UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

School of Ocean and Earth Science

Deep-Sea Macrofaunal Biodiversity of the Whittard Canyon (NE Atlantic)

by

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Thesis for the degree of Doctor of Philosophy

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ABSTRACT

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DEEP-SEA MACROFAUNAL BIODIVERSITY OF THE WHITTARD CANYON (NE ATLANTIC)

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Submarine canyons are topographically complex features that incise continental and oceanic island margins. Due to their high environmental variability, faunal patterns and the drivers of these patterns within canyons remain poorly understood. With this in mind, benthic macrofaunal samples were collected from three branches (Western, Central and Eastern) of the Whittard Canyon, a major feature on the Celtic margin (NE Atlantic), and one site on the adjacent slope to the west of the canyon. A total of 136 core samples (each core 78.5 cm^2 surface area) was collected at depths of ~ 3500 m during 22 deployments of a hydraulically-dampened Megacorer at these four main sites. The samples yielded 4444 macrofaunal individuals (>300-µm sieve fraction) that were identified to higher taxon level; these included 2225 polychaetes identified to species level and 410 macrofaunal nematodes (>500-µm sieve fraction) identified to genus level. Macrofaunal abundance varied significantly among sites, and decreased from the Eastern branch (6249 ± standard deviation 1363 ind. m^{-2}) to the slope site (2744 ± SD 269 ind. m^{-2}). Ordination of macrofauna higher taxa and polychaete family and species level assemblages revealed that the Central and Eastern branches were substantially similar, while the Western branch and slope sites were relatively distinct. A similar pattern was evident in a corresponding ordination of environmental variables across the sites. In contrast, ordination of macrofaunal nematode assemblages grouped the three canyon sites together while the slope site was distinct. A total of 110 polychaete morphospecies was recorded, of which 46 species were found only in the canyon. *Paramphinome jeffreysii* was the most abundant species followed by *Aurospio* sp. B. Forty-eight nematode genera were identified, with *Paramesacanthion* and *Metacylicolaimus* being the most abundant. The canyon branches had broadly similar levels of polychaete species richness and diversity; these metrics and evenness values were higher on the slope than inside the canyon, while dominance was correspondingly lower on the slope. Polychaete feeding modes and nematode feeding groups shifted across the study site. Omnivorous polychaetes and predatory nematodes were more abundant inside the canyon compared with the slope site. Additional polychaetes were collected for molecular analysis (CO1 and 16S genes) from shallower parts (~ 1000 m) of the canyon and nearby Goban Spur. A total of 109 sequences was obtained from 139 specimens resulted in the identification of 33 polychaete species, of which 5 could be assigned Latin binomial names based on phylogenetic analyses. Only one of these species (*P. jeffreysii*) occurred at the deeper (3500 m) sites. Overall, this project highlighted the variability of macrofaunal assemblages within the soft-sediment habitat of a submarine canyon. This variation probably reflects the dynamic environmental conditions, which are influenced by the topographic profiles of individual canyon branches.

Table of Contents

List of Tables

List of Figures

List of Accompanying Materials

1x CD-ROM

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I, Laetitia Mary Gunton declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research. I confirm that:

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3. Where I have consulted the published work of others, this is always clearly attributed;
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Chapter 1: Introduction

1.1 The Heterogeneous Deep-sea Environment

The deep seafloor is the largest ecosystem on Earth (Ramirez-Llodra et al. 2011). The oceans cover 71 % of the Earth's surface and the deep seafloor, defined as the area beyond the shelf break (200-300 m water depth; UNESCO, 2009), occupies 91 % of this area (Harris et al. 2014). Despite its enormous size, the floor of the deep ocean is the least explored part of the planet. Only 5 % has been surveyed with remote instruments and less than 0.01 % has been sampled and studied in any detail (Ramirez-Llodra et al. 2010a). Nevertheless, our knowledge has improved dramatically in recent decades and we now know much more about this remote region than we did in the middle of the last century. Benthic (i.e. seafloor) deep-sea habitats are now believed to harbour some of the highest levels of local (alpha) species diversity on the planet (Hessler & Sanders 1967, Sanders 1968, Sanders & Hessler 1969, Grassle & Maciolek 1992, Snelgrove & Smith 2002, Stuart et al. 2003, Rex & Etter 2010). This high diversity is found mainly in a "thin veneer", comprising the top few centimetres of seafloor sediment (Rex & Etter 2010). The discovery of chemosynthetic environments, such as hydrothermal vents (Corliss et al. 1979) and cold seeps (Paull et al. 1984), in the deep sea was a major discovery that altered our understanding of the processes maintaining life on Earth (Baker et al. 2010).

Approximately 1 million species have been described on earth, around 98 % of these are invertebrates from 30 phyla (Ramirez-Llodra et al. 2010a). All invertebrate phyla except Onchophora are found in the world's oceans (Ramirez-Llodra et al. 2010a). Some phyla such as Echinoderms are only found in aquatic environments. There are no exclusively deep-sea phyla. Indeed, the soft-bottom deep-sea fauna is similar to that of shallow-water fauna at higher taxonomic levels (Thistle 2003). Sea cucumbers, sea anemones, polychaete worms, nematode worms and formainiferans are common components of deep-sea fauna. However, at the lower taxonomic levels there are fewer similarities with shallow-water fauna and most species found in the deep sea are not found in shallow water. Some taxa are exclusive to the deep-sea, for example, xenophyophores, a protist taxon, have not been found above 500 m depth (Tendal 1996).

Far from being a homogenous expanse, the deep sea is a heterogeneous environment that varies both temporally and spatially. Temporal variation operates at different scales at the deep seafloor (Glover et al. 2010). The drivers of environmental change can occur daily, in the form of strong current events (benthic storms) (Thistle et al. 1991), or seasonally and inter-annually, as varying pulses of food (Billett et al. 1983, Gooday & Turley 1990, Beaulieu 2002, Gooday 2002). Longer term processes, such as decadal changes in abyssal food supply potentially caused by climatic oscillations (e.g., El Niño Southern Oscillation (ENSO); Ruhl & Smith 2004, Ruhl 2008, Ruhl et al. 2008), and possibly human-induced climate change (Glover et al. 2010, Smith et al. 2013, Jones et al. 2014, Kuhnz et al. 2014) also influence deep-sea environments.

In terms of spatial (habitat) heterogeneity, the deep sea encompasses a wide range of environments, from gentle slopes and smooth expanses of abyssal plain, to the deep topographic depressions of ocean trenches (Ramirez-Llodra et al., 2010a). On a much smaller scale, spatial heterogeneity is also found in the sediment grain-size diversity (Etter & Grassle 1992, Leduc et al. 2012b) of the soft, sedimentary habitats that make up most of the deep-sea environment. Biogenic structures add further structural complexity, providing habitats for other organisms, especially below 2000 m where hard substrata are limited (Buhl-Mortensen et al. 2010). For example, at very small spatial scales, juvenile nematodes have been reported to occupy the tests of the arenaceous foraminifera *Vanhoeffenella gaussi* (Hope & Tchesunov 1999).

