	-1.064 to 1.912

* All macrofauna body size values are in log gram.

† Indicates the mean, all else represent the differences between the mean.

‡ Indicates the standard error of the mean, all else represent the standard error of the difference.

†† Indicates the confidence interval of the mean, all else represent the confidence interval of the difference.

8.3 Appendix C. Parameter estimates with variability measures explaining meiofaunal body size

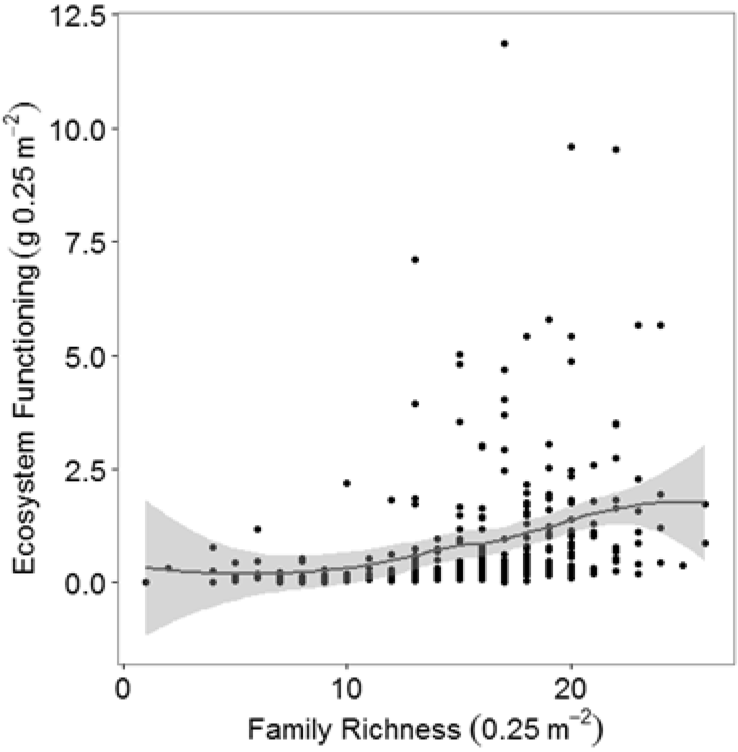
	Mean Body Size*	**Standard Error**	**Confidence Interval 0.5% - 99.5%**
Depth	-6.300×10^{-5}†	8.300×10^{-6}‡	-8.449×10^{-5} to -4.164×10^{-5}††
Sieve Size	2.342	3.598×10^{-1}	1.415 to 3.269
Area Sampled	-5.789×10^{-1}	1.261×10^{-1}	-9.036×10^{-1} to -2.539×10^{-1}
Antarctica	-1.946×10^{-1}	3.722×10^{-2}	-2.905×10^{-1} to -9.87×10^{-2}
Arctic Ocean	-1.698×10^{-3}	9.917×10^{-2}	-2.571×10^{-1} to 2.537×10^{-1}
Central Atlantic	-1.560×10^{-1}	6.816×10^{-2}	-3.316×10^{-1} to 1.957×10^{-2}
Caribbean	8.917×10^{-1}	7.383×10^{-2}	7.015×10^{-1} to 1.082
East Atlantic	4.687×10^{-1}	1.295×10^{-1}	1.350×10^{-1} to 8.024×10^{-1}
Gulf of Mexico	1.420×10^{-1}	4.058×10^{-2}	3.749×10^{-2} to 2.466×10^{-1}
Mediterranean	3.003×10^{-1}	5.262×10^{-2}	1.647×10^{-1} to 4.358×10^{-2}
Northeast Atlantic	7.482×10^{-1}	6.688×10^{-2}	5.759×10^{-1} to 9.204×10^{-1}
Northwest Atlantic	9.908×10^{-1}	4.884×10^{-2}	8.650×10^{-1} to 1.117
Southeast Pacific	-4.828	5.570×10^{-1}	-6.263 to -3.393
Southwest Pacific	-1.246×10^{-1}	3.976×10^{-2}	-2.270×10^{-1} to -2.215×10^{-2}
West Atlantic	-8.512×10^{-1}	1.866×10^{-1}	-1.332 to -3.706×10^{-1}
West Pacific	3.829×10^{-1}	5.564×10^{-2}	2.396×10^{-1} to 5.262×10^{-1}
Gastrotricha	7.433×10^{-1}	6.446×10^{-1}	-9.170×10^{-1} to -2.404
Bivalvia	2.123	1.403×10^{-1}	1.761 to 2.484
Foraminifera	-1.229×10^{-1}	3.359×10^{-2}	-2.095×10^{-1} to -3.639×10^{-2}
Kinorhyncha	1.159×10^{-1}	1.350×10^{-1}	-2.320×10^{-1} to 4.637×10^{-1}
Maxillopoda	3.564×10^{-1}	5.790×10^{-2}	2.072×10^{-1} to 5.055×10^{-1}
Nematoda	-1.487×10^{-1}	3.157×10^{-2}	-2.300×10^{-1} to -6.739×10^{-2}
Ostracoda	1.429	6.044×10^{-2}	1.273 to 1.584
Polychaeta	1.344	4.797×10^{-2}	1.221 to 1.468
Undetermined	1.382	9.687×10^{-2}	1.132 to 1.631
Turbellaria	-1.734	1.461×10^{-1}	-2.110 to -1.358

* All meiofaunal body size values are in log microgram.
† Indicates the mean, all else represent the differences between the mean.
‡ Indicates the standard error of the mean, all else represent the standard error of the difference.
†† Indicates the confidence interval of the mean, all else represent the confidence interval of the difference.

8.4 Appendix D. The indicator variables used for each latent variable in the structural equation model.

Latent variable	Indicator variable
Habitat Heterogeneity	bathymetry rugosity (25-cell) bathymetric position index (125-cell) slope roughness
Fishing Intensity	log vessel monitoring system (3km) log vessel monitoring system (point 3km) log trawling 3km
Family Evenness	Pielou's J
Functional Evenness	functional evenness
Family Richness	family richness
Functional Dispersion	functional richness
Ecosystem Efficiency	seafloor total organic carbon: sea surface particulate organic carbon biomass: seafloor organic carbon
Ecosystem Functioning	biomass
Density	number of individuals per box core
Current Speed	velocity velocity mean 10 years zonal velocity meridional velocity
Temperature	temperature temperature mean 10 years temperature minimum 10 years
Food Availability	particulate organic carbon total organic carbon organic carbon chlorophyll at the sea surface
Sediment Characteristics	percent clay percent silt percent sand particle size diversity
Biogenic Habitats	sponge density

8.5 Appendix E. Unstandardized biodiversity – ecosystem functioning relationship based on deep-sea polychaete family data collected in the northwest Atlantic



Relationships between bristle worms (Polychaeta) family richness as a measure of taxonomic diversity and ecosystem functioning (secondary biomass production). The shaded area indicates the 95% confidence interval of the slope.

8.6 Appendix F. NEREIDA dataset

Box core	Abundance (0.25 m²)	Biomass (g / 0.25 m²)	Latitude	Longitude	Temperature (°Celsius)	Salinity (PSU)
BC 10	267	1.575	48.33285	-44.477783	3.67206	34.856
BC 100	79	0.0115	48.65536	-44.892432	3.503475	34.826
BC 101	31	0.0865	48.72117	-45.142583	3.46953	34.818
BC 102	191	0.3302	48.88592	-44.799423	3.35457	34.836
BC 103	9	0.1118	48.78314	-44.799897	3.414565	34.831
BC 104	201	0.3978	48.41467	-44.995615	3.60707	34.81
BC 105	151	0.2071	48.52899	-45.14873	3.57301	34.813
BC 106	310	0.4362	48.40559	-45.412003	3.624945	34.809
BC 107	103	0.399	48.16895	-45.80259	3.61119	34.789
BC 108	199	0.345	48.22478	-45.611148	3.56698	34.774
BC 109	146	0.433	48.40829	-45.616593	3.539545	34.79
BC 11	477	2.5949	48.10294	-44.311668	3.543925	34.815
BC 110	222	0.1676	48.24685	-46.085797	3.690605	34.831
BC 111	66	0.2786	48.11707	-46.209395	3.55205	34.766
BC 112	15	0.099	47.94299	-46.190862	3.55853	34.755
BC 113	122	0.2117	47.83205	-46.366503	3.59791	34.76
BC 114	68	0.9503	48.10065	-46.489187	3.814445	34.843
BC 115	356	0.7053	48.04051	-46.407497	3.74094	34.82
BC 116	93	0.3289	47.77852	-46.490737	3.577715	34.743
BC 117	136	0.5126	47.93021	-46.48257	3.96887	34.9
BC 118	24	0.0451	47.86495	-46.621273	3.557025	34.725
BC 119	82	0.7416	47.66513	-46.736855	3.55132	34.709
BC 12	51	0.3101	47.75245	-43.821217	3.55436	34.851
BC 120	35	0.4583	48.05001	-45.854585	3.57081	34.763
BC 121	19	0.1039	48.11424	-46.049118	3.612725	34.79
BC 122	131	0.2764	47.97346	-46.022177	3.563595	34.759
BC 123	228	0.2551	47.80713	-45.970363	3.633985	34.766
BC 124	158	0.1666	47.95525	-45.881133	3.859375	34.86
BC 125	100	0.165	47.81591	-46.191097	3.580515	34.756
BC 126	188	0.4674	47.67853	-46.317032	3.56889	34.744
BC 129	176	0.2026	47.79294	-46.07698	3.58721	34.754
BC 13	60	0.2827	48.00889	-44.082348	3.59272	34.844
BC 130	200	0.5565	47.66687	-46.126705	3.832895	34.853
BC 131	224	0.5513	47.[illegible]	-46.39168	3.578365	34.739
BC 132	270	0.2173	47.[illegible]	-46.22735	3.591945	34.747

BC 133	66	0.2145	47.64635	-46.545888	3.989785	34.913
BC 135	10	0.2154	47.49396	-46.550833	3.580825	34.738
BC 136	25	1.1659	47.32698	-46.686695	3.55858	34.722
BC 137	129	0.1074	47.33708	-46.92681	3.503605	34.68
BC 138	99	0.2581	47.4877	-46.812372	3.50701	34.688
BC 139	428	1.8119	47.80681	-46.759853	3.54151	34.7
BC 14	27	0.108	48.0564	-43.938418	3.510765	34.863
BC 140	110	0.2022	47.98679	-46.664525	3.941775	34.862
BC 141	201	1.302	48.02608	-46.553963	3.569045	34.744
BC 142	183	0.9553	48.02327	-46.790102	3.499085	34.699
BC 143	255	1.73	47.84224	-46.864792	3.5003	34.672
BC 144	332	0.7362	47.76218	-46.881718	3.63962	34.718
BC 145	450	1.4867	47.94591	-46.801396	3.55151	34.706
BC 146	203	0.8858	47.24142	-46.54713	3.551915	34.713
BC 147	359	0.76517	47.12435	-46.661447	3.65418	34.764
BC 148	137	0.284	47.26799	-46.827453	3.46537	34.674
BC 149	307	1.47539	47.11757	-46.896608	3.43274	34.659
BC 150	284	0.98696	47.2144	-46.779053	3.53898	34.711
BC 151	252	0.3828	47.24026	-46.675719	3.80186	34.833
BC 152	257	0.70057	47.12938	-46.782223	3.52445	34.705
BC 153	239	0.767	47.4038	-47.090147	3.387535	34.603
BC 154	32	0.0968	47.48018	-46.953715	3.591105	34.701
BC 156	199	0.2677	47.56618	-47.011242	3.435965	34.628
BC 157	414	2.45657	47.21546	-47.1216905	3.566805	34.682
BC 158	441	1.05898	47.22566	-46.9875525	3.409685	34.636
BC 159	103	0.6296	47.02885	-47.152397	3.29284	34.568
BC 16	36	0.2035	48.22586	-44.216458	3.56383	34.85
BC 160	261	0.5888	47.10706	-47.033336	3.542225	34.695
BC 161	77	0.5241	46.90268	-47.117354	3.292535	34.578
BC 162	103	0.1853	46.72792	-46.778908	3.4352	34.673
BC 163	279	0.3521	46.70696	-46.952975	3.384125	34.643
BC 164	48	0.1719	46.90296	-46.683998	3.559105	34.716
BC 165	78	0.3733	46.91942	-46.859465	3.4458	34.67

BC 166	66	0.1094	46.76548	-46.568432	3.706835	34.771
BC 167	81	0.1651	46.83661	-46.7058	3.4769	34.686
BC 168	218	1.96788	46.97322	-46.8220079	3.48897	34.69
BC 169	323	1.21622	46.84946	-46.849505	3.47051	34.684
BC 17	8	0.0059	48.20882	-44.008336	3.429715	34.85
BC 170	236	0.96268	46.9583	-47.0017818	3.5516	34.707
BC 171	228	1.03557	46.80979	-47.0761699	3.65482	34.74
BC 172	211	1.4162	46.52488	-46.7378067	3.528825	34.723
BC 174	82	0.5779	46.47437	-46.4781383	3.595095	34.748
BC 175	150	0.0972	46.57968	-46.5258783	3.5093	34.708
BC 176	135	0.34475	46.54966	-46.748065	3.470675	34.697
BC 177	172	0.38985	46.38696	-46.7427783	3.440105	34.693
BC 18	41	0.1971	47.83565	-43.816364	3.498705	34.851
BC 180	188	1.0962	46.50532	-47.0486274	3.40097	34.633
BC 181	38	0.0701	46.34755	-46.133794	3.59471	34.765
BC 182	96	0.1908	46.36563	-46.523245	3.58307	34.75
BC 183	30	0.0405	46.40546	-46.276562	3.60131	34.757
BC 185	46	0.0557	46.26219	-46.169858	3.55451	34.767
BC 186	24	0.0838	46.24935	-45.89913	3.481695	34.764
BC 187	25	0.1483	46.3081	-45.542292	3.49673	34.79
BC 188	30	0.21411	46.39593	-44.991085	3.426055	34.798
BC 189	67	0.1469	46.40072	-44.644855	3.329605	34.809
BC 19	369	0.2556	47.87237	-44.045492	3.512205	34.819
BC 190	14	0.0934	46.35464	-44.63193	3.258065	34.814
BC 191	52	0.3342	46.40221	-44.87772	3.4003	34.8
BC 192	68	0.173	46.36816	-45.218535	3.440065	34.791
BC 196	19	0.1375	46.31408	-45.25863	3.473375	34.819
BC 197	30	0.2172	46.20161	-45.509482	3.413855	34.813
BC 199	43	0.2145	46.26096	-45.702667	3.533685	34.795

BC 20	51	0.1222	47.67518	-43.586403	3.411935	34.867
BC 200	45	0.1169	46.19234	-45.973477	3.457835	34.767
BC 201	32	0.1141	46.13706	-46.051443	3.44309	34.772
BC 202	44	0.0787	46.17144	-45.737228	3.42292	34.79
BC 204	119	0.2228	46.32638	-46.282752	3.98551	34.892
BC 206	73	0.2288	46.23981	-46.099765	3.54126	34.773
BC 207	63	0.2804	46.27359	-46.287857	3.78612	34.832
BC 208	128	0.4909	46.28084	-46.59581	3.49521	34.721
BC 21	9	0.2714	47.82125	-43.586861	3.33668	34.869
BC 210	62	0.0783	45.97087	-46.705375	3.494165	34.747
BC 212	23	0.0238	46.04031	-46.726408	3.4166	34.714
BC 213	54	0.1985	45.90368	-46.73563	3.38604	34.729
BC 214	43	0.0877	45.84128	-46.5615	3.354535	34.745
BC 215	413	1.1399	46.32631	-46.792828	3.57451	34.743
BC 216	75	0.2658	46.40429	-46.611658	3.517445	34.723
BC 217	79	0.5952	46.48311	-46.381003	3.792215	34.817
BC 218	118	0.1701	45.85208	-46.343501	3.9143	34.928
BC 219	57	0.3759	45.99996	-46.316342	3.41979	34.751
BC 22	233	0.4832	47.60993	-43.842953	3.52767	34.833
BC 220	32	0.0861	46.06608	-45.877667	3.325425	34.785
BC 221	30	0.0917	45.8869	-46.221192	3.29603	34.765
BC 222	15	0.09133	46.07793	-46.235512	3.43452	34.758
BC 223	34	0.2849	45.86193	-46.213837	3.27492	34.769
BC 224	40	0.29312	45.81879	-46.472764	3.309775	34.749
BC 225	30	0.091	45.79689	-46.763145	3.422485	34.774
BC 226	70	0.1562	45.9005	-46.906008	3.336615	34.715
BC 227	141	0.2111	46.20572	-46.727023	3.482285	34.722
BC 228	576	1.20885	46.2357	-46.884952	3.56809	34.744

BC 229	158	0.24396	46.1169	-46.860092	3.66994	34.808
BC 23	42	0.1272	47.58599	-43.66193	3.44783	34.849
BC 230	143	0.61933	46.04508	-47.016612	3.40729	34.708
BC 231	284	0.68746	46.1691	-47.122856	3.65725	34.76
BC 232	61	0.2048	45.87262	-47.025565	3.43054	34.759
BC 234	41	0.0677	45.9241	-47.230868	3.24937	34.649
BC 235	94	0.1266	46.05024	-47.06403	3.33162	34.67
BC 236	559	5.7894	46.21465	-47.264795	3.23532	34.567
BC 237	395	1.0107	46.0028	-47.40861	3.20249	34.576
BC 238	693	5.67187	46.11715	-47.408847	3.12972	34.522
BC 239	1026	5.41123	46.04133	-47.556305	3.17619	34.526
BC 240	181	1.0188	45.98123	-47.4989	3.155015	34.542
BC 241	340	4.0231	45.9915	-47.63416	3.2844	34.559
BC 242	87	0.3659	45.89343	-47.504976	3.22473	34.586
BC 243	144	0.4578	45.89329	-47.39285	3.226045	34.616
BC 244	58	0.1986	45.8096	-47.26644	3.458335	34.774
BC 245	176	4.6928	45.77313	-47.679401	3.261365	34.59
BC 246	79	0.2173	45.77153	-47.368638	3.352045	34.72
BC 247	66	0.4634	45.6746	-47.551068	3.172865	34.612
BC 248	487	4.7907	45.81595	-47.844141	3.106095	34.481
BC 249	238	3.0229	45.74179	-47.863102	3.693405	34.718
BC 250	118	1.3985	45.69267	-47.698752	3.509325	34.712
BC 251	65	0.0955	45.53052	-47.664755	3.34234	34.717
BC 252	31	0.2066	45.44931	-47.687799	3.233085	34.699
BC 253	31	0.2949	45.53862	-47.800047	3.12739	34.576

BC 254	378	4.8485	45.40503	-48.473474	2.86444	34.33
BC 255	632	11.86975	45.54133	-48.300931	2.820095	34.327
BC 256	452	2.3316	45.68086	-47.995107	3.02778	34.448
BC 257	98	0.7555	45.58334	-48.007353	3.30981	34.587
BC 258	177	1.8136	45.51559	-48.2253	2.96838	34.407
BC 259	54	0.0423	45.4539	-47.902997	3.23141	34.623
BC 260	108	0.2303	45.31279	-48.287926	3.101715	34.509
BC 262	131	0.3828	45.4853	-48.027408	3.17742	34.553
BC 263	40	0.1842	45.44079	-48.105937	3.44678	34.661
BC 265	536	9.5756	45.34218	-48.578862	2.956175	34.356
BC 266	482	5.4116	45.39354	-48.573554	2.81591	34.291
BC 267	112	0.386	45.2606	-48.393954	3.13315	34.513
BC 268	241	1.933	45.19692	-48.57526	3.744885	34.759
BC 271	69	0.2668	45.29009	-48.545726	2.969225	34.382
BC 272	445	1.7424	45.17352	-48.432661	3.12591	34.526
BC 274	1074	9.5306	45.29341	-48.643125	2.853445	34.3
BC 275	578	5.6495	45.08107	-48.764118	3.218165	34.46
BC 276	624	3.5108	44.87559	-48.876227	3.03952	34.364
BC 277	398	1.7033	45.16177	-48.656226	3.09459	34.423
BC 278	264	0.2426	45.02532	-48.47121	3.22428	34.596
BC 279	577	0.4547	44.95577	-48.649178	3.857585	34.846
BC 280	459	3.7021	44.75542	-48.928715	3.060175	34.369
BC 281	459	2.176	44.65233	-48.92333	3.086775	34.397
BC 282	784	7.0979	44.56295	-48.986643	2.96247	34.314
BC 283	356	1.1147	44.71009	-48.852817	3.096365	34.425
BC 284	49	0.1303	44.75707	-48.64636	3.21071	34.593
BC 285	115	0.2317	44.59182	-48.807696	3.73262	34.844

BC 286	72	0.4388	44.44134	-48.874663	3.242865	34.512
BC 287	299	1.6348	44.33695	-48.913085	3.13796	34.431
BC 288	220	0.6557	44.52733	-48.812352	3.426565	34.672
BC 289	434	3.5498	44.40251	-48.925912	3.13374	34.417
BC 291	528	5.0017	44.16465	-48.904741	3.188065	34.464
BC 292	144	0.3441	44.3239	-48.789028	3.23419	34.572
BC 293	383	3.0487	44.22145	-48.799668	3.259625	34.581
BC 294	309	1.838	43.82097	-48.872853	3.30585	34.584
BC 296	276	1.6582	44.04334	-48.95546	3.44712	34.556
BC 297	129	1.5528	44.00944	-48.84397	3.409945	34.629
BC 298	225	2.1936	43.79576	-48.979608	3.28024	34.49
BC 299	122	0.4712	43.64411	-48.855105	3.39426	34.679
BC 300	872	1.7529	43.70218	-48.972787	3.29767	34.525
BC 301	282	0.8187	43.37386	-49.044497	3.334615	34.583
BC 302	211	0.5053	43.46674	-48.945854	3.28739	34.604
BC 303	135	0.4062	43.54652	-48.863422	3.232555	34.612
BC 304	335	0.75209	43.60274	-49.009933	3.3972	34.58
BC 305	1088	1.8138	43.56847	-49.134607	3.32245	34.474
BC 306	119	1.7824	43.50976	-49.048388	3.33233	34.55
BC 307	65	0.5177	43.31955	-49.039938	3.33663	34.597
BC 308	354	2.4745	43.40467	-49.179617	3.444245	34.553
BC 309	453	2.5277	43.32305	-49.211087	3.386135	34.522
BC 31	44	0.094	47.12188	-43.364808	3.374215	34.891
BC 310	300	0.8604	43.26444	-49.259145	3.63381	34.625
BC 311	57	0.2536	43.21002	-49.055385	3.502195	34.689
BC 314	100	0.382	43.14692	-48.988067	3.87807	34.929
BC 315	91	0.4589	43.23926	-48.88407	3.26905	34.664
BC 316	187	0.8769	43.35574	-48.767735	3.16994	34.672
BC 317	137	0.6062	43.03717	-49.317803	3.51394	34.644
BC 318	255	2.9961	43.19814	-49.284235	3.3984	34.531
BC 319	16	0.1974	43.10677	-49.178988	3.380705	34.605

BC 320	41	0.1115	42.99951	-49.130942	3.3784	34.665
BC 321	22	0.0125	43.17259	-49.426762	3.40148	34.471
BC 324	132	0.5308	42.88703	-49.34797	3.336725	34.621
BC 327	271	0.7054	42.95627	-49.698117	3.383255	34.459
BC 328	232	1.4897	43.08989	-49.49725	3.59731	34.576
BC 329	73	0.1535	42.77282	-49.728203	3.67815	34.774
BC 33	63	0.0786	47.06629	-43.41113	3.2485	34.851
BC 330	387	2.2829	43.01471	-49.633418	3.52925	34.521
BC 331	23	0.053	42.89898	-49.642023	3.761175	34.739
BC 332	133	0.1622	42.80966	-49.600912	3.331	34.588
BC 333	130	0.3753	42.85993	-49.711062	3.4215	34.551
BC 334	552	3.4881	42.8791	-49.807808	3.8919	34.68
BC 337	2	0.3209	42.74993	-49.963937	3.60643	34.633
BC 339	278	1.2493	42.80837	-49.887942	3.670325	34.614
BC 34	2	0.0031	47.12099	-43.454868	3.416015	34.871
BC 340	187	1.2995	42.73294	-50.391928	3.663825	34.609
BC 341	24	0.1341	42.69787	-50.314186	3.80461	34.759
BC 342	142	1.6266	42.73853	-50.275582	3.456285	34.498
BC 343	44	0.3096	42.67821	-50.207522	3.485265	34.597
BC 344	59	0.1053	42.63339	-50.525742	3.428925	34.583
BC 345	168	1.0041	42.74492	-50.443747	3.497585	34.505
BC 346	240	0.7792	42.80861	-50.68371	3.58329	34.492
BC 347	60	0.2194	42.69866	-50.647695	3.630385	34.653
BC 348	40	0.2169	42.68725	-50.953882	3.485935	34.6
BC 35	30	0.1256	46.99951	-43.61749	3.57447	34.866
BC 352	33	0.2014	42.82005	-50.991065	3.596275	34.585
BC 353	84	0.42992	42.89087	-51.028243	3.56508	34.497
BC 354	56	0.26691	42.82183	-51.12025	3.51061	34.539
BC 356	85	0.1088	42.90873	-50.836415	3.819495	34.538
BC 357	9	0.0297	42.97406	-51.000927	3.950215	34.686

BC 358	45	0.335	42.60369	-50.654552	3.49995	34.652
BC 36	4	0.0061	46.99904	-43.414448	3.30107	34.859
BC 361	73	0.0652	42.59757	-50.177525	3.30527	34.588
BC 362	132	1.2475	42.71002	-50.132512	3.55447	34.618
BC 363	122	0.2156	42.65872	-50.120983	3.405645	34.599
BC 364	71	0.2686	42.60478	-50.359372	3.36946	34.59
BC 365	147	0.2467	42.67158	-50.039907	3.396015	34.596
BC 366	46	0.1703	42.71711	-49.990873	3.43792	34.589
BC 367	99	0.18	42.73106	-49.866435	3.366155	34.57
BC 368	4	0.777	42.77263	-49.966402	3.612035	34.614
BC 369	98	0.5102	42.94036	-49.56829	3.69829	34.698
BC 37	11	0.1845	46.99633	-43.257257	3.20253	34.893
BC 370	36	0.5456	42.8253	-49.40316	3.479385	34.726
BC 371	114	0.4809	43.00527	-48.925453	3.2314	34.676
BC 38	42	0.0452	46.94592	-43.305547	3.079675	34.854
BC 4	60	0.7663	48.41311	-44.324025	3.501785	34.846
BC 40	37	0.0511	46.85148	-43.423193	3.27199	34.866
BC 41	30	0.025	46.91927	-43.514881	3.595275	34.888
BC 44	77	0.264	46.73167	-43.8603833	3.549725	34.872
BC 45	22	0.0177	46.75804	-43.907944	3.374955	34.825
BC 47	42	0.0342	46.65335	-43.992368	3.312485	34.83
BC 5	101	0.2825	48.76025	-44.729503	3.427075	34.836
BC 50	97	0.3316	48.20928	-47.400668	3.317385	34.661
BC 51	125	0.4949	48.20445	-47.162947	3.43565	34.718
BC 52	87	0.6489	48.21528	-47.470725	3.32039	34.663
BC 53	111	0.9192	48.2045	-47.729037	3.26348	34.622
BC 57	128	1.6047	48.1732	-47.570122	3.297965	34.63
BC 58	169	1.8422	48.09197	-47.428573	3.45559	34.668
BC 59	245	1.17832	48.35984	-46.343913	3.54508	34.802
BC 6	117	0.2867	48.44703	-44.182957	3.388015	34.843
BC 60	105	0.3334	48.27856	-46.480163	3.48144	34.761
BC 61	36	0.4423	48.21245	-46.61206	3.53278	34.759
BC 63	114	3.9337	48.2204	-47.033507	3.446055	34.731
BC 67	355	2.9386	48.15659	-46.861343	3.53744	34.739

BC 68	200	1.45158	48.31712	-46.522115	3.557125	34.809
BC 7	87	1.753	48.74029	-44.302632	3.33811	34.856
BC 70	198	1.1306	48.27279	-46.769075	3.763645	34.88
BC 71	107	0.14778	48.44175	-46.245362	3.4514	34.793
BC 72	242	0.3607	48.385	-46.46675	3.41137	34.768
BC 73	121	2.73795	48.35247	-46.641945	3.38278	34.752
BC 74	445	1.96	48.11572	-46.771702	3.545345	34.733
BC 76	340	1.9618	48.19968	-46.711683	3.471175	34.731
BC 77	10	0.0837	48.30121	-46.248355	3.621265	34.812
BC 78	79	0.874	48.49789	-45.615245	3.538325	34.801
BC 79	33	0.05216	48.46628	-46.031745	3.56478	34.821
BC 80	49	0.2017	48.55692	-45.516732	3.58922	34.822
BC 81	65	0.4711	48.35188	-45.819818	3.695475	34.841
BC 82	73	1.8566	48.38918	-45.94971	3.517895	34.787
BC 83	19	0.5195	48.51944	-45.782932	3.541505	34.813
BC 84	86	0.22717	48.57029	-46.001203	3.46232	34.819
BC 85	329	0.616	48.65602	-45.670817	3.55471	34.842
BC 86	130	0.15431	48.75519	-45.529195	3.59248	34.868
BC 87	10	0.1215	48.62485	-45.44584	3.516755	34.813
BC 88	6	0.148	48.70996	-45.354043	3.74131	34.889
BC 89	66	1.17143	48.97448	-45.27298	3.338655	34.842
BC 9	12	0.1227	48.32696	-44.473582	3.597125	34.838
BC 90	152	1.09725	48.86489	-45.383997	3.396305	34.831
BC 91	220	0.3962	48.91961	-45.189502	3.409445	34.844
BC 92	65	0.0651	48.94067	-45.053663	3.36176	34.838
BC 93	114	0.29056	48.84762	-45.271517	3.505075	34.853
BC 94	65	0.1607	48.64766	-45.17561	3.60143	34.84
BC 95	132	0.1593	48.54497	-45.327613	3.77091	34.867
BC 96	139	0.674	48.60848	-45.11685	3.52351	34.814

BC 97	114	0.313	48.54657	-44.946767	3.52486	34.812
BC 98	150	0.1598	48.41076	-44.77322	3.542545	34.808
BC 99	111	0.6281	48.57652	-44.763305	3.543945	34.834

BC	Particulate organic carbon (mg/m³)	Chlorophyll (mg/m³)	Zonal velocity (m/s)	Meridional velocity (m/s)	Velocity (m/s)	Biomass measured by
BC 10	134.709175	0.79825	0.02482	-0.0226	0.03357	IECS
BC 100	129.653565	0.83119	0.04836	-0.0118	0.04978	IECS
BC 101	141.580295	0.932565	0.05777	0.00394	0.0579	IECS
BC 102	131.66997	0.80422	0.08852	-0.02002	0.09075	IECS
BC 103	130.85481	0.811145	0.07533	-0.020465	0.07806	IECS
BC 104	136.90721	0.899335	0.00431	-0.001975	0.00474	IECS
BC 105	136.714195	1.002705	0.00996	-0.001275	0.01004	IECS
BC 106	151.2203	1.01893	0.00411	-0.003875	0.0057	IECS
BC 107	131.127975	0.850885	0.00052	-0.011045	0.01107	IECS
BC 108	132.49353	0.896095	0.0068	-0.0054	0.00869	IECS
BC 109	140.301065	1.06743	0.01182	-0.00507	0.01288	IECS
BC 11	132.67147	0.90744	0.01428	-0.01545	0.02104	IECS
BC 110	135.822555	0.95274	0.00869	-0.0053	0.01036	IECS
BC 111	134.96048	0.93194	0.00971	-0.01189	0.01537	IECS
BC 112	157.73766	1.14133	-0.0015	-0.02676	0.0268	IECS
BC 113	139.85804	1.025765	-0.0027	-0.03958	0.03967	IECS
BC 114	138.31794	0.97038	0.01856	-0.001875	0.01876	IECS
BC 115	134.579005	0.911995	0.00168	-0.025235	0.02533	IECS
BC 116	135.316455	0.937405	0.00013	-0.035695	0.0357	IECS
BC 117	139.988025	1.014605	-0.0091	-0.02782	0.02929	IECS
BC 118	131.485275	0.857115	0.01047	-0.02464	0.02678	IECS
BC 119	126.38912	0.76112	0.00278	-0.03009	0.03022	IECS
BC 12	128.45992	0.725525	0.03993	-0.049115	0.0633	IECS
BC 120	133.87311	0.90303	0.00527	-0.00838	0.0099	IECS
BC 121	133.280805	0.886285	-0.0041	-0.024655	0.02499	IECS
BC 122	139.29911	0.940385	0.00303	-0.01408	0.0144	IECS
BC 123	154.81397	1.01158	0.00337	-0.00735	0.00809	IECS
BC 124	140.84429	0.94288	0.00305	-0.00342	0.00459	IECS
BC 125	157.192535	1.24329	0.00151	-0.023105	0.02315	IECS
BC 126	143.123	1.00237	0.00265	-0.028805	0.02893	IECS
BC 129	148.60617	0.985535	0.00341	-0.011685	0.01217	IECS
BC 13	132.258445	0.73862	0.02947	-0.033815	0.04485	IECS

BC 130	145.873655	1.006985	0.00476	-0.00611	0.00799	IECS
BC 131	137.64907	0.90814	-0.0056	-0.02517	0.02579	IECS
BC 132	141.44578	0.96527	0.00012	-0.017295	0.0173	IECS
BC 133	135.087245	0.872115	-0.0171	-0.056595	0.05914	IECS
BC 135	129.706435	0.820645	-0.0132	-0.036815	0.0391	IECS
BC 136	126.791755	0.76163	-0.0198	-0.052125	0.05576	IECS
BC 137	125.97828	0.68901	-0.0026	-0.043335	0.04341	IECS
BC 138	120.809995	0.67313	-0.003	-0.035095	0.03522	IECS
BC 139	127.54589	0.779325	0.00947	-0.028395	0.02994	IECS
BC 14	141.61968	0.729425	0.06893	-0.082635	0.10761	IECS
BC 140	137.189885	0.86562	-0.0007	-0.01956	0.01959	IECS
BC 141	146.930235	0.992135	0.01946	-0.01854	0.02692	IECS
BC 142	127.644815	0.777585	0.03201	-0.012995	0.03455	IECS
BC 143	128.647865	0.772035	0.01477	-0.02174	0.0263	IECS
BC 144	127.53534	0.764535	0.00955	-0.02139	0.02344	IECS
BC 145	127.160885	0.76061	0.02046	-0.01771	0.02709	IECS
BC 146	131.438655	0.79733	-0.0027	-0.01931	0.0195	IECS
BC 147	128.823425	0.749525	-0.0054	-0.02402	0.02462	JG
BC 148	124.699915	0.714365	-0.0093	-0.04887	0.04975	IECS
BC 149	120.55991	0.670975	-0.0049	-0.056815	0.05703	JG
BC 150	125.95104	0.738185	-0.014	-0.05974	0.06136	JG
BC 151	127.94862	0.756905	-0.0186	-0.07067	0.07308	IECS
BC 152	126.02478	0.726135	-0.0084	-0.05595	0.05658	JG
BC 153	129.066735	0.70157	0.00563	-0.033905	0.03437	IECS
BC 154	125.76153	0.71233	-1E-05	-0.035055	0.03506	IECS
BC 156	124.52906	0.72139	0.00719	-0.02953	0.03039	IECS
BC 157	120.539425	0.65286	0.00645	-0.034105	0.03471	JG
BC 158	119.0818	0.647485	0.00125	-0.04437	0.04439	JG
BC 159	114.370665	0.590315	0.00655	-0.044635	0.04511	IECS
BC 16	200.463115	0.76702	0.04844	-0.04698	0.06748	IECS
BC 160	118.69801	0.642875	-0.0014	-0.06108	0.0611	JG
BC 161	120.067655	0.644935	0.00539	-0.054015	0.05428	IECS
BC 162	129.30673	0.696955	0.0022	-0.04533	0.04538	IECS
BC 163	123.44998	0.66752	0.00985	-0.06724	0.06796	IECS

BC 164	123.10189	0.653945	-0.0022	-0.00767	0.00797	IECS
BC 165	125.406415	0.68329	-0.0014	-0.060275	0.06029	IECS
BC 166	126.055415	0.676475	-0.0043	0.00086	0.00439	IECS
BC 167	125.63147	0.681965	-0.0011	-0.02468	0.02471	IECS
BC 168	126.48166	0.68736	-0.0037	-0.05963	0.05974	JG
BC 169	123.86305	0.667135	-0.0007	-0.06101	0.06101	JG
BC 17	156.062935	0.74709	0.06394	-0.047335	0.07956	IECS
BC 170	122.34351	0.66707	0.00025	-0.074815	0.07482	JG
BC 171	121.043135	0.64093	0.00541	-0.075875	0.07607	JG
BC 172	123.675535	0.669915	-0.0012	-0.036085	0.03611	JG
BC 174	129.31853	0.70668	-0.0047	-0.00145	0.00488	IECS
BC 175	128.68137	0.70091	-0.0051	-0.008575	0.00999	IECS
BC 176	124.9379	0.679205	0.00012	-0.040955	0.04096	JG
BC 177	127.54174	0.71143	-0.0032	-0.030445	0.03062	JG
BC 18	128.062105	0.720845	0.05316	-0.057505	0.07831	IECS
BC 180	122.338	0.664205	0.00727	-0.068545	0.06893	IECS
BC 181	149.94781	0.886655	-0.0698	0.00945	0.07382	IECS
BC 182	150.83308	0.942885	0.03733	-0.028405	0.04982	IECS
BC 183	146.32773	0.872995	-0.0633	-0.06266	0.08918	IECS
BC 185	147.92182	0.87364	-0.0834	-0.077755	0.11414	IECS
BC 186	145.1405	0.840935	-0.1358	-0.113325	0.17689	IECS
BC 187	147.91348	0.851325	-0.0982	-0.188875	0.21361	IECS
BC 188	145.28265	0.82643	-0.1548	-0.138895	0.20821	JG
BC 189	140.91416	0.815425	-0.0956	-0.18682	0.21282	IECS
BC 19	130.044485	0.74034	0.01988	-0.024725	0.03173	IECS
BC 190	141.39608	0.8098	-0.1058	-0.186245	0.21688	IECS
BC 191	145.18802	0.822635	-0.1539	-0.149875	0.21506	IECS
BC 192	143.605475	0.830245	-0.1202	-0.158555	0.19924	IECS
BC 196	146.697265	0.85927	-0.1126	-0.20157	0.23267	IECS
BC 197	152.761335	0.84515	-0.193	-0.265075	0.32793	IECS
BC 199	145.292675	0.8352	-0.1222	-0.194095	0.22938	IECS
BC 20	128.98948	0.727855	0.05777	-0.071165	0.09166	IECS

BC 200	159.488395	0.918415	-0.1529	-0.111615	0.18938	IECS
BC 201	146.17619	0.907425	-0.1553	-0.121745	0.19742	IECS
BC 202	150.238635	0.827555	-0.1275	-0.197605	0.23616	IECS
BC 204	146.299285	0.873955	0.21326	-0.30782	0.37453	IECS
BC 206	148.681515	0.896105	-0.1045	-0.072455	0.12733	IECS
BC 207	147.85855	0.87005	-0.3064	-0.09309	0.32224	IECS
BC 208	152.09027	0.95888	0.01741	-0.00419	0.02216	IECS
BC 21	129.92203	0.75498	0.0597	-0.064165	0.08764	IECS
BC 210	140.24684	0.802785	-0.1195	0.012785	0.1204	IECS
BC 212	144.651405	0.86162	-0.1295	-0.014985	0.13109	IECS
BC 213	138.124935	0.75902	-0.1373	-0.026	0.13982	IECS
BC 214	140.068525	0.78384	-0.1199	-0.12741	0.17666	IECS
BC 215	142.596125	0.89127	-0.078	-0.18948	0.20535	IECS
BC 216	146.93351	0.954785	0.00492	-0.09262	0.09283	IECS
BC 217	144.85043	0.8847	-0.0886	0.042945	0.09855	IECS
BC 218	156.37035	0.8361	-0.1182	-0.37617	0.41203	IECS
BC 219	154.40985	0.87084	-0.1331	-0.14442	0.19696	IECS
BC 22	126.670395	0.716315	0.01909	-0.034685	0.03959	IECS
BC 220	149.31075	0.84344	-0.1324	-0.195885	0.23813	IECS
BC 221	154.72176	0.857175	-0.1406	-0.17969	0.22825	IECS
BC 222	149.082285	0.91099	-0.1198	-0.164275	0.2036	JG
BC 223	160.47629	0.860995	-0.1355	-0.188305	0.232	IECS
BC 224	146.65613	0.809895	-0.1139	-0.16199	0.20072	JG
BC 225	134.90177	0.75962	-0.2043	-0.10545	0.22998	IECS
BC 226	136.45801	0.77094	-0.1448	-0.02204	0.14665	IECS
BC 227	149.11912	0.915725	-0.0368	-0.017315	0.04213	IECS
BC 228	144.59028	0.89866	-0.0923	-0.139875	0.1678	JG
BC 229	144.630185	0.88156	-0.1502	0.016345	0.1514	JG

BC 23	128.148575	0.71124	0.03997	-0.0899	0.09838	IECS
BC 230	139.247955	0.835185	-0.146	-0.130855	0.19616	JG
BC 231	136.826065	0.829465	-0.247	-0.36582	0.4415	JG
BC 232	135.816585	0.78891	-0.221	-0.03829	0.22425	IECS
BC 234	136.93822	0.82711	-0.1442	-0.183195	0.23329	IECS
BC 235	139.515605	0.84921	-0.1457	-0.14443	0.20541	IECS
BC 236	133.4208	0.78623	-0.1335	-0.248125	0.28211	JG
BC 237	133.373795	0.782505	-0.0966	-0.243035	0.26162	JG
BC 238	132.753025	0.771415	-0.1252	-0.25572	0.28501	JG
BC 239	133.385895	0.76695	-0.1598	-0.28348	0.32555	JG
BC 240	133.27448	0.779115	-0.1364	-0.26531	0.29853	IECS
BC 241	133.645385	0.770025	-0.1668	-0.298455	0.34199	IECS
BC 242	134.21186	0.79621	-0.1521	-0.272595	0.3125	IECS
BC 243	134.944655	0.82501	-0.1436	-0.204335	0.25076	IECS
BC 244	136.324185	0.84435	-0.2315	-0.154745	0.27957	IECS
BC 245	132.16566	0.78925	-0.143	-0.29654	0.32924	IECS
BC 246	135.4349	0.816925	-0.1444	-0.200925	0.24777	IECS
BC 247	134.163315	0.798555	-0.1452	-0.20801	0.25407	IECS
BC 248	129.47835	0.729425	-0.1868	-0.26567	0.32595	IECS
BC 249	131.906535	0.76071	-0.2329	-0.357815	0.42694	IECS
BC 250	133.08074	0.79839	-0.1262	-0.20211	0.23827	IECS
BC 251	132.08694	0.763015	-0.1202	-0.180515	0.21717	IECS
BC 252	131.0461	0.73938	-0.1928	-0.265995	0.32851	IECS
BC 253	133.05542	0.79699	-0.1384	-0.236	0.27358	IECS
BC 254	140.937625	0.77817	-0.1405	-0.222975	0.2639	IECS

BC 255	148.11949	0.78563	-0.1489	-0.225985	0.27084	IECS
BC 256	133.02989	0.811735	-0.1369	-0.251765	0.28672	IECS
BC 257	140.32889	0.837215	-0.2278	-0.3417	0.41066	IECS
BC 258	153.633625	0.80094	-0.1717	-0.251215	0.30441	IECS
BC 259	133.12201	0.767155	-0.1404	-0.220595	0.26152	IECS
BC 260	140.4142	0.779485	-0.1655	-0.25757	0.30615	IECS
BC 262	148.56784	0.80719	-0.1897	-0.302525	0.35711	IECS
BC 263	136.502445	0.765955	-0.2566	-0.372715	0.45251	IECS
BC 265	136.60029	0.742965	-0.1337	-0.210455	0.24985	IECS
BC 266	137.165555	0.74755	-0.1138	-0.195895	0.22684	IECS
BC 267	141.31085	0.77622	-0.1718	-0.283005	0.33118	IECS
BC 268	141.22242	0.733955	-0.1832	-0.37969	0.42159	IECS
BC 271	136.321335	0.74312	-0.1543	-0.238925	0.28474	IECS
BC 272	147.12147	0.83054	-0.1657	-0.237745	0.29072	IECS
BC 274	135.42823	0.73162	-0.126	-0.205505	0.24148	IECS
BC 275	145.98628	0.76156	-0.1041	-0.24529	0.26664	IECS
BC 276	138.101585	0.737625	-0.1158	-0.201345	0.23274	IECS
BC 277	140.03967	0.75194	-0.1271	-0.24059	0.2724	IECS
BC 278	135.23925	0.7654	-0.1788	-0.193775	0.26882	IECS
BC 279	135.523025	0.756835	-0.0771	-0.44293	0.44961	IECS
BC 280	135.17751	0.736445	-0.1304	-0.16444	0.2126	IECS
BC 281	134.802915	0.740425	-0.1099	-0.171105	0.20611	IECS
BC 282	134.600765	0.743265	-0.0092	-0.157365	0.15778	IECS
BC 283	135.118705	0.74263	-0.1331	-0.19917	0.24183	IECS
BC 284	136.61079	0.76659	-0.1382	-0.211245	0.25356	JG
BC 285	140.62776	0.76276	0.3955	-0.30508	0.50914	IECS
BC 286	137.908075	0.766445	0.05209	-0.185685	0.19353	JG
BC 287	141.243005	0.77424	0.04031	-0.147575	0.15369	IECS

BC 288	132.2199	0.723815	0.12383	-0.143885	0.20307	IECS
BC 289	136.387815	0.75125	0.03791	-0.14495	0.15036	IECS
BC 291	152.89256	0.80169	0.04241	-0.1567	0.16346	IECS
BC 292	141.81781	0.783045	0.05286	-0.1709	0.18015	IECS
BC 293	142.502905	0.78994	0.05143	-0.170165	0.17937	IECS
BC 294	141.102245	0.78204	-0.0516	-0.17233	0.18188	IECS
BC 296	142.592145	0.78124	0.01241	-0.22529	0.22565	IECS
BC 297	141.523055	0.77265	-0.0712	-0.17314	0.19136	IECS
BC 298	141.344195	0.75403	-0.0622	-0.16502	0.17812	IECS
BC 299	145.68961	0.81008	0.05539	-0.23026	0.23741	IECS
BC 300	159.081035	0.762975	-0.051	-0.18195	0.18957	IECS
BC 301	137.353225	0.786075	-0.0288	-0.170135	0.17272	IECS
BC 302	136.9985	0.80461	-0.0184	-0.15859	0.15977	IECS
BC 303	140.61903	0.8275	-0.0137	-0.179655	0.18027	IECS
BC 304	148.088295	0.78655	-0.0394	-0.2102	0.21388	IECS
BC 305	145.321065	0.78018	-0.0907	-0.159015	0.18408	IECS
BC 306	143.828145	0.77482	-0.0608	-0.166095	0.17757	IECS
BC 307	140.41821	0.810425	-0.0075	-0.13621	0.13642	IECS
BC 308	132.772785	0.74502	-0.0351	-0.18895	0.19229	IECS
BC 309	136.494805	0.756345	-0.0312	-0.14445	0.14783	IECS
BC 31	130.03799	0.68861	0.06759	-0.10229	0.1226	IECS
BC 310	135.88095	0.74664	-0.0939	-0.247825	0.26505	IECS
BC 311	141.56112	0.81686	0.1189	-0.132855	0.18856	IECS
BC 314	141.47447	0.8184	-0.1171	-0.16766	0.22037	IECS
BC 315	137.636105	0.895705	0.0331	-0.166945	0.17089	IECS
BC 316	135.080245	0.958695	0.01641	-0.14322	0.1443	IECS
BC 317	138.1417	0.790205	-0.1554	-0.21983	0.26929	IECS
BC 318	135.596115	0.743895	-0.1018	-0.171235	0.19955	IECS
BC 319	136.130885	0.79085	-0.1076	-0.190185	0.21895	IECS
BC 320	142.63034	0.81024	-0.1389	-0.20891	0.25157	IECS

BC 321	141.081875	0.777975	-0.1183	-0.135195	0.18025	IECS
BC 324	143.726745	0.829465	-0.1389	-0.200975	0.24434	IECS
BC 327	152.96781	0.81855	-0.1385	-0.1616	0.21295	IECS
BC 328	143.34452	0.793885	-0.1266	-0.156065	0.20112	IECS
BC 329	130.11327	0.743	-0.2245	-0.329535	0.39875	IECS
BC 33	125.71821	0.66411	0.02934	-0.114795	0.11849	IECS
BC 330	151.620465	0.83563	-0.0086	-0.144865	0.14563	IECS
BC 331	135.083045	0.770015	-0.1317	-0.23882	0.27272	IECS
BC 332	137.60601	0.79449	-0.1722	-0.21072	0.27213	IECS
BC 333	142.050805	0.808855	-0.1813	-0.20528	0.27391	IECS
BC 334	144.891935	0.82422	-0.1524	-0.23661	0.28151	IECS
BC 337	146.137475	0.82619	-0.2466	-0.261965	0.35974	IECS
BC 339	144.51986	0.82671	-0.2471	-0.26807	0.36456	IECS
BC 34	128.475805	0.692405	0.04247	-0.11238	0.12014	IECS
BC 340	170.76278	1.115	-0.2212	-0.115595	0.24981	IECS
BC 341	171.787355	1.068385	-0.1055	-0.23925	0.26939	IECS
BC 342	159.264795	1.059515	-0.1405	-0.10445	0.17534	IECS
BC 343	149.61283	0.94815	-0.1241	-0.1319	0.18311	IECS
BC 344	156.60355	0.866925	-0.1487	-0.06274	0.16161	IECS
BC 345	170.116895	0.97737	-0.158	-0.08719	0.1805	IECS
BC 346	170.89041	0.964985	-0.1341	-0.022395	0.13615	IECS
BC 347	152.754725	0.87983	-0.2743	0.110335	0.29739	IECS
BC 348	161.68412	1.04337	-0.1536	0.08236	0.17562	IECS
BC 35	124.604825	0.66747	-0.009	-0.117955	0.1183	IECS
BC 352	166.089205	0.96928	-0.18	0.09544	0.20419	IECS
BC 353	164.64586	0.969205	-0.1613	0.08824	0.18489	JG
BC 354	161.69092	0.88208	-0.1858	0.07566	0.20102	JG
BC 356	182.43787	0.993865	-0.2409	0.09485	0.26149	IECS
BC 357	186.32095	1.368455	-0.1381	0.067145	0.15374	IECS
BC 358	150.403035	0.83955	-0.1398	-0.03163	0.1434	IECS
BC 36	123.97685	0.65723	0.02061	-0.13836	0.13989	IECS

BC 361	142.7788	0.90422	-0.1393	-0.14995	0.20629	IECS
BC 362	150.14819	0.92936	-0.1253	-0.180935	0.22297	IECS
BC 363	142.919135	0.91249	-0.1338	-0.17045	0.21963	IECS
BC 364	139.290615	1.152465	-0.134	-0.099365	0.16809	IECS
BC 365	142.01232	0.85269	-0.1435	-0.187375	0.23833	IECS
BC 366	146.22931	0.83016	-0.2087	-0.231055	0.31149	IECS
BC 367	137.583785	0.784235	-0.1781	-0.225275	0.28718	IECS
BC 368	146.116135	0.827125	-0.244	-0.255635	0.35337	IECS
BC 369	142.62156	0.81238	-0.2142	-0.24281	0.3238	IECS
BC 37	125.27963	0.6693	0.03474	-0.18332	0.18658	IECS
BC 370	137.284625	0.80032	-0.1348	-0.149385	0.20255	IECS
BC 371	136.16957	0.805135	-0.1215	-0.176405	0.21585	IECS
BC 38	124.480295	0.661	0.01879	-0.1222	0.12364	IECS
BC 4	139.167435	0.789465	0.05499	-0.04938	0.07391	IECS
BC 40	123.44796	0.65361	-0.0237	-0.08437	0.08764	IECS
BC 41	123.42061	0.65304	-0.0258	-0.1726	0.17452	IECS
BC 44	124.825355	0.67183	-0.0544	-0.07917	0.09606	IECS
BC 45	123.12566	0.64486	-0.0227	-0.052785	0.05745	IECS
BC 47	125.555315	0.64575	-0.0271	-0.05459	0.06095	IECS
BC 5	133.862015	0.835425	0.07817	-0.030315	0.08384	IECS
BC 50	148.83741	0.978395	0.11199	-0.00146	0.112	IECS
BC 51	134.67752	0.897615	0.11285	0.01035	0.11332	IECS
BC 52	144.736055	0.97354	0.11959	-0.00219	0.11961	IECS
BC 53	134.58318	0.90232	0.1233	-0.006085	0.12345	IECS
BC 57	140.30939	0.95876	0.11347	-0.003485	0.11352	IECS
BC 58	144.42803	0.94024	0.07302	0.00229	0.07305	IECS
BC 59	136.50972	1.027205	0.04878	0.04226	0.06454	JG
BC 6	136.4716	0.702085	0.05806	-0.056	0.08066	IECS
BC 60	145.913035	1.112985	0.06673	0.022935	0.07056	IECS
BC 61	135.7208	0.84986	0.07777	0.009535	0.07835	IECS
BC 63	134.54976	0.888465	0.09555	0.01825	0.09728	IECS
BC 67	131.921145	0.79995	0.07431	0.013745	0.07557	IECS
BC 68	146.241805	0.691605	0.10075	0.0461	0.11079	JG
BC 7	125.18889	0.690075	0.06308	-0.05791	0.08564	IECS

BC 70	129.228335	0.808725	0.17433	0.061575	0.18488	JG
BC 71	141.77695	1.101475	0.07509	0.04613	0.08813	JG
BC 72	135.025375	0.881045	0.06849	0.03664	0.07767	JG
BC 73	133.887935	0.89584	0.07489	0.031055	0.08107	JG
BC 74	127.03706	0.77086	0.05426	-0.004095	0.05441	IECS
BC 76	133.09185	0.815005	0.07038	0.01363	0.07169	IECS
BC 77	140.642565	1.06311	0.05214	0.01562	0.05443	IECS
BC 78	136.28512	0.955275	0.02053	0.00619	0.02146	IECS
BC 79	162.94551	1.20557	0.0333	0.05015	0.06021	JG
BC 80	132.382585	0.91143	0.02151	0.010655	0.024	IECS
BC 81	130.947565	0.885055	0.0092	-0.00994	0.01388	IECS
BC 82	143.382135	1.12928	0.03471	0.01668	0.03851	IECS
BC 83	137.511945	1.01738	0.04946	0.037565	0.06211	IECS
BC 84	137.14124	0.90122	0.04218	0.067315	0.07944	JG
BC 85	131.964045	0.831245	0.07338	0.0608	0.09529	JG
BC 86	134.582435	0.824735	0.0362	0.078385	0.08634	JG
BC 87	132.81383	0.86449	0.04205	0.019045	0.04616	IECS
BC 88	132.473575	0.863755	0.06386	0.02919	0.07022	IECS
BC 89	132.911945	0.8475	0.12269	0.039655	0.12894	JG
BC 9	134.55641	0.80382	0.02366	-0.020925	0.03159	IECS
BC 90	137.52168	0.853795	0.09509	0.04351	0.10457	JG
BC 91	136.63064	0.86509	0.12618	0.02158	0.12801	JG
BC 92	140.660505	0.97883	0.11669	0.002515	0.11672	JG
BC 93	134.834495	0.85168	0.11053	0.04037	0.11767	JG
BC 94	135.78692	0.962765	0.04083	0.002605	0.04091	JG
BC 95	138.5052	0.925315	-0.0058	-0.001765	0.00604	IECS
BC 96	132.593935	0.89148	0.02699	-0.00148	0.02703	IECS
BC 97	133.683965	0.892305	0.02043	-0.00634	0.02139	IECS
BC 98	141.183	0.797335	0.01075	-0.006175	0.0124	IECS
BC 99	141.469335	0.963675	0.04173	-0.02045	0.04647	IECS

BC	Multibeam bathymetry (m)	Cruise	Collection year	Collection month	Sediment total carbon % in top 0-2 cm
BC 10	907.9379883	1	2009	June	3.520
BC 100	1127.25	2	2009	July	3.550
BC 101	1195.569946	2	2009	July	3.360
BC 102	1494.290039	2	2009	July	3.660
BC 103	1354.430054	2	2009	July	2.830
BC 104	690.3150024	2	2009	July	3.390
BC 105	801.1489868	2	2009	July	3.590
BC 106	738.6569824	2	2009	July	3.720
BC 107	855.4509888	2	2009	July	3.660
BC 108	707.2700195	2	2009	July	3.370
BC 109	931.2739868	2	2009	July	3.140
BC 11	691.8070068	1	2009	June	3.810
BC 110	1166.630005	2	2009	July	3.840
BC 111	1165.339966	2	2009	July	3.070
BC 112	1098.48999	2	2009	July	3.390
BC 113	1173.390015	2	2009	July	3.550
BC 114	1112.890015	2	2009	July	3.220
BC 115	1164.729981	2	2009	July	3.000
BC 116	1169.290039	2	2009	July	2.640
BC 117	1164.040039	2	2009	July	2.990
BC 118	1132.229981	2	2009	July	2.670
BC 119	1077.859985	2	2009	July	2.620
BC 12	884.309021	1	2009	June	4.100
BC 120	814.901001	2	2009	July	3.100
BC 121	1090.900024	2	2009	July	3.310
BC 122	899.5189819	2	2009	July	3.140
BC 123	735.2020264	3	2009	August	3.090
BC 124	748.7199707	3	2009	August	3.090
BC 125	1063.189941	3	2009	August	3.630
BC 126	1129.819946	3	2009	August	3.030
BC 129	898.2620239	3	2009	August	3.110
BC 13	824.7030029	1	2009	June	3.840
BC 130	953.9099731	3	2009	August	3.280
BC 131	1059.319946	3	2009	August	3.290
BC 132	1006.659973	3	2009	August	3.390
BC 133	1167.430054	3	2009	August	2.580

BC 135	1160.48999	3	2009	August	2.960
BC 136	1154.939941	3	2009	August	3.020
BC 137	1077.949951	3	2009	August	2.470
BC 138	1124.949951	3	2009	August	2.770
BC 139	896.1799927	3	2009	August	2.250
BC 14	1116.099976	1	2009	June	4.390
BC 140	954.7290039	3	2009	August	2.490
BC 141	1118.069946	3	2009	August	2.770
BC 142	720.2130127	3	2009	August	1.130
BC 143	745.1630249	3	2009	August	1.230
BC 144	794.8200073	3	2009	August	1.570
BC 145	773.6719971	3	2009	August	1.700
BC 146	875.71698	3	2009	August	2.900
BC 147	1116.900024	3	2009	August	3.260
BC 148	1150.800049	3	2009	August	2.720
BC 149	1160.180054	3	2009	August	3.120
BC 150	1153.949951	3	2009	August	3.070
BC 151	1148.089966	3	2009	August	3.120
BC 152	1160.969971	3	2009	August	3.120
BC 153	839.0869751	3	2009	August	1.380
BC 154	987.2269897	3	2009	August	2.320
BC 156	826.5859985	3	2009	August	2.060
BC 157	909.1920166	3	2009	August	1.680
BC 158	1105.709961	3	2009	August	2.860
BC 159	960.4849854	3	2009	August	1.610
BC 16	1024.199951	1	2009	June	3.890
BC 160	1104.209961	3	2009	August	2.460
BC 161	1031.430054	3	2009	August	2.180
BC 162	1145.48999	3	2009	August	3.350
BC 163	1210.219971	3	2009	August	3.380
BC 164	741.3699951	3	2009	August	4.050
BC 165	1192.449951	3	2009	August	2.580
BC 166	910.5230103	3	2009	August	3.170

BC 167	1041.670044	3	2009	August		2.630
BC 168	1182.579956	3	2009	August		2.760
BC 169	1199.430054	3	2009	August		2.800
BC 17	1262.459961	1	2009	June		3.200
BC 170	1165.569946	3	2009	August		2.400
BC 171	1089.25	3	2009	August		2.020
BC 172	1124.02002	3	2009	August		3.050
BC 174	781.3560181	3	2009	August		2.940
BC 175	1010.570007	3	2009	August		3.540
BC 176	1132.199951	3	2009	August		3.560
BC 177	1185.199951	3	2009	August		3.770
BC 18	994.947998	1	2009	June		4.280
BC 180	723.1459961	3	2009	August		1.230
BC 181	873.0889893	4	2010	June	na	
BC 182	891.3410034	4	2010	June		3.422
BC 183	918.0269775	4	2010	June		3.571
BC 185	1326.790039	4	2010	June		5.521
BC 186	792.5499878	4	2010	June		6.014
BC 187	990.4030151	4	2010	June		5.469
BC 188	1206.290039	4	2010	June		5.690
BC 189	1926.089966	4	2010	June		5.468
BC 19	721.9169922	1	2009	June		3.780
BC 190	1467.150024	4	2010	June		5.627
BC 191	1458.52002	4	2010	June		5.728
BC 192	1238.26001	4	2010	June	na	
BC 196	1601.98999	4	2010	June		5.542
BC 197	1442.189941	4	2010	June		5.401
BC 199	786.4639893	4	2010	June		5.490
BC 20	1315.390015	1	2009	June		5.560
BC 200	938.3850098	4	2010	June		5.345
BC 201	1369.130005	4	2010	June		5.105

BC 202	1196.479981	4	2010	June	5.437
BC 204	1000.049988	4	2010	June	3.212
BC 206	1094.469971	4	2010	June	4.511
BC 207	851.1010132	4	2010	June	3.509
BC 208	968.7520142	4	2010	June	3.247
BC 21	1484.229981	1	2009	June	3.950
BC 210	811.7180176	4	2010	June	4.706
BC 212	1340.199951	4	2010	June	4.739
BC 213	728.026001	4	2010	June	5.590
BC 214	1516.359985	4	2010	June	5.046
BC 215	1262.23999	4	2010	June	2.976
BC 216	1061.630005	4	2010	June	3.291
BC 217	957.1069946	4	2010	June	3.280
BC 218	1307.319946	4	2010	June	4.262
BC 219	929.9439697	4	2010	June	3.560
BC 22	702.3400269	1	2009	June	4.000
BC 220	1546.810059	4	2010	June	6.166
BC 221	1258.540039	4	2010	June	4.994
BC 222	1580.050049	4	2010	June	4.321
BC 223	1499.130005	4	2010	June	4.990
BC 224	1349.869995	4	2010	June	5.087
BC 225	1706.150024	4	2010	June	5.860
BC 226	1670.719971	4	2010	June	5.520
BC 227	1150.300049	4	2010	June	3.213
BC 228	1307.849976	4	2010	June	3.077
BC 229	1424.969971	4	2010	June	4.240
BC 23	1016.320007	1	2009	June	5.260
BC 230	1306.469971	4	2010	June	3.839

BC 231	1444.109985	5	2010	July	2.969
BC 232	1783.699951	5	2010	July	5.675
BC 234	1929.48999	5	2010	July	4.527
BC 235	1431.579956	5	2010	July	4.079
BC 236	668.3699951	5	2010	July	1.147
BC 237	1520.050049	5	2010	July	3.280
BC 238	805.7269897	5	2010	July	1.108
BC 239	801.1939697	5	2010	July	0.923
BC 240	1246.479981	5	2010	July	2.405
BC 241	710.9249878	5	2010	July	1.148
BC 242	1491.359985	5	2010	July	3.488
BC 243	1639.719971	5	2010	July	3.406
BC 244	1989.73999	5	2010	July	5.835
BC 245	1333.589966	5	2010	July	2.187
BC 246	1932.329956	5	2010	July	4.870
BC 247	1371.439941	5	2010	July	3.367
BC 248	701.1170044	5	2010	July	0.780
BC 249	933.382019	5	2010	July	1.614
BC 250	1315.459961	5	2010	July	2.607
BC 251	1730.099976	5	2010	July	3.545
BC 252	2121.949951	5	2010	July	4.833
BC 253	1501.27002	5	2010	July	3.492
BC 254	931.309021	5	2010	July	0.957
BC 255	841.9089966	5	2010	July	0.993
BC 256	797.9219971	5	2010	July	0.860

BC 257	1232.689941	5	2010	July		1.833
BC 258	1129.810059	5	2010	July		1.135
BC 259	1526.459961	5	2010	July		3.237
BC 260	1465.780029	5	2010	July		2.669
BC 262	1400.680054	5	2010	July		2.977
BC 263	1447.560059	5	2010	July	na	
BC 265	994.3599854	5	2010	July		1.468
BC 266	720.9190063	5	2010	July		0.603
BC 267	1784.560059	5	2010	July		2.088
BC 268	1481.969971	5	2010	July		1.233
BC 271	1625.219971	5	2010	July		0.987
BC 272	1549.77002	5	2010	July		2.182
BC 274	700.6970215	5	2010	July		0.835
BC 275	1007.570007	5	2010	July		1.321
BC 276	1213.410034	5	2010	July		0.907
BC 277	1052.560059	5	2010	July		0.935
BC 278	1684.579956	5	2010	July		2.869
BC 279	1466.930054	5	2010	July		2.055
BC 280	1483.579956	5	2010	July		2.370
BC 281	1628.23999	5	2010	July		2.658
BC 282	1028.880005	5	2010	July		1.705
BC 283	1650.25	5	2010	July		1.823
BC 284	1647.060059	5	2010	July		3.157
BC 285	1827.569946	5	2010	July		2.544
BC 286	1444.609985	5	2010	July		2.252
BC 287	753.7940063	5	2010	July		0.515
BC 288	1970.079956	5	2010	July		1.395
BC 289	835.6450195	5	2010	July		0.452

BC 291	896.1829834	5	2010	July		0.572
BC 292	1726.76001	5	2010	July		1.379
BC 293	1654.119995	5	2010	July		2.732
BC 294	1752.219971	5	2010	July		2.332
BC 296	730.8220215	5	2010	July		0.418
BC 297	1434.569946	5	2010	July		1.812
BC 298	622.5040283	6	2010	August		0.331
BC 299	2294.310059	6	2010	August		2.057
BC 300	1764.790039	6	2010	August		2.659
BC 301	1864.319946	6	2010	August		2.307
BC 302	2087.949951	6	2010	August		2.758
BC 303	2226.729981	6	2010	August		2.941
BC 304	1374.910034	6	2010	August		1.413
BC 305	1757.579956	6	2010	August		2.570
BC 306	1390.530029	6	2010	August		1.539
BC 307	1382.650024	6	2010	August		2.594
BC 308	969.7550049	6	2010	August		0.831
BC 309	841.5469971	6	2010	August		0.809
BC 31	1648.52002	1	2009	June		5.270
BC 310	1369.369995	6	2010	August		1.088
BC 311	1261.48999	6	2010	August		1.226
BC 314	1564.630005	6	2010	August		2.730
BC 315	2254.290039	6	2010	August		1.896
BC 316	1889.229981	6	2010	August		2.787
BC 317	1186.640015	6	2010	August		1.368
BC 318	862.1660156	6	2010	August		0.734
BC 319	1315.099976	6	2010	August		1.900
BC 320	2070.75	6	2010	August		2.650
BC 321	588.9829712	6	2010	August	na	
BC 324	1871.439941	6	2010	August		2.387