This thesis will focus on submarine canyons, environmentally complex deep-sea features that dissect continental margins and are characterised by high spatial and temporal heterogeneity (Tyler et al. 2009, Levin et al. 2010, De Leo et al. 2014). RRS *James Cook* cruise 036 (JC036) to the Whittard Canyon, during which the Megacore samples for this thesis were collected, was part of the multidisciplinary HERMIONE (**H**otspot **E**cosystem **R**esearch and **M**an's **I**mpact **on** **E**uropean seas) project. This project was a continuation of HERMES (**H**otspot **E**cosystem **R**esearch on the **M**argins of **E**uropean **S**eas). HERMES was a large multidisciplinary European Commission sponsored project set up to study the environmental heterogeneity of Europe's continental margins (Weaver & Gunn 2009). It focused on key "biodiversity hotspots" such as cold seeps, cold-water coral locations, carbonate mounds, canyons, anoxic environments, presence of gas hydrates and deep-water currents.

1.1.1 Geomorphology

The deep sea can be divided into four depth zones: upper bathyal (301- 800 m), lower bathyal (801-3500 m), abyssal (3501-6500 m) and hadal (> 6500 m) (Watling et al. 2013). These zones encompass a wide range of geomorphological features and habitats (Ramirez-Llodra et al., 2010a, UNESCO, 2009, Harris et al., 2014)(Figure 1.1). The upper bathyal zone begins at the shelf break and coincides with the upper part of the continental margin (i.e. the upper continental slope). The lower bathyal zone comprises the lower continental margins (i.e. the lower continental slope and rise) as well as the slopes of oceanic islands and seamounts. Also lying within the lower bathyal zone are large parts of mid-ocean ridges. These are vast mountain systems located along tectonic spreading centres that stretch for huge distances. The Mid-Atlantic Ridge is thought to account for 44.7 % of the bathyal habitat in the North Atlantic (Priede et al. 2013). The abyssal zone covers the largest area of the ocean floor (85 %) (Harris et al. 2014), most of it consists of abyssal plains, large areas of flat or gently sloping ocean floor (although extensively populated by abyssal hills, Durden et al. (2015a)). The hadal (ultra-abyssal) areas are restricted to trenches associated with subduction zones (with the exception of the Romanche Fracture Zone in the equatorial Atlantic) (Watling et al. 2013). Trenches are long, narrow, steep-sided depressions in the ocean floor, in some cases reaching depths of > 10, 000 m.

Continental margins, the focus for this thesis, mark the transition between the thick granitic continental crust and the thin basaltic oceanic crust and encompass the continental shelf, slope and rise (Levin & Sibuet, 2012). They range from 100 to 4000 m depth and comprise around 15 % of global seabed (Levin & Dayton, 2009). They are areas of relatively high primary production, derived from photosynthetic production in the upper water column. They are also believed to play an important role in the biogeochemical cycling of carbon, nitrogen and other elements in the oceans (Walsh 1991). Continental margins are the most geologically diverse areas of the deep-sea floor and display a considerable degree of habitat heterogeneity (Levin & Dayton, 2009, Levin et al. 2010, Menot et al. 2010). They encompass large topographic features such as ridges, scarps, hills, mounds and submarine canyons.

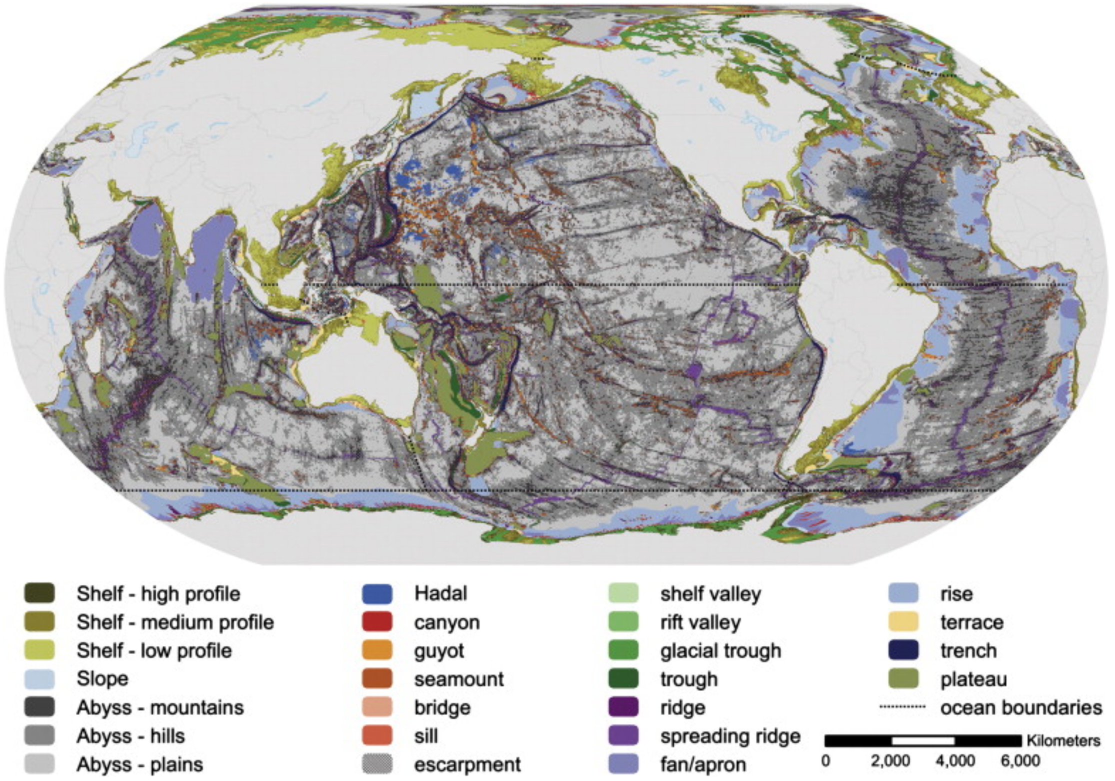


Figure 1.1 **Map of geomorphological features of the world's oceans.**
From Harris et al. (2014)

1.1.2 Biogeographic provinces

The deep-ocean floor can also be divided into biogeographical provinces (see papers in Gebruk et al. 1997). These are the geographic centres of distributions of benthic organisms. Most recently, Watling et al. (2013) proposed 28 such provinces, 14 of them located in the lower bathyal and 14 in the abyssal zone. These provinces were mainly determined by the water-mass characteristics (such as temperature, salinity, oxygen content and hydrography) and the particulate organic flux to the ocean floor. These variables were thought to be good proxies for benthic organism distribution. The North Atlantic (the focus for this study) includes the North Atlantic Bathyal and North Atlantic Abyssal biogeographic provinces. The North Atlantic Bathyal province extends along the Mid-Atlantic Ridge from the Reykjanes Ridge to the equator and along the eastern and western margins of the North Atlantic. The North Atlantic Abyssal province includes all areas north of the equator under the influence of the North Atlantic Deep water, although it is divided into eastern and western parts by the Mid-Atlantic Ridge (Watling et al. 2013).