BC 327	581.78302	6	2010	August	0.520
BC 328	631.4710083	6	2010	August	0.762
BC 329	1903.439941	6	2010	August	2.150
BC 33	1285.880005	1	2009	June	6.170
BC 330	785.723999	6	2010	August	1.116
BC 331	1276.339966	6	2010	August	1.769
BC 332	1877.48999	6	2010	August	2.005
BC 333	1456.920044	6	2010	August	2.230
BC 334	705.9310303	6	2010	August	0.926
BC 337	1216.560059	6	2010	August	2.490
BC 339	723.9500122	6	2010	August	0.812
BC 34	1169.699951	1	2009	June	6.610
BC 340	1075	6	2010	August	1.459
BC 341	1848.780029	6	2010	August	1.580
BC 342	1456.599976	6	2010	August	0.832
BC 343	1371.819946	6	2010	August	2.688
BC 344	1882.280029	6	2010	August	3.044
BC 345	920.1400146	6	2010	August	1.054
BC 346	1223.23999	6	2010	August	1.407
BC 347	1339.180054	6	2010	August	2.336
BC 348	1474.670044	6	2010	August	2.142
BC 35	811.723999	1	2009	June	5.020
BC 352	1407.199951	6	2010	August	2.036
BC 353	1483.810059	6	2010	August	1.620
BC 354	1983.51001	6	2010	August	2.902
BC 356	778.492981	6	2010	August	1.774
BC 357	1004.780029	6	2010	August	2.251
BC 358	1616.469971	6	2010	August	2.021
BC 36	1186.369995	1	2009	June	5.590
BC 361	1988.609985	6	2010	August	2.099
BC 362	1130.920044	6	2010	August	1.010

BC 363	1654.099976	6	2010	August	2.505
BC 364	1774.48999	6	2010	August	2.425
BC 365	1538.479981	6	2010	August	1.888
BC 366	1613.969971	6	2010	August	2.780
BC 367	1638.349976	6	2010	August	2.674
BC 368	1001.059998	6	2010	August	1.056
BC 369	1183.369995	6	2010	August	1.650
BC 37	1849.560059	1	2009	June	1.460
BC 370	1633.369995	6	2010	August	2.482
BC 371	1966.930054	6	2010	August	2.508
BC 38	1536.140015	1	2009	June	5.090
BC 4	1181.189941	1	2009	May	3.290
BC 40	1322.73999	1	2009	June	3.870
BC 41	997.572998	1	2009	June	5.760
BC 44	1780.640015	1	2009	June	5.950
BC 45	881.1920166	1	2009	June	6.990
BC 47	1496.560059	1	2009	June	4.470
BC 5	1392.839966	1	2009	May	3.120
BC 50	1427.160034	1	2009	June	2.810
BC 51	1372.859985	1	2009	June	2.300
BC 52	1464.02002	1	2009	June	2.860
BC 53	1521.780029	1	2009	June	2.910
BC 57	1273.52002	1	2009	June	2.510
BC 58	664.7659912	1	2009	June	0.680
BC 59	985.0059814	1	2009	June	2.460
BC 6	1679.630005	1	2009	May	3.090
BC 60	871.7719727	1	2009	June	2.080
BC 61	829.0570068	1	2009	June	2.000
BC 63	1445.560059	1	2009	June	2.460
BC 67	760.0529785	2	2009	July	1.280
BC 68	1050.329956	2	2009	July	1.650
BC 7	1787.400024	1	2009	May	2.720
BC 70	1233.680054	2	2009	July	1.830

BC 71	1264.060059	2	2009	July		2.910
BC 72	1439.420044	2	2009	July		2.620
BC 73	1613.339966	2	2009	July		2.850
BC 74	687.2399902	2	2009	July		1.490
BC 76	819.822998	2	2009	July		1.720
BC 77	1080.5	2	2009	July		2.770
BC 78	1029.089966	2	2009	July		3.520
BC 79	1028.459961	2	2009	July		2.620
BC 80	983.9420166	2	2009	July		3.860
BC 81	1158.369995	2	2009	July		3.360
BC 82	1139.01001	2	2009	July		3.040
BC 83	1155.910034	2	2009	July		2.870
BC 84	1507.619995	2	2009	July		3.100
BC 85	1105.630005	2	2009	July		2.790
BC 86	1151.530029	2	2009	July		2.940
BC 87	1082.140015	2	2009	July	na	
BC 88	1161.890015	2	2009	July		3.810
BC 89	1575.890015	2	2009	July		3.520
BC 9	900.8179932	1	2009	June		3.920
BC 90	1325.229981	2	2009	July		3.260
BC 91	1281.569946	2	2009	July		2.850
BC 92	1402.229981	2	2009	July		2.890
BC 93	1187.829956	2	2009	July		2.890
BC 94	1019.559998	2	2009	July		3.290
BC 95	836.84198	2	2009	July		3.410
BC 96	931.2849731	2	2009	July		3.820
BC 97	878.9940186	2	2009	July		3.580
BC 98	760.7009888	2	2009	July		3.570
BC 99	1057.780029	2	2009	July		3.830

BC	Sediment organic carbon % in top 0-2cm	Sediment inorganic carbon % in top 0-2cm	Sediment clay % in top 0-2cm	Sediment silt % in top 0-2cm	Sediment sand % in top 0-2cm
BC 10	0.240	3.280	17.135	52.39	30.465
BC 100	0.340	3.210	13.3165959	35.711924	50.971481
BC 101	0.320	3.040	17.7552143	46.82886	35.415893
BC 102	0.530	3.130	na	na	na
BC 103	0.420	2.410	25.045535	64.81931	10.13514
BC 104	0.460	2.930	21.390397	70.40742	8.2021655
BC 105	0.340	3.250	13.4534554	54.97144	31.575082
BC 106	0.270	3.450	23.745504	61.35274	14.901733
BC 107	0.380	3.280	11.6043448	63.48069	24.914995
BC 108	0.310	3.060	13.7197965	68.16682	18.113392
BC 109	0.340	2.800	12.8672415	61.97201	25.16072
BC 11	0.410	3.400	19.97	61.01	19.0604
BC 110	0.390	3.450	12.6238423	65.877167	21.498983
BC 111	0.520	2.550	23.603462	68.0613	8.3352603
BC 112	0.670	2.720	25.035023	69.249063	5.7159193
BC 113	0.310	3.240	14.2518914	67.147448	18.600659
BC 114	0.430	2.790	17.6393635	58.48244	23.878181
BC 115	0.480	2.520	13.9781888	69.652444	16.36937
BC 116	0.410	2.230	18.8532031	60.0879	21.058909
BC 117	0.630	2.360	21.491831	67.24692	11.261274
BC 118	0.600	2.070	16.6132333	60.04446	23.342309
BC 119	0.720	1.900	18.2849701	61.38223	20.332807
BC 12	0.250	3.850	18.416	53.07	28.485
BC 120	0.430	2.670	12.0986451	60.612281	27.289062
BC 121	0.380	2.930	14.2339736	70.57213	15.193896
BC 122	0.350	2.790	13.1952769	63.776729	23.028006
BC 123	0.390	2.700	12.8779718	51.69363	35.428443
BC 124	0.370	2.720	12.2804802	59.91626	27.803249
BC 125	0.290	3.340	12.1223621	69.528352	18.349255
BC 126	0.340	2.690	13.6415564	63.800292	22.558154
BC 129	0.350	2.760	12.7060084	62.273346	25.020625
BC 13	0.300	3.540	18.676	55.78	25.545
BC 130	0.440	2.840	14.4084679	67.061489	18.530025
BC 131	0.400	2.890	14.0205335	64.756051	21.223393
BC 132	0.410	2.980	12.3082679	69.164027	18.527697
BC 133	0.410	2.170	13.3057926	48.770497	37.923723

BC 135	0.460	2.500	15.8263236	57.057103	27.116597
BC 136	0.520	2.500	21.807836	67.22111	10.971024
BC 137	0.560	1.910	17.9740065	61.13568	20.8903
BC 138	0.640	2.130	18.8784745	59.749	21.37251
BC 139	0.640	1.610	14.9171442	63.45782	21.625042
BC 14	0.330	4.060	22.761	52.16	25.132
BC 140	0.780	1.710	21.880324	62.56774	15.551936
BC 141	0.600	2.170	21.161246	68.8961	9.9426399
BC 142	0.360	0.770	8.4387194	31.175917	60.38537
BC 143	0.410	0.820	9.191574	33.707725	57.100691
BC 144	0.520	1.050	14.7486725	50.48679	34.764536
BC 145	0.520	1.180	14.0068641	55.36564	30.627483
BC 146	0.310	2.590	11.1131552	40.318266	48.568556
BC 147	0.350	2.910	14.8078819	64.87923	20.31288
BC 148	0.460	2.260	19.787893	61.26587	18.946224
BC 149	0.500	2.620	22.606123	64.26265	13.131228
BC 150	0.560	2.510	22.702171	69.48434	7.8134918
BC 151	0.450	2.670	18.850837	59.73796	21.411209
BC 152	0.510	2.610	20.466844	59.49496	20.038198
BC 153	0.470	0.910	13.2995132	36.740357	49.960146
BC 154	0.630	1.690	18.8913926	60.08018	21.028408
BC 156	0.500	1.560	15.4232582	53.42939	31.147361
BC 157	0.530	1.150	14.2739904	40.89544	44.830564
BC 158	0.570	2.290	19.0283824	60.14953	20.822102
BC 159	0.550	1.060	15.794932	42.13804	42.067016
BC 16	0.340	3.550	26.348	52.05	21.594
BC 160	0.450	2.010	15.9096518	54.867855	29.222511
BC 161	0.670	1.510	16.5676643	44.90281	38.529543
BC 162	0.240	3.110	11.1165871	60.644814	28.238588
BC 163	0.640	2.740	21.48564	57.45124	21.063162
BC 164	0.290	3.760	11.891309	34.32526	53.783432
BC 165	0.380	2.200	17.5202716	69.5155	12.964222
BC 166	0.320	2.850	13.3740397	50.20181	36.424136

BC 167	0.310	2.320	8.1572178	55.937739	35.905046
BC 168	0.430	2.330	16.5651515	68.46916	14.965666
BC 169	0.530	2.270	17.3254866	66.2696	16.404907
BC 17	0.640	2.560	40.101	59.879	0
BC 170	0.570	1.830	18.3416574	70.36923	11.289103
BC 171	0.730	1.290	17.739774	62.8639	19.396338
BC 172	0.340	2.710	11.2102658	83.760645	5.0291026
BC 174	0.300	2.640	5.1367354	19.822695	75.040585
BC 175	0.370	3.170	12.0175803	66.768882	21.21353
BC 176	0.330	3.230	10.4130429	77.214548	12.372417
BC 177	0.460	3.310	13.1055846	81.43927	5.4551416
BC 18	0.250	4.030	17.244	49.4	33.347
BC 180	0.460	0.770	4.962255	15.992107	79.045636
BC 181	na	na	na	na	na
BC 182	0.197	3.225	12.98498	40.25502	46.76005
BC 183	0.392	3.179	12.49662	49.97116	37.53222
BC 185	1.189	4.332	na	na	na
BC 186	0.352	5.662	8.51446	20.74022	70.74532
BC 187	0.215	5.254	8.72632	27.06067	64.21300
BC 188	0.430	5.260	6.41387	26.97000	66.61614
BC 189	0.453	5.015	11.73574	27.21047	61.05380
BC 19	0.320	3.460	16.446	56.13	27.4237
BC 190	0.313	5.314	13.16343	26.15531	60.68125
BC 191	0.367	5.361	9.89997	26.61430	63.48573
BC 192	na	na	12.13025	36.06031	51.80943
BC 196	0.238	5.304	8.28416	21.81180	69.90405
BC 197	0.175	5.226	10.06716	30.36767	59.56518
BC 199	0.126	5.364	6.84053	22.71242	70.44704
BC 20	0.170	5.390	9.335	20.843	69.823
BC 200	0.171	5.175	9.53318	33.27621	57.19059
BC 201	0.108	4.997	9.00188	32.55994	58.43819

BC 202	0.153	5.284	8.32713	28.40919	63.26367
BC 204	0.146	3.066	11.07847	44.14159	44.77994
BC 206	0.177	4.335	10.50490	45.03649	44.45859
BC 207	0.102	3.407	10.67776	31.15302	58.16918
BC 208	0.198	3.049	9.97210	39.57478	50.45312
BC 21	0.140	3.810	4.036	7.788	88.174
BC 210	0.156	4.556	na	na	na
BC 212	0.400	4.340	14.85831	67.21904	17.92266
BC 213	0.145	5.446	na	na	na
BC 214	0.249	4.797	12.52028	67.13544	20.34428
BC 215	0.436	2.541	15.61286	66.79155	17.59557
BC 216	0.201	3.090	11.75817	65.33649	22.90535
BC 217	0.244	3.036	12.85093	48.47119	38.67790
BC 218	0.252	4.010	11.17157	43.91603	44.91241
BC 219	0.212	3.348	12.62850	47.77470	39.59680
BC 22	0.330	3.670	18.491	59.35	22.143
BC 220	0.365	5.802	na	na	na
BC 221	0.540	4.454	13.36047	39.45620	47.18333
BC 222	0.494	3.827	15.28354	56.20111	28.51534
BC 223	0.628	4.362	na	na	na
BC 224	0.265	4.822	10.59862	38.72279	50.67861
BC 225	0.603	5.257	15.48107	62.86541	21.65351
BC 226	0.653	4.867	18.15852	66.39128	15.45019
BC 227	0.403	2.810	11.30008	50.81632	37.88360
BC 228	0.800	2.277	19.83541	65.82504	14.33954
BC 229	0.797	3.443	18.70021	71.86896	9.43084
BC 23	0.290	4.970	18.327872	48.57537	33.096721
BC 230	0.753	3.086	18.99160	63.65885	17.34954

BC 231	2.001	0.968	23.36224	56.16711	20.47067
BC 232	0.823	4.852	22.55948	64.49331	12.94719
BC 234	0.592	3.935	16.05421	57.73312	26.21264
BC 235	0.953	3.126	21.36266	72.52924	6.10811
BC 236	0.412	0.735	9.89504	34.77915	55.32579
BC 237	1.650	1.630	21.07857	52.82578	26.09565
BC 238	0.281	0.828	10.97527	36.92649	52.09824
BC 239	0.264	0.659	8.76013	25.21262	66.02724
BC 240	0.949	1.456	15.73164	65.26270	19.00566
BC 241	0.294	0.854	7.99953	25.23370	66.76677
BC 242	1.324	2.164	16.75839	68.10330	15.13829
BC 243	0.815	2.591	19.35802	58.61962	22.02235
BC 244	0.764	5.071	15.72847	53.91105	30.36050
BC 245	0.831	1.356	14.71843	49.84331	35.43825
BC 246	0.554	4.316	13.82837	49.76813	36.40350
BC 247	1.055	2.312	16.32228	68.76743	14.91029
BC 248	0.220	0.560	7.32441	20.82911	71.84648
BC 249	0.353	1.261	8.26991	38.71540	53.01468
BC 250	0.735	1.872	15.14817	48.07440	36.77743
BC 251	0.816	2.729	21.76867	62.38224	15.84911
BC 252	0.898	3.935	17.52655	57.72561	24.74785
BC 253	1.331	2.161	14.41506	71.77919	13.80574
BC 254	0.547	0.410	8.93401	31.59951	59.46650
BC 255	0.520	0.473	8.81278	32.27062	58.91660
BC 256	0.291	0.569	5.01165	15.58924	79.39911

BC 257	0.742	1.092	14.16833	49.01956	36.81211
BC 258	0.333	0.802	8.46580	33.80760	57.72660
BC 259	0.853	2.385	16.17013	64.90568	18.92419
BC 260	0.679	1.990	18.40733	54.63112	26.96153
BC 262	0.969	2.008	15.65000	51.80249	32.54753
BC 263	na	na	na	na	na
BC 265	0.687	0.781	7.93783	36.93599	55.12618
BC 266	0.233	0.370	6.19934	20.45490	73.34576
BC 267	0.380	1.708	12.09919	40.92294	46.97789
BC 268	0.414	0.819	10.96364	56.35793	32.67840
BC 271	0.321	0.666	na	na	na
BC 272	0.484	1.698	15.23594	35.91020	48.85383
BC 274	0.425	0.410	6.40557	25.95630	67.63816
BC 275	0.555	0.766	8.27323	36.00528	55.72153
BC 276	0.447	0.460	8.37714	38.53678	53.08604
BC 277	0.365	0.570	8.26637	29.86845	61.86520
BC 278	0.786	2.083	16.77249	53.12146	30.10602
BC 279	1.010	1.045	18.53193	47.76169	33.70638
BC 280	2.370	0.000	9.63463	63.28059	27.08480
BC 281	2.625	0.033	11.05061	65.45966	23.48977
BC 282	0.628	1.077	8.69239	43.27750	48.03007
BC 283	0.928	0.896	20.67204	59.62285	19.70511
BC 284	0.996	2.161	19.32009	60.47006	20.20985
BC 285	1.044	1.500	13.47052	60.43501	26.09447
BC 286	1.635	0.617	16.93018	50.30334	32.76653
BC 287	0.226	0.289	5.62696	17.49052	76.88253
BC 288	0.326	1.069	10.42412	39.73400	49.84188
BC 289	0.197	0.255	5.43896	23.66363	70.89743

BC 291	0.209	0.363	7.81707	25.51274	66.67018
BC 292	0.438	0.942	12.06398	35.25200	52.68402
BC 293	1.558	1.174	16.33495	64.24183	19.42319
BC 294	1.274	1.058	na	na	na
BC 296	0.122	0.296	4.53598	16.46520	78.99882
BC 297	0.986	0.826	13.90894	55.38476	30.70630
BC 298	0.151	0.180	3.73887	13.93651	82.32464
BC 299	1.135	0.922	11.29654	56.09248	32.61097
BC 300	1.955	0.704	13.67073	55.13147	31.19781
BC 301	1.205	1.102	19.02629	55.69762	25.27606
BC 302	1.597	1.161	22.40848	60.88115	16.71035
BC 303	1.496	1.445	21.49348	65.29697	13.20955
BC 304	0.667	0.746	12.51731	45.22483	42.25787
BC 305	1.468	1.102	12.94035	59.24678	27.81285
BC 306	0.605	0.934	10.85994	50.01175	39.12827
BC 307	1.647	0.947	22.13264	62.80917	15.05820
BC 308	0.472	0.359	8.59515	31.18820	60.21666
BC 309	0.339	0.470	8.82537	29.92132	61.25331
BC 31	0.190	5.080	10.4274125	19.267676	70.30492
BC 310	0.738	0.350	10.78149	36.77316	52.44536
BC 311	0.692	0.534	13.88046	44.67249	41.44704
BC 314	2.730	0.000	21.38084	56.46273	22.15641
BC 315	1.205	0.691	14.59578	44.15646	41.24770
BC 316	2.107	0.680	19.24645	61.51708	19.23646
BC 317	1.190	0.178	13.98017	43.68073	42.33909
BC 318	0.664	0.070	7.68082	24.30292	68.01626
BC 319	1.900	0.000	17.96765	54.52439	27.50801
BC 320	2.650	0.000	17.59973	57.53942	24.86079
BC 321	na	na	na	na	na
BC 324	2.041	0.346	17.49057	60.49864	22.01076

BC 327	0.520	0.000	5.94798	21.75350	72.29852
BC 328	0.647	0.115	8.03839	26.89799	65.06362
BC 329	2.150	0.000	17.57781	54.05964	28.36256
BC 33	0.210	5.960	8.0448462	12.210269	79.744876
BC 330	0.990	0.126	7.98710	32.73578	59.27711
BC 331	1.651	0.118	14.93982	49.34668	35.71353
BC 332	1.870	0.136	17.00588	55.09103	27.90307
BC 333	2.230	0.000	15.73541	54.25331	30.01127
BC 334	0.687	0.239	11.21760	37.35532	51.42708
BC 337	2.490	0.000	17.07925	50.44331	32.47749
BC 339	0.631	0.181	4.85026	15.40673	79.74299
BC 34	0.270	6.340	8.6805001	11.652421	79.667067
BC 340	1.105	0.354	13.91910	43.01928	43.06161
BC 341	1.580	0.000	11.47052	46.58938	41.94012
BC 342	0.604	0.228	9.53481	36.64092	53.82428
BC 343	0.768	1.920	15.58198	38.46689	45.95113
BC 344	2.338	0.706	17.21377	58.62918	24.15704
BC 345	0.694	0.366	12.00399	44.34208	43.65392
BC 346	0.978	0.429	9.54145	50.94897	39.50961
BC 347	1.709	0.627	12.02929	58.67956	29.29120
BC 348	1.367	0.775	16.46766	52.98544	30.54691
BC 35	0.300	4.720	18.4329327	58.22394	23.343118
BC 352	0.911	1.125	15.86071	51.98152	32.15775
BC 353	0.958	0.662	13.88868	39.74922	46.36211
BC 354	2.004	0.898	21.52331	55.33627	23.14041
BC 356	1.465	0.309	9.99159	46.89627	43.11214
BC 357	1.293	0.958	13.66262	55.73645	30.60093
BC 358	1.273	0.748	19.02509	53.63201	27.34288
BC 36	0.220	5.370	9.2946809	15.107612	75.597706
BC 361	1.343	0.756	16.29613	50.58077	33.12310
BC 362	0.663	0.347	10.14552	38.67425	51.18026

BC 363	2.093	0.412	17.15088	54.49692	28.35217
BC 364	2.372	0.053	17.03603	64.31794	18.64605
BC 365	1.208	0.680	12.15812	50.96205	36.87982
BC 366	2.780	0.000	21.21591	57.15734	21.62673
BC 367	2.410	0.264	18.35738	56.40832	25.23433
BC 368	0.790	0.266	na	na	na
BC 369	1.161	0.489	11.78918	50.24749	37.96334
BC 37	0.150	1.310	na	na	na
BC 370	1.832	0.650	19.19111	60.54378	20.26513
BC 371	1.544	0.964	16.66149	57.73066	25.60787
BC 38	0.200	4.890	na	na	na
BC 4	0.410	2.880	26.953	55.59	17.428
BC 40	0.170	3.700	na	na	na
BC 41	0.330	5.430	9.4884059	24.314879	66.196724
BC 44	0.230	5.720	6.718992	14.528738	78.752286
BC 45	0.270	6.720	4.1323487	18.662377	77.20529
BC 47	0.230	4.240	na	na	na
BC 5	0.420	2.700	27.148	70.786	2.061
BC 50	0.480	2.330	20.1429981	74.72149	5.1354917
BC 51	0.320	1.980	14.4890485	68.219206	17.291739
BC 52	0.500	2.360	21.551495	72.43564	6.0128839
BC 53	0.530	2.380	21.921275	71.71986	6.3588289
BC 57	0.490	2.020	21.347812	67.31424	11.337959
BC 58	0.110	0.570	2.6313467	5.529751	91.838913
BC 59	0.490	1.970	19.0822136	65.38432	15.533458
BC 6	0.370	2.720	29.444	62.075	8.449
BC 60	0.360	1.720	12.5351051	60.47082	26.994061
BC 61	0.390	1.610	14.1744873	56.75043	29.075081
BC 63	0.440	2.020	18.862428	66.3154	14.822183
BC 67	0.210	1.070	4.1675479	14.584071	81.248396
BC 68	0.290	1.360	8.3043922	45.327583	46.367993
BC 7	0.240	2.480	13.989	33.828	52.184
BC 70	0.340	1.490	12.3338392	51.504209	36.161945

BC 71	0.500	2.410	19.3614555	75.31013	5.328414
BC 72	0.450	2.170	21.458662	70.05627	8.485049
BC 73	0.540	2.310	25.060552	70.60681	4.3326488
BC 74	0.360	1.130	12.3858969	41.116207	46.49789
BC 76	0.380	1.340	12.0439086	53.226903	34.729196
BC 77	0.340	2.430	14.7312968	65.966971	19.301737
BC 78	0.200	3.320	12.7213962	54.435543	32.843085
BC 79	0.310	2.310	14.1739931	67.620345	18.20566
BC 80	0.320	3.540	13.8218877	72.98261	13.195504
BC 81	0.480	2.880	23.241514	64.98017	11.778316
BC 82	0.550	2.490	21.746675	70.90085	7.3524828
BC 83	0.350	2.520	16.3188137	55.368576	28.312632
BC 84	0.740	2.360	21.091263	59.209457	19.699303
BC 85	0.270	2.520	11.8840802	58.046344	30.069602
BC 86	0.400	2.540	23.178635	71.56522	5.2561572
BC 87	na	na	na	na	na
BC 88	0.390	3.420	17.8060485	59.0977	23.096247
BC 89	0.460	3.060	23.024983	63.16214	13.812897
BC 9	0.360	3.560	28.615	55.14	16.204
BC 90	0.730	2.530	30.369438	64.100957	5.5296309
BC 91	0.500	2.350	25.085696	66.22149	8.6928042
BC 92	0.450	2.440	24.983146	63.51802	11.49884
BC 93	0.450	2.440	24.447055	61.01475	14.5382
BC 94	0.350	2.940	12.1185648	69.08337	18.798051
BC 95	0.270	3.140	11.9234855	45.386599	42.689939
BC 96	0.300	3.520	11.5646558	62.880225	25.55512
BC 97	0.250	3.330	12.8160356	53.370415	33.813542
BC 98	0.250	3.320	9.96611	52.491897	37.541973
BC 99	0.330	3.500	14.2989356	57.37484	28.326216

BC	Sediment gravel % in top 0-2cm	Sediment particle size diversity (S-W)	Within Closed Area	Geological setting	2003-2012 no vms records within 5km radius
BC 10	0.00000	2.174464	N	draped over failed seabed	29
BC 100	0.00000	2.319084	N	smooth areas	84
BC 101	0.00000	2.142341	N	draped over MTDs	121
BC 102	na	na	N	sediment drifts	66
BC 103	0.00000	2.065284	N	smooth areas	148
BC 104	0.00000	2.014714	N	na	22
BC 105	0.00000	2.14637	N	smooth areas	50
BC 106	0.00000	2.105053	N	smooth areas	270
BC 107	0.00000	2.062227	N	smooth areas	398
BC 108	0.00000	2.098149	N	smooth areas	661
BC 109	0.00000	2.041688	N	rough topography of MTDs	154
BC 11	0.00000	2.078054	N	smooth areas	34
BC 110	0.00000	2.115939	N	smooth areas	24
BC 111	0.00000	2.039849	N	smooth areas	27
BC 112	0.00000	1.988081	Y	draped over MTDs	107
BC 113	0.00000	2.072539	Y	smooth areas	55
BC 114	0.00000	2.10276	N	draped over MTDs	179
BC 115	0.00000	2.028569	N	smooth areas	45
BC 116	0.00000	2.113452	N	smooth areas	92
BC 117	0.00000	2.07898	N	smooth areas	64
BC 118	0.00000	2.199733	N	draped over failed seabed	245
BC 119	0.00000	2.199294	N	draped over failed seabed	163
BC 12	0.00000	2.148189	N	smooth areas	91
BC 120	0.00000	2.134219	N	smooth areas	627
BC 121	0.00000	2.042957	Y	draped over MTDs	94
BC 122	0.00000	2.145472	N	smooth areas	275
BC 123	0.00000	1.914375	N	gullies cutting smooth areas	286
BC 124	0.00000	1.941131	N	smooth areas	761
BC 125	0.00000	2.054085	N	draped over MTDs	142
BC 126	0.00000	2.052822	N	sediment waves	41
BC 129	0.00000	2.113814	N	gullies cutting smooth areas	326
BC 13	0.00000	2.142544	N	smooth areas	30
BC 130	0.00000	2.054918	N	draped over MTDs	322
BC 131	0.00000	2.111534	Y	draped over MTDs	78
BC 132	0.00000	2.087529	N	sediment waves	155
BC 133	0.00000	2.188814	N	smooth areas	52

BC 135	0.00000	2.216472	N	smooth areas	60
BC 136	0.00000	2.056821	N	smooth areas	68
BC 137	0.00000	2.186327	N	rough topography of MTDs	52
BC 138	0.00000	2.218308	N	draped over MTDs	67
BC 139	0.00000	2.15093	N	draped over failed seabed	1047
BC 14	0.00000	2.202833	Y	draped over failed seabed	24
BC 140	0.00000	2.179188	N	draped over failed seabed	1286
BC 141	0.00000	2.058578	N	draped over failed seabed	137
BC 142	0.00000	2.073737	N	draped over failed seabed	638
BC 143	0.00000	1.932806	N	smooth areas	619
BC 144	0.00000	2.070069	N	smooth areas	605
BC 145	0.00000	1.969654	N	draped over failed seabed	771
BC 146	0.00000	2.158254	N	gullies cutting smooth areas	461
BC 147	0.00000	2.151775	N	draped over MTDs	671
BC 148	0.00000	2.187703	N	smooth areas	74
BC 149	0.00000	2.121248	Y	smooth areas	50
BC 150	0.00000	2.017051	N	smooth areas	59
BC 151	0.00000	2.220054	N	draped over MTDs	63
BC 152	0.00000	2.217613	N	smooth areas	67
BC 153	0.00000	2.069245	N	draped over failed seabed	605
BC 154	0.00000	2.131248	N	draped over gullies	147
BC 156	0.00000	2.219945	N	draped over gullies	558
BC 157	0.00000	2.221508	N	draped over failed seabed	298
BC 158	0.00000	2.20269	N	draped over MTDs	53
BC 159	0.00000	2.264554	N	gullies associated with failed seabed	233
BC 16	0.00000	2.197322	N	draped over gullies	143
BC 160	0.00000	2.205633	N	draped over MTDs	63
BC 161	0.00000	2.285037	N	gullies associated with failed seabed	118
BC 162	0.00000	2.069815	N	draped over failed seabed	1869
BC 163	0.00000	2.247645	Y	smooth areas	31
BC 164	0.00000	2.321788	N	failed seabed stepped	102
BC 165	0.00000	1.97682	Y	smooth areas	61
BC 166	0.00000	1.998649	N	draped over MTDs	109

BC 167	0.00000		1.884955	N	sediment drifts	1361
BC 168	0.00000		2.008609	Y	smooth areas	109
BC 169	0.00000		2.05732	N	smooth areas	107
BC 17	0.00000		1.826929	Y	draped over gullies	2
BC 170	0.00000		1.993301	Y	draped over MTDs	52
BC 171	0.00000		2.039398	N	gullies associated with failed seabed	49
BC 172	0.00000		1.732293	N	draped over failed seabed	2209
BC 174	0.00000		2.190545	N	failed seabed mixed	68
BC 175	0.00000		1.862069	N	draped over MTDs	1343
BC 176	0.00000		1.803882	N	draped over failed seabed	2104
BC 177	0.00000		1.802337	N	sediment drifts	2225
BC 18	0.00000		2.148905	N	smooth areas	153
BC 180	0.00000		2.082364	N	canyon head>400m walls	29
BC 181	na	na		N	canyon head>400m walls	59
BC 182	0.00000		2.273517	N	draped over MTDs	518
BC 183	0.00000		2.114151	N	draped over MTDs	97
BC 185	na	na		N	canyon head>400m walls	36
BC 186	0.00000		2.020193	N	draped over failed seabed	21
BC 187	0.00000		2.01486	N	canyon head>400m walls	41
BC 188	0.00000		2.110442	N	inter canyon area	20
BC 189	0.00000		2.221999	N	canyon head>400m floor	12
BC 19	0.00000		2.078058	N	draped over failed seabed	52
BC 190	0.00000		2.21464	N	inter canyon area	8
BC 191	0.00000		2.067067	N	inter canyon area	9
BC 192	0.00000		2.209181	N	inter canyon area	25
BC 196	0.00000		1.993935	N	gullies associated with failed seabed	17
BC 197	0.00000		2.13196	N	draped over failed seabed	29
BC 199	0.00000		1.976982	N	draped over failed seabed	22
BC 20	0.00000		2.135566	Y	draped over failed seabed	7
BC 200	0.00000		2.055876	N	draped over failed seabed	59
BC 201	0.00000		2.058021	N	gullies cutting smooth areas	30

BC 202	0.00000		1.993548	N	draped over failed seabed	54
BC 204	0.00000		2.154704	N	draped over MTDs	27
BC 206	0.00000		2.091609	N	gullies associated with failed seabed	85
BC 207	0.00000		2.143897	N	failed seabed mixed	24
BC 208	0.00000		2.164401	N	draped over MTDs	694
BC 21	0.00000		1.748201	Y	draped over failed seabed	5
BC 210	na	na		N	failed seabed stepped	21
BC 212	0.00000		1.922422	N	failed seabed stepped	56
BC 213	na	na		N	smooth areas	10
BC 214	0.00000		1.862005	N	failed seabed stepped	22
BC 215	0.00000		2.039924	N	smooth areas	1220
BC 216	0.00000		1.976331	N	draped over MTDs	1623
BC 217	0.00000		2.033631	N	sediment drifts	100
BC 218	0.00000		2.132813	N	failed seabed stepped	17
BC 219	0.00000		1.937241	N	failed seabed stepped	18
BC 22	0.00000		2.08762	N	iceberg pits	64
BC 220	na	na		N	inter canyon area	8
BC 221	0.00000		2.269945	Y	failed seabed stepped	9
BC 222	0.00000		2.014725	N	canyon head>400m floor	20
BC 223	na	na		Y	failed seabed stepped	9
BC 224	0.00000		2.133728	N	failed seabed stepped	24
BC 225	0.00000		2.014125	N	failed seabed stepped	18
BC 226	0.00000		2.051887	N	rough topography of MTDs	12
BC 227	0.00000		1.972243	N	failed seabed stepped	209
BC 228	0.00000		2.075294	N	smooth areas	446
BC 229	0.00000		1.985365	N	failed seabed stepped	37
BC 23	0.00000		2.088688	N	draped over failed seabed	62
BC 230	0.00000		2.047992	N	failed seabed stepped	34

BC 231	0.00000	2.231802	Y	canyon head>400m floor	33
BC 232	0.00000	2.036971	N	rough topography of MTDs	20
BC 234	0.00000	2.091628	N	canyon head>400m floor	66
BC 235	0.00000	1.955156	N	rough topography of MTDs	48
BC 236	0.00000	2.376454	Y	iceberg pits	24
BC 237	0.00000	2.252729	Y	failed seabed stepped	73
BC 238	0.00000	2.177061	Y	rough topography of MTDs	21
BC 239	0.00000	1.974171	N	rough topography of MTDs	43
BC 240	0.00000	2.127859	Y	rough topography of MTDs	54
BC 241	0.00000	2.170042	N	rough topography of MTDs	92
BC 242	0.00000	2.089856	Y	rough topography of MTDs	55
BC 243	0.00000	2.245464	Y	failed seabed stepped	44
BC 244	0.00000	2.254319	N	failed seabed stepped	20
BC 245	0.00000	2.206725	Y	draped over MTDs	49
BC 246	0.00000	2.26824	N	failed seabed stepped	14
BC 247	0.00000	2.099217	N	draped over MTDs	21
BC 248	0.00000	2.023794	N	failed seabed stepped	201
BC 249	0.00000	2.166388	N	failed seabed stepped	293
BC 250	0.00000	2.236204	Y	draped over MTDs	23
BC 251	0.00000	2.190344	N	failed seabed stepped	16
BC 252	0.00000	2.272625	N	failed seabed stepped	12
BC 253	0.00000	2.055202	N	failed seabed stepped	17
BC 254	0.00000	1.989893	N	failed seabed stepped	618
BC 255	0.00000	1.909847	N	failed seabed stepped	517
BC 256	0.00000	2.031385	N	failed seabed stepped	344

BC 257	0.00000	2.201276	Y	failed seabed stepped	45
BC 258	0.00000	2.076302	N	failed seabed stepped	131
BC 259	0.00000	2.159877	N	failed seabed stepped	18
BC 260	0.00000	2.242995	Y	canyon head>400m walls	18
BC 262	0.00000	2.277365	Y	failed seabed stepped	21
BC 263	na	na	Y	failed seabed stepped	30
BC 265	0.00000	2.156922	N	failed seabed stepped	571
BC 266	0.00000	2.138302	N	inter canyon area	79
BC 267	0.00000	2.252	Y	failed seabed stepped	19
BC 268	0.00000	2.18395	Y	canyon head>400m floor	42
BC 271	na	na	N	canyon head>400m floor	238
BC 272	0.00000	2.319665	Y	inter canyon area	15
BC 274	0.00000	1.8952	N	inter canyon area	1441
BC 275	0.00000	1.946498	N	canyon head>400m walls	2371
BC 276	0.00000	2.075706	N	shelf indenting canyon walls	906
BC 277	0.00000	2.003028	N	inter canyon area	1117
BC 278	0.00000	2.308951	N	shelf indenting canyon walls	20
BC 279	0.00000	2.280629	Y	canyon head>400m walls	21
BC 280	0.00000	2.118065	N	canyon head>400m floor	305
BC 281	0.00000	2.123047	N	canyon head>400m floor	200
BC 282	0.00000	2.139307	N	shelf indenting canyon walls	382
BC 283	0.00000	2.162606	N	inter canyon area	28
BC 284	0.00000	2.20625	N	inter canyon area	26
BC 285	0.00000	2.235511	N	inter canyon area	28
BC 286	0.00000	2.274027	N	inter canyon area	132
BC 287	0.00000	2.075299	N	inter canyon area	497
BC 288	0.00000	2.158594	N	inter canyon area	31
BC 289	0.00000	1.889683	N	canyon head>400m walls	416

BC 291	0.00000		1.920663	N	canyon head>400m walls	532
BC 292	0.00000		2.259458	Y	canyon head>400m floor	28
BC 293	0.00000		2.163486	Y	canyon head>400m floor	33
BC 294	na	na		N	canyon head>400m walls	71
BC 296	0.00000		1.954783	N	inter canyon area	382
BC 297	0.00000		2.207263	N	inter canyon area	42
BC 298	0.00000		1.872408	N	iceberg pits	677
BC 299	0.00000		2.201429	N	shelf indenting canyon walls	18
BC 300	0.00000		2.262199	N	shelf indenting canyon walls	534
BC 301	0.00000		2.210615	N	shelf indenting canyon floor	51
BC 302	0.00000		2.156732	N	shelf indenting canyon walls	17
BC 303	0.00000		2.069222	N	canyon head>400m walls	12
BC 304	0.00000		2.140662	N	canyon head>400m floor	977
BC 305	0.00000		2.152714	N	shelf indenting canyon floor	245
BC 306	0.00000		2.011337	N	shelf indenting canyon walls	518
BC 307	0.00000		2.060648	N	inter canyon area	99
BC 308	0.00000		1.824018	N	shelf indenting canyon walls	205
BC 309	0.00000		1.774071	N	inter canyon area	269
BC 31	0.00000		2.115176	N	steep flanks>6.4deg	2
BC 310	0.00000		1.923483	N	shelf indenting canyon walls	552
BC 311	0.00000		2.165956	N	inter canyon area	51
BC 314	0.00000		2.247133	N	inter canyon area	14
BC 315	0.00000		2.260479	N	shelf indenting canyon floor	5
BC 316	0.00000		2.18931	N	inter canyon area	6
BC 317	0.00000		1.973085	N	inter canyon area	158
BC 318	0.00000		2.107673	N	inter canyon area	537
BC 319	0.00000		2.194541	N	inter canyon area	99
BC 320	0.00000		2.216623	N	shelf indenting canyon walls	3
BC 321	na	na		N	inter canyon area	113
BC 324	0.00000		2.188154	N	canyon head>400m floor	10

BC 327	0.00000	1.843286	N	iceberg pits	339
BC 328	0.00000	1.933093	N	iceberg pits	74
BC 329	0.00000	2.235468	N	canyon head>400m walls	8
BC 33	0.00000	2.095745	Y	rough topography of MTDs	5
BC 330	0.00000	1.994416	N	shelf indenting canyon floor	245
BC 331	0.00000	2.253302	N	inter canyon area	23
BC 332	0.00000	2.204299	N	inter canyon area	6
BC 333	0.00000	2.175229	N	inter canyon area	28
BC 334	0.00000	2.095974	N	shelf indenting canyon walls	300
BC 337	0.00000	2.270649	N	canyon head>400m floor	177
BC 339	0.00000	2.046488	N	inter canyon area	192
BC 34	0.00000	1.961843	N	rough topography of MTDs	5
BC 340	0.00000	2.183355	N	inter canyon area	76
BC 341	0.00000	2.163449	N	shelf indenting canyon walls	309
BC 342	0.00000	2.050064	N	shelf indenting canyon floor	322
BC 343	0.00000	2.270456	N	inter canyon area	295
BC 344	0.00000	2.214703	N	canyon head>400m walls	3
BC 345	0.00000	2.130527	N	canyon head>400m walls	73
BC 346	0.00000	2.113582	N	canyon head>400m floor	69
BC 347	0.00000	2.147231	N	inter canyon area	12
BC 348	0.00000	2.203775	N	inter canyon area	6
BC 35	0.00000	2.095118	N	smooth areas	9
BC 352	0.00000	2.22102	N	inter canyon area	23
BC 353	0.00000	2.279216	N	canyon head>400m floor	59
BC 354	0.00000	2.289143	Y	canyon head>400m walls	9
BC 356	0.00000	2.055375	N	canyon head>400m floor	100
BC 357	0.00000	2.03138	N	canyon head>400m floor	174
BC 358	0.00000	2.233863	N	inter canyon area	3
BC 36	0.00000	2.143324	N	steep flanks>6.4deg	3
BC 361	0.00000	2.219732	N	inter canyon area	6
BC 362	0.00000	2.06569	N	canyon head>400m walls	399

BC 363	0.00000		2.260549	N	canyon head>400m walls	51
BC 364	0.00000		2.097769	N	inter canyon area	2
BC 365	0.00000		2.278907	N	inter canyon area	55
BC 366	0.00000		2.176187	N	canyon head>400m floor	327
BC 367	0.00000		2.219949	N	canyon head>400m floor	14
BC 368	na	na		N	canyon head>400m floor	196
BC 369	0.00000		2.189949	N	inter canyon area	25
BC 37	na	na		N	steep flanks>6.4deg	3
BC 370	0.00000		2.169223	N	inter canyon area	14
BC 371	0.00000		2.222029	N	inter canyon area	3
BC 38	na	na		N	rough topography of MTDs	2
BC 4	0.00000		2.133936	N	draped over gullies	82
BC 40	na	na		Y	failed seabed mixed	1
BC 41	0.00000		2.149049	N	na	1
BC 44	0.00000		1.960409	N	na	10
BC 45	0.00000		1.944699	N	failed seabed mixed	8
BC 47	na	na		N	inter canyon area	3
BC 5	0.00000		1.925934	N	draped over MTDs	146
BC 50	0.00000		1.922497	N	inter canyon area	831
BC 51	0.00000		1.894819	N	inter canyon area	1413
BC 52	0.00000		1.956412	N	inter canyon area	308
BC 53	0.00000		1.968259	N	gullies cutting smooth areas	1451
BC 57	0.00000		2.001645	N	gullies cutting smooth areas	5454
BC 58	0.00000		1.745863	N	iceberg pits	2425
BC 59	0.00000		2.041167	N	failed seabed stepped	1507
BC 6	0.00000		2.071972	Y	draped over MTDs	9
BC 60	0.00000		2.00489	N	draped over failed seabed	4044
BC 61	0.00000		1.977562	N	draped over failed seabed	2281
BC 63	0.00000		1.996171	N	failed seabed stepped	469
BC 67	0.00000		2.109588	N	smooth areas	1538
BC 68	0.00000		2.032813	N	failed seabed stepped	1369
BC 7	0.00000		2.25832	N	draped over MTDs	6
BC 70	0.00000		2.241182	N	gullies associated with failed seabed	289

BC 71	0.00000	1.920491	N	failed seabed stepped	188
BC 72	0.00000	1.987155	Y	failed seabed stepped	45
BC 73	0.00000	1.965314	Y	gullies associated with failed seabed	24
BC 74	0.00000	2.243007	N	draped over failed seabed	642
BC 76	0.00000	1.913845	N	rough topography of MTDs	1378
BC 77	0.00000	2.035349	N	draped over failed seabed	319
BC 78	0.00000	1.986969	N	na	7
BC 79	0.00000	1.970308	N	draped over failed seabed	2119
BC 80	0.00000	1.873128	Y	draped over failed seabed	51
BC 81	0.00000	2.063219	N	rough topography of MTDs	20
BC 82	0.00000	1.979836	N	draped over MTDs	73
BC 83	0.00000	2.077551	N	rough topography of MTDs	115
BC 84	0.00000	2.21347	Y	failed seabed stepped	22
BC 85	0.00000	2.090132	N	sediment drifts	1629
BC 86	0.00000	1.954633	N	failed seabed stepped	652
BC 87	na	na	N	rough topography of MTDs	69
BC 88	0.00000	2.204052	N	draped over MTDs	195
BC 89	0.00000	2.106053	Y	failed seabed stepped	2
BC 9	0.00000	2.156841	N	draped over failed seabed	28
BC 90	0.00000	1.99951	Y	failed seabed stepped	39
BC 91	0.00000	2.04334	N	sediment drifts	68
BC 92	0.00000	2.084901	N	sediment drifts	85
BC 93	0.00000	2.135574	N	sediment drifts	584
BC 94	0.00000	1.986348	Y	smooth areas	56
BC 95	0.00000	2.124546	N	smooth areas	121
BC 96	0.00000	2.108587	Y	smooth areas	73
BC 97	0.00000	1.931937	N	smooth areas	48
BC 98	0.00000	2.029332	N	smooth areas	29
BC 99	0.00000	2.186022	N	smooth areas	88

BC	2003-2012 no vms records within 3km radius	2003-2012 no vms records within 1km radius	2003-2012 vms record point density within 5km radius	2003-2012 vms record point density within 3km radius
BC 10	14	4	0.356507	0.459781
BC 100	31	0	1.069521	1.131768
BC 101	50	6	1.54062	1.803756
BC 102	16	3	0.840338	0.565884
BC 103	46	8	1.884395	1.626917
BC 104	3	0	0.280113	0.282942
BC 105	12	2	0.63662	0.424413
BC 106	86	8	3.425014	3.076996
BC 107	131	24	5.054761	4.597809
BC 108	254	25	8.377916	8.841941
BC 109	24	1	1.948056	0.848826
BC 11	8	0	0.432901	0.282942
BC 110	5	1	0.305577	0.176839
BC 111	9	0	0.343775	0.31831
BC 112	27	3	1.362366	0.95493
BC 113	15	2	0.700282	0.530517
BC 114	69	8	2.279099	2.475744
BC 115	12	0	0.572958	0.424413
BC 116	33	3	1.17138	1.167136
BC 117	24	3	0.814873	0.848826
BC 118	105	20	3.132169	3.713615
BC 119	60	10	2.075381	2.122066
BC 12	31	8	1.158648	1.096401
BC 120	241	41	7.983212	8.558999
BC 121	29	3	1.184113	1.061033
BC 122	106	3	3.501409	3.748983
BC 123	107	10	3.641465	3.784351
BC 124	326	58	9.67662	11.600627
BC 125	51	9	1.808	1.803756
BC 126	21	4	0.522028	0.742723
BC 129	128	11	4.188958	4.527074
BC 13	9	0	0.381972	0.31831
BC 130	148	8	4.087099	5.234429
BC 131	19	0	0.980394	0.671988
BC 132	48	8	1.948056	1.662285
BC 133	10	2	0.662085	0.353678

BC 135	18	0	0.763944	0.63662
BC 136	23	1	0.840338	0.813459
BC 137	16	3	0.662085	0.565884
BC 138	18	4	0.840338	0.63662
BC 139	396	19	13.318086	14.005635
BC 14	7	0	0.343775	0.247574
BC 140	506	99	16.373861	18.355869
BC 141	45	3	1.744338	1.591549
BC 142	218	17	8.123268	7.674805
BC 143	229	9	7.855888	8.06385
BC 144	255	32	7.690367	9.01878
BC 145	282	45	9.816677	9.97371
BC 146	83	5	5.831437	2.864789
BC 147	296	23	8.517973	10.468859
BC 148	29	4	0.942197	1.096401
BC 149	16	2	0.63662	0.565884
BC 150	22	1	0.751211	0.778091
BC 151	19	0	0.789408	0.671988
BC 152	33	4	0.85307	1.167136
BC 153	185	12	7.703099	6.507669
BC 154	48	7	1.871662	1.697653
BC 156	206	35	7.104677	7.674805
BC 157	144	26	3.806986	5.092958
BC 158	15	0	0.674817	0.530517
BC 159	79	13	2.979381	2.829421
BC 16	52	2	1.820733	1.839124
BC 160	20	2	0.802141	0.707355
BC 161	38	9	1.502423	1.343975
BC 162	748	90	23.745918	26.348986
BC 163	9	1	0.394704	0.31831
BC 164	29	2	1.298704	1.025665
BC 165	23	5	0.776676	0.813459
BC 166	33	5	1.387831	1.061033

BC 167	492	68	17.443382	17.365572
BC 168	44	4	1.362366	1.556182
BC 169	28	2	1.362366	0.919562
BC 17	2	0	0.025465	0.070736
BC 170	26	1	0.662085	0.919562
BC 171	10	2	0.623887	0.353678
BC 172	970	71	28.113129	34.20063
BC 174	16	1	0.865803	0.565884
BC 175	609	63	17.112339	21.503601
BC 176	1041	157	26.738031	36.747108
BC 177	989	100	28.355045	34.943352
BC 18	53	12	1.948056	1.874492
BC 180	9	0	0.369239	0.31831
BC 181	21	1	0.763944	0.742723
BC 182	235	36	6.595381	8.276057
BC 183	38	0	1.235042	1.343975
BC 185	6	1	0.445634	0.212207
BC 186	4	3	0.26738	0.141471
BC 187	12	1	0.509296	0.424413
BC 188	9	1	0.254648	0.31831
BC 189	2	0	0.152789	0.070736
BC 19	37	6	0.662085	1.308607
BC 190	3	3	0.101859	0.106103
BC 191	4	1	0.114592	0.141471
BC 192	16	2	0.31831	0.565884
BC 196	8	1	0.216451	0.282942
BC 197	9	1	0.369239	0.31831
BC 199	10	0	0.292845	0.353678
BC 20	2	0	0.089127	0.070736
BC 200	19	3	0.751211	0.884194
BC 201	8	0	0.381972	0.282942

BC 202	23	3	0.674817	0.813459
BC 204	12	1	0.343775	0.424413
BC 206	41	2	1.069521	1.450078
BC 207	10	0	0.305577	0.353678
BC 208	309	33	8.874479	10.964007
BC 21	1	0	0.063662	0.035368
BC 210	4	1	0.280113	0.141471
BC 212	12	2	0.713014	0.424413
BC 213	5	1	0.127324	0.176839
BC 214	15	1	0.280113	0.530517
BC 215	207	7	15.597184	7.356495
BC 216	481	67	20.588284	16.94116
BC 217	41	14	1.273239	1.450078
BC 218	4	0	0.216451	0.141471
BC 219	3	0	0.229183	0.106103
BC 22	26	3	0.814873	0.919562
BC 220	3	0	0.101859	0.106103
BC 221	1	0	0.114592	0.035368
BC 222	10	0	0.254648	0.353678
BC 223	6	1	0.114592	0.212207
BC 224	3	0	0.305577	0.106103
BC 225	10	2	0.229183	0.353678
BC 226	6	1	0.152789	0.212207
BC 227	50	1	2.673803	1.839124
BC 228	100	12	5.665916	3.466041
BC 229	12	2	0.471099	0.495149
BC 23	20	4	0.789408	0.707355
BC 230	18	2	0.432901	0.63662

BC 231	17	2	0.420169	0.601252
BC 232	5	0	0.254648	0.176839
BC 234	47	0	0.840338	1.697653
BC 235	16	0	0.611155	0.565884
BC 236	10	2	0.305577	0.353678
BC 237	30	2	0.916732	1.061033
BC 238	8	0	0.26738	0.282942
BC 239	14	1	0.547493	0.495149
BC 240	16	3	0.700282	0.565884
BC 241	37	3	1.17138	1.273239
BC 242	30	1	0.700282	1.061033
BC 243	8	0	0.560225	0.282942
BC 244	9	1	0.254648	0.31831
BC 245	19	1	0.623887	0.671988
BC 246	4	0	0.178254	0.141471
BC 247	8	1	0.254648	0.282942
BC 248	80	7	2.546479	2.829421
BC 249	115	8	3.730592	4.067293
BC 250	6	1	0.292845	0.176839
BC 251	4	0	0.190986	0.141471
BC 252	5	0	0.152789	0.176839
BC 253	5	0	0.216451	0.176839
BC 254	254	20	7.86862	8.983413
BC 255	243	30	6.595381	8.594367
BC 256	131	15	4.379944	4.633177

BC 257	21	1	0.572958	0.742723
BC 258	59	7	1.667944	2.086698
BC 259	9	0	0.229183	0.31831
BC 260	8	0	0.229183	0.282942
BC 262	5	2	0.26738	0.176839
BC 263	5	0	0.381972	0.176839
BC 265	123	13	7.33386	4.314868
BC 266	14	0	0.993127	0.495149
BC 267	7	0	0.241916	0.247574
BC 268	12	1	0.547493	0.424413
BC 271	48	1	3.068507	1.697653
BC 272	9	0	0.190986	0.31831
BC 274	365	9	18.385578	12.838499
BC 275	1037	111	30.175777	36.676373
BC 276	205	2	11.561015	7.356495
BC 277	311	11	14.247551	10.964007
BC 278	8	0	0.254648	0.282942
BC 279	11	1	0.26738	0.389045
BC 280	99	11	3.896113	3.501409
BC 281	57	12	2.533747	1.414711
BC 282	112	11	4.863775	3.996557
BC 283	8	1	0.356507	0.282942
BC 284	10	0	0.331042	0.31831
BC 285	4	0	0.356507	0.141471
BC 286	24	1	1.680676	0.884194
BC 287	175	26	6.315268	6.189359
BC 288	7	1	0.394704	0.247574
BC 289	175	38	5.283944	6.224727

BC 291	292	53	6.773634	10.327388
BC 292	12	1	0.356507	0.424413
BC 293	14	1	0.420169	0.495149
BC 294	13	4	0.916732	0.459781
BC 296	150	0	4.83831	5.269797
BC 297	8	1	0.547493	0.282942
BC 298	218	29	8.581635	7.60407
BC 299	8	1	0.241916	0.247574
BC 300	158	27	6.582648	6.047888
BC 301	4	0	0.649352	0.141471
BC 302	6	2	0.203718	0.212207
BC 303	5	1	0.152789	0.176839
BC 304	335	35	12.43955	12.237247
BC 305	68	6	3.144902	2.405008
BC 306	107	3	6.582648	3.784351
BC 307	40	2	1.260507	1.414711
BC 308	18	4	2.559211	0.601252
BC 309	60	0	3.425014	2.122066
BC 31	2	0	0.025465	0.070736
BC 310	217	43	7.028282	8.240689
BC 311	19	2	0.649352	0.671988
BC 314	4	1	0.178254	0.141471
BC 315	1	0	0.063662	0.035368
BC 316	1	0	0.076394	0.035368
BC 317	65	15	2.011719	2.263537
BC 318	255	11	6.811831	8.452896
BC 319	21	0	1.273239	0.742723
BC 320	0	0	0.038197	0
BC 321	26	3	1.451493	0.990297
BC 324	3	0	0.114592	0.106103

BC 327	131	14	4.341747	4.633177
BC 328	16	0	0.916732	0.565884
BC 329	2	0	0.101859	0.070736
BC 33	2	0	0.063662	0.070736
BC 330	75	3	3.093972	2.617215
BC 331	11	0	0.292845	0.389045
BC 332	1	0	0.089127	0.035368
BC 333	8	0	0.356507	0.282942
BC 334	94	3	3.806986	3.32457
BC 337	60	1	2.253634	2.122066
BC 339	47	2	2.44462	1.662285
BC 34	1	0	0.063662	0.035368
BC 340	29	2	0.967662	1.025665
BC 341	74	22	3.959775	2.617215
BC 342	46	3	4.112564	1.591549
BC 343	54	0	3.743324	1.909859
BC 344	2	0	0.038197	0.070736
BC 345	3	0	0.929465	0.106103
BC 346	15	1	0.878535	0.530517
BC 347	5	0	0.152789	0.176839
BC 348	3	0	0.076394	0.106103
BC 35	2	0	0.114592	0.070736
BC 352	6	2	0.292845	0.212207
BC 353	16	1	0.751211	0.565884
BC 354	1	0	0.114592	0.035368
BC 356	21	2	1.311437	0.778091
BC 357	65	5	2.215437	2.298905
BC 358	1	0	0.038197	0.035368
BC 36	1	1	0.038197	0.035368
BC 361	0	0	0.076394	0
BC 362	197	6	5.10569	6.932082

BC 363	6	0	0.649352	0.212207
BC 364	1	0	0.025465	0.035368
BC 365	9	0	0.687549	0.31831
BC 366	198	16	4.163493	6.896714
BC 367	5	0	0.178254	0.176839
BC 368	42	1	2.521014	1.485446
BC 369	6	0	0.305577	0.212207
BC 37	1	1	0.038197	0.035368
BC 370	6	0	0.178254	0.212207
BC 371	2	0	0.038197	0.070736
BC 38	0	0	0.025465	0
BC 4	31	3	1.044056	1.096401
BC 40	1	0	0.012732	0.035368
BC 41	1	0	0.012732	0.035368
BC 44	2	1	0.127324	0.070736
BC 45	5	1	0.101859	0.176839
BC 47	0	0	0.038197	0
BC 5	53	4	1.871662	1.909859
BC 50	101	1	10.669747	3.748983
BC 51	300	38	17.889015	10.539594
BC 52	37	4	4.010705	1.308607
BC 53	231	20	18.385578	8.099218
BC 57	2088	139	69.200569	73.529587
BC 58	622	24	31.194368	22.387794
BC 59	465	23	19.098593	16.375275
BC 6	2	0	0.114592	0.070736
BC 60	1504	143	51.477074	53.546795
BC 61	773	87	29.029861	27.445385
BC 63	96	8	5.946029	3.359938
BC 67	495	41	19.607889	17.542412
BC 68	378	39	17.379721	13.369016
BC 7	4	0	0.076394	0.141471
BC 70	58	2	3.71786	2.086698

BC 71	30	2	2.368226	1.061033
BC 72	6	1	0.572958	0.212207
BC 73	9	1	0.305577	0.31831
BC 74	223	40	8.174198	7.887012
BC 76	579	67	17.54524	20.442568
BC 77	88	5	4.03617	3.112363
BC 78	3	0	0.089127	0.106103
BC 79	934	141	26.979946	32.998123
BC 80	22	0	0.649352	0.778091
BC 81	8	0	0.254648	0.282942
BC 82	25	0	0.929465	0.884194
BC 83	51	2	1.451493	1.803756
BC 84	8	0	0.292845	0.282942
BC 85	689	130	20.72834	24.403757
BC 86	214	28	8.301522	7.674805
BC 87	28	1	0.878535	0.95493
BC 88	72	3	2.482817	2.581847
BC 89	1	0	0.025465	0.035368
BC 9	11	1	0.356507	0.389045
BC 90	5	1	0.496563	0.176839
BC 91	14	0	0.85307	0.459781
BC 92	34	3	1.082254	1.202504
BC 93	227	32	7.435719	8.028482
BC 94	25	6	0.713014	0.884194
BC 95	42	5	1.54062	1.485446
BC 96	31	1	0.942197	1.096401
BC 97	16	2	0.611155	0.565884
BC 98	7	0	0.369239	0.247574
BC 99	26	1	1.120451	0.919562

BC	2003-2012 vms record point density within 1km radius	2008-2012 trawl density trawl length per km² 5km radius	2008-2012 trawl density trawl length per km² 3km radius	2008-2012 trawl density trawl length per km² 1km radius
BC 10	1.273239	0.3218645	0.314577	0.625692
BC 100	0	0.6743916	0.739397	0.829235
BC 101	1.909859	0.981624	1.263583	2.004853
BC 102	0.95493	1.0916913	0.79008	1.233911
BC 103	2.546479	4.5509524	5.469474	4.607926
BC 104	0	0	0	0
BC 105	0.63662	1.0144846	0.657238	0.329075
BC 106	2.546479	9.782258	9.090721	9.701111
BC 107	7.957747	11.4267263	11.696314	13.124125
BC 108	7.639437	23.1059475	27.739346	32.520702
BC 109	0.31831	3.8976576	0.410354	0
BC 11	0	1.2598686	1.63968	0.445977
BC 110	0.31831	0	0	0
BC 111	0	0.0775702	0	0
BC 112	0.95493	0.3597796	0.072465	0
BC 113	0.63662	0	0	0
BC 114	2.546479	2.05656	0.882648	0.617835
BC 115	0	0.125486	0.202967	0.30753
BC 116	0.95493	0.1878118	0.17217	0
BC 117	0.95493	0.2261697	0.201354	0.197745
BC 118	6.366198	3.8124907	4.114298	2.298619
BC 119	3.183099	1.364051	1.342813	1.435349
BC 12	2.546479	0.7619519	0.60909	0.568112
BC 120	12.414085	20.2946701	21.316305	25.894073
BC 121	0.95493	0.408448	0	0
BC 122	0.95493	3.5456035	3.030698	4.812539
BC 123	3.183099	6.3445902	7.681598	6.787204
BC 124	17.507044	25.2164955	31.602272	39.470146
BC 125	4.138029	3.1532354	3.302676	3.767983
BC 126	1.273239	0.0873559	0	0
BC 129	3.501409	3.5171237	3.166143	2.455952
BC 13	0	0.5062623	0.206072	0
BC 130	2.546479	3.8745182	4.201344	2.156319
BC 131	0	0.0117115	0	0
BC 132	2.546479	1.9321839	2.486419	2.419754
BC 133	0.63662	0.1506765	0.212205	0.636585

BC 135	0	0.1631378	0.2169	0.626818
BC 136	0.31831	0.1516129	0.200984	0
BC 137	0.95493	0.1618484	0.189238	0
BC 138	1.273239	0.1003742	0	0
BC 139	6.047888	20.6047096	22.622345	17.831083
BC 14	0	0	0	0
BC 140	31.512678	28.1088467	34.044235	51.471642
BC 141	0.95493	1.5765932	1.251615	1.558313
BC 142	5.411268	15.0428648	15.626256	22.610504
BC 143	3.183099	14.2253294	12.625756	12.206017
BC 144	9.867606	10.5639095	11.944447	12.931176
BC 145	14.642255	17.985054	17.184595	16.37763
BC 146	1.909859	6.8299327	2.026381	0.622993
BC 147	7.639437	13.0023308	16.650187	11.696737
BC 148	1.591549	0.1247654	0.201806	0.292207
BC 149	0.63662	0.1450506	0.20238	0.274422
BC 150	0.31831	0.2015562	0.295722	0
BC 151	0	0	0	0
BC 152	1.273239	0.0165317	0	0
BC 153	3.819719	6.723454	5.548762	2.806909
BC 154	2.228169	1.0732764	0.439833	0
BC 156	11.140846	7.3113933	8.108754	9.004508
BC 157	8.276057	3.4569063	4.146638	6.074911
BC 158	0	0.2049729	0	0
BC 159	4.138029	1.4436247	1.98726	1.18907
BC 16	0.63662	1.1433613	0.630331	0
BC 160	0.63662	0.2255649	0.217986	0.611116
BC 161	2.864789	0.8632018	0.903878	0.930284
BC 162	28.9662	56.5690918	68.130562	66.180328
BC 163	0.31831	0	0	0
BC 164	0.63662	0.5830635	0.385079	0.91596
BC 165	1.591549	0.1163026	0.16927	0
BC 166	1.591549	2.3602362	1.136944	0.63649

BC 167	21.326763	27.7877426	31.797453	40.051369
BC 168	1.273239	0.2496854	0.311066	0
BC 169	0.63662	1.2624586	0.322182	0
BC 17	0	0	0	0
BC 170	0.31831	0	0	0
BC 171	0.63662	0.0754078	0	0
BC 172	22.281692	78.1970978	96.123932	96.399063
BC 174	0.31831	0.6426435	0.315951	0
BC 175	20.053522	52.0626831	65.387291	89.928429
BC 176	49.974651	77.613411	104.086082	130.661407
BC 177	31.194368	84.3740997	99.527977	111.64875
BC 18	3.819719	0.9016635	1.148834	2.22365
BC 180	0	0.116853	0.144604	0
BC 181	0.31831	0.9985136	0.188717	0
BC 182	11.140846	38.9214134	50.175613	50.386719
BC 183	0	2.5843027	3.694482	4.419129
BC 185	0.31831	0.3328513	0	0
BC 186	0.95493	0.195722	0.21183	0.631252
BC 187	0.31831	0.2929929	0.177292	0
BC 188	0.63662	0.1765942	0.322625	0.815004
BC 189	0	0.1081486	0.024647	0
BC 19	1.909859	2.2587807	3.514667	4.920711
BC 190	0.95493	0	0	0
BC 191	0.63662	0.0868796	0.041048	0
BC 192	0.63662	0	0	0
BC 196	0.31831	0.043865	0.01929	0
BC 197	0.31831	0	0	0
BC 199	0	0.2038484	0.199727	0
BC 20	0	0	0	0
BC 200	0.95493	0.9247395	0.968905	0.607035
BC 201	0	0	0	0

BC 202	0.95493	0.3543505	0.323035	0.635628
BC 204	0.31831	0.1120832	0.135538	0
BC 206	0.63662	2.0200913	2.557761	1.871733
BC 207	0	0.2066893	0.117537	0
BC 208	10.504227	57.8175354	74.252174	71.732765
BC 21	0	0	0	0
BC 210	0.31831	0	0	0
BC 212	0.63662	0.1300733	0.207741	0.489064
BC 213	0.31831	0	0	0
BC 214	0.31831	0	0	0
BC 215	2.228169	43.2649651	28.684299	8.853997
BC 216	21.008453	59.034523	51.785694	43.57613
BC 217	4.456338	3.1286099	4.544284	6.411159
BC 218	0	0	0	0
BC 219	0	0	0	0
BC 22	0.95493	2.3250563	3.171374	3.891253
BC 220	0	0	0	0
BC 221	0	0	0	0
BC 222	0	0	0	0
BC 223	0.31831	0	0	0
BC 224	0	0	0	0
BC 225	0.63662	0	0	0
BC 226	0.31831	0	0	0
BC 227	0.31831	6.450017	2.490616	0
BC 228	3.819719	10.0381107	7.232416	6.000772
BC 229	0.63662	0.1503095	0.208295	0.554557
BC 23	1.273239	0.0228012	0	0
BC 230	0.63662	0.1240903	0.196872	0