1.1.3 Physical environment

Much of the deep sea is devoid of sunlight (all light has effectively disappeared by 1 km depth; Gage and Tyler 1991), food is generally limited, pressure is high, increasing by 1 atmosphere (10^5 Pascals) per 10 m increase in depth, temperatures vary from 4°C to - 1°C, salinity is usually around 35 PSU, and most of the water overlying the deep-sea floor is saturated with oxygen (5-6 ml l^{-1}) (Thistle 2003). In combination, these characteristics make the deep sea very different from any other ecosystem on earth.

Most regions of the deep sea are also essentially physically stable. The speed of near-bottom flow 1 m above the sea floor in the bathyal zone is generally less than 10 cm s^{-1}, and less than 4 cm s^{-1} at abyssal depths, these speeds varying little in magnitude from day to day (Thistle 2003). Nevertheless, dynamic physical processes have been recorded, including tidal currents, and strong episodic currents capable of eroding sediments. These "benthic storms" (Kerr 1980, Richardson et al. 1981) are well documented at the High Energy Benthic Boundary Layer Experiment site (HEBBLE) in the northwestern Atlantic (Nowell et al. 1982), where bottom current speeds reach over 0.2 m s^{-1} (Hollister & McCave 1984). On ocean margins, slumps, slides, debris flows and turbidity currents are forms of gravity-driven sediment transport. These processes can transport very large volumes of sediment over great distances into the deep sea (Masson et al. 1996). Turbidity currents are "gravity flows in which sediment grains are maintained in suspension by fluid turbulence" and are initiated by landslides (Masson et al. 2006). They are important processes around oceanic islands and on continental margins, especially in submarine canyons. As a consequence of the 1755 Lisbon earthquake a large turbidity current is thought to have flowed through the Setúbal canyon out onto the Tagus abyssal plain (Thomson & Weaver, 1994). Few direct observations of turbidity currents have been made. However, in 1929 on the Grand Banks, Newfoundland, a turbidity current was recorded that reached velocities of up to 25 ms^{-1} and broke submarine telegraph cables in its path (Heezen & Ewing, 1952). On longer time scales, catastrophic slope failures and landslides occur on the ocean floor (Masson 1996). One such large slide, the Nuuanu Slide, occurred on the flanks of the Hawaiian Islands, this slide left deposits reaching a thickness of 2 km and having a volume of 5000 km^3 (Masson et al. 1996).

1.1.4 Food supply

Except at chemosynthetic systems (e.g., vents, seeps), benthic life in the deep sea is overwhelmingly dependant on the delivery of organic matter from the upper ocean, and on material that is laterally advected from the adjacent continents (Rowe & Staresinic 1979, Gage

& Tyler 1991). The organic matter that reaches the deep-sea floor is mostly the direct product of photosynthesis in the euphotic zone and arrives in the form of particles that settle through the water column. This Particulate Organic Matter (POM) consists of the small remains of phyto- and zoo-plankton (faecal pellets, crustacean molts, salp carcasses and salp faeces) (Wiebe et al. 1979), bacteria and cyanobacteria (Pfannkuche & Lochte 1993), macroaggregates (Gooday & Turley 1990, Gooday, 2002), terrrigenous material including large plant remains (e.g. wood) (Turner 1973, Amon et al. 2015a,b), marine macrophyte detritus (e.g. *Thalassia* and *Sargassum*)(Grassle & Morse-Porteous 1987), large vertebrate carcasses (e.g. dead whales) (Smith & Baco 2003). Large vertebrate falls deliver exceptional, though highly localised pulses of organic matter to the sea floor. For example, whales falls may enrich local sediments with the equivalent of ~ 2000-years of typical organic flux (Smith & Baco 2003). Material originating from jellyfish and salp blooms has been observed to sink rapidly to the abyssal seafloor (~ 4000m) providing major inputs of organic matter (Billett et al. 2006, Smith et al. 2014).

Much of the POM that reaches the seafloor, however, does so as rapidly sinking macroaggregates, termed ‘phytodetritus’ (Thiel et al. 1989). This consists of phytoplankton and zooplankton remains (small chlorophytes, ebriaceans, diatoms, coccolithophorids, silicoflagellates, dinoflagellates, tintinnids, radiolarians, phaeodarians, acantharians, foraminifers, pteropods), crustacean moults and eggs, radiolarian faecal pellets (“minpellets”) and both heterotrophic bacteria and cyanobacteria (Billett et al. 1983, Lochte & Turley 1988). These constituents become aggregated together in a gelatinous and membranous matrix (Thiel et al. 1989).

Depending on the residence time of the sinking material in the water column, it arrives at the sediment surface in a more-or-less advanced state of degradation (Lochte & Turley 1988, Turley et al. 1995, Wakeham et al. 1997). As POM descends through the water column, it is partially remineralised and consumed by biota (Turley et al. 1995, Buesseler et al. 2007), with only 0.5 - 2 % of surface production reaching the abyssal seafloor from the open ocean (Buesseler et al. 2007). Bacteria are also very important contributors to the solubilisation and remineralisation of POM (Turley, 2000).

Particulate Organic Carbon (POC) flux decreases with distance from the productive coastal waters (Pfannkuche et al. 1983). It also varies regionally (Yool et al. 2007) and seasonally (Billett et al. 1983, Rice et al. 1986, Bett et al. 2001, Gooday 2002) as a result of variations in the productivity of the upper ocean. In areas that experience strong spring blooms, such as the North Atlantic, large fast-sinking aggregates of phytodetritus can settle in a period of weeks to the abyssal seafloor where they form patchy deposits (Billett et al. 1983, Lampitt 1985). During the period 1991-1994, time-lapse camera records at the Porcupine Abyssal Plain indicated that phytodetritus arrived at the seafloor in late May to early June where it accumulated for a couple of months until late July, phytodetritus cover then decreased for two months before disappearing in early October (Bett et al. 2001). The persistence of phytodetritus on the seafloor is mainly a balance between the rate at which it is deposited and the rate at which it is consumed by benthic organisms.

Exceptions to the dependence on food derived from surface production are found in chemosynthetic ecosystems, mainly at hydrothermal vents along mid-ocean ridges and cold seeps on continental margins. At these sites primary production depends on chemosynthetic bacteria that use hydrogen sulphide and methane to fix carbon (Van Dover 2000).