BC 231	0.63662	0	0	0
BC 232	0	0	0	0
BC 234	0	0	0	0
BC 235	0	0.0899468	0	0
BC 236	0.63662	0	0	0
BC 237	0.63662	0	0	0
BC 238	0	0	0	0
BC 239	0.31831	0.0584751	0	0
BC 240	0.95493	0	0	0
BC 241	0.95493	0.1537626	0.186552	0
BC 242	0.31831	0	0	0
BC 243	0	0	0	0
BC 244	0.31831	0	0	0
BC 245	0.31831	0	0	0
BC 246	0	0	0	0
BC 247	0.31831	0	0	0
BC 248	2.228169	2.3813791	1.979525	1.364191
BC 249	2.546479	5.9341884	7.180797	8.333181
BC 250	0.31831	0	0	0
BC 251	0	0	0	0
BC 252	0	0	0	0
BC 253	0	0	0	0
BC 254	6.366198	9.2663641	10.577578	6.022558
BC 255	9.867606	13.9184895	20.453701	26.439152
BC 256	4.774648	5.4505548	3.697093	0

BC 257	0.31831	0.0475793	0	0
BC 258	2.228169	2.3639588	2.805758	3.438421
BC 259	0	0	0	0
BC 260	0	0	0	0
BC 262	0.63662	0	0	0
BC 263	0	0	0	0
BC 265	4.138029	5.7448788	4.561473	2.510959
BC 266	0	0.2083338	0.130946	0
BC 267	0	0	0	0
BC 268	0.31831	0.1891689	0.130305	0
BC 271	0.63662	1.6979001	0.567153	0
BC 272	0	0	0	0
BC 274	2.864789	62.1943855	61.589851	16.229301
BC 275	34.059158	106.5900497	141.243591	122.587273
BC 276	0.95493	11.1016874	2.19887	0.334452
BC 277	3.501409	35.1960754	26.67565	30.853598
BC 278	0	0	0	0
BC 279	0.31831	0	0	0
BC 280	3.501409	1.1840686	0.368015	0
BC 281	3.819719	0.5528315	0.084121	0
BC 282	3.501409	3.7051714	2.380236	0
BC 283	0.31831	0	0	0
BC 284	0	0	0	0
BC 285	0	0	0	0
BC 286	0.31831	1.9349401	0.322407	0
BC 287	8.276057	7.7550674	7.228143	4.276348
BC 288	0.31831	0	0	0
BC 289	12.095776	7.1706638	7.465743	7.675076

BC 291	17.507044	8.5768118	12.575662	19.443527
BC 292	0.31831	0	0	0
BC 293	0.31831	0.1182577	0.176873	0
BC 294	1.273239	0.0144807	0	0
BC 296	0	2.563761	2.000998	1.851954
BC 297	0.31831	0.0983041	0.00168	0
BC 298	9.230987	13.8931065	10.73707	7.056746
BC 299	0.31831	0.2789473	0.31926	0
BC 300	8.276057	8.6120129	6.979541	7.419639
BC 301	0	0.747847	0	0
BC 302	0.63662	0	0	0
BC 303	0.31831	0	0	0
BC 304	11.459156	34.2093048	34.322132	41.40015
BC 305	1.909859	2.328177	2.799415	3.633049
BC 306	0.95493	4.9021001	2.056912	0
BC 307	0.63662	2.404577	1.090325	0
BC 308	1.273239	6.167769	0.211282	0.526591
BC 309	0	4.8414006	3.51272	0.914686
BC 31	0	0	0	0
BC 310	13.687325	6.1429086	5.031883	2.833477
BC 311	0.63662	0.8368182	0.294995	0
BC 314	0.31831	0	0	0
BC 315	0	0	0	0
BC 316	0	0	0	0
BC 317	4.774648	2.5720913	3.687852	5.878295
BC 318	3.819719	8.0369949	9.470194	5.372404
BC 319	0	0.8709901	0.405076	0.585926
BC 320	0	0	0	0
BC 321	0.95493	0.4405799	0.179133	0
BC 324	0	0.2444689	0.375654	0

BC 327	4.456338	5.1082649	3.994681	0.44663
BC 328	0	0.5511061	0.137222	0
BC 329	0	0.0956551	0	0
BC 33	0	0	0	0
BC 330	0.95493	1.2501562	0.585462	0.631585
BC 331	0	0.1235978	0.19274	0
BC 332	0	0.1199716	0.176075	0
BC 333	0	0.0891883	0	0
BC 334	0.95493	3.3738556	2.65528	3.130328
BC 337	0.31831	0.4844238	0.237825	0.619647
BC 339	0.63662	2.3587062	1.031613	0.328296
BC 34	0	0	0	0
BC 340	0.63662	1.7428223	1.296179	0
BC 341	7.002818	5.7242827	1.584684	0.625158
BC 342	0.95493	9.6019096	3.164764	0.427529
BC 343	0	15.0472336	6.713401	0.636581
BC 344	0	0	0	0
BC 345	0	0.9351069	0	0
BC 346	0.31831	0.6449925	0.061699	0
BC 347	0	0	0	0
BC 348	0	0	0	0
BC 35	0	0.1216492	0.185394	0
BC 352	0.63662	0	0	0
BC 353	0.31831	0	0	0
BC 354	0	0.0884434	0.049649	0
BC 356	0.63662	0.5737063	0.203745	0
BC 357	1.591549	2.3754044	2.841485	0.638854
BC 358	0	0	0	0
BC 36	0.31831	0	0	0
BC 361	0	0	0	0
BC 362	1.909859	23.9629364	32.537296	21.326885

BC 363	0	0.3464519	0	0
BC 364	0	0	0	0
BC 365	0	0.1443306	0	0
BC 366	5.092958	5.7826943	4.309647	0.017657
BC 367	0	0	0	0
BC 368	0.31831	1.2063369	0.508314	0.152914
BC 369	0	0.0478817	0	0
BC 37	0.31831	0	0	0
BC 370	0	0.0380676	0	0
BC 371	0	0	0	0
BC 38	0	0	0	0
BC 4	0.95493	1.1242449	1.61038	2.700821
BC 40	0	0	0	0
BC 41	0	0	0	0
BC 44	0.31831	0	0	0
BC 45	0.31831	0.0644769	0.107602	0.293296
BC 47	0	0	0	0
BC 5	1.273239	4.6349177	4.008492	5.010834
BC 50	0.31831	31.1626606	12.108688	1.183686
BC 51	11.459156	42.8633003	32.359348	15.925449
BC 52	1.273239	15.5299511	2.794683	1.85656
BC 53	6.047888	15.9084377	10.707407	3.941664
BC 57	45.518314	203.0870361	218.294281	183.991867
BC 58	7.957747	62.0127068	43.789932	20.887756
BC 59	7.002818	44.7012176	37.495544	19.877745
BC 6	0	0	0	0
BC 60	44.563385	60.1230736	64.538246	44.729694
BC 61	27.692961	47.7807922	44.978481	33.955635
BC 63	2.546479	13.2176514	7.720544	2.411555
BC 67	12.732395	35.1852226	33.775463	28.773174
BC 68	12.414085	15.3889217	14.561513	18.945869
BC 7	0	0	0	0
BC 70	0.63662	7.0038347	4.179601	2.468181

BC 71	0.63662	4.588696	1.398136	1.061715
BC 72	0.31831	0	0	0
BC 73	0.31831	0.0245447	0	0
BC 74	12.732395	16.5206337	13.573033	16.999865
BC 76	21.326763	34.9564056	39.242588	29.959892
BC 77	1.591549	8.6656027	8.365638	5.679047
BC 78	0	0	0	0
BC 79	44.563385	76.0682983	93.038185	91.4627
BC 80	0	0	0	0
BC 81	0	0	0	0
BC 82	0	0.2364512	0	0
BC 83	0.63662	1.3305616	1.283614	1.483909
BC 84	0	0.3438504	0.38728	0
BC 85	42.335217	54.6740646	74.110016	143.732162
BC 86	8.912677	25.1923027	23.063581	6.042431
BC 87	0.31831	0.3350175	0.420238	1.150049
BC 88	0.95493	3.2838721	2.161438	0.931154
BC 89	0	0	0	0
BC 9	0.31831	0.2749197	0.213396	0.62888
BC 90	0.31831	1.4144679	0	0
BC 91	0	2.2235429	0.563699	0
BC 92	0.95493	1.1419609	1.199326	2.07854
BC 93	10.185916	26.0946503	30.414116	34.997002
BC 94	1.909859	0.2517476	0.408979	0.540637
BC 95	1.591549	1.3451769	1.624866	1.934638
BC 96	0.31831	0.1242037	0.197423	0
BC 97	0.63662	0.4745857	0.207162	0
BC 98	0	0.3231455	0.271025	0.518832
BC 99	0.31831	0.3327808	0.192619	0

BC	2008-2012 trawl density trawl length per km² 2km radius	2008-2012 trawl density trawl length per km² 200m radius	Modelled 10 year max bottom current velocity (m/s)	Modelled 10 year mean bottom current velocity (m/s)
BC 10	0.11329	0	0.0951485	0.041542
BC 100	0.616063	0	0.129428	0.0721467
BC 101	0.726796	3.1214499	0.14757	0.0852625
BC 102	1.18603	3.1830699	0.198558	0.161461
BC 103	1.86498	0	0.167575	0.137579
BC 104	0.338237	0	0.0575059	0.031326
BC 105	0.186836	0	0.0725585	0.0324538
BC 106	6.4534998	10.8555002	0.0496142	0.0239118
BC 107	10.9307003	15.9463997	0.0727802	0.0367351
BC 108	29.5049	39.0806007	0.0481271	0.0196885
BC 109	0.460473	0	0.0879304	0.0420066
BC 11	2.1640799	0	0.0695815	0.0227668
BC 110	0	0	0.0977575	0.0385079
BC 111	0	0	0.0960648	0.0447757
BC 112	0.106343	0	0.129744	0.0733085
BC 113	0	0	0.140124	0.0886609
BC 114	0.316153	1.88682	0.0661454	0.0364737
BC 115	0.302968	0	0.0783836	0.0435146
BC 116	0.253511	0	0.123352	0.0750618
BC 117	0.303143	0	0.09119	0.0497854
BC 118	3.90604	2.0071299	0.0881462	0.0449194
BC 119	1.16609	0	0.0936413	0.0481121
BC 12	0.905355	0	0.146437	0.0905762
BC 120	22.7798996	34.0817986	0.0442619	0.0179577
BC 121	0.0314906	0	0.126725	0.07222
BC 122	4.2406201	10.3227997	0.0684963	0.0302316
BC 123	10.2145004	0	0.048952	0.0140736
BC 124	37.2883987	51.4179001	0.0352799	0.009216
BC 125	4.3861299	5.8379898	0.0947914	0.040973
BC 126	0	0	0.104537	0.0564748
BC 129	4.6748099	0	0.0525783	0.0164416
BC 13	0.311369	0	0.118645	0.0551991
BC 130	6.0457902	5.1680698	0.0441656	0.0183716
BC 131	0	0	0.0837359	0.0492056
BC 132	3.72735	2.7918799	0.0561134	0.0275871
BC 133	0.318314	3.18014	0.117195	0.0712298

BC 135	0.32018	2.05825	0.13383	0.0786775
BC 136	0.303452	0	0.18547	0.12052
BC 137	0	0	0.121056	0.0681946
BC 138	0	0	0.103737	0.0570756
BC 139	18.7014008	4.8192	0.0891237	0.0455924
BC 14	0	0	0.18072	0.148565
BC 140	25.9505997	42.9864006	0.0757701	0.0406058
BC 141	1.13019	1.41774	0.0715347	0.0382112
BC 142	9.6926298	11.8143997	0.0806293	0.0474637
BC 143	13.2256002	12.9496002	0.0752175	0.0350713
BC 144	12.8299999	9.0558796	0.0787037	0.0357166
BC 145	17.4960995	10.9814997	0.0712212	0.0371735
BC 146	2.5260501	2.4712601	0.0591796	0.0203935
BC 147	9.5867395	0	0.0843764	0.0310414
BC 148	0.30319	0	0.161095	0.10339
BC 149	0	0	0.172222	0.112086
BC 150	0.351006	0	0.178049	0.115399
BC 151	0	0	0.167115	0.0976728
BC 152	0	0	0.178192	0.111362
BC 153	6.8622198	3.68641	0.0931895	0.0407806
BC 154	0.430399	0	0.0913496	0.0425125
BC 156	9.7268295	1.17264	0.0842077	0.0377815
BC 157	4.9176898	5.8113699	0.105115	0.0494355
BC 158	0	0	0.128438	0.0747544
BC 159	1.10911	0	0.121081	0.0641932
BC 16	0.893598	0	0.135843	0.0877166
BC 160	0.317291	1.97066	0.138924	0.0858008
BC 161	0.304099	0	0.142955	0.0860498
BC 162	47.4887009	43.7901993	0.176011	0.0842836
BC 163	0	0	0.194872	0.140396
BC 164	0.579361	0	0.0979307	0.0370977
BC 165	0	0	0.203237	0.125214
BC 166	1.2322	3.18239	0.0538536	0.0171192

BC 167	26.9039001	36.9948006	0.0962936	0.0384217
BC 168	0	0	0.195292	0.112782
BC 169	0.488633	0	0.210035	0.124513
BC 17	0	0	0.171333	0.131967
BC 170	0	0	0.171509	0.114081
BC 171	0	0	0.153333	0.101956
BC 172	67.4047012	66.264801	0.154689	0.0688359
BC 174	0.328735	0	0.072421	0.0261889
BC 175	59.0494995	108.9160004	0.0587706	0.0256939
BC 176	74.2796021	118.2170029	0.17068	0.0791732
BC 177	64.395401	82.2169037	0.123753	0.0651922
BC 18	1.22797	6.0615401	0.16855	0.131926
BC 180	0	0	0.211499	0.127412
BC 181	0	0	0.0411374	0.0143033
BC 182	63.2401009	73.4789963	0.056928	0.01729
BC 183	0.427859	0	0.0539868	0.0178744
BC 185	0	0	0.0521856	0.0193618
BC 186	0.318059	3.0828199	0.104707	0.0547781
BC 187	0	0	0.114434	0.0661071
BC 188	0.477141	0	0.131779	0.0711268
BC 189	0.0360113	0	0.186612	0.113743
BC 19	4.9806299	11.1577997	0.08591	0.0275143
BC 190	0	0	0.198698	0.116589
BC 191	0.0526084	0	0.129482	0.0676151
BC 192	0	0	0.118266	0.0630107
BC 196	0	0	0.139547	0.0733284
BC 197	0	0	0.156435	0.0859407
BC 199	0.29982	0	0.104733	0.0556431
BC 20	0	0	0.206554	0.156991
BC 200	0.249351	0	0.109062	0.0589237
BC 201	0	0	0.102651	0.05116

BC 202	0.318359	3.1143601	0.15312	0.0843009
BC 204	0.213836	0	0.063167	0.0161672
BC 206	0.903951	2.3092	0.0628965	0.0266229
BC 207	0.15814	0	0.0575967	0.0196144
BC 208	90.4005966	86.107399	0.0697895	0.0196431
BC 21	0	0	0.18147	0.125963
BC 210	0	0	0.091715	0.0372835
BC 212	0.313071	0	0.0682977	0.0259996
BC 213	0	0	0.110781	0.0489816
BC 214	0	0	0.218302	0.0985704
BC 215	18.3381004	3.1025801	0.161788	0.0858894
BC 216	48.5810013	35.2588005	0.0503536	0.017557
BC 217	0.8862	3.1777899	0.0639234	0.023768
BC 218	0	0	0.193752	0.0984837
BC 219	0	0	0.147598	0.0737695
BC 22	4.4071498	8.7908697	0.10081	0.0415262
BC 220	0	0	0.173306	0.100816
BC 221	0	0	0.182663	0.102928
BC 222	0	0	0.117291	0.060606
BC 223	0	0	0.182335	0.102475
BC 224	0	0	0.216965	0.106617
BC 225	0	0	0.15259	0.0731859
BC 226	0	0	0.0823563	0.0421946
BC 227	2.3717599	0	0.0565768	0.0159734
BC 228	5.2982702	2.27247	0.114481	0.056047
BC 229	0.31157	0	0.068532	0.0297785
BC 23	0	0	0.205783	0.165715
BC 230	0	0	0.0881727	0.0407557

BC 231	0	0	0.142161	0.0833622
BC 232	0	0	0.0841423	0.0386259
BC 234	0	0	0.103887	0.0432691
BC 235	0	0	0.0970605	0.0450092
BC 236	0	0	0.136232	0.0816808
BC 237	0	0	0.141246	0.0778054
BC 238	0	0	0.130242	0.0744226
BC 239	0	0	0.122215	0.0679819
BC 240	0	0	0.14177	0.0777523
BC 241	0	0	0.122441	0.0678464
BC 242	0	0	0.15259	0.083517
BC 243	0	0	0.134858	0.07166
BC 244	0	0	0.0971757	0.0394146
BC 245	0	0	0.156297	0.0911039
BC 246	0	0	0.125552	0.0605046
BC 247	0	0	0.142819	0.0828228
BC 248	1.73379	0	0.116164	0.0607825
BC 249	6.6533198	9.2343998	0.12708	0.0723746
BC 250	0	0	0.156328	0.0921918
BC 251	0	0	0.149298	0.0811662
BC 252	0	0	0.142001	0.077995
BC 253	0	0	0.149077	0.0903046
BC 254	10.3612003	5.8239598	0.0997273	0.0497457
BC 255	25.2838001	32.8504982	0.105855	0.0517639
BC 256	3.9572101	0	0.114987	0.0605045

BC 257	0	0	0.136341	0.0756025
BC 258	2.9683299	8.6116199	0.121774	0.0638371
BC 259	0	0	0.151636	0.0938189
BC 260	0	0	0.133323	0.0752271
BC 262	0	0	0.148601	0.0875671
BC 263	0	0	0.145164	0.0841994
BC 265	3.0238199	0	0.0917297	0.0430442
BC 266	0.199437	0	0.0837545	0.0358119
BC 267	0	0	0.138993	0.0812525
BC 268	0.201871	0	0.142354	0.0700614
BC 271	0.0767785	0	0.121119	0.0644466
BC 272	0	0	0.162269	0.0940342
BC 274	51.9800987	0	0.0951166	0.0430942
BC 275	129.1679993	81.949501	0.0977334	0.052547
BC 276	2.1080301	0	0.0977174	0.0463748
BC 277	21.3304996	35.6594009	0.127501	0.0679713
BC 278	0	0	0.185227	0.100605
BC 279	0	0	0.153245	0.0832346
BC 280	0.597977	0	0.113084	0.0516979
BC 281	0.109771	0	0.130277	0.0563514
BC 282	3.27459	0	0.124148	0.062369
BC 283	0	0	0.132885	0.0565681
BC 284	0	0	0.134173	0.0665567
BC 285	0	0	0.156939	0.0634643
BC 286	0.256668	0	0.201977	0.104067
BC 287	7.5675702	3.18152	0.226119	0.12887
BC 288	0	0	0.180383	0.0754054
BC 289	7.6331501	15.8177004	0.202193	0.113622

BC 291	13.0382004	17.6954002	0.250516	0.134796
BC 292	0	0	0.235697	0.129754
BC 293	0.262058	0	0.265824	0.146921
BC 294	0	0	0.25194	0.109246
BC 296	2.5722599	6.16433	0.147698	0.0764176
BC 297	0	0	0.196916	0.0897564
BC 298	12.4245996	16.8554001	0.164447	0.0864607
BC 299	0.473626	0	0.130695	0.046205
BC 300	5.7329202	4.2587299	0.125594	0.0595687
BC 301	0	0	0.156147	0.0606854
BC 302	0	0	0.158708	0.0594984
BC 303	0	0	0.117229	0.040332
BC 304	29.8059998	10.2468004	0.0826673	0.0345421
BC 305	4.2301898	9.8530302	0.0602518	0.0238075
BC 306	2.2804101	0	0.0789988	0.022022
BC 307	1.10725	0	0.166162	0.0717245
BC 308	0.311287	0	0.086788	0.0322035
BC 309	2.68135	0	0.104288	0.0424323
BC 31	0	0	0.233012	0.175061
BC 310	4.1210699	3.0259399	0.0950459	0.0406036
BC 311	0.334926	0	0.198486	0.0835795
BC 314	0	0	0.216228	0.0924856
BC 315	0	0	0.201202	0.0961973
BC 316	0	0	0.18652	0.0960229
BC 317	5.20649	8.2986202	0.0970714	0.0396138
BC 318	12.3669996	5.0431199	0.0782215	0.0321027
BC 319	0.0102262	0	0.118088	0.052064
BC 320	0	0	0.149905	0.0695228
BC 321	0.352811	0	0.0678374	0.0210455
BC 324	0.563561	0	0.135475	0.0643444

BC 327	5.4026198	0	0.0862188	0.0319977
BC 328	0.213211	0	0.072152	0.0237052
BC 329	0	0	0.132883	0.058139
BC 33	0	0	0.304322	0.243778
BC 330	0.693592	2.95228	0.0751015	0.0243635
BC 331	0.290547	0	0.0965212	0.0367824
BC 332	0.262378	0	0.120725	0.0528942
BC 333	0	0	0.107161	0.0476426
BC 334	3.9879	3.16804	0.106337	0.0421466
BC 337	0.355852	1.76205	0.147852	0.0641227
BC 339	1.54767	0	0.128394	0.0581264
BC 34	0	0	0.25961	0.191408
BC 340	1.8347501	0	0.121016	0.0392926
BC 341	1.3774101	0	0.152268	0.0599892
BC 342	2.8873	0	0.13736	0.0499624
BC 343	3.0664599	3.18086	0.181076	0.0837549
BC 344	0	0	0.166642	0.0675089
BC 345	0	0	0.0990225	0.030353
BC 346	0	0	0.0684704	0.0175442
BC 347	0	0	0.146923	0.0491518
BC 348	0	0	0.146873	0.0514015
BC 35	0.27785	0	0.23051	0.167426
BC 352	0	0	0.084854	0.0247108
BC 353	0	0	0.0513081	0.0147255
BC 354	0.0698689	0	0.0882152	0.0274115
BC 356	0.282755	0	0.0538596	0.0100689
BC 357	1.68559	3.0811501	0.029883	0.0075163
BC 358	0	0	0.204755	0.0842749
BC 36	0	0	0.335612	0.278396
BC 361	0	0	0.188538	0.0934331
BC 362	21.8551998	4.9124999	0.18134	0.0839567

BC 363	0	0	0.187902	0.09721
BC 364	0	0	0.18108	0.0847941
BC 365	0	0	0.178913	0.0964485
BC 366	2.8271899	0	0.158042	0.0729856
BC 367	0	0	0.141254	0.0690209
BC 368	0.744514	0	0.142803	0.0606616
BC 369	0	0	0.0947524	0.0417184
BC 37	0	0	0.36079	0.268846
BC 370	0	0	0.16958	0.0872851
BC 371	0	0	0.171887	0.0735092
BC 38	0	0	0.350236	0.275643
BC 4	0.316419	0	0.151902	0.107415
BC 40	0	0	0.191081	0.117514
BC 41	0	0	0.264684	0.200857
BC 44	0	0	0.144996	0.106868
BC 45	0.163334	0	0.13943	0.104857
BC 47	0	0	0.146404	0.105308
BC 5	1.75033	1.60509	0.172126	0.130566
BC 50	12.2094002	0	0.290704	0.177737
BC 51	32.4659996	17.8115005	0.24944	0.153767
BC 52	4.0774999	5.3698802	0.301683	0.187536
BC 53	8.3290596	2.16661	0.3154	0.19677
BC 57	165.4409943	108.0619965	0.28805	0.178924
BC 58	45.1915016	8.1426401	0.13469	0.105214
BC 59	21.1702003	12.7924004	0.152407	0.114451
BC 6	0	0	0.179566	0.138502
BC 60	44.0029984	22.5093002	0.153793	0.116897
BC 61	32.882	8.6978798	0.165605	0.116178
BC 63	9.3143702	0	0.21552	0.140086
BC 67	19.5972004	20.8574009	0.160558	0.107696
BC 68	9.2132196	5.5226998	0.188613	0.141402
BC 7	0	0	0.178508	0.132228
BC 70	2.54685	0	0.206542	0.153068

BC 71	1.77045	0	0.176797	0.142493
BC 72	0	0	0.190777	0.149462
BC 73	0	0	0.208453	0.158777
BC 74	7.4328599	10.6953001	0.126324	0.0820269
BC 76	30.4339008	16.816	0.1734	0.12206
BC 77	2.4155099	0	0.109603	0.0696719
BC 78	0	0	0.108765	0.0537101
BC 79	65.6294022	64.6395035	0.14458	0.110231
BC 80	0	0	0.112481	0.0559195
BC 81	0	0	0.0974702	0.0440232
BC 82	0	0	0.114494	0.0608792
BC 83	0.47946	0	0.142704	0.0905434
BC 84	0	0	0.175951	0.138312
BC 85	50.3352013	91.254303	0.168108	0.128664
BC 86	18.1161995	0	0.193467	0.152893
BC 87	0	0	0.124115	0.0658195
BC 88	1.7036999	0	0.157934	0.0980129
BC 89	0	0	0.258493	0.216308
BC 9	0	0	0.0946284	0.0408069
BC 90	0	0	0.216414	0.176351
BC 91	0.584581	0	0.245066	0.199204
BC 92	0.997491	3.16207	0.229498	0.189932
BC 93	21.6410007	46.1227989	0.217915	0.171949
BC 94	0	0	0.111069	0.0461893
BC 95	1.20482	2.3569601	0.0789881	0.0344528
BC 96	0	0	0.0944446	0.0337926
BC 97	0	0	0.0838934	0.0302661
BC 98	0.313179	0	0.0675818	0.0315334
BC 99	0	0	0.110387	0.056373

BC	Modelled bottom temperature 10 year minimum (°C)	Modelled bottom temperature 10 year mean (°C)	Seafloor rugosity (5 cell moving window)	Seafloor rugosity (25 cell moving window)
BC 10	3.59284	4.0479202	0.0000005	0.0000027
BC 100	3.5530901	3.971	0.0000012	0.0000052
BC 101	3.5457201	3.9493001	0.0000008	0.0000049
BC 102	3.4238501	3.75032	0.0000002	0.0000033
BC 103	3.48599	3.85378	0.0000006	0.0000038
BC 104	3.66436	4.12218	0.0000002	0.0000008
BC 105	3.62621	4.0844202	-0.0000001	0.0000004
BC 106	3.6585901	4.1129398	0.0000002	0.0000039
BC 107	3.6398799	4.0920601	0.0000001	0.0000017
BC 108	3.66466	4.1227102	0.0000002	0.0000011
BC 109	3.6113999	4.0546699	0.0000004	0.0004887
BC 11	3.6296599	4.0968499	0.0000005	0.0000212
BC 110	3.6031001	4.03052	0.0000008	0.0000027
BC 111	3.6180401	4.05018	0.0000001	0.0000009
BC 112	3.6108601	4.0503602	0.000001	0.0000017
BC 113	3.6264901	4.0651202	0	0.0000008
BC 114	3.66065	4.12151	0.0000015	0.0000026
BC 115	3.6542001	4.09268	0.0000001	0.0000009
BC 116	3.6465399	4.0837498	0.0000001	0.0000004
BC 117	3.6549001	4.0975399	0.0000014	0.0000066
BC 118	3.6544001	4.13731	0.0000786	0.0004156
BC 119	3.6535599	4.14329	0.0000024	0.0000219
BC 12	3.5718901	4.0194898	0.0000003	0.0000027
BC 120	3.6499801	4.1010599	0.0000002	0.000002
BC 121	3.6080899	4.0444298	0.0000002	0.0000222
BC 122	3.61906	4.0696502	0.0000006	0.0000018
BC 123	3.6703999	4.1240101	0.0000008	0.0000597
BC 124	3.65854	4.118	0.0000013	0.0000117
BC 125	3.6149099	4.0581899	0.0000002	0.0000026
BC 126	3.6165299	4.05408	0.0000001	0.0000014
BC 129	3.6359401	4.0860901	0.0000005	0.0000052
BC 13	3.5973899	4.0555601	0.0000002	0.0000026
BC 130	3.6224501	4.0721202	0.0000002	0.0000049
BC 131	3.6178701	4.05795	0.0000005	0.0000127
BC 132	3.6184499	4.0626502	0.0000002	0.0000297

BC 133	3.6472399	4.0820999	0.0000001	0.0000003
BC 135	3.6299	4.0659599	0	0.0000003
BC 136	3.63569	4.0706301	0.0000001	0.0000002
BC 137	3.67399	4.1245899	0.0000017	0.000019
BC 138	3.6626	4.1195798	0	0.0000015
BC 139	3.65119	4.1996498	0.000002	0.0000196
BC 14	3.49174	3.8879099	0.0000005	0.000007
BC 140	3.6565001	4.1769199	0.0000769	0.0003093
BC 141	3.6573701	4.13727	0.0000001	0.000001
BC 142	3.64784	4.2133598	0.0000189	0.0002307
BC 143	3.62603	4.2320099	0.0000001	0.0000021
BC 144	3.6230099	4.2307301	0.0000002	0.0000012
BC 145	3.64013	4.22121	0.000006	0.0000717
BC 146	3.65698	4.1080999	0.0000392	0.0006741
BC 147	3.6407399	4.0801601	0.000003	0.000533
BC 148	3.65646	4.0848999	0.0000001	0.0000007
BC 149	3.6619301	4.0873899	0.0000002	0.0000011
BC 150	3.6410201	4.0738902	-0.0000001	0.0000002
BC 151	3.63484	4.07161	0.0000005	0.0000039
BC 152	3.6395199	4.0732899	0.0000005	0.0000009
BC 153	3.5982299	4.2396598	0.0000069	0.0001349
BC 154	3.65029	4.1934299	0.0000005	0.0000156
BC 156	3.60741	4.2396202	0.0000016	0.0000055
BC 157	3.6208301	4.2261701	0.0000016	0.0000076
BC 158	3.6729701	4.1356301	0.0000011	0.0000036
BC 159	3.6152799	4.2297902	0.0000128	0.000891
BC 16	3.5544701	3.99053	0.0000027	0.0000153
BC 160	3.67823	4.1401401	0.0000006	0.0000063
BC 161	3.6542399	4.1988502	0.0001469	0.0008143
BC 162	3.6450801	4.0734301	0.0000011	0.0000174
BC 163	3.6713099	4.09023	0.0000001	0.0000034
BC 164	3.66189	4.1054602	0.0000111	0.0000821
BC 165	3.6478801	4.0784602	0.0000001	0.0000007

BC 166	3.67272	4.1407599	0.0005343	0.0033785
BC 167	3.6487	4.0881701	0.0000093	0.0008903
BC 168	3.6405301	4.0725999	0	0.0000004
BC 169	3.64745	4.0780902	0.0000002	0.0000011
BC 17	3.44818	3.8045001	0.0000171	0.0002351
BC 170	3.68346	4.1070399	0	0.0000005
BC 171	3.6731701	4.1614499	0.0000086	0.0000628
BC 172	3.64852	4.0767999	0.0000014	0.0000126
BC 174	3.64382	4.1174598	0.0000024	0.0000417
BC 175	3.6465001	4.11307	0.0000001	0.0000007
BC 176	3.6498101	4.07759	0.0000014	0.0000485
BC 177	3.6375401	4.0750999	0.0000358	0.0001245
BC 18	3.53723	3.96035	0.0000003	0.0000054
BC 180	3.65415	4.2063999	0.0000041	0.0001879
BC 181	3.6333399	4.1386099	0.0000651	0.0004881
BC 182	3.6401601	4.1115599	0.0000104	0.0000595
BC 183	3.6408999	4.1455002	0.0000011	0.0000112
BC 185	3.5817499	4.0662298	0.0000023	0.0011961
BC 186	3.57235	4.0787802	0.000002	0.0000622
BC 187	3.54387	4.0152202	0.0000565	0.0004147
BC 188	3.5269499	3.9569499	0.0000542	0.0155731
BC 189	3.4846001	3.8780701	0.000164	0.017656
BC 19	3.6282401	4.0959301	0.0000065	0.0000558
BC 190	3.4200101	3.7316699	0.0000054	0.000201
BC 191	3.52194	3.9424701	0.0001098	0.0016602
BC 192	3.5373199	3.9728301	0.0002661	0.0014338
BC 196	3.4709499	3.8350699	0.0000834	0.0009372
BC 197	3.4254301	3.76405	0.000209	0.0004058
BC 199	3.5415399	4.0231199	0.0000128	0.0001867
BC 20	3.4419799	3.7904601	0.0000009	0.0000128
BC 200	3.52789	4.0016699	0.0000125	0.0015938