1.2 Deep-Sea Communities

1.2.1 Size groups

Deep–sea benthic organisms are categorised into four size groups: mega-, macro-, meio-, and nanobenthic. The largest organism size group, the megafauna (> a few centimetres), are animals large enough to be identified in photographs and caught in trawls. This group includes mobile megafauna that can swim (e.g. large scavenging amphipods, cephalopods and fish) or crawl across the surface of the seafloor (e.g. ophiuroids, asteroids, echinoids, holothurians, large polychaetes, hemichordates, pycnogonids and some decapods), as well as some burrowing fauna (e.g. echiurans). The sessile megafauna includes sponges, bryozoans and cnidarians such as hydroids, sea pens, sea fans and cold-water corals (Gage & Tyler 1991).

The deep-sea macrofauna are organisms retained on a c. 300 µm mesh sieve (Hessler & Jumars 1974). This definition differs from that for shallow-water macrofauna, which are regarded as organisms retained on a c. 1 mm sieve (Mare 1942). Macrofaunal taxa in the deep sea are less abundant than in shallow water and thus a smaller mesh size is needed to compensate for the decreased density (Bett 2013, 2014). The macrofauna includes small peracarid crustaceans (cumaceans, tanaids, amphipods and isopods), molluscs (bivalves, gastropods and scaphopods), vermiform taxa (e.g. mainly polychaetes and sometimes sipunculids but also rarer taxa such as oligochaetes and nemerteans) and small ophiuroids and holothurians are occasionally encountered (Gage & Tyler 1991). These constitute the macrofauna *sensu strictu,* i.e. excluding meiofaunal taxa that are retained on a 300-µm mesh. This thesis will focus on the macrofauna, particularly the polychaetes, which are typically the dominant macrofaunal taxon in deep-sea sediments (e.g. Grassle & Maciolek 1992, Hessler & Jumars 1974). The polychaetes constitute a class within the phylum Annelida, the segmented worms, and are ubiquitous in the marine environment, from shallow water to hadal depths. Their body segments incorporate a pair of fleshy protrusions called parapodia that bear bristles called chaetae, which are made of chitin. Adults can range in size from under 1 mm to over 6 m (Rouse & Pleijel 2001). The class Polychaeta is very diverse with around 80 known families and 11,590 currently valid marine, non-fossil species (World Polychaete Database, Read 2015). However, there are many undescribed deep-sea species. For example, Grassle & Maciolek (1992) reported that 64 % (236 species) of the 367 species of benthic polychaetes in their samples from the continental slope and rise off the eastern coast of the United States (1500 – 2500 m depth) were undescribed.

The meiofauna pass through a 500 µm (or 1000 µm) mesh but are retained on a 44 µm (or 32 µm) mesh (Giere 2009). This group consists of protozoans (mainly foraminifera) and multicellular (metazoan) animals. Nematodes are generally the most abundant and species-rich metazoan taxon among the deep-sea meiofauna, typically representing 80 - 99 % of total metazoan abundance within this size fraction (Vincx et al. 1994). Other components of the meiofauna generally found in the deep sea include harpacticoid copepods, benthic ostracods as well as the juvenile and larval stages of macrofaunal organisms such as polychaetes and bivalves that constitute the 'temporary meiofauna' (Gage & Tyler 1991). Specimens belonging to meiofaunal taxa may be retained on a 300 µm mesh, these are excluded from the macrofauna *sensu strictu,* but are included in the macrofauna *sensu lato* (Bett, 2014).

The nanofauna, the smallest size group, includes organisms in the size range 2 - 40 (or 50) µm (Thiel 1983). This group is made up mainly of single-celled organisms (prokaryotes, yeast-like cells and protists) together with the juvenile stages of meiobenthic metazoans (Thiel 1983, Gage & Tyler 1991).

1.2.2 Functional grouping

1.2.2.1 Feeding groups

Deep-sea organisms can be assigned to a number of different feeding groups. Few direct observations of feeding modes have been made in the deep sea although some studies have analysed gut contents (e.g. Sokolova, 2000). These analyses are hampered by the swim bladders of benthopelagic fish, which on recovery eject the gut contents out of the mouth, as well as the gastric mills of scavenging crustaceans that grind food down making it unidentifiable (Gage & Tyler 1991). Most of what is known about deep-sea feeding groups is essentially inferred from shallow-water species (Thistle 2003). However, increased use of molecular methods for gut contents analysis (Olsen et al. 2014) and increased availability of photography and video image data of deep-sea habitats, are leading to considerable advanaces radical in our understanding of deep-sea organisms' feeding behaviour (Durden et al. 2015b).

The majority (> 80 %) of taxa in the deep sea are deposit feeders (Thiel 1979, Jumars & Gallagher 1982). In general terms, deposit feeders rapidly consume large volumes of sediment with a relatively low food value (Jumars et al. 1990). Deep-sea deposit feeders may have a larger gut volume compared with their shallow-water relatives (Allen & Sanders 1966, Penry & Jumars 1990) this is thought to increase food assimilation efficiency, necessary for organisms feeding on food-poor deep-sea sediments. Deposit feeders can be divided into two types depending on which sediment horizon they feed on: surface deposit feeders and sub-surface deposit feeders.

Suspension feeders collect material from the water column. They typically decrease in overall importance with increasing depth (Jumars & Gallagher 1982, Gage & Tyler 1991). This shift in feeding strategy with depth is found in all major taxa. For example, most deep-water bivalves are deposit feeders or carnivores and few are suspension feeders, whereas a much larger proportion of shallow-water bivalves are suspension feeders (Jumars & Gallagher 1982). Suspension feeders may be found in greater numbers where topographic features enhance bottom current speeds (Genin et al. 1986).

Carnivores select and eat other living organisms, they are generally rare in deep-sea communities (Jumars & Gallagher 1982). This feeding mode is often inferred from an organism's feeding apparatus, for example, deep-sea nematodes with large teeth in their buccal cavity are thought to be carnivorous, by analogy with shallow-water species with similar teeth (Jensen 1992). Carnivores are more strongly affected by the decrease in food availability in the deep sea compared with other feeding types. This may reflect the progressive loss of energy from lower to higher trophic levels (Rex et al. 1990). The low density of prey in the deep sea is also thought to make this feeding method unprofitable (Thistle 2003). Carnivory is also practiced by generalist scavengers, which become more important with depth. With increasing depth scavengers become highly specialised and more motile, for example, giant scavenging amphipods such as *Eurythenes gryllus* and *Alicella gigantean* (Gage and Tyler, 1991).

Herbivores are also found in the deep sea. Wood-boring bivalves (subfamily Xylophagainae) make numerous bore holes in blocks of wood deployed on the deep-sea floor and gut analysis shows that they are ingesting the wood (Turner 1973, Amon et al. 2015b). In a recent study, Amon et al. (2015a) found numerous invertebrate species living on mango wood that had been deployed for a period of tow year at the Southwest Indian Ridge (732- 750 m depth). Taxa inhabiting the wood included polychaetes, pycnogonids, amphipods and bivalves. There are also deep-sea species that use ephemeral plant structures for food; these include polychaetes, echiurans, gastropods and isopods, that are reported to ingest seagrass blades and fragments of coconut husks (Wolff 1976).