BC 201	3.4898601	3.91751	0.0000586	0.0003696
BC 202	3.47649	3.8833001	0.0000156	0.000072
BC 204	3.6154001	4.1188898	0.0000052	0.0001301
BC 206	3.5629799	4.0467801	0.00001	0.0001314
BC 207	3.5994401	4.1030302	0.0000054	0.0003898
BC 208	3.62603	4.1041498	0.0000048	0.0000312
BC 21	3.36415	3.65114	0.0000074	0.0039034
BC 210	3.5606301	4.0644598	0.0000853	0.0026078
BC 212	3.5685599	4.0457602	0.0000033	0.0001239
BC 213	3.5246201	3.9940701	0.0000015	0.0000416
BC 214	3.5010099	3.93559	0.0000017	0.0001744
BC 215	3.6410699	4.0714302	0.0000013	0.0000121
BC 216	3.6363299	4.08286	0.0000002	0.0000026
BC 217	3.6475101	4.13901	0.0000006	0.0000092
BC 218	3.47843	3.8902199	0.0000915	0.0005884
BC 219	3.5527699	4.0415502	0.0000069	0.0001916
BC 22	3.6079099	4.0743399	0.0000115	0.0000085
BC 220	3.4101901	3.7202401	0.0000193	0.000276
BC 221	3.46348	3.8354101	0.0000176	0.0013992
BC 222	3.5186501	3.9665501	0.0000031	0.0027752
BC 223	3.4444201	3.7874501	0.0000314	0.0015258
BC 224	3.4756	3.87273	0.0000224	0.0001377
BC 225	3.4616899	3.83127	0.0000011	0.0000262
BC 226	3.4583099	3.8364401	0.0000024	0.0000346
BC 227	3.58724	4.0436001	0.0000025	0.0004164
BC 228	3.61622	4.0546098	0.0000002	0.0000037
BC 229	3.5271599	3.9744401	0.0000292	0.0003203
BC 23	3.51893	3.9358201	0.0000006	0.0000228

BC 230	3.5032101	3.9105999	0.0000018	0.0002677
BC 231	3.68134	4.10777	0.0000321	0.0039249
BC 232	3.44171	3.78143	0.0000276	0.0002787
BC 234	3.4805	3.82407	0.001078	0.0058563
BC 235	3.5243001	3.9322901	0.0000046	0.0000363
BC 236	3.6224999	4.2261801	0.0000005	0.000004
BC 237	3.6807401	4.1069102	0.0000479	0.0006286
BC 238	3.63451	4.2361302	0.0000204	0.0001912
BC 239	3.58588	4.2334399	0.0000215	0.0000909
BC 240	3.6770699	4.1642799	0.0000135	0.0003122
BC 241	3.5093999	4.19207	0.0000038	0.000098
BC 242	3.6754701	4.09411	0.0000011	0.000043
BC 243	3.5539601	3.9283099	0.0000103	0.0001271
BC 244	3.43255	3.73125	0.000048	0.0002043
BC 245	3.677	4.1201	0.0000046	0.000083
BC 246	3.4478199	3.7648699	0.0003341	0.0017607
BC 247	3.5132501	3.87479	0.0000009	0.00035
BC 248	3.5352299	4.20329	0.0000302	0.0001923
BC 249	3.6533401	4.2220602	0.0000164	0.0002609
BC 250	3.6314001	4.0433302	0.0000001	0.0000017
BC 251	3.4491701	3.7639999	0.0000377	0.0019931
BC 252	3.38956	3.64832	0.0003103	0.0024809
BC 253	3.53036	3.9017501	0.0000109	0.0001036
BC 254	3.6322401	4.2497001	0.0000219	0.0002735
BC 255	3.47948	4.1766901	0.0000088	0.0000724

BC 256	3.65325	4.2470198	0.0002415	0.0018116
BC 257	3.68753	4.1430502	0.0000654	0.0008578
BC 258	3.66994	4.2480898	0.0000235	0.0006357
BC 259	3.5163901	3.8715701	0.0000107	0.0000939
BC 260	3.59922	3.9798801	0.0000085	0.0001621
BC 262	3.64516	4.0626101	0.0000365	0.0001534
BC 263	3.6484201	4.0694699	0.0000045	0.0000814
BC 265	3.63782	4.25594	0.0016134	0.0070745
BC 266	3.4619901	4.1756802	0.00034	0.0068377
BC 267	3.58077	3.93381	0.0000659	0.0008091
BC 268	3.6812401	4.1154099	0.0032343	0.0096095
BC 271	3.6939199	4.1729498	0.0010104	0.0207813
BC 272	3.53756	3.86359	0.0000744	0.0018019
BC 274	3.6287899	4.2641101	0.0001747	0.0016127
BC 275	3.63028	4.2453198	0.0001185	0.0008466
BC 276	3.6981299	4.2106299	0.0001935	0.000553
BC 277	3.6805401	4.2002201	0.000006	0.0000985
BC 278	3.4853401	3.7913799	0.0000033	0.0006645
BC 279	3.6182599	4.01689	0.0002156	0.001623
BC 280	3.70714	4.2262101	0.0016062	0.0093858
BC 281	3.69121	4.1704602	0.0009218	0.017371
BC 282	3.63343	4.2564301	0.0004809	0.0112203
BC 283	3.65131	4.0366502	0.0000985	0.0004857
BC 284	3.4581399	3.7095699	0.0001959	0.0013384
BC 285	3.5536201	3.83687	0.0001224	0.0020642
BC 286	3.6512499	4.0545998	0.0026979	0.0183175
BC 287	3.7282	4.21346	0.0000411	0.0005905
BC 288	3.5493801	3.8319299	0.000706	0.0169653

BC 289	3.7239599	4.2273102	0.0023082	0.0144924
BC 291	3.71208	4.2164602	0.0000696	0.0011631
BC 292	3.5266299	3.8420899	0.0001709	0.0015421
BC 293	3.5564401	3.89746	0.0010178	0.0033833
BC 294	3.6231999	4.00384	0.0004056	0.0041969
BC 296	3.66605	4.25102	0.0027142	0.0185143
BC 297	3.6101	3.9877801	0.0003044	0.0019861
BC 298	3.6702299	4.2445798	0.0000153	0.0007426
BC 299	3.5426099	3.8301301	0.0014729	0.02539
BC 300	3.68506	4.1662898	0.0011548	0.0455024
BC 301	3.6145999	3.99282	0.0003114	0.0015985
BC 302	3.5394499	3.8217499	0.0000471	0.0014711
BC 303	3.4544101	3.70034	0.0046802	0.0232846
BC 304	3.6656301	4.0947599	0.0049573	0.0174087
BC 305	3.6688199	4.2375698	0.0059702	0.0498785
BC 306	3.6577799	4.0485001	0.0079593	0.0447986
BC 307	3.60411	3.9829299	0.0001172	0.0015523
BC 308	3.6908901	4.2365098	0.0002201	0.003323
BC 309	3.68363	4.2558699	0.0004033	0.0015811
BC 31	3.3594799	3.6345699	0.0012525	0.0102665
BC 310	3.6791601	4.2727399	0.0016169	0.0081723
BC 311	3.6070001	4.0023999	0.0007526	0.0151425
BC 314	3.54232	3.8864901	0.0000076	0.0010359
BC 315	3.4595101	3.72036	0.0013235	0.0292559
BC 316	3.35969	3.5752001	0.0000281	0.0006287
BC 317	3.6660099	4.1108799	0.0000014	0.0002304
BC 318	3.70117	4.2508602	0.0001351	0.001379
BC 319	3.64185	4.0643101	0.0000612	0.0003614
BC 320	3.5434599	3.8855801	0.0001771	0.0043431
BC 321	3.61268	4.3129401	0.0001199	0

BC 324	3.5431001	3.88778	0.0000376	0.0030727
BC 327	3.71404	4.3464999	0.0000439	0.0028102
BC 328	3.6788499	4.3138099	0.0000828	0.0026295
BC 329	3.5814199	3.9377501	0.0002128	0.0016451
BC 33	3.42061	3.7616401	0.0000024	0.0000658
BC 330	3.6817999	4.33356	0.0018841	0.0184397
BC 331	3.6958699	4.1453199	0.0002103	0.0016551
BC 332	3.54123	3.8668799	0.0001604	0.0004796
BC 333	3.6975501	4.1567101	0.0006992	0.0065543
BC 334	3.72663	4.3485799	0.0001189	0.0043525
BC 337	3.7079699	4.16922	0.0028377	0.012301
BC 339	3.75933	4.30586	0.000048	0.0008007
BC 34	3.45647	3.8306201	0.0000019	0.0000973
BC 340	3.7218399	4.2150102	0.0004133	0.003728
BC 341	3.6514101	4.0964799	0.0002275	0.0122774
BC 342	3.7305901	4.2503901	0.0026627	0.0321423
BC 343	3.61761	4.0188198	0.0002403	0.0027871
BC 344	3.55057	3.8986399	0.0000109	0.0030749
BC 345	3.7280099	4.2368999	0.0018277	0.0198557
BC 346	3.7564099	4.3034401	0.0018423	0.0302312
BC 347	3.6292901	4.0526199	0.0000089	0.0003449
BC 348	3.55076	3.9047501	0.0010043	0.0053217
BC 35	3.5697401	4.0311298	0.0000001	0.0000003
BC 352	3.61954	4.02424	0.0001643	0.0004987
BC 353	3.6488099	4.05092	0.0054223	0.0312128
BC 354	3.5821199	3.93155	0.0013046	0.0120134
BC 356	3.7374101	4.3881698	0.001918	0.0056378
BC 357	3.76405	4.2753601	0.0068643	0.017419
BC 358	3.5176599	3.8405199	0.000138	0.0009724
BC 36	3.43016	3.78687	0.0000089	0.0000908
BC 361	3.47384	3.7290699	0.0014049	0.0131974

BC 362	3.67239	4.1300702	0.0002124	0.0019508
BC 363	3.56409	3.9210801	0.0000276	0.0004897
BC 364	3.5046699	3.7994101	0.0000669	0.0020148
BC 365	3.56461	3.9284401	0.0010294	0.0056074
BC 366	3.63571	4.0575199	0.003251	0.0119376
BC 367	3.6010001	3.9886999	0.0004058	0.0019335
BC 368	3.7525101	4.2632699	0.0114446	0.0306876
BC 369	3.68347	4.1351099	0.000176	0.0094073
BC 37	3.1640301	3.3951299	0.0018253	0.0218472
BC 370	3.4823999	3.7881	0.0000227	0.000456
BC 371	3.43172	3.69155	0.0000271	0.0002325
BC 38	3.3185501	3.5631199	0.0001189	0.0005033
BC 4	3.51631	3.9212	0.0000003	0.0000136
BC 40	3.4031999	3.70344	0.0001554	0.0045201
BC 41	3.49476	3.91997	0.0000011	0.0000038
BC 44	3.50494	3.90359	0.000313	0.0037394
BC 45	3.5655401	4.0123	0.0009147	0.0035155
BC 47	3.47542	3.84323	0.0003111	0.0029972
BC 5	3.48364	3.8521199	0.0000001	0.000005
BC 50	3.58657	3.9705501	0.0000128	0.0003391
BC 51	3.6037099	3.99806	0.0000066	0.0002221
BC 52	3.5794101	3.9584701	0.0003063	0.0036838
BC 53	3.6008201	3.9863501	0.0001032	0.0008508
BC 57	3.6444199	4.0752401	0.0000017	0.0003842
BC 58	3.6465299	4.2121501	0.0000231	0.0003067
BC 59	3.5652101	3.9668901	0.0000302	0.0002044
BC 6	3.4145501	3.74418	0.0000156	0.0003423
BC 60	3.6113901	4.0232301	0.0000144	0.00014
BC 61	3.6626999	4.1007099	0.0000002	0.0000038
BC 63	3.5922799	3.98264	0.0001558	0.0008013
BC 67	3.6663101	4.1466298	0.0000015	0.0000996
BC 68	3.5541	3.9417	0.0000075	0.0001833
BC 7	3.35129	3.62696	0.0000008	0.000015

BC 70	3.5711401	3.9592199	0.0000066	0.0000705
BC 71	3.49031	3.8455901	0.000116	0.000378
BC 72	3.4899099	3.8385899	0.0000113	0.0000413
BC 73	3.4681699	3.7989299	0.0000026	0.0000712
BC 74	3.6649599	4.1834402	0.0000163	0.0001738
BC 76	3.6682401	4.1202698	0.0000042	0.0000302
BC 77	3.6064701	4.0250502	0.0000018	0.0000077
BC 78	3.5929401	4.0279002	0.0000001	0.0000041
BC 79	3.55042	3.9474399	0.0000014	0.0000292
BC 80	3.59569	4.0346999	0.0000004	0.0000017
BC 81	3.59378	4.01616	0.0000016	0.0000115
BC 82	3.58622	4.00632	0.0000008	0.0000092
BC 83	3.5643699	3.9760499	0.0000002	0.0000013
BC 84	3.45979	3.8006101	0.0000075	0.0002989
BC 85	3.5134101	3.8891499	0.0000003	0.000006
BC 86	3.48698	3.84936	0.0000011	0.0000204
BC 87	3.562	3.9895401	0.000001	0.0000358
BC 88	3.5501499	3.95383	0.0000001	0.0000036
BC 89	3.35605	3.6323299	0.0000078	0.0006541
BC 9	3.5933599	4.0490499	0.0000005	0.0000029
BC 90	3.43116	3.75665	0.0000052	0.0000641
BC 91	3.42786	3.7535901	0.0000004	0.0000093
BC 92	3.4132199	3.7298901	0.0000009	0.0000041
BC 93	3.4712701	3.8253601	0.0000002	0.0000026
BC 94	3.5815499	4.0127101	0.0000002	0.0000031
BC 95	3.6159101	4.06991	0.0000001	0.0000005
BC 96	3.5866001	4.0322399	0	0.0000009
BC 97	3.6069701	4.0594401	0.0000003	0.0000029
BC 98	3.63205	4.0948901	0.0000003	0.0000015
BC 99	3.5573299	3.98961	0.0000005	0.0000029

BC	Bathymetric position index (25 cell window)	Bathymetric position index (50 cell window)	Bathymetric position index (75 cell window)	Bathymetric position index (100 cell window)
BC 10	-0.241638	-1.25287	-3.23755	-4.4022799
BC 100	1.07996	1.80115	2.2045901	2.7126501
BC 101	-0.421509	-3.4121101	-8.5249004	-14.7428999
BC 102	1.27759	3.37537	5.3800001	8.0130596
BC 103	0.48877	3.18274	4.7193599	6.3698702
BC 104	0.284058	0.424438	5.75494	14.2052002
BC 105	0.461243	1.52606	3.40485	6.1003399
BC 106	1.2605	6.6068702	12.6398001	18.6317005
BC 107	0.717712	1.87	2.5431499	3.1159101
BC 108	-0.925659	3.7781999	17.4314003	31.3824005
BC 109	-15.0998001	-26.4547997	-28.9664001	-25.9836006
BC 11	4.59552	16.1611004	33.3804016	52.1609993
BC 110	-1.32275	-2.73877	-4.9626498	-7.9373798
BC 111	0.356934	-0.555298	-0.903442	-1.80396
BC 112	0.779297	-0.133057	-1.5323499	-4.6359901
BC 113	-0.4104	-0.776489	-1.57397	-3.4285901
BC 114	0.912354	-0.918823	-2.4586201	-5.1988502
BC 115	-0.0561523	-0.873047	-2.10815	-4.1315899
BC 116	0.266724	0.547729	0.549072	0.500366
BC 117	2.4500699	3.08447	2.27563	0.691528
BC 118	-20.5473995	-31.1271992	-38.4679985	-46.2692986
BC 119	4.3682899	4.7541499	1.5929	-2.5167201
BC 12	0.404358	1.76685	2.8585801	4.34656
BC 120	0.0079956	-2.5463901	-5.9398198	-11.0763998
BC 121	-2.0622599	-7.8378901	-12.7715998	-18.0072994
BC 122	0.28595	2.3283701	4.0960698	6.48492
BC 123	1.41351	18.2008991	37.3000984	52.8804016
BC 124	-2.8950801	-6.5233798	-4.2614698	7.6633902
BC 125	1.51563	1.60718	-0.757202	-4.2564702
BC 126	0.0673828	-0.490112	-2.06848	-4.60181
BC 129	1.5058	3.2084999	1.68335	-1.91766
BC 13	-1.3158	-1.40405	-1.39636	1.65924
BC 130	-1.3809201	-9.3873901	-22.7672005	-26.6630993
BC 131	2.07446	2.07898	-1.76563	-8.96387
BC 132	3.5715899	1.27777	-4.5795298	-14.6166
BC 133	0.118896	0.185303	-0.272705	-0.835327

BC 135	0.19458	-0.607788	-2.4588599	-5.4450698
BC 136	0.363403	0.434082	0.253906	-0.530884
BC 137	4.78967	11.6794004	13.8816004	13.4320002
BC 138	-0.963501	-3.52197	-7.0889902	-11.2161999
BC 139	1.26868	3.2059901	4.3540001	7.3562598
BC 14	-0.904419	-3.3768301	-1.88623	6.2578101
BC 140	13.4076004	16.3686008	18.2236996	15.5152998
BC 141	-0.114746	-1.20032	-4.4986601	-9.6870098
BC 142	7.5626202	18.0300007	31.1053009	42.9903984
BC 143	-0.648376	-0.065918	5.3555899	15.6529999
BC 144	0.0239258	0.350403	1.49646	6.60706
BC 145	-6.4103398	-10.0313997	-12.6461	-9.25037
BC 146	10.0024004	8.8168898	28.5070992	51.6082001
BC 147	-21.8423004	-50.8148994	-77.6722031	-100.8339996
BC 148	-0.31311	-2.9256599	-5.0559101	-6.7246099
BC 149	-0.694214	-1.20239	-2.1886001	-3.7990699
BC 150	-0.182983	-0.440918	-0.611572	-1.28027
BC 151	-1.09338	-3.4147899	-6.3919702	-11.2714005
BC 152	-0.992798	-2.3728001	-4.2073998	-6.1366
BC 153	8.2387695	7.4365201	3.21613	4.24261
BC 154	0.220215	0.867981	-0.932251	-4.2087402
BC 156	1.17206	-0.180786	-1.05457	5.7430401
BC 157	-1.40662	-3.75806	-9.5827599	-14.4956999
BC 158	0.605225	-4.6560102	-10.5437002	-16.3822002
BC 159	-23.5205002	-39.8782997	-50.5363998	-61.1330986
BC 16	1.35034	-3.3463099	-3.4809	-2.93823
BC 160	-1.92126	-4.3840299	-10.5586996	-17.2619991
BC 161	-12.1400995	-22.2949009	-30.9286003	-43.2840996
BC 162	-4.5513902	-11.849	-19.6233006	-25.5016003
BC 163	-1.1301301	-3.05615	-5.4910898	-7.9644799
BC 164	3.7092299	29.0993996	70.6857986	120.4520035
BC 165	-0.857666	-1.75427	-3.29895	-5.4201698
BC 166	-52.6086998	-87.0514984	-111.4810028	-108.939003

BC 167	-20.1618004	-51.8079987	-68.6190033	-77.7352982
BC 168	-0.361694	-1.1920201	-3.87537	-8.4384804
BC 169	-0.878052	-2.0258801	-3.5327101	-6.8198199
BC 17	7.8990502	45.5928001	97.6404037	161.6430054
BC 170	-0.309082	-2.9561801	-6.7441401	-11.9961996
BC 171	-1.03479	-7.44031	-15.5640001	-25.8134003
BC 172	2.14099	4.5152602	1.91956	-0.64917
BC 174	1.0992399	23.1315002	64.098999	98.774498
BC 175	-0.811768	-6.17731	-12.5234003	-28.2672005
BC 176	3.12012	3.3563199	-0.338013	-4.8066401
BC 177	9.85254	7.2480502	2.6892099	0.191284
BC 18	1.02728	1.28387	1.54413	3.2370601
BC 180	7.1847501	15.7938004	12.6674004	8.0352802
BC 181	20.8502998	22.0049	1.02777	-7.3424702
BC 182	5.1957402	-3.7535999	-24.6471996	-41.4578018
BC 183	-1.4317	-7.13306	-26.2791996	-59.6422005
BC 185	-28.5398998	-79.8058014	-122.3980026	-161.1710052
BC 186	-4.0830698	-1.20026	4.6209698	10.6182003
BC 187	-15.8383999	-17.0813007	-0.9552	14.6820002
BC 188	103.7490005	115.2710037	87.7870026	62.9630013
BC 189	-137.4909973	-320.7950134	-418.4559937	-455.1210022
BC 19	-6.2645898	5.6167598	21.5482006	36.1743011
BC 190	12.3984003	100.8759995	227.5500031	311.3720093
BC 191	34.0247993	16.2973995	38.8830986	27.1758003
BC 192	15.5824003	80.5121994	94.4082031	87.6315994
BC 196	26.7367992	67.3087997	123.1149979	180.8630066
BC 197	-9.64221	0.739746	14.4827003	32.8264008
BC 199	11.9509001	22.3575993	34.9197006	52.0479012
BC 20	0.767334	44.0822983	89.0708008	137.1369934
BC 200	37.5681992	60.9169998	78.4402008	93.9621964
BC 201	24.4808006	52.3167	78.4901962	96.7139969

BC 202	1.2445101	21.6443005	50.3787994	82.2464981
BC 204	-14.2950001	-54.9109001	-89.0884018	-109.7180023
BC 206	-1.78882	12.4970999	12.9343996	6.2717299
BC 207	19.0317993	16.5149994	18.7784996	19.7411003
BC 208	-4.14502	-28.4761009	-59.5158997	-61.9561005
BC 21	50.9389992	172.852005	266.4159851	278.4790039
BC 210	12.4516001	26.6511002	63.9958	92.3170013
BC 212	-1.13208	-57.448101	-146.5010071	-187.0619965
BC 213	6.2388301	45.8400002	118.8789978	236.5220032
BC 214	-9.1635704	-39.5969009	-98.8401031	-149.2030029
BC 215	-2.88062	-6.65625	-13.4800997	-33.4275017
BC 216	0.605957	-9.28613	-21.9617004	-30.1825008
BC 217	-2.9953599	-15.3605003	-60.2723007	-103.2529984
BC 218	-24.0914001	-25.3826008	-21.5559006	-17.7395992
BC 219	4.8039598	7.6849399	14.4406996	29.1781006
BC 22	-3.2787499	-1.75482	5.4617901	24.0681
BC 220	-1.3207999	23.1399002	78.8134003	150.7630005
BC 221	31.6527004	50.6594009	57.8800011	82.4364014
BC 222	-56.9375	-171.6009979	-238.1560059	-277.4609985
BC 223	-13.2665997	-50.6769981	-59.361599	-36.8619003
BC 224	9.9475098	35.2607002	73.908699	106.447998
BC 225	1.13025	-4.1663799	-11.7918997	-31.3827991
BC 226	1.8063999	0.376099	-5.1226802	-29.2390003
BC 227	-12.7945995	-29.4950008	-30.8910007	-23.1306
BC 228	-0.621094	-27.2192001	-54.892601	-67.7371979
BC 229	-18.0018005	-44.6239014	-65.8302994	-85.935997
BC 23	4.35742	6.7485399	10.0579004	13.2182999
BC 230	25.3656998	66.6707993	88.4119034	106.737999

BC 231	-48.6367989	-102.1299973	-131.3600006	-158.6309967
BC 232	-4.10742	4.5261202	-1.86243	-9.7376699
BC 234	-72.4031982	-120.1060028	-151.0149994	-175.8359985
BC 235	2.77087	1.27332	5.4774199	12.2890997
BC 236	1.56854	22.4543991	55.1010017	97.4019012
BC 237	-26.3311005	-68.5309982	-106.5270004	-138.3090057
BC 238	8.8101797	7.9643602	6.25842	30.8127003
BC 239	2.3217199	-13.5440998	1.75867	44.1735001
BC 240	-17.1965008	-21.5671005	-23.8153	-31.7068005
BC 241	9.4591103	46.3437996	77.2987976	114.8320007
BC 242	5.4301801	9.2668505	-3.2460899	-31.9255009
BC 243	-8.9305401	-11.8660002	-10.8957996	-7.0507798
BC 244	-8.2430401	1.98914	16.5783997	15.0192003
BC 245	-6.3835402	-23.1287994	-48.5327988	-71.2424011
BC 246	-36.0746002	-43.3282013	-43.4249001	-48.2550011
BC 247	16.0202999	43.6567001	68.4658966	93.0653992
BC 248	-11.0551996	-9.6378803	23.7761002	68.2432022
BC 249	1.29419	4.2421899	6.3015099	3.43048
BC 250	0.549438	0.732422	1.51428	3.4497099
BC 251	-4.7979698	7.0822802	5.2981	10.908
BC 252	-54.7703018	-72.3107986	-89.9433975	-115.0630035
BC 253	-8.0657997	-6.7697802	-4.41467	1.80396
BC 254	-7.9116201	-10.9524002	23.0238991	60.1719017
BC 255	-0.736572	28.5811996	66.2343979	106.8150024
BC 256	33.0191994	42.2498016	46.2941017	76.6830978

BC 257	17.323	17.3118992	9.4531298	-7.2301002
BC 258	-5.6473398	-13.1820002	-21.9855003	-29.2898998
BC 259	-3.2694099	4.33533	15.6906996	28.8353996
BC 260	-5.9678998	-9.18787	-11.2960997	-2.44946
BC 262	12.5031996	15.7039003	16.9552994	15.4947996
BC 263	-7.0155001	-7.7744098	-12.4580002	-17.4962006
BC 265	108.2139969	99.1975021	75.8281021	65.876297
BC 266	65.8121033	127.4440002	161.0509949	207.2279968
BC 267	-14.3182001	-61.4264984	-119.7149963	-137.4949951
BC 268	-100.1169968	-149.0529938	-170.003006	-185.628006
BC 271	-155.5050049	-273.3869934	-324.5469971	-350.0769958
BC 272	55.1626015	131.7660065	138.1390076	151.3540039
BC 274	61.4152985	196.9779968	314.95401	374.6690063
BC 275	13.3017998	-17.0666008	-25.8230991	-4.6264
BC 276	28.6359997	85.4574966	89.023201	60.5872002
BC 277	5.9895	16.3034992	32.736599	63.1929016
BC 278	21.2388992	47.8585014	71.1094971	72.387001
BC 279	-3.0546899	-27.4712009	-26.8516998	-16.1905994
BC 280	-112.7089996	-223.9429932	-261.894989	-242.5930023
BC 281	-141.4109955	-218.1369934	-267.1270142	-317.2619934
BC 282	-36.1613007	-119.1080017	-97.8451996	-36.4380989
BC 283	-14.9724998	49.7391014	97.4757996	98.9422989
BC 284	13.0890999	110.0960007	183.345993	216.1490021
BC 285	27.1737003	24.5862999	36.6990013	40.2471008
BC 286	-109.3710022	-67.9207001	-60.4822006	-58.6581001
BC 287	24.1494999	51.4140015	116.7669983	153.5950012
BC 288	132.8350067	118.836998	11.0818005	-79.3977966
BC 289	93.8656998	78.3500977	66.0355988	70.966301

BC 291	-12.7757998	-23.8257999	-30.1826992	7.0243502
BC 292	-42.1110001	-68.5479965	-63.3037987	-52.9916
BC 293	-72.8024979	-61.6183014	-78.2062988	-92.1843033
BC 294	39.7275009	-22.5072994	-60.5522003	-105.9459991
BC 296	163.3589935	164.1829987	165.5460052	245.0059967
BC 297	50.0653992	92.4247971	89.1790009	157.5449982
BC 298	40.1813011	151.9080048	260.1610107	387.7279968
BC 299	-158.7409973	-297.7680054	-340.5020142	-336.2290039
BC 300	-217.4499969	-396.3680115	-453.4620056	-442.3670044
BC 301	0.897705	-186.2359924	-305.9020081	-360.1579895
BC 302	32.2645988	-12.4561005	-72.8606033	-126.5049973
BC 303	152.7559967	151.0209961	101.3740005	34.8264008
BC 304	-137.7570038	-165.7910004	-131.1289978	-6.5327101
BC 305	-245.0549927	-465.9150085	-568.1820068	-583.9849854
BC 306	240.6940002	364.4700012	351.6340027	260.7780151
BC 307	-31.8297005	22.3167992	101.9189987	174.2559967
BC 308	29.3934002	111.8010025	119.6650009	97.7873001
BC 309	-29.1107998	-36.9928017	23.5214996	130.5630035
BC 31	93.110199	161.2299957	135.0130005	84.2328033
BC 310	-112.4749985	-279.8880005	-377.243988	-404.1149902
BC 311	98.5038986	151.7799988	183.8829956	189.1889954
BC 314	-23.1436005	-26.9437008	-11.8202	-0.311035
BC 315	-164.6809998	-270.394989	-307.6359863	-320.5480042
BC 316	1.16357	-19.6732998	13.2510996	91.7382965
BC 317	-11.4534998	-16.6707001	9.7966299	53.8288994
BC 318	4.51086	102.9339981	169.279007	199.2429962
BC 319	-4.03369	25.1100998	79.5447006	94.1177979
BC 320	-25.1868992	-164.5359955	-218.2960052	-261.9580078
BC 321	58.8046989	189.302002	353.303009	396.8399963
BC 324	-57.6315994	-143.2570038	-191.5140076	-214.723999

BC 327	35.3284988	103.3840027	204.7599945	306.0480042
BC 328	45.6641006	131.1809998	168.8679962	204.4869995
BC 329	-14.4995003	-30.9111004	-49.0101013	-69.6527023
BC 33	-7.5255098	-9.5596905	-1.56287	19.4913006
BC 330	-25.2021008	64.4301987	148.5050049	179.6419983
BC 331	5.7465801	78.6423035	88.4815979	69.2340012
BC 332	27.2213001	42.5601006	44.4606018	28.0023994
BC 333	77.114502	38.4926987	-24.7444992	-85.0414963
BC 334	-28.4279995	144.2810059	225.1380005	273.9809875
BC 337	-96.9824982	-124.0680008	-124.3040009	-98.674202
BC 339	-13.6900997	12.1638002	98.7578964	229.2550049
BC 34	0.626587	7.2785602	21.7301998	47.5334015
BC 340	-15.3943996	6.5463901	8.2594004	61.0942001
BC 341	-134.8569946	-275.9779968	-354.5369873	-419.5660095
BC 342	-193.1569977	-356.3559875	-398.5339966	-351.0069885
BC 343	60.0037003	97.4384003	116.4020004	144.9279938
BC 344	-47.9188004	-107.9169998	-132.8990021	-153.5639954
BC 345	151.3190002	137.2890015	145.7489929	180.3820038
BC 346	-159.1269989	-254.8289948	-272.0180054	-269.368988
BC 347	-4.8131099	42.3061981	92.0605011	102.0130005
BC 348	23.6431007	111.7129974	156.4589996	184.3470001
BC 35	0.150757	1.55164	3.7767301	7.1846299
BC 352	4.4418898	2.1947	11.6948004	25.1616993
BC 353	-70.1791	-60.385601	-95.8883972	-127.6480026
BC 354	-81.2469025	-141.7610016	-174.5399933	-205.6840057
BC 356	-45.3986015	-56.8040009	-14.7217999	34.7053986
BC 357	-135.4900055	-148.8110046	-111.4980011	-57.5251007
BC 358	-1.1763901	47.4474983	94.9344025	144.7299957
BC 36	1.73499	6.2540302	13.0718002	23.3866005
BC 361	123.2009964	199.2489929	155.4790039	76.8904037
BC 362	-20.4960995	-31.6886005	-29.8234997	5.93396

BC 363	15.4126997	39.5278015	28.5837002	-2.37341
BC 364	47.4375992	66.0086975	81.6376038	109.5510025
BC 365	92.7046967	135.3699951	157.276001	143.5800018
BC 366	-107.3450012	-202.2810059	-244.6300049	-271.2780151
BC 367	-16.8929005	-12.0770998	-39.2322006	-60.2354012
BC 368	-143.1569977	-173.1210022	-130.052002	-44.2288017
BC 369	96.1048965	218.6109924	271.5289917	238.0509949
BC 37	59.4810982	114.887001	165.8659973	176.0769958
BC 370	30.2844009	79.107399	100.2789993	167.2109985
BC 371	-13.0363998	-19.3584995	-21.4060001	-21.3388996
BC 38	-11.8892002	-5.67554	3.6472199	24.0813007
BC 4	-0.368896	2.51489	6.7779498	10.6773996
BC 40	50.1957016	115.0360031	206.602005	285.1889954
BC 41	2.5636599	5.0078702	8.4580097	15.7063999
BC 44	-52.6674004	-151.4170074	-206.0090027	-225.6640015
BC 45	49.3394012	93.1884003	144.3829956	213.8710022
BC 47	58.2981987	146.7100067	215.1049957	255.2310028
BC 5	0.486206	0.124634	-1.6792001	-3.6054699
BC 50	17.3339996	66.0056992	61.8069	53.5507011
BC 51	-12.5811005	-8.8101797	-0.413452	-0.423706
BC 52	59.5099983	84.6616974	71.4806976	63.5199013
BC 53	-25.7924995	-27.4466991	-42.4854012	-59.9636993
BC 57	7.4016099	3.2025101	1.01868	-7.1991
BC 58	4.4292598	26.4374008	73.0139008	127.4779968
BC 59	11.9254999	31.9764004	64.9417038	99.7761002
BC 6	-19.0879002	-61.1414986	-74.168602	-77.2855988
BC 60	10.7641001	27.7238007	52.2004013	78.1996002
BC 61	1.22601	13.7349997	29.7577991	48.2252007
BC 63	-33.7499008	-48.0488014	-56.9165001	-66.2573013
BC 67	14.4520998	40.7868004	51.5449982	61.1619987
BC 68	1.54626	6.4786401	24.3377991	50.1823997
BC 7	-0.770874	-6.6048598	-13.2515001	-19.6518993
BC 70	-2.8298299	-1.27319	12.9008999	27.5296993

BC 71	20.0422001	26.6007004	34.2919006	49.4623985
BC 72	-7.2504902	-10.4042997	-8.9244404	-6.0264902
BC 73	-6.9072299	-17.6182995	-26.0056992	-35.4928017
BC 74	3.89923	21.2702999	41.5826988	57.1889992
BC 76	-2.7136199	0.859863	14.0186996	34.1996002
BC 77	-2.1368401	-4.1392798	-7.0664101	-10.0139999
BC 78	-3.23071	-16.5771008	-15.6362	-12.5109997
BC 79	-1.81726	4.073	21.6984005	49.4477997
BC 80	-0.0753784	1.74713	4.2699599	6.2061801
BC 81	-4.2629399	-16.2212009	-27.9713001	-39.0158997
BC 82	-2.83289	-5.97229	-8.5904503	-11.4473
BC 83	-0.450073	-2.9982901	-8.0697002	-14.7191
BC 84	-17.5543995	-39.4707985	-48.2421989	-49.8731995
BC 85	2.57043	9.3959999	22.8400993	43.8611984
BC 86	3.8532701	16.3495998	31.6798	52.0775986
BC 87	-2.53894	-9.5274696	-15.3365002	-20.3253002
BC 88	0.66394	-0.196899	-4.0545702	-9.6289101
BC 89	-18.9221001	-28.0412998	-24.1338997	-15.7707996
BC 9	1.25677	0.626465	-1.0854501	-2.4257801
BC 90	3.89856	1.32458	9.9025898	21.6793995
BC 91	3.2901599	9.4726601	19.6581001	32.5283012
BC 92	1.38428	3.8331299	9.2000704	16.6156998
BC 93	1.2789299	6.0675001	14.4661999	26.375
BC 94	1.82446	4.4576402	7.1851802	9.7017803
BC 95	0.838806	3.1215799	7.02771	11.9468002
BC 96	0.826294	3.1756599	6.6207299	11.1751003
BC 97	0.587891	1.96759	4.0538301	6.8183599
BC 98	1.02386	3.6089499	7.88977	11.0346003
BC 99	-0.0672607	0.297729	1.40918	2.4812

BC	Bathymetric position index (125 cell window)	Bathymetric position index (150 cell window)	Multibeam slope angle (°)	Radial aspect from -1 west to 1 east	Radial aspect from -1 south to 1 north
BC 10	-4.3997202	-3.8790901	1.44328	0.655069	0.755569
BC 100	3.0139201	2.8226299	1.18243	0.374222	0.927339
BC 101	-21.5466003	-28.9445	0.459741	-0.147842	0.989011
BC 102	11.9982996	16.9813004	1.28008	0.512674	0.858584
BC 103	8.2424297	9.8790302	0.507354	0.842616	0.538516
BC 104	23.5258007	33.4538994	0.626923	0.170944	0.985281
BC 105	9.5759296	13.8787003	0.53907	0.0748494	0.997195
BC 106	25.6623001	33.2349014	0.531215	-0.523903	0.851778
BC 107	3.0436399	2.7416401	0.65233	-0.883031	0.469315
BC 108	44.7296982	57.6463013	1.29443	-0.825268	0.564741
BC 109	-19.993	-14.4219999	1.15591	-0.955274	0.295722
BC 11	70.7904968	89.9459991	1.13993	0.796713	0.604358
BC 110	-12.8304005	-20.0084991	0.118147	0.497859	-0.867258
BC 111	-4.3499799	-8.61304	0.0387797	0.608097	0.793863
BC 112	-8.7982197	-13.2198	1.15678	-0.9451	0.326782
BC 113	-6.2717299	-9.9738798	0.0578676	0.850883	0.525356
BC 114	-9.8703604	-17.4451008	0.826066	0.713022	-0.701142
BC 115	-6.6416001	-10.0938997	0.188717	-0.359186	-0.933266
BC 116	-0.216675	-2.35449	0.0593843	0.987562	-0.157233
BC 117	-2.1226799	-6.6662598	0.290059	-0.758941	0.651159
BC 118	-54.7853012	-63.4348984	1.01334	0.707475	-0.706739
BC 119	-8.1929903	-14.3864002	1.25098	0.951452	-0.307797
BC 12	6.24438	9.1686401	1.65176	0.94077	0.339045
BC 120	-11.4561005	-4.05475	0.692092	-0.77328	0.634064
BC 121	-23.6355991	-29.0380001	1.41202	-0.893056	0.449946
BC 122	10.2080002	13.9749002	0.775931	-0.919858	0.392251
BC 123	66.9756012	80.6912994	1.94549	-0.772725	0.634741
BC 124	20.3491993	33.0788994	1.37739	-0.883023	0.469331
BC 125	-8.1711397	-12.4019003	0.8622	-0.987271	0.15905
BC 126	-8.02637	-12.2117004	0.609913	-0.849721	0.527233
BC 129	0.605042	10.0257998	1.07433	-0.922771	0.38535
BC 13	15.2360001	31.7730999	1.19423	0.840562	0.541715
BC 130	-17.1655006	-5.7604399	1.06528	-0.94569	0.325071
BC 131	-18.3834991	-30.2448997	0.446488	-0.933286	0.359134
BC 132	-24.7607994	-25.6348	0.905533	-0.943822	0.330453
BC 133	-1.82715	-4.02771	0.0935766	-0.91559	0.402113

BC 135	-9.1090097	-12.7434998	0.0297852	0.68606	0.727545
BC 136	-2.13904	-4.5950899	0.0240215	0.931229	0.364436
BC 137	11.0457001	6.53613	0.120959	0.396082	0.918215
BC 138	-16.2418995	-22.0337009	0.610508	0.913732	-0.406318
BC 139	11.4442997	16.5755997	1.25129	0.685551	-0.728025
BC 14	23.4524994	51.5619011	1.3723	0.816979	0.576667
BC 140	12.4474001	8.5072002	3.5843799	0.97707	0.21292
BC 141	-17.2586994	-28.125	0.731058	0.957409	-0.288736
BC 142	53.7184982	63.2767982	0.849057	0.885289	0.465042
BC 143	27.5296993	41.8391991	0.837055	0.900331	-0.435207
BC 144	18.9113998	33.0377998	0.826897	0.760746	-0.649049
BC 145	3.99475	23.3390007	0.679588	0.942976	0.332861
BC 146	75.6591034	95.8930969	5.2498598	-0.682717	0.730682
BC 147	-101.2600021	-95.2274017	0.297489	0.764046	0.645162
BC 148	-8.2627001	-9.9025898	0.0999595	0.99823	-0.0594742
BC 149	-6.17908	-9.3929396	0.118968	0.716354	-0.697737
BC 150	-3.0601799	-5.91675	0.0129489	-0.374493	-0.92723
BC 151	-23.9379005	-41.5189018	0.456382	-0.985487	0.169748
BC 152	-8.7657499	-14.3156004	0.0599902	-0.0116591	-0.999932
BC 153	14.2368002	28.8603992	1.61062	0.999938	-0.0111285
BC 154	-8.5198402	-13.6527996	1.37091	0.992282	-0.124001
BC 156	17.4577999	31.0091991	1.24423	0.976361	-0.216145
BC 157	-1.24554	12.8646002	1.64432	0.981505	-0.191437
BC 158	-22.1606007	-29.3493996	0.695102	0.958962	-0.283534
BC 159	-49.4692993	-34.0135002	2.0776801	0.37191	0.928269
BC 16	-2.85712	-3.22015	0.752528	0.287173	0.957879
BC 160	-24.4030991	-33.3213005	0.636713	0.74942	-0.662095
BC 161	-58.9174004	-61.0003014	4.8152099	0.976857	0.213895
BC 162	-28.8453007	-30.6989994	1.78154	-0.9986	0.0528976
BC 163	-10.5970001	-19.3658009	0.466693	0.995234	-0.0975104
BC 164	162.2669983	192.5630035	1.77405	-0.982627	0.185592
BC 165	-9.97791	-20.0678997	0.0559222	-0.593242	-0.805024
BC 166	-85.1808014	-67.2259979	2.9679201	-0.748672	-0.662941

BC 167	-81.3735962	-71.4929962	1.43634	-0.0137685	0.999905
BC 168	-19.0358009	-33.675499	0.08208	-0.251514	-0.967854
BC 169	-13.6696997	-27.3169994	0.207456	-0.896162	-0.443726
BC 17	200.4060059	196.5330048	2.17314	0.647507	0.76206
BC 170	-19.3251991	-29.1009998	0.507941	0.991243	-0.132047
BC 171	-37.2378998	-50.8671989	1.538	0.871765	0.489924
BC 172	-2.66626	-2.4492199	2.3873401	-0.982274	-0.187453
BC 174	114.3030014	118.5270004	2.2406199	0.488542	0.87254
BC 175	-51.7967987	-65.697403	0.0518964	-0.447214	-0.894427
BC 176	-8.7741699	-10.2644997	2.1199999	-0.913217	-0.407474
BC 177	-3.8111601	-17.0636005	2.4000199	-0.999294	0.037562
BC 18	6.2764902	11.1070995	1.1602401	0.912668	0.408703
BC 180	32.8689003	76.0578995	2.40868	-0.537798	-0.843073
BC 181	1.27692	9.7814302	2.6570201	-0.962659	-0.270716
BC 182	-57.0158997	-66.5572968	1.0481499	-0.897868	0.440264
BC 183	-80.0994034	-89.7863998	0.949685	-0.812648	-0.582755
BC 185	-210.2980042	-262.5469971	3.1431701	-0.756727	-0.653731
BC 186	22.6702003	47.4576988	3.1740601	0.202806	-0.979219
BC 187	23.6441994	35.1292	3.0878699	0.414927	0.909855
BC 188	96.0428009	151.6309967	8.24296	-0.191763	-0.981441
BC 189	-445.5880127	-420.8900146	4.0109401	-0.917794	-0.397058
BC 19	50.6837006	65.6819992	1.6351399	0.728755	0.684774
BC 190	356.0809937	404.3150024	3.0018799	0.347801	-0.937568
BC 191	38.4402008	68.4481964	6.7494302	-0.348314	-0.937378
BC 192	115.0650024	200.5939941	6.46523	0.822291	-0.569068
BC 196	228.128006	241.5469971	3.36184	0.0972042	-0.995264
BC 197	56.9132996	73.9152985	5.57166	0.607005	-0.794698
BC 199	73.3989029	105.5500031	2.39889	-0.35211	-0.935959
BC 20	166.1380005	190.1880035	2.6480801	0.969901	0.243499
BC 200	116.2900009	149.7890015	3.01806	-0.135359	-0.990797
BC 201	102.8190002	100.3099976	5.37499	-0.355539	-0.934661

BC 202	110.7789993	130.7480011	2.8878601	0.136903	-0.990585
BC 204	-123.6279984	-136.4589996	1.0161901	0.961865	-0.273523
BC 206	-4.3189702	-16.7007999	2.6245201	-0.650189	-0.759773
BC 207	20.6784992	17.8941994	5.1714602	0.891971	0.452092
BC 208	-59.6032982	-63.6226006	0.663117	0.724586	-0.689184
BC 21	256.8309937	232.2429962	1.27834	0.981352	0.192219
BC 210	111.1340027	134.753006	5.6976399	-0.988149	-0.1535
BC 212	-212.0449982	-232.6390076	1.3958499	0.231262	-0.972892
BC 213	351.3410034	431.3710022	0.686679	-0.685675	-0.727908
BC 214	-186.4129944	-208.0019989	1.39847	-0.755347	0.655326
BC 215	-67.1818008	-101.6849976	0.204261	-0.918572	-0.395255
BC 216	-47.296299	-60.9333	0.113654	-0.736618	-0.676309
BC 217	-131.029007	-140.2539978	0.565463	-0.919324	-0.393501
BC 218	-3.0167201	20.2252007	3.42309	-0.20728	-0.978282
BC 219	44.5625992	57.5331001	1.66678	0.991325	-0.131433
BC 22	46.4603996	69.1622009	0.905527	0.938107	0.346345
BC 220	205.8379974	238.8500061	2.4349599	-0.275051	-0.96143
BC 221	131.7030029	197.6699982	2.4679501	0.453812	-0.891098
BC 222	-298.4360046	-315.5280151	0.678425	0.978569	-0.20592
BC 223	23.6898994	93.3058014	1.04296	0.998084	-0.0618678
BC 224	122.9449997	123.6220016	2.4909899	-0.298007	-0.954564
BC 225	-45.2845001	-48.6281013	1.52253	0.0854616	-0.996341
BC 226	-61.0358009	-79.3925018	1.01895	0.582179	-0.813061
BC 227	-12.6138	-10.7677002	2.0346899	-0.998869	0.0475488
BC 228	-68.0950012	-70.637001	0.694862	-0.99546	-0.0951809
BC 229	-101.6119995	-105.5449982	1.62297	0.732567	-0.680695
BC 23	17.9848003	37.1845016	1.51476	0.952615	0.304179
BC 230	122.8759995	138.8049927	1.53866	-0.940062	-0.341004

BC 231	-182.8209991	-202.151001	1.37831	0.974067	0.226259
BC 232	-15.8744001	-16.3640003	0.696724	-0.963605	-0.26733
BC 234	-190.246994	-199.5650024	2.9166501	-0.909336	-0.416063
BC 235	18.8180008	27.2709999	1.16892	-0.999292	0.0376109
BC 236	156.5059967	222.5579987	1.75139	0.787924	-0.615773
BC 237	-162.9669952	-183.9230042	0.759339	0.969241	-0.246113
BC 238	73.0998001	126.348999	2.66046	0.480097	-0.877216
BC 239	90.990799	139.4170074	2.68488	0.690182	-0.723636
BC 240	-44.5349007	-58.2971992	4.4721498	0.675854	-0.737036
BC 241	158.6000061	203.5579987	3.5909901	0.828439	-0.560079
BC 242	-62.3378983	-83.6094971	1.84056	0.677614	-0.735418
BC 243	-1.59436	-0.276489	0.917642	0.0991514	-0.995072
BC 244	7.42419	-3.0415001	2.1255901	0.879386	-0.47611
BC 245	-91.7490005	-110.8310013	1.06376	0.439558	0.898214
BC 246	-54.9653015	-59.4667015	2.9798801	0.588195	-0.808719
BC 247	118.1999969	146.2039948	1.07514	0.649899	-0.760021
BC 248	116.0240021	161.8950043	2.8593099	0.914891	-0.403701
BC 249	10.2528	31.7586994	3.5961399	0.979108	-0.203341
BC 250	4.63098	5.7701402	0.777511	0.217978	-0.975954
BC 251	14.3776999	22.2861004	5.0201702	0.92625	0.376909
BC 252	-131.8159943	-156.0319977	3.7052801	0.993193	-0.116479
BC 253	8.8266602	18.3250008	0.857814	0.989764	0.142715
BC 254	105.2440033	151.8399963	4.3119202	0.847239	-0.531212
BC 255	145.8240051	182.0070038	3.1787	0.549821	-0.835282
BC 256	118.9889984	157.4799957	7.2846298	-0.663332	-0.748325

BC 257	-28.9368992	-47.8499985	1.3626	0.437244	0.899343
BC 258	-17.2987003	-0.937134	5.2657399	0.97584	-0.218488
BC 259	44.0486984	61.6764984	1.13061	0.473158	-0.880978
BC 260	18.6410007	47.9828987	1.50534	-0.331068	-0.943607
BC 262	12.1169004	7.9450698	1.23646	0.124218	-0.992255
BC 263	-20.0494003	-17.2821999	0.993134	0.642291	-0.766461
BC 265	91.3611984	124.9290009	12.2356005	-0.929331	-0.369248
BC 266	260.4190063	306.6340027	11.7441998	-0.881663	-0.471879
BC 267	-154.6719971	-184.302002	7.8499398	-0.776291	-0.630375
BC 268	-195.8939972	-191.8249969	2.4092901	0.816526	-0.577308
BC 271	-358.8269958	-348.7319946	2.3362801	0.90336	0.428883
BC 272	155.3009949	158.4799957	4.1082501	0.999625	-0.0273713
BC 274	400.2640076	412.2950134	4.9168	0.998854	0.0478602
BC 275	18.3171005	41.3964005	4.9896002	0.942144	-0.335208
BC 276	27.6515007	22.2945995	5.7692699	0.848979	-0.528427
BC 277	87.6809998	109.1689987	2.5344801	0.865802	-0.500387
BC 278	69.6230011	69.0651016	7.9962201	0.998142	-0.0609238
BC 279	-11.7874002	-14.1752996	3.98948	0.979837	0.1998
BC 280	-197.6649933	-158.4550018	8.5818596	0.943885	0.330276
BC 281	-298.4259949	-240.0390015	6.05832	0.961498	0.274811
BC 282	31.6117992	101.6809998	19.3577995	0.545036	0.838413
BC 283	33.7825012	-54.0996017	6.5303402	0.975283	-0.22096
BC 284	266.303009	316.7730103	7.2379198	0.46046	0.887681
BC 285	9.8350801	-38.3142014	6.1856499	0.982958	0.183827
BC 286	-87.3516998	-115.2850037	9.5323	0.328383	0.944545
BC 287	226.0870056	298.1629944	4.8150702	0.993536	0.113521
BC 288	-181.9550018	-282.9869995	5.7713099	0.99728	-0.0737107
BC 289	137.0149994	222.2109985	6.4074602	0.689762	0.724037

BC 291	93.1802979	190.3130035	7.7957602	0.997358	0.0726481
BC 292	-45.6594009	-75.5078964	3.5553501	0.949267	-0.314471
BC 293	-103.189003	-135.4120026	5.5731401	0.857348	0.514738
BC 294	-155.4029999	-137.3580017	10.6752996	0.789817	0.613342
BC 296	329.4179993	395.131012	7.89537	0.774121	0.633037
BC 297	185.4290009	190.8769989	5.3374	0.993657	0.112457
BC 298	519.1799927	619.0180054	4.6501999	0.878378	-0.477966
BC 299	-339.9289856	-375.9259949	4.5897498	0.848982	0.528421
BC 300	-421.1069946	-381.2510071	1.4916199	0.89798	-0.440036
BC 301	-364.7170105	-358.9320068	1.65219	0.942587	-0.33396
BC 302	-145.8769989	-170.8090057	7.6440902	0.137194	0.990544
BC 303	-31.9230995	-81.9350967	11.5306997	0.144709	-0.989474
BC 304	121.2559967	205.9909973	3.3445599	0.982742	0.184982
BC 305	-567.8010254	-527.6129761	5.5541201	-0.214465	-0.976732
BC 306	172.8930054	138.1620026	7.0130801	-0.997792	0.066414
BC 307	193.9499969	164.8480072	1.92026	0.0959496	-0.995386
BC 308	97.9821014	128.8139954	8.1188402	0.430003	-0.902828
BC 309	182.973999	215.8930054	2.0001199	0.952106	0.305768
BC 31	63.9508018	35.4669991	13.0557003	0.909045	0.416698
BC 310	-394.3829956	-355.4289856	3.6605799	0.807043	-0.590492
BC 311	179.298996	170.6660004	4.6577001	0.952551	0.30438
BC 314	5.2274199	32.5303001	0.717958	0.818777	0.574111
BC 315	-312.098999	-327.9500122	4.55478	0.812313	-0.583221
BC 316	150.3430023	177.8309937	1.51876	0.307545	0.951533
BC 317	109.6529999	143.4179993	1.44187	0.687558	-0.72613
BC 318	230.852005	231.0220032	1.4871	0.37474	-0.92713
BC 319	77.0663986	57.7645988	4.17698	-0.19583	-0.980638
BC 320	-295.4750061	-324.480011	13.8628998	0.967853	0.251517
BC 321	396.7609863	391.947998	1.20684	0.939995	-0.341188
BC 324	-217.098999	-199.2480011	0.88337	-0.430522	-0.90258

BC 327	410.3619995	506.0320129	6.5289502	0.94502	-0.327012
BC 328	278.7420044	333.6239929	1.42064	0.440421	-0.897791
BC 329	-103.8690033	-156.5670013	6.2148099	0.614258	-0.789105
BC 33	68.1107025	106.7030029	2.94399	0.984094	0.177651
BC 330	207.3540039	239.1109924	7.91043	0.0612492	-0.998123
BC 331	73.5960999	119.7580032	6.5601702	0.0264199	-0.999651
BC 332	18.6026993	-13.5402002	2.7936101	-0.130873	-0.991399
BC 333	-86.3440018	-51.8274994	10.6429996	0.240233	-0.970715
BC 334	340.9630127	404.4750061	7.6114101	0.797792	-0.602932
BC 337	-34.6287003	35.1071014	4.8805399	0.124775	-0.992185
BC 339	329.0499878	421.9880066	8.5832005	0.748015	-0.663681
BC 34	90.5594025	131.5509949	4.47192	0.990456	0.137826
BC 340	126.6699982	181.3990021	7.1504102	-0.237183	-0.971465
BC 341	-471.3210144	-460.0939941	2.68295	0.290519	-0.956869
BC 342	-303.3900146	-250.6380005	12.3353996	0.562236	-0.826977
BC 343	151.1940002	149.4700012	6.43957	-0.823238	-0.567696
BC 344	-177.4819946	-193.2489929	4.5977602	-0.769632	-0.638488
BC 345	227.8000031	278.6430054	6.62466	-0.842575	-0.538578
BC 346	-233.598999	-191.7359924	3.5675099	0.675793	-0.737091
BC 347	116.9349976	119.4720001	0.719338	-0.178197	-0.983995
BC 348	198.8190002	211.451004	4.73142	-0.0419086	-0.999121
BC 35	17.4657001	33.0031013	0.983706	0.97067	-0.240418
BC 352	33.6697006	39.1735001	2.6096499	-0.960309	-0.278938
BC 353	-161.9649963	-187.9349976	14.5670004	-0.801055	-0.59859
BC 354	-235.197998	-267.1489868	3.8259699	-0.998166	0.060535
BC 356	84.0070038	127.3939972	5.62849	0.352601	-0.935774
BC 357	-6.36414	33.9136009	4.5577998	-0.112148	-0.993692
BC 358	169.9889984	189.4689941	2.89869	-0.411129	-0.911577
BC 36	37.0065002	53.8651009	3.7002399	0.978186	0.207731
BC 361	18.3567009	-45.2672997	5.3866901	0.231505	-0.972834
BC 362	82.9324036	174.9980011	12.5277004	-0.407988	-0.912987

BC 363	-16.1119003	-48.5068016	5.2923102	0.605918	-0.795527
BC 364	102.9020004	79.0823975	3.8106599	0.489371	-0.872076
BC 365	104.3899994	36.6400986	4.64186	-0.298713	-0.954343
BC 366	-264.1799927	-209.8179932	9.7214403	0.16856	-0.985691
BC 367	-66.7222977	-84.8389969	4.8555598	0.951825	-0.306643
BC 368	44.2401009	133.022995	5.1402102	0.8095	-0.58712
BC 369	190.1900024	151.7030029	4.4397602	0.0530295	-0.998593
BC 37	147.2810059	102.8850021	12.8506002	0.432057	0.901846
BC 370	206.2330017	213.2899933	1.4026901	0.174524	-0.984653
BC 371	-26.4745998	-47.966301	3.21175	0.607733	-0.794142
BC 38	94.0615005	188.0140076	4.9683099	0.9791	-0.20338
BC 4	17.6842003	31.6968002	1.85497	0.649885	0.760032
BC 40	322.7269897	315.6900024	2.20491	-0.191482	-0.981496
BC 41	32.678299	62.4674988	1.39285	0.873829	-0.486234
BC 44	-300.8179932	-337.8670044	13.5959997	0.987561	0.157235
BC 45	297.4349976	395.3649902	7.0700202	0.89948	-0.436962
BC 47	222.9400024	174.5679932	5.8261499	-0.371112	-0.928588
BC 5	-4.7778301	-5.7452402	0.673101	0.663185	0.748455
BC 50	38.5358009	24.8773994	3.0534899	-0.240628	0.970617
BC 51	-5.1733398	-11.5497999	3.1761401	-0.214313	0.976765
BC 52	54.4580994	37.1455994	0.766844	0.195824	0.980639
BC 53	-74.5178986	-89.9280014	0.841946	0.364087	0.931365
BC 57	-19.6991997	-30.0653	4.7741199	0.574897	0.818226
BC 58	181.4559937	233.2290039	3.44853	-0.504814	0.863228
BC 59	134.7160034	169.6230011	2.73787	-0.350768	0.936462
BC 6	-78.1519012	-78.2317963	1.4359699	0.994003	-0.109356
BC 60	110.0159988	144.2969971	0.22306	0.983009	-0.183558
BC 61	70.0822983	95.5746002	1.20751	0.89507	-0.445926
BC 63	-75.6104965	-81.9599991	3.1749799	-0.268417	0.963303
BC 67	75.5139999	101.6579971	1.32576	-0.535593	0.844476
BC 68	82.4452972	115.947998	1.70011	-0.515855	0.856676
BC 7	-22.3806992	-21.9832001	1.05725	0.700161	-0.713986
BC 70	40.5956993	52.0638008	3.8959799	-0.498431	0.866929

BC 71	69.4261017	89.8541031	5.5820799	-0.460063	0.887886
BC 72	-2.5395501	4.1348901	5.3554101	-0.469897	0.882721
BC 73	-44.699501	-51.5634995	4.49821	-0.51391	0.857844
BC 74	75.3622971	98.6519012	1.55101	0.888595	0.458692
BC 76	57.0509987	85.2316971	0.984605	-0.182559	0.983195
BC 77	-12.0303001	-9.8436298	0.701644	0.669596	-0.742726
BC 78	-11.9525003	-13.0447998	1.39526	-0.786538	0.617542
BC 79	83.7382965	118.9179993	0.135568	-0.976962	0.213415
BC 80	8.8999596	11.0122004	1.42709	-0.64488	0.764284
BC 81	-50.5681992	-65.202301	0.773293	-0.953738	0.300639
BC 82	-14.5629997	-17.9034004	0.497521	0.894225	-0.447617
BC 83	-20.9971008	-26.6238003	0.097089	0.26594	-0.963989
BC 84	-47.1764984	-39.3686981	4.73667	-0.616885	0.787053
BC 85	66.7452011	90.8141022	0.500976	0.675507	-0.737353
BC 86	75.6492996	101.4309998	1.51051	-0.532693	0.846309
BC 87	-25.4375992	-30.6587009	1.2221	0.181326	0.983423
BC 88	-16.3859997	-23.9309006	0.285812	0.494311	0.869285
BC 89	-6.7650099	-8.9471397	3.09673	-0.965458	0.26056
BC 9	-2.6456299	-2.37219	1.13027	0.643537	0.765415
BC 90	36.7120018	52.7403984	3.3655601	-0.724749	0.689013
BC 91	49.4341011	70.0531998	1.49765	-0.0160841	0.999871
BC 92	25.8430996	37.6235008	1.5614901	0.346741	0.937961
BC 93	42.1236992	58.7039986	0.18696	0.996404	0.0847325
BC 94	11.6433001	13.0916996	1.2502199	-0.0160383	0.999871
BC 95	18.1480999	25.4892998	0.758218	-0.207198	0.978299
BC 96	16.6588993	22.7700005	1.15731	0.154913	0.987928
BC 97	10.2502003	14.2454996	0.684465	0.410878	0.91169
BC 98	13.9970999	20.0800991	0.683929	0.510988	0.859588
BC 99	3.8952601	6.0299101	1.3864	0.524909	0.851159

BC	Roughness index (3 cell window)	Standard deviation of bathymetry values (3 cell window)	Sponge density (Kenchington et al 2014) (kg/km²)	Rao entrophy	Functional dispersion	Functional evenness
BC 10	5.32581	1.54256	0.150266	0.122505	0.31634412	0.592418
BC 100	4.03442	1.26405	0.000001	0.151169	0.36448353	0.767287
BC 101	1.37036	0.491894	0.023249	0.165902	0.38989352	0.6713852
BC 102	4.5950899	1.36833	0.000286	0.14499	0.35716598	0.6317508
BC 103	1.8479	0.543981	0	0.141208	0.35655556	0.7667398
BC 104	1.89575	0.670017	0.019872	0.110229	0.28193346	0.5787835
BC 105	1.51416	0.576193	0.000622	0.098343	0.26642595	0.5419072
BC 106	1.91052	0.567539	0.009803	0.08227	0.21898169	0.611683
BC 107	2.3134201	0.697542	0.002	0.115094	0.29958343	0.7077441
BC 108	4.7100801	1.38366	0.015153	0.141463	0.34811084	0.6758571
BC 109	3.7988901	1.23693	0.033592	0.144151	0.35867189	0.7227688
BC 11	4.1795001	1.21842	0.023353	0.097977	0.2759613	0.4960113
BC 110	0.423828	0.133009	0.254036	0.126954	0.33057249	0.4459477
BC 111	0.137939	0.041481	0.220948	0.178849	0.4078892	0.7122013
BC 112	3.85059	1.23647	0.037927	0.144694	0.37351781	0.9028036
BC 113	0.207764	0.0619381	0.377989	0.165466	0.39082932	0.7114995
BC 114	3.0579801	0.883248	0.011993	0.152866	0.36404415	0.7212932
BC 115	0.637695	0.20177	0.109719	0.108458	0.29165073	0.6592513
BC 116	0.18335	0.0639598	0.240099	0.130501	0.33560686	0.6514827
BC 117	1.06274	0.310775	0.270135	0.156196	0.38356788	0.5521103
BC 118	3.81128	1.11983	0.023952	0.178963	0.41439961	0.7230706
BC 119	4.14258	1.33867	0.015339	0.145094	0.3723634	0.5616095
BC 12	5.5406499	1.7664	0.323405	0.142935	0.34524239	0.7721344
BC 120	2.54791	0.739639	0.280877	0.158348	0.3917631	0.5993959
BC 121	4.9602098	1.50907	0.194327	0.163861	0.40130578	0.8721691
BC 122	2.6675401	0.829615	0.051582	0.142188	0.3527058	0.5211302
BC 123	7.1763301	2.0808401	0.332912	0.166928	0.39424971	0.5851287
BC 124	4.8677402	1.4717	0.701543	0.166635	0.3966235	0.5719482
BC 125	2.5819099	0.921175	0.01352	0.125188	0.31598472	0.7495164
BC 126	2.1914101	0.651148	0.043361	0.14572	0.36109509	0.6356623
BC 129	3.6824999	1.14879	0.028932	0.119268	0.30844881	0.5856861
BC 13	4.3239698	1.27677	1.030855	0.155033	0.37803718	0.7354282
BC 130	3.54791	1.13938	0.004101	0.138935	0.34302379	0.6056399
BC 131	1.51477	0.478005	0.01292	0.147557	0.36193731	0.5632239
BC 132	3.01843	0.967478	0.003231	0.121922	0.31338916	0.503173
BC 133	0.320923	0.0998588	0.046967	0.130874	0.33583772	0.71449

BC 135	0.109375	0.0322068	0.137273	0.181598	0.42190444	0.8043985
BC 136	0.0804443	0.025864	0.409583	0.18488	0.42199095	0.6791893
BC 137	0.412476	0.130298	0.068729	0.15871	0.39142077	0.5989175
BC 138	2.11182	0.652835	0.04182	0.134351	0.34103365	0.5882914
BC 139	4.6279898	1.33762	0.001081	0.129538	0.33404138	0.4727551
BC 14	5.0070801	1.46691	5.318373	0.191695	0.43272202	0.8464037
BC 140	11.1415997	3.8394101	0.0001	0.144839	0.35726857	0.550738
BC 141	2.3908701	0.781879	0.017744	0.138841	0.35002715	0.5104301
BC 142	3.0316801	0.913819	0.007439	0.157141	0.37991679	0.5960372
BC 143	2.92804	0.89482	0.019489	0.142572	0.35685714	0.6086444
BC 144	3.0521901	0.883931	0.018019	0.112823	0.28932167	0.5045097
BC 145	2.2609899	0.727675	0.011331	0.130081	0.326707	0.5375934
BC 146	19.5034008	5.6304798	0.105064	0.14625	0.35627526	0.6896147
BC 147	1.09741	0.318587	0.228842	0.103985	0.29583236	0.4826474
BC 148	0.275024	0.106836	0.356261	0.133835	0.33758591	0.6801143
BC 149	0.44104	0.127508	0.621313	0.113372	0.29595759	0.6763635
BC 150	0.0449219	0.0138763	0.445578	0.105858	0.28276831	0.6056363
BC 151	1.37988	0.487451	0.380792	0.127759	0.32886528	0.5700491
BC 152	0.184082	0.065926	0.431768	0.122031	0.31804231	0.6629536
BC 153	4.3975201	1.72348	0.011916	0.148677	0.36315992	0.5263582
BC 154	4.0025601	1.46407	0.008034	0.15072	0.37647118	0.6211728
BC 156	3.8766501	1.3292201	0.011485	0.150175	0.37926819	0.582557
BC 157	5.04211	1.7572	0.01171	0.127798	0.33247202	0.3901404
BC 158	2.25916	0.743073	0.15259	0.154479	0.37801583	0.4687936
BC 159	7.06323	2.22066	0.108461	0.154489	0.36698155	0.6037282
BC 16	2.4625199	0.806098	0.470982	0.162512	0.3905791	0.7131424
BC 160	2.3538799	0.680971	0.396474	0.157625	0.38533577	0.5215666
BC 161	14.9926996	5.16185	0.878602	0.160497	0.3822763	0.7624102
BC 162	4.90063	1.9046299	1.59622	0.145009	0.36708635	0.6503626
BC 163	1.33362	0.49875	8.466702	0.138873	0.33954368	0.5777729
BC 164	5.4335299	1.90065	0.188839	0.201097	0.43886479	0.7068539
BC 165	0.204224	0.0599509	1.430077	0.173422	0.40301821	0.7831958
BC 166	11.0421	3.2416501	0.015595	0.157462	0.38870078	0.6194302