1.2.2.2 Mobility

Deep-sea organisms are either sessile, motile or hemi-sessile. Sessile organisms, for example, sponges and soft and stony corals, remain fixed in the same location. They are usually restricted by the availability of suitable hard substrata, such as exposed rock outcrops on the continental slope, seamounts, oceanic spreading centres, as well as manganese nodules, stones dropped from icebergs, and hydrothermal vents edifices (Gage & Tyler 1991).

Motile organisms either swim, burrow or crawl across the sediment surface, although most spend the majority of their time stationary or moving very slowly. Deep-sea fish have been recorded to swim at 10 cm s^{-1} over the abyssal plain in the NE Atlantic (Bagley & Priede 1997) and deep-sea holothurians moved at 1 - 2 cm min^{-1} (Gage 1991). Echiuran worms and the anemone *Iosactis vagabunda* have hemi-sessile life styles. Echiurans extend their proboscis out from their burrow onto the sediment surface and make sweeping feeding excursions (Bett & Rice 1993). When they have fully utilised the surface detritus around their central burrow they burrow to a new feeding location (Ohta 1984, Bett et al. 1995). The anemone *Iosactis vagabunda* has been observed to move between feeding burrow locations both over the sediment surface and beneath the surface (Durden et al. 2015b).

1.2.3 Biomass and abundance trends with depth

Benthic abundance and biomass decreases with distance from land and with depth, reflecting the fact that these metrics are positively correlated with food availability (Thiel 1975, Rowe 1991, Smith & Demopoulos 2003, Wei et al. 2010, Johnson et al. 2007). Terrestrial runoff and productivity in the surface waters is highest near the continental margins. Also, organic matter degrades as it settles through the water column and hence the greater the depth, the greater the degree of degradation, as predicted by the standard flux attenuation equation (Marsay et al. 2015). As a result, the amount of food reaching the ocean floor decreases with increasing depth. Indeed, abyssal macrofaunal density is very low (10s -100s individuals m^{-2}) (McClain et al. 2009, Wei et al. 2010). However, this decline is far from uniform (Gage 2003) and regions of high productivity can show elevated abundance and biomass, regardless of their depth (Rex & Etter 2010). Thus, topographic depressions in the ocean floor, for example, trenches and canyons that trap sediments and organic matter, may show elevated faunal abundance and biomass for their depth (Thiel 1975, Rowe et al. 1982, Rowe 1983, Vetter 1994).

The decline in abundance and biomass is seen in the megafauna (Lampitt et al. 1986), macrofauna (Rowe 1983) and meiofauna (Shirayama 1983, Bett et al. 1994, Vincx et al. 1994) but is also not uniform across size groups. In terms of abundance the megafauna declines faster than the macrofauna, which in turn declines faster than the meiofauna (Thiel 1983, Rex et al. 2006, Wei et al. 2010). For biomass, the megafauna and macrofauna declined at very similar rates but faster than the meiofauna (Rex et al. 2006, Wei et al. 2010). Bacteria abundance and biomass does not appear to decline with depth (Rex et al. 2006, Wei et al. 2010). As a result, apparent average body size decreases with depth and the ocean-floor benthos tends to be dominated by small organisms to a greater extent than in shallow water (i.e large animals are rare).

1.2.4 Diversity

1.2.4.1 Diversity terminology

Species diversity is ‘a measure of diversity that incorporates both number of species in an assemblage and some measure of their relative abundance’ (Gotelli & Chao 2013). The number of species in the unit of study is termed ‘species richness’ and the variation in species abundances is termed ‘species evenness’ (Magurran, 2004). Diversity indices are single statistics that measure diversity. They can incorporate both richness and evenness (heterogeneity measure) with different indices applying a different weighting to each component. This thesis follows the methods for measuring diversity summarised by Magurran (2004).

Species diversity can be measured at different spatial scales. Local (alpha) diversity reflects diversity within a habitat (Whittaker 1960), in other words within samples from a particular locality. Estimates of local diversity in different habitat types within a region can be pooled together to give regional diversity (Gamma diversity) estimates (Whittaker 1972). Rex & Etter, (2005) define a region in the deep sea as a basin or a large topographic feature. The degree of diversity at the regional scale can be viewed as a composite of overlapping species distribution ranges (Stevens, 1989). Turnover (beta) diversity is ‘the degree of change in species composition along a gradient’ (Grey 2000), it links local and regional scales of diversity, high beta diversity will increase regional diversity. This between-habitat diversity can be calculated by comparing differences between local diversity relative to regional diversity (Whittaker 1960, 1972).

1.2.4.2 Deep-sea Diversity

From the beginning of serious deep-sea exploration in late 1860s until the mid 1960s, benthic species diversity was generally believed to be much lower in the deep sea than in shallow-water settings (Ekman 1953, Marshall 1954, Bruun 1957). Before the 1960s, most deep-sea sampling was conducted using coarse-mesh trawls and dredges (Mills 1983). These yielded low numbers of species and individuals, retaining only the larger-sized megafaunal animals. The Danish Ingolf expeditions (North Atlantic) of 1895 and 1896 were an exception. In these expeditions a silk gauze was used to sieve mud collected from trawls and dredges, from which scientists recovered diverse, small invertebrates (tanaids and isopods) (Hansen 1913,1916 in Levin & Gooday 2003). With the introduction of new sampling equipment, notably the epibenthic sled (Hessler & Sanders 1967) and the box-corer (Hessler & Jumars 1974), quantitative sediment samples could be obtained and sieved on finer meshes. These methods yielded a high density and diversity of small sediment-dwelling macrofaunal animals (Sanders et al. 1965). The deep-sea floor is now believed to harbour some of the highest levels of local (alpha) species diversity on Earth (Hessler & Sanders 1967, Sanders 1968, Sanders & Hessler 1969, Grassle & Maciolek 1992, Snelgrove & Smith 2002, Stuart et al. 2003, Rex & Etter 2010). However, whether or not deep-sea diversity actually exceeds that of shallow-water settings is still disputed (Gray 1994, Gray et al. 1997, McClain & Schlacher 2015).

There are two large-scale (macro-ecological) diversity patterns in the deep sea: (i) a latitudinal gradient of decreasing alpha diversity from the equator to the poles (Rex 1981, Rex et al. 1993, 2000, Rex & Etter 2010) and (ii) a parabolic distribution of alpha diversity with depth (Paterson & Lambshead 1995). The latitudinal gradient is much more pronounced in the North than the South Atlantic. The poleward decrease in species richness has been shown for gastropods, isopod and bivalves in the North Atlantic (Rex et al. 1993, Rex et al. 2000; Rex & Etter, 2010) and for benthic foraminifera in the North and South Atlantic (Culver & Buzas 2000). Cumaceans also displayed a peak in diversity at the equator in samples from the North and South Atlantic, however, the eastern North Atlantic basin showed a significant relationship whereas the western basin did not (Gage et al. 2004). Conversely, nematodes did not appear to display a poleward decrease in diversity (Lambshead et al. 2000). There is still debate about the existence of latitudinal gradients of diversity in the South Atlantic especially when the species-rich Southern Ocean is included (Clarke & Crame 1997, Gray 2001, Brandt et al. 2007).

The parabolic depth pattern is particularly well established in the North Atlantic, with peaks at intermediate (i.e. bathyal) depths and reduced levels of diversity at upper bathyal and abyssal depths (Rex 1981, Rex 1983, Maciolek et al. 1987, Etter & Grassle 1992, Paterson & Lambshead 1995, Levin et al. 2001, Rex & Etter 2010). However, this depth pattern is not universal for all regions of the deep sea and the depth at which this peak occurs varies tremendously between taxa (Rex et al. 1997, Bett 2001, Stuart et al. 2003). Rowe et al. (1982) reported a macrofaunal diversity peak at around 3000 m followed by lower diversity values around 3660 m in the Northwest Atlantic, whereas Etter & Grassle (1992) reported a macrofauna diversity peak between 1200 m and 1500 m in the same region. Rex (1983) reported that the diversity peak was located at around 2000 m for polychaetes but around 3000 m for other taxa (gastropods, protobranchia and cumaceans) in the Northwest Atlantic. In the Northeast Atlantic, there is evidence for a diversity peak for polychaetes at 1500 m (Paterson & Lambshead, 1995), although Bett (2001) recorded a diversity peak at 400 m for macrofauna and Gage et al. (2000) failed to find clear evidence for a peak in macrofaunal diversity at 1400 m in this region.

1.3 Biological Sampling Methods

Sampling the deep-sea benthos is logistically very challenging as a result of the extreme hydrostatic pressure at depth, the large distance from the surface to the seafloor and the distance from land (Jamieson et al. 2013). Collecting deep-sea samples is therefore both time consuming and expensive. The types of sampling equipment used will depend on the type of fauna and seafloor substratum that needs to be sampled.

1.3.1 Trawls and sleds

Trawling is used for collecting large numbers of megafauna. There are many types of trawls, beam and otter trawls, both of which are adapted from coastal fishing trawls and are pulled across the seabed at the end of a long wire attached to a winch on the research vessel. The most common trawl used in the deep sea is the Agassiz trawl, a double-sided beam trawl (Gage & Tyler 1991). It is often fitted with a main net of 20 mm mesh size and the cod-end (where the catch is retained) lined with netting of 10 mm mesh (Gage & Tyler 1991). The epibenthic sled (e.g. Hessler & Sanders 1967) is used to collect macrofauna from the top few centimetres of seafloor sediments. It consists of a net that is mounted on a metal frame attached to sled runners to stop it sinking into the sediment. The original epibenthic sled was later modified with the addition of an odometer and camera, as well as an upper ('suprabenthic') net designed to catch near-bottom plankton and lighter organisms stirred up from the sediment by the passage of the sled (Rice et al. 1982). Recently, it has been adapted to improve the ability to sample not only on soft sediments but also on steep slopes, between rocks and glacier moraines (Brenke et al.

2005). Trawls and sleds yield qualitative samples, as they do not collect every individual in their path and often obtain reduced numbers, especially of smaller bodied taxa (Bett et al. 2001).

1.3.2 Grabs and corers

Grabs and corers are used to collect samples for macrofauna, meiofauna and nanofauna. The first quantitative samples from the deep sea were taken using grabs. These are mechanical devices lowered down through the water column to the seafloor where they are triggered and penetrate the seafloor to grab a sample of sediment. Most grabs are a variation of the original Petersen grab (Petersen & Boysen-Jensen 1911). A version of the Petersen grab was first used by Spärk during the Galathea Expedition of 1950-1952 to depths of 2000 - 10120 m with a 68 % success rate (Thorson 1957) and still remains in use today. The Okean grab was used by Russian scientists during their worldwide sampling programmes in the 1950s and 1960s (Gage & Bett, 2005). Campbell, Day and van Veen grabs have also been used for deep-sea sampling (Gage & Bett, 2005, Jamieson et al. 2013). Grabs, however, generate bow-waves as they approach the sediment surface (Jamieson et al. 2013). Bow-waves are hydraulic disturbances created in front of a sampling device. These disturbances cause the surficial, light sediment particles to be blown away along with the light-bodied fauna living on the surface sediments (Wigley 1967), causing them to be excluded from the collected sample. This leads to an underestimation of organisms living on the surface sediments (Bett et al. 1994).

Box corers consist of a detachable, square, open-ended steel box attached to a weighted column, the top of which is attached, in turn, to the winch cable. On contact with the seafloor, the metal box sinks into the sediment. As the corer is lifted from the sediment a weighted spade is released and closes the bottom of the box (Gage and Tyler 1991). Box cores take a sample of known area. The commonly-used USNEL-type box corer, for example, collects a sample of 0.25 m^2 to a sediment depth (> 20 cm) that encompasses the vertical distribution of most benthic organisms. However, box corers, like grabs, produce a bow wave as the corer comes into contact with the seabed (Bett et al. 1994).

Tube corers collect sediment samples that are far less disturbed compared with other sediment sampling methods. The Craib corer (Craib 1965), which uses a hydraulic damper to slow the descent of a single plastic tube into the sediment, thereby minimising disturbance of the surface sediment, is an important example. Using the same hydraulic dampening principle, the Barnett-Watson multiple corer was developed to carry up to 12 core tubes simultaneously (Barnett et al. 1984). This was a major advance in deep-sea sediment sampling as the hydraulic dampening decreased the bow wave effect and multiple samples could be taken at once. Different types of multicorer are now commercially available with differing numbers of core tubes in a range of sizes. Multicores are often the preferred instrument for deep-sea sediment sampling for meiofauna and increasingly for macrofauna (instead of box corers, epibenthic sleds). Megacorers are a type of multiple corer (Fig 1.2), and the Bowers and Connelly design was used in the present study to obtain quantitative macrofaunal samples. Megacorers collect a more accurate sample for quantitative macrofaunal analysis than box corers (Gage & Bett 2005). Compared with Megacorers, box cores underestimate the faunal abundance by 48 - 66 %. This is because, as noted above, a box corer produces a large bow wave as it approaches the seabed whereas a bow wave is minimised in the case of the Megacorer. The Megacorer collects up to 12 more-or-less undisturbed samples in plastic tubes (diameter 100 mm), which penetrate 20 - 40 cm into fine-grained deep-sea sediments (Gage & Bett 2005). The corer consists of an outer framework supporting a hydraulically dampened, weighted coring head equipped with a variable number of plastic core tubes. The corer is lowered at the end of a cable to the seabed and when the frame contacts the seabed, the core tubes descend slowly into the sediment, dampened by the hydraulic mechanism. Hauling on the cable releases lids that seal the top of each core tube and, as the core tubes are pulled from the sediment, a sliding plate that seals the bottom of the tube (Jamieson et al. 2013). In this way, the sediment is retained inside the tubes. The corer can then be brought on deck, the sediment extruded from each tube and sliced into the desired sediment horizons.

Push corers and modified Eckman corers (small box corers) can be used with manned submersibles and remotely operated vehicles (ROVs). Push corers are typically around 60 mm diameter by 300 mm length. They have a ‘T-handle’ on the top to allow the pilot to grasp the corer using a manipulator arm. Once at the seabed, each core tube is individually lifted out of the tool tray and carefully pushed into the sediment, a valve at the top allows the water to escape. As the corer is pulled back out of the sediment, the suction closes the valve and helps to retain the sediment sample. The core tube is then carefully pushed down onto a bung inside a quiver on the submersible. These core samples can be taken from precise locations, although they sample a much smaller area than a box corer or a Megacorer (Jamieson et al. 2013).

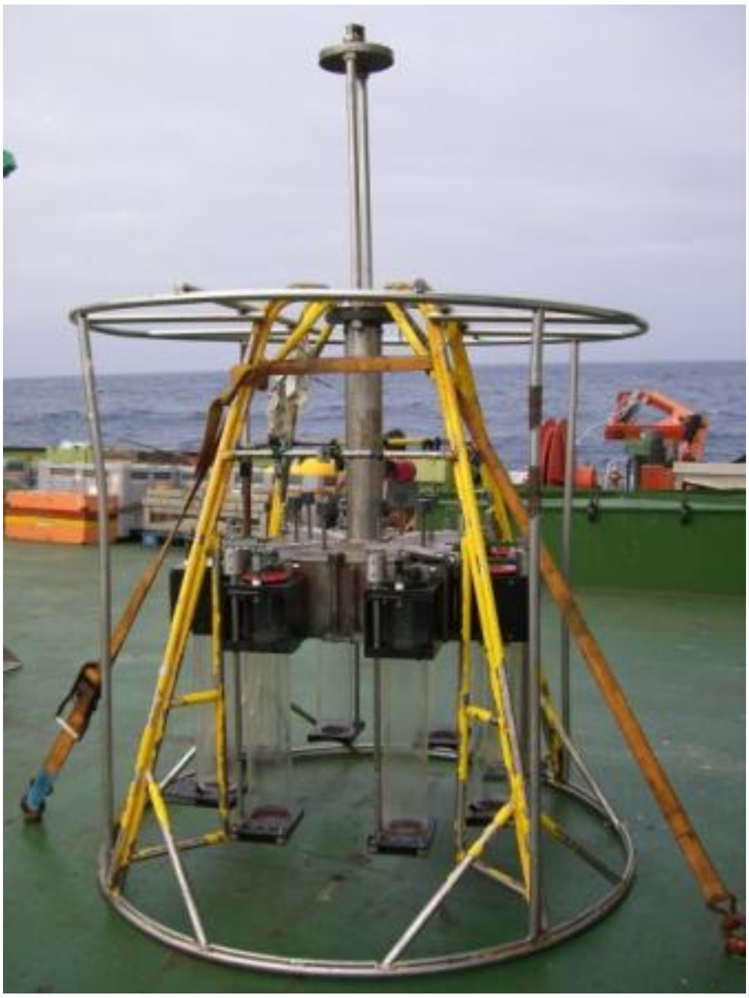


Figure 1.2 Megacorer sampling equipment

1.3.3 Photography and video

Photographs and videos of the deep-sea floor are increasingly used to provide non-destructive methods for studying deep-sea megafaunal assemblages. Megafaunal organisms are sparsely dispersed on the seafloor and some are highly mobile, allowing them to escape capture by mechanical sampling devices. Photographic transects using towed camera sledges (e.g. Rice et al. 1982, Barker et al. 1999), towed camera platforms (e.g. WASP and SHRIMP; Jones et al. 2009) or more recently, ROVs (e.g. Morgan et al. 2015) and autonomous vehicles (AUVs , e.g. NOCS Autosub, Morris et al. 2014), have been used to make quantitative assessments of deep-sea megafauna (Jamieson et al. 2013). Free standing cameras such as 'Bathysnap' (Lampitt & Burnham 1983, Bett 2003) can be deployed at the sea bed for long periods of time to record temporal changes (e.g. Gooday et al. 1993, Rice et al.1994, Durden et al. 2015b).

1.4 Submarine Canyons

Submarine canyons are major topographic features in the deep sea found on continental and volcanic island margins around the world. Submarine canyons were first discussed over 150 years ago by Dana (1863), who described a valley in the Bay of New York, but it was not until Shepard and Dill's (1966) book, which gave detailed descriptions of submarine canyons, that interest in canyons increased. Submarine canyons are either shelf-incising with or without direct connections to rivers, or, blind canyons, those that are confined to the continental slope (Huang et al. 2014). There are believed to be around 9477 distinct, large submarine canyons in the world's oceans, 2076 of which are shelf-incising and 7401 incise the slope only (Harris et al. 2014). Canyons account for 2% of the total ocean floor and on average 11% of the continental slope area (Harris et al. 2014). Canyons are found more frequently on active than passive margins (Harris & Whiteway 2011). However, there have been relatively few investigations of canyons compared with other deep-sea environments such as seamounts and hydrothermal vents (Ramirez- Llodra et al. 2010a). The global distribution and high frequency of canyons found along the continental slope suggests that they play an important role in the connectivity of the continental shelf to the abyssal plain. Canyons are also important areas for pelagic and demersal fisheries (Würtz 2012) and cetacean feeding grounds (Hooker et al. 1999). They may act as nursery grounds for some fish species by providing higher food availability and attractive habitat structures such as rocky walls, boulders and detritus patches (Stefanescu et al. 1994, Vetter & Dayton 1999).

Active canyons are believed to be very unstable environments. Their steep topography influences hydrodynamic regimes by focusing internal tides in the upper reaches (Gardner 1989). They are subject to tidal currents, episodic slumps, turbidity flows and dense shelf water cascading, which periodically transport sediments downslope (Gardner 1989, Canals et al. 2006, de Stigter et al. 2007). In this way, submarine canyons play an important role as fast track conduits for the transport of material from the shelf to abyssal depths (Puig et al. 2003) (Fig. 1.3). Particulate organic carbon (Palanques et al. 2005), macrophyte detritus (Vetter & Dayton 1998, 1999, Harrold et al. 1998), sediment (Arzola et al. 2008) and even pollutants (Palanques et al. 2008) are brought down through the canyons out onto the adjacent abyssal plain.

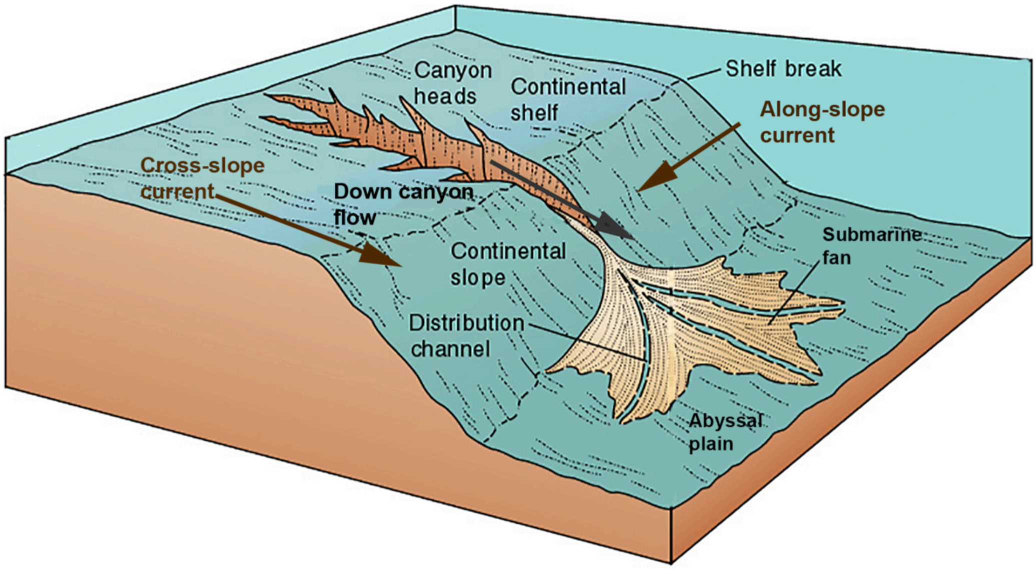


Figure 1.3 Schematic of submarine canyon

Enhanced food supply inside canyons compared with the surrounding continental slope and abyssal plain has led to the idea that canyons are deep-sea biomass ‘hotspots’ (Vetter 1994, De Leo et al. 2010). This may be true for some canyons, which have an elevated faunal density compared with the adjacent slope e.g. the Hudson Canyon off New York (Rowe et al. 1982), the Merenguera Canyon in the Catalan Sea (Sardà et al. 1994), the Setubal Canyon on the Iberian margin (Gage et al. 1995) and the La Jolla Canyon system off the coast of California (Vetter & Dayton 1999)). However, others show either no significant enhancement of biomass, such as the Carson Canyon in the northwest Atlantic (Houston & Haedrich 1984), or a lower density inside the canyon, for example, the Newport Canyon off the coast of California (Maurer et al. 1994). The density and biomass of the benthic fauna within canyons is dependent on the physical disturbance regime (Okey 1997) and the quantity and quality of organic matter funnelled into the canyon (Rowe et al. 1982, Vetter & Dayton 1998).

Canyons add to the habitat heterogeneity on continental margins. Attributes such as extreme topography, diverse current regimes, varying substratum types, and detrital funnelling from the continental shelf will serve to increase habitat heterogeneity within canyons (Figure 1.4) (Levin et al. 2010). Currents may distribute organic matter and sediment in a patchy manner (McClain & Barry 2010). For the same reasons, mean sediment grain size and diversity can be expected to vary throughout a canyon. Different substrata will increase sediment particle size diversity, which often positively correlates to macrofaunal (Etter & Grassle 1992) and meiofaunal diversity (Leduc et al. 2012b). Sessile megafauna add to the habitat complexity inside canyons, for example, deep-water corals can be found throughout canyon systems, providing refuge for diverse faunal communities (Mortensen & Buhl-Mortensen 2005, Buhl-Mortensen et al. 2010, Huvenne et al. 2011). It is expected that all of these factors act to increase environmental heterogeneity, particularly within active canyons, and thereby to enhance diversity compared with the adjacent slope (Tews et al. 2004). Shelf-incising canyons are thought to encompass greater habitat heterogeneity and are more likely to intersect currents along the shelf (Huang et al. 2014). In a study of two canyons off South Australia, the du Couedic (100- 1500 m depth) and Bonney (100-2000 m depth) canyons, the shelf-incising (du Couedic) canyon had a higher benthic megafaunal biomass and species richness than the 'blind' canyon (Currie & Sorokin 2013). This was attributed to different hydrodynamic regimes and structure (depth range, morphology and proximity to adjacent canyon) of the two canyons.

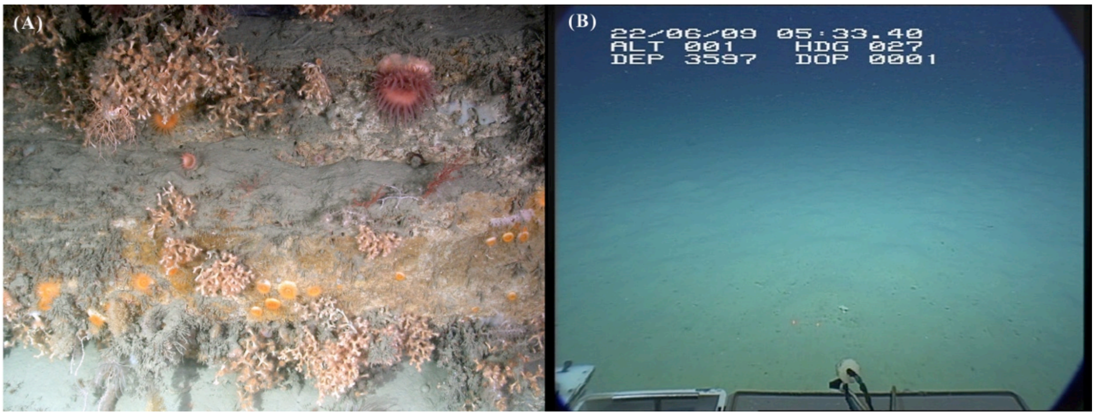


Figure 1.4 **Habitat heterogeneity inside the Whittard Submarine Canyon.**
A) Steep vertical wall with cold-water corals attached. B) Flat area of soft sediment.

There is no general agreement on whether alpha species diversity is higher inside canyons (Vetter & Dayton 1998, 1999, Schlacher et al. 2007, Vetter et al. 2010, De Leo et al. 2012) or higher on the adjacent slope (Gage et al. 1995, Curdia et al. 2004, Garcia et al. 2007, Koho et al. 2007, Ingels et al. 2009). Faunal diversity is also reported to change down the canyon axis and out onto the canyon fan (Tyler et al. 2009), for example, for foraminifera (Duros et al. 2011) and polychaetes (Paterson et al. 