BC 167	4.0384498	1.5378799	0.130489	0.157815	0.3777246	0.7873563
BC 168	0.261963	0.0877259	0.511846	0.108777	0.29342137	0.5738885
BC 169	0.723511	0.221449	2.422476	0.114844	0.30715814	0.5310955
BC 17	8.0177002	2.3275199	1.169433	0.24584	0.49414476	0.9221133
BC 170	1.49292	0.542854	1.701913	0.125003	0.32329026	0.5791659
BC 171	5.4958501	1.64643	2.825592	0.14944	0.366834	0.6684722
BC 172	7.32019	2.55371	2.036067	0.129228	0.34107444	0.5186037
BC 174	7.9766798	2.39518	0.038709	0.19365	0.43200871	0.7161664
BC 175	0.183533	0.0556375	0.029224	0.102111	0.27687834	0.6449863
BC 176	7.3282499	2.2669499	2.103455	0.10952	0.2927825	0.6581147
BC 177	6.6385498	2.5695801	3.066901	0.124334	0.33235196	0.5536979
BC 18	4.0153198	1.24038	2.413412	0.183971	0.42116031	0.6470631
BC 180	8.7211304	2.57725	2.365827	0.177699	0.41487846	0.5275016
BC 181	8.6121197	2.8478	0.078117	0.203958	0.44448633	0.7720298
BC 182	3.6823699	1.12851	0.014985	0.164939	0.39001068	0.6952744
BC 183	3.41382	1.0115	0.061204	0.18169	0.41371295	0.6912508
BC 185	11.6056004	3.36165	0.236107	0.192436	0.42896448	0.7183681
BC 186	9.8262901	3.39486	0.257503	0.158787	0.38192957	0.7086946
BC 187	10.7131996	3.30634	0.641056	0.161032	0.37976064	0.759899
BC 188	25.3938999	8.8630695	0	0.176844	0.40999115	0.7946258
BC 189	13.8304005	4.3169198	0.000059	0.154943	0.37651505	0.6369792
BC 19	6.04602	1.74835	0.020367	0.142943	0.34461633	0.5665958
BC 190	10.1016998	3.21155	0	0.221984	0.46691103	0.8184013
BC 191	22.7443008	7.2492599	0	0.148767	0.36311089	0.6585786
BC 192	23.6294994	6.9433398	0.000059	0.208389	0.45081558	0.7980947
BC 196	9.64429	3.6045301	0	0.172893	0.402723	0.8023912
BC 197	20.5111008	5.97929	0.540738	0.199652	0.43529032	0.8293563
BC 199	8.0792799	2.56426	0.617823	0.176724	0.39385892	0.7214175
BC 20	8.4180899	2.8324599	0.473588	0.187877	0.41491214	0.8141494
BC 200	8.9191303	3.2311599	0.259079	0.171463	0.39508101	0.737006
BC 201	18.1644001	5.7613702	0.19482	0.175833	0.40811731	0.751635

BC 202	8.52637	3.09108	0.548791	0.160203	0.3860055	0.6198548
BC 204	3.27057	1.08603	0.108717	0.136415	0.33681273	0.6587838
BC 206	9.6833496	2.80703	0.252075	0.162803	0.39062251	0.6171073
BC 207	18.2637005	5.5438399	0.187878	0.190636	0.43297054	0.707
BC 208	2.4549	0.710429	0.022599	0.100057	0.25216658	0.6349758
BC 21	3.96436	1.37049	0.085459	0.191029	0.40086352	0.7436053
BC 210	17.0813999	6.1136999	0.073852	0.201018	0.44315843	0.7693144
BC 212	4.39709	1.49221	0.124094	0.182615	0.41772758	0.8979023
BC 213	2.5355799	0.73381	0.017151	0.205449	0.44900553	0.6923767
BC 214	5.1549101	1.4946001	0.124217	0.166695	0.39354122	0.7654162
BC 215	0.705322	0.219683	4.831776	0.108872	0.29722623	0.5940176
BC 216	0.419922	0.121894	0.01658	0.176021	0.41308272	0.6120356
BC 217	1.93933	0.604422	0.090899	0.106244	0.28039401	0.6231907
BC 218	10.5992002	3.6638701	2.111229	0.137	0.3406134	0.597761
BC 219	4.8607202	1.78064	1.855125	0.190699	0.42717401	0.7538666
BC 22	3.05145	0.971195	0.20794	0.158879	0.37486572	0.5905175
BC 220	7.8787799	2.60535	0.091418	0.161306	0.37800144	0.8043604
BC 221	8.6976299	2.64082	6.157172	0.213399	0.45781382	0.8285712
BC 222	2.09412	0.724925	1.148144	0.186746	0.42647684	0.8712829
BC 223	2.99597	1.12058	5.905505	0.166535	0.38353882	0.8288906
BC 224	8.1685801	2.6675701	0.232747	0.177345	0.41180962	0.735135
BC 225	4.30408	1.62664	0	0.136851	0.33079297	0.701279
BC 226	3.7390101	1.09149	0.06138	0.164088	0.38369188	0.6283559
BC 227	5.57727	2.1761799	0.408023	0.146919	0.35807749	0.6562088
BC 228	1.97095	0.742147	20.977606	0.093064	0.24687887	0.6258721
BC 229	6.0050001	1.73878	5.629676	0.165513	0.39165079	0.6519896
BC 23	4.98669	1.6191601	0.628995	0.194878	0.43694514	0.7553408
BC 230	5.16711	1.64649	5.781866	0.140422	0.34441873	0.6347227

BC 231	4.3105502	1.4755	21.165382	0.185033	0.41815139	0.6261
BC 232	2.2581799	0.762949	0.012006	0.169115	0.39994322	0.765129
BC 234	10.1094999	3.2007899	1.071213	0.17604	0.40389513	0.6180495
BC 235	3.1704099	1.24769	5.940724	0.141599	0.34887538	0.7048876
BC 236	6.4291401	1.87183	16.579613	0.176595	0.41645909	0.5362968
BC 237	2.4693601	0.835536	34.54134	0.13646	0.33997982	0.6079498
BC 238	9.4785204	2.8475699	34.240887	0.195993	0.4382092	0.5656931
BC 239	9.9525099	2.8730199	15.824565	0.161681	0.39468602	0.5722499
BC 240	16.5641994	4.7894802	24.615778	0.205671	0.44397693	0.6448601
BC 241	13.0468998	3.84166	9.838553	0.158135	0.38014187	0.6561835
BC 242	6.8161602	1.96856	13.197752	0.181878	0.41832962	0.6999159
BC 243	2.6226799	0.982607	10.491956	0.155866	0.37309856	0.5291254
BC 244	7.4682598	2.27443	0	0.176621	0.40757919	0.6985423
BC 245	3.72998	1.1399699	5.201109	0.136781	0.33743036	0.5375388
BC 246	10.9209995	3.2314999	0	0.19331	0.42983409	0.7719106
BC 247	3.9620399	1.14869	0.270713	0.168522	0.39780608	0.605672
BC 248	9.8836699	3.0617001	2.758047	0.168033	0.39926084	0.6662877
BC 249	11.1466999	3.84655	3.603846	0.18461	0.42259497	0.4510486
BC 250	2.43433	0.830818	4.465073	0.184698	0.42403172	0.6790291
BC 251	17.1504002	5.3803802	0.649431	0.17274	0.397727	0.7113212
BC 252	10.802	3.9809599	0.07869	0.146451	0.35062312	0.7187503
BC 253	2.5651901	0.920209	3.323554	0.156906	0.379928	0.651498
BC 254	15.5909996	4.6171699	2.092045	0.17116	0.41097815	0.537622
BC 255	11.5409002	3.40172	1.628093	0.147293	0.36000473	0.579984
BC 256	27.0578995	7.8345299	2.461137	0.190957	0.43286611	0.5440107

BC 257	4.7880902	1.47483	4.377264	0.173819	0.40424969	0.754635
BC 258	16.5233994	5.6367898	3.819099	0.143902	0.35369293	0.418338
BC 259	4.0296602	1.21488	1.46499	0.128745	0.32880521	0.6764947
BC 260	5.0283198	1.61103	6.333755	0.140213	0.3467229	0.694736
BC 262	3.6110799	1.32375	3.362164	0.167938	0.39284843	0.7313626
BC 263	3.6663799	1.0631599	3.818937	0.164752	0.39366973	0.7126445
BC 265	42.358799	13.3130999	5.285128	0.176833	0.41361163	0.7219164
BC 266	42.1230011	12.7313995	2.593151	0.185371	0.425972	0.6689669
BC 267	29.1646996	8.4517298	5.382258	0.135729	0.33753599	0.6866782
BC 268	8.8085899	2.98334	12.693507	0.178819	0.41040778	0.5392238
BC 271	8.6925001	2.6087799	8.860729	0.179481	0.41454197	0.6972699
BC 272	11.4273996	4.39885	5.075793	0.135021	0.33383699	0.6159781
BC 274	13.7547998	5.2781301	6.09224	0.168081	0.40040371	0.3846308
BC 275	16.7325001	5.3580899	7.472814	0.175867	0.41154208	0.533943
BC 276	20.8570995	6.1929302	14.129236	0.131933	0.33101324	0.4798756
BC 277	9.0585899	2.70961	9.905922	0.133573	0.33340979	0.5755188
BC 278	22.3097	8.6022396	2.188229	0.142829	0.35800767	0.5200135
BC 279	12.2896004	4.2881699	15.596958	0.153726	0.36541527	0.5361018
BC 280	28.8372002	9.2769403	2.927872	0.126399	0.33002066	0.5550577
BC 281	19.7199993	6.5303102	0.245793	0.097188	0.28817484	0.5938001
BC 282	72.9262009	21.5102005	0.038058	0.157765	0.39145522	0.5282054
BC 283	20.5048008	7.0082102	1.771026	0.173674	0.40424707	0.6078873
BC 284	25.6189995	7.7775102	0.77718	0.143372	0.34721569	0.7899436
BC 285	18.9864998	6.6441898	0.039067	0.165108	0.39708409	0.7210932
BC 286	31.9619007	10.3569002	2.026732	0.184472	0.42514038	0.6851549
BC 287	13.9743004	5.1584301	3.585548	0.13859	0.34329061	0.5471553
BC 288	16.7837009	6.2056499	0.162567	0.14411	0.3564262	0.5757114
BC 289	23.8610992	6.95154	2.154936	0.150595	0.37594966	0.5731484

BC 291	21.7751007	8.3714304	2.19478	0.161412	0.39971777	0.4217863
BC 292	11.7684002	3.8128099	4.52493	0.133908	0.34552682	0.6385321
BC 293	20.0326004	6.00139	3.881186	0.132864	0.34619785	0.6078893
BC 294	39.6831017	11.5489998	0.121507	0.133772	0.35078041	0.6618249
BC 296	29.1478996	8.5541201	0.954976	0.169189	0.40168589	0.5481092
BC 297	15.4507999	5.7308402	1.409912	0.191435	0.43238765	0.6484294
BC 298	16.5645008	4.9834599	0.096937	0.169834	0.40720791	0.4825142
BC 299	16.5119991	5.0230098	0.098533	0.029092	0.09488832	0.5333564
BC 300	5.1828599	1.7237999	0.135368	0.148065	0.36862782	0.4541968
BC 301	5.5401602	1.79296	0.010385	0.163414	0.39603667	0.6552913
BC 302	22.6896992	8.22085	0.0017	0.142576	0.35297878	0.6209694
BC 303	34.7661018	12.5769997	0.026786	0.183797	0.42023785	0.6212546
BC 304	12.3169003	4.0038099	0.07929	0.158698	0.3883559	0.6361514
BC 305	20.2789001	6.3501101	0.143838	0.116744	0.3166862	0.4480541
BC 306	22.9540005	7.8060899	0.054306	0.198046	0.43688653	0.6620408
BC 307	5.5423598	2.0738699	0.000655	0.223606	0.46770203	0.5871519
BC 308	28.6856995	8.7638502	0.091712	0.183331	0.42236984	0.5364366
BC 309	6.97717	2.1846299	0.040081	0.166637	0.4013578	0.5618491
BC 31	46.1516991	14.2347002	7.163545	0.166434	0.3772997	0.7192341
BC 310	13.6084003	4.0533199	0.034637	0.159017	0.38847277	0.6267091
BC 311	15.2334003	5.0134501	0	0.152936	0.37500621	0.6828503
BC 314	2.6224401	0.773676	0	0.163286	0.39594644	0.6258988
BC 315	16.8367004	4.97439	0	0.148426	0.34574269	0.739347
BC 316	4.9527602	1.62185	0	0.19844	0.43540071	0.6859652
BC 317	5.3372798	1.5419199	0.021693	0.16444	0.39048292	0.6515073
BC 318	5.0499902	1.60298	0.040117	0.157707	0.36992151	0.6525361
BC 319	12.8961	4.4766798	0.000007	0.164201	0.39648261	0.8308546
BC 320	45.0915985	15.1141005	0	0.159059	0.38507513	0.7128485
BC 321	4.0990601	1.31478	0.184839	0.080049	0.17846698	0.5669377
BC 324	3.0794699	0.958575	0	0.181556	0.41711494	0.6192919

BC 327	21.7493992	7.00212	0.053092	0.153465	0.37938789	0.5667638
BC 328	5.0328398	1.53369	0.247548	0.16775	0.40202023	0.577142
BC 329	22.9260006	6.67168	0.000845	0.199312	0.43855398	0.7527277
BC 33	8.96558	3.15026	19.25453	0.159902	0.38510807	0.6218666
BC 330	22.4130001	8.5770197	0.135886	0.182462	0.42213952	0.5575085
BC 331	18.2332001	7.0499001	0.034999	0.207839	0.44254956	0.7438097
BC 332	8.2114296	3.0060999	0.007346	0.158775	0.37479416	0.6499513
BC 333	34.1068993	11.5304003	0.013097	0.207186	0.44532455	0.6426778
BC 334	28.0979996	8.18641	0.009379	0.17875	0.41681659	0.501281
BC 337	16.1685009	5.34021	0.028099	0.053254	0.23076923	NA
BC 339	32.0073013	9.2486601	0.015227	0.176372	0.41264985	0.625741
BC 34	13.2296	4.7885499	19.897259	0	0	NA
BC 340	22.7273006	7.7041001	0.04075	0.151969	0.36738275	0.6123533
BC 341	8.8964796	2.8862901	0.021274	0.114618	0.28867952	0.692988
BC 342	45.5956993	13.4935999	0.025908	0.182376	0.42072828	0.6131213
BC 343	23.5128002	6.9191799	0.0111	0.228139	0.47028462	0.7139632
BC 344	16.9885006	4.9251299	0.004274	0.151767	0.36797908	0.6325072
BC 345	24.0720005	7.16608	0.046818	0.189492	0.42559315	0.6819845
BC 346	13.0352001	3.87344	0.012419	0.150202	0.36431035	0.674968
BC 347	2.18225	0.772112	0.005951	0.184883	0.41863805	0.7352266
BC 348	14.8484001	5.16541	0	0.136424	0.34758096	0.7992609
BC 35	3.1159101	1.0512201	20.944201	0.180394	0.40517634	0.774001
BC 352	8.4877901	2.82812	0.001246	0.146522	0.3384644	0.7155914
BC 353	54.6026993	16.1443005	0.001719	0.181365	0.40549171	0.8202741
BC 354	10.9394999	4.1810298	0	0.205655	0.44748143	0.7039945
BC 356	19.1026993	6.0860801	0.00983	0.176865	0.41124222	0.5036577
BC 357	18.0340996	5.4533901	0.003031	0.132661	0.34403754	0.772784
BC 358	10.0727997	3.1224201	0	0.148505	0.37558342	0.7654842
BC 36	11.4819002	3.96034	22.572979	0.196006	0.43960375	0.8842199
BC 361	17.0851994	5.8320198	-9999	0.188532	0.42629445	0.763319
BC 362	43.8917007	13.6041002	0.021967	0.187468	0.42885987	0.576638

BC 363	19.4584999	5.6754699	0.013245	0.175731	0.41314142	0.6922418
BC 364	13.5839005	4.0832901	0.003742	0.186937	0.41573348	0.7618346
BC 365	15.1845999	5.0067902	0.019906	0.185722	0.41690468	0.6107159
BC 366	29.7922001	10.5511999	0.027122	0.183915	0.41780589	0.7589265
BC 367	16.0552006	5.2430301	0.009688	0.185895	0.4228576	0.6010454
BC 368	18.8225994	6.2358699	0.030336	0.175666	0.41816927	0.96832
BC 369	12.2108002	4.7678599	0.081927	0.188285	0.42780478	0.6275
BC 37	45.6819992	14.0091	0.248634	0.17683	0.40989914	0.8127718
BC 370	4.26123	1.5026799	0.000032	0.146966	0.35459811	0.7619408
BC 371	11.8177004	3.44086	0	0.145042	0.35342903	0.7212534
BC 38	15.3577003	5.3224401	2.660611	0.133649	0.3567966	0.7450162
BC 4	6.8392301	1.98236	1.449766	0.146596	0.35624382	0.7387947
BC 40	6.7985802	2.3724101	13.33863	0.180761	0.4061074	0.8380895
BC 41	4.96631	1.4897799	31.946341	0.128343	0.31526814	0.699755
BC 44	41.5507011	14.8305998	1.992655	0.191423	0.4286197	0.635687
BC 45	25.0109005	7.6686802	1.471683	0.149029	0.35929436	0.7088695
BC 47	20.0112	6.2751698	0.755065	0.19275	0.42163296	0.792827
BC 5	2.49475	0.720203	0	0.133085	0.33156227	0.653659
BC 50	9.6982403	3.2688701	0.015067	0.167511	0.38983641	0.6722763
BC 51	9.91541	3.39768	0.017261	0.163205	0.38714693	0.7708418
BC 52	3.0246601	0.886541	0.006993	0.169878	0.40258447	0.6764961
BC 53	2.8715799	0.920383	0.000121	0.196533	0.43843034	0.5843363
BC 57	17.4666996	5.1160002	0.004047	0.147542	0.36271269	0.6883803
BC 58	12.3620996	3.6937699	0.026798	0.168934	0.39571433	0.5760192
BC 59	9.2648296	2.93452	4.95156	0.136522	0.3516362	0.4968766
BC 6	4.1351299	1.5369	1.697636	0.18898	0.42748025	0.7137148
BC 60	0.780151	0.25529	4.640854	0.155979	0.38515514	0.5169121
BC 61	4.24194	1.29094	3.154047	0.153193	0.3840161	0.8023177
BC 63	10.2347002	3.40484	0.079129	0.165082	0.39598532	0.5542025
BC 67	4.79181	1.4177001	0.0564	0.175954	0.41482527	0.4990896
BC 68	6.10535	1.81756	7.081107	0.129337	0.31814298	0.741678
BC 7	3.9039299	1.12918	0	0.164034	0.39331461	0.6863676
BC 70	13.9408998	4.1709499	0.374978	0.18101	0.41472832	0.6567352

BC 71	19.8521996	6.0006299	22.036587	0.18249	0.41901158	0.5437635
BC 72	19.0098991	5.7402601	4.627711	0.100752	0.26649762	0.6268994
BC 73	16.1989002	4.8192701	6.400169	0.194206	0.43224985	0.6745241
BC 74	5.4169302	1.66219	0.005751	0.152211	0.37652467	0.4846384
BC 76	2.98926	1.05244	0.450278	0.136563	0.34403658	0.5510021
BC 77	2.5996101	0.751355	4.482356	0.166036	0.39464321	0.8709011
BC 78	5.1406298	1.4926	0.049871	0.144403	0.35928908	0.755723
BC 79	0.477661	0.151703	8.957119	0.170163	0.39600368	0.7744123
BC 80	5.2634902	1.5255001	0.033426	0.139266	0.35462553	0.6728343
BC 81	2.5367401	0.826422	0.084457	0.164276	0.39050613	0.7689529
BC 82	1.75757	0.534049	1.259825	0.108682	0.28796425	0.6446906
BC 83	0.31897	0.104844	0.211381	0.163222	0.39784509	0.7671423
BC 84	17.4580994	5.07512	7.108299	0.174109	0.40365377	0.7241528
BC 85	1.85291	0.535584	2.87872	0.121652	0.32431604	0.4927047
BC 86	5.4477501	1.61462	12.115713	0.134901	0.35248949	0.6751915
BC 87	3.70996	1.3053401	0.478767	0.123018	0.31565949	0.8013893
BC 88	1.02124	0.305766	0.770835	0.189513	0.42891508	0.9017813
BC 89	9.96387	3.3130901	12.40034	0.200465	0.44192094	0.7090629
BC 9	4.1744399	1.20885	0.149004	0.158161	0.371353	0.8154237
BC 90	12.4347	3.59794	9.439569	0.119525	0.30637409	0.6752791
BC 91	3.98242	1.60114	10.934052	0.108185	0.29162368	0.5826874
BC 92	5.2585402	1.66993	1.572325	0.181519	0.41644954	0.7561976
BC 93	0.538696	0.200221	10.493631	0.08467	0.23320666	0.6324684
BC 94	3.32581	1.33654	0.003574	0.081336	0.22690006	0.7075155
BC 95	2.3540599	0.81036	0.002875	0.127845	0.32380595	0.6529509
BC 96	3.4630699	1.23713	0.000886	0.100082	0.27575566	0.689679
BC 97	2.3849499	0.733033	0.004347	0.099244	0.26660301	0.6641215
BC 98	2.4570301	0.731375	0.041614	0.177649	0.40746608	0.7234246
BC 99	4.9982901	1.48225	0.013871	0.166915	0.38316895	0.7244421

BC	Family Richness	Pielou's *J'*	Shannon-Wiener H
BC 10	23	0.701044	2.198121
BC 100	17	0.756095	2.142178
BC 101	13	0.798562	2.04827
BC 102	21	0.773839	2.355971
BC 103	6	0.935945	1.676988
BC 104	17	0.54651	1.54838
BC 105	13	0.677607	1.738027
BC 106	13	0.492928	1.264336
BC 107	13	0.64004	1.641671
BC 108	19	0.647066	1.905247
BC 109	15	0.723565	1.95945
BC 11	21	0.633195	1.927775
BC 110	16	0.685419	1.900384
BC 111	14	0.818001	2.158751
BC 112	6	0.866133	1.551901
BC 113	21	0.836118	2.54558
BC 114	17	0.7518	2.130011
BC 115	16	0.647482	1.795201
BC 116	16	0.771191	2.138197
BC 117	18	0.758477	2.192281
BC 118	9	0.895983	1.968677
BC 119	13	0.757357	1.942581
BC 12	16	0.740133	2.052084
BC 120	8	0.638271	1.327248
BC 121	8	0.896508	1.864237
BC 122	16	0.796124	2.207325
BC 123	20	0.779288	2.334539
BC 124	18	0.801719	2.317265
BC 125	12	0.731139	1.816812
BC 126	18	0.799727	2.311508
BC 129	18	0.639278	1.847752
BC 13	12	0.828537	2.058837
BC 130	18	0.694005	2.005933
BC 131	20	0.770687	2.308773
BC 132	19	0.729161	2.146969
BC 133	14	0.843918	2.227149

BC 135	7	0.942681	1.834372
BC 136	6	0.786274	1.408813
BC 137	17	0.797065	2.258254
BC 138	15	0.743703	2.013984
BC 139	20	0.567871	1.701191
BC 14	12	0.942853	2.342903
BC 140	14	0.710271	1.874445
BC 141	18	0.721085	2.084205
BC 142	15	0.711672	1.927242
BC 143	13	0.714144	1.831744
BC 144	14	0.523096	1.380481
BC 145	15	0.63751	1.72641
BC 146	20	0.761862	2.282335
BC 147	19	0.75861	2.233681
BC 148	21	0.702684	2.139337
BC 149	18	0.68428	1.977824
BC 150	18	0.636394	1.839416
BC 151	19	0.721668	2.124907
BC 152	16	0.731741	2.028818
BC 153	20	0.705966	2.114886
BC 154	12	0.857301	2.130312
BC 156	17	0.715937	2.028403
BC 157	17	0.698992	1.980393
BC 158	20	0.741687	2.221895
BC 159	12	0.68058	1.691178
BC 16	12	0.86801	2.156923
BC 160	18	0.753826	2.178839
BC 161	11	0.752303	1.803944
BC 162	15	0.79247	2.146048
BC 163	20	0.719988	2.15689
BC 164	17	0.864209	2.448489
BC 165	13	0.820294	2.104012
BC 166	15	0.844532	2.287036

BC 167	15	0.800773	2.168533
BC 168	18	0.650522	1.880249
BC 169	19	0.753865	2.219709
BC 17	7	0.97957	1.906155
BC 170	14	0.766738	2.023467
BC 171	20	0.821797	2.461883
BC 172	16	0.807604	2.239154
BC 174	16	0.856479	2.374665
BC 175	20	0.656258	1.965972
BC 176	16	0.657234	1.82224
BC 177	18	0.779612	2.253369
BC 18	12	0.804293	1.998592
BC 180	19	0.756585	2.227718
BC 181	15	0.873794	2.366277
BC 182	16	0.735238	2.038514
BC 183	13	0.89792	2.303119
BC 185	18	0.90012	2.601682
BC 186	11	0.867473	2.080108
BC 187	10	0.885836	2.039713
BC 188	13	0.931459	2.389145
BC 189	13	0.790439	2.027437
BC 19	22	0.726717	2.246314
BC 190	9	0.941735	2.069202
BC 191	16	0.814472	2.258196
BC 192	19	0.909863	2.679036
BC 196	12	0.938947	2.333197
BC 197	17	0.931198	2.638284
BC 199	16	0.832696	2.308723
BC 20	14	0.845747	2.231975
BC 200	17	0.87261	2.47229
BC 201	11	0.889545	2.133035

BC 202	13	0.801169	2.054959
BC 204	21	0.720162	2.192549
BC 206	16	0.821329	2.277207
BC 207	18	0.879635	2.542473
BC 208	16	0.485399	1.345812
BC 21	4	0.828871	1.14906
BC 210	17	0.914808	2.591846
BC 212	8	0.861054	1.790512
BC 213	15	0.902629	2.444364
BC 214	16	0.886834	2.458825
BC 215	20	0.713666	2.137952
BC 216	16	0.81753	2.266673
BC 217	13	0.650337	1.668082
BC 218	17	0.78067	2.211805
BC 219	20	0.885039	2.65134
BC 22	22	0.776376	2.399811
BC 220	10	0.912163	2.100332
BC 221	15	0.932817	2.526115
BC 222	8	0.929966	1.93381
BC 223	12	0.911482	2.264949
BC 224	14	0.865455	2.283986
BC 225	11	0.917209	2.199372
BC 226	14	0.71227	1.879721
BC 227	23	0.789916	2.476778
BC 228	24	0.562409	1.787367
BC 229	18	0.806511	2.331116
BC 23	17	0.88452	2.506035
BC 230	18	0.833791	2.409965

BC 231	22	0.802709	2.481207
BC 232	14	0.834298	2.201761
BC 234	13	0.852845	2.187504
BC 235	20	0.840126	2.516792
BC 236	19	0.719509	2.11855
BC 237	21	0.639721	1.947644
BC 238	23	0.753719	2.363283
BC 239	20	0.678741	2.033326
BC 240	19	0.728072	2.143764
BC 241	17	0.663909	1.880997
BC 242	17	0.860203	2.437138
BC 243	19	0.751403	2.212461
BC 244	17	0.873127	2.473756
BC 245	17	0.633143	1.793828
BC 246	21	0.875635	2.66589
BC 247	13	0.830076	2.129104
BC 248	15	0.738823	2.000769
BC 249	16	0.716673	1.98704
BC 250	20	0.802118	2.402931
BC 251	17	0.805037	2.28084
BC 252	10	0.882222	2.031391
BC 253	9	0.875123	1.922841
BC 254	20	0.670132	2.007537
BC 255	17	0.523235	1.482437
BC 256	20	0.796671	2.386612

BC 257	19	0.770549	2.268833
BC 258	12	0.690014	1.71462
BC 259	13	0.768297	1.970643
BC 260	17	0.758931	2.150214
BC 262	25	0.791911	2.549064
BC 263	15	0.818615	2.21685
BC 265	20	0.756786	2.267129
BC 266	18	0.754571	2.18099
BC 267	18	0.748326	2.162939
BC 268	24	0.757291	2.406712
BC 271	18	0.796033	2.300832
BC 272	26	0.687736	2.240709
BC 274	22	0.681072	2.105224
BC 275	24	0.754285	2.397158
BC 276	22	0.625506	1.933466
BC 277	18	0.636046	1.838409
BC 278	21	0.766448	2.33347
BC 279	24	0.723943	2.300729
BC 280	17	0.76104	2.156189
BC 281	18	0.633647	1.831475
BC 282	13	0.661229	1.69602
BC 283	23	0.730613	2.290834
BC 284	16	0.77328	2.143986
BC 285	15	0.7116	1.927048
BC 286	16	0.843847	2.33964
BC 287	16	0.642133	1.780371
BC 288	20	0.566601	1.697384
BC 289	15	0.640061	1.733318

BC 291	15	0.651543	1.764412
BC 292	17	0.640295	1.814092
BC 293	19	0.675481	1.988911
BC 294	22	0.566619	1.751442
BC 296	15	0.705826	1.911411
BC 297	18	0.86041	2.486904
BC 298	10	0.854134	1.966716
BC 299	6	0.321616	0.576258
BC 300	20	0.654953	1.962064
BC 301	18	0.714706	2.065765
BC 302	17	0.599414	1.698267
BC 303	23	0.832855	2.611412
BC 304	18	0.755337	2.183205
BC 305	20	0.56709	1.698851
BC 306	21	0.810741	2.46832
BC 307	16	0.827632	2.294682
BC 308	20	0.684527	2.05066
BC 309	19	0.638925	1.881275
BC 31	9	0.74764	1.642733
BC 310	23	0.665903	2.087934
BC 311	12	0.837604	2.081369
BC 314	17	0.737863	2.090522
BC 315	18	0.756866	2.187625
BC 316	26	0.834086	2.717532
BC 317	20	0.689021	2.064123
BC 318	16	0.654669	1.815127
BC 319	10	0.949942	2.187322
BC 320	11	0.86543	2.075211
BC 321	4	0.409048	0.567061
BC 324	22	0.762798	2.35784

BC 327	19	0.642929	1.893065
BC 328	15	0.711566	1.926956
BC 329	18	0.853898	2.468084
BC 33	14	0.820117	2.164336
BC 330	23	0.712566	2.234246
BC 331	8	0.851561	1.770771
BC 332	20	0.671945	2.012967
BC 333	18	0.788688	2.279601
BC 334	22	0.695585	2.150083
BC 337	2	1	0.693147
BC 339	19	0.717463	2.112525
BC 34	1		0
BC 340	21	0.751352	2.287509
BC 341	6	0.650647	1.165804
BC 342	22	0.752313	2.325431
BC 343	14	0.885208	2.336116
BC 344	12	0.745886	1.853458
BC 345	18	0.758767	2.19312
BC 346	22	0.751755	2.323707
BC 347	17	0.84448	2.392592
BC 348	12	0.831628	2.066518
BC 35	11	0.937846	2.248856
BC 352	11	0.688951	1.652032
BC 353	19	0.852506	2.510151
BC 354	15	0.88047	2.384356
BC 356	13	0.811752	2.082103
BC 357	5	0.886683	1.427061
BC 358	15	0.850441	2.303037
BC 36	4	1	1.386294
BC 361	16	0.885161	2.454187
BC 362	19	0.823674	2.425258

BC 363	19	0.758683	2.233895
BC 364	17	0.855495	2.423801
BC 365	22	0.819468	2.533009
BC 366	15	0.866098	2.345436
BC 367	18	0.807436	2.333792
BC 368	4	1	1.386294
BC 369	14	0.828015	2.18518
BC 37	6	0.889721	1.594167
BC 370	13	0.826174	2.119094
BC 371	17	0.855613	2.424135
BC 38	10	0.882772	2.032657
BC 4	16	0.840639	2.330747
BC 40	10	0.816621	1.880339
BC 41	9	0.727743	1.599015
BC 44	17	0.831387	2.355495
BC 45	8	0.830656	1.7273
BC 47	12	0.879231	2.184808
BC 5	18	0.717827	2.074787
BC 50	19	0.826233	2.432794
BC 51	17	0.856965	2.427965
BC 52	20	0.769534	2.305319
BC 53	15	0.757037	2.050095
BC 57	19	0.774245	2.279717
BC 58	19	0.800069	2.355756
BC 59	16	0.749805	2.078902
BC 6	16	0.893562	2.47748
BC 60	13	0.706009	1.810878
BC 61	5	0.700718	1.127762
BC 63	13	0.82904	2.126446
BC 67	17	0.706435	2.001482
BC 68	16	0.668619	1.853806
BC 7	18	0.756384	2.186231
BC 70	21	0.819621	2.495354

BC 71	17	0.82551	2.338845
BC 72	17	0.565991	1.603572
BC 73	22	0.829987	2.565526
BC 74	19	0.618203	1.82026
BC 76	18	0.554211	1.601877
BC 77	7	0.898329	1.748067
BC 78	15	0.696201	1.885347
BC 79	12	0.911163	2.264154
BC 80	13	0.819067	2.100865
BC 81	15	0.90013	2.437597
BC 82	13	0.668351	1.714286
BC 83	8	0.882531	1.835171
BC 84	15	0.850972	2.304474
BC 85	16	0.663512	1.839645
BC 86	12	0.778507	1.934517
BC 87	7	0.942681	1.834372
BC 88	5	0.969724	1.56071
BC 89	15	0.812671	2.200754
BC 9	8	0.872497	1.814308
BC 90	20	0.683863	2.048672
BC 91	18	0.68477	1.979239
BC 92	14	0.860162	2.270016
BC 93	9	0.550254	1.209031
BC 94	9	0.604577	1.328392
BC 95	16	0.679048	1.882721
BC 96	14	0.600872	1.585735
BC 97	11	0.553224	1.326574
BC 98	17	0.818736	2.319653
BC 99	17	0.785037	2.224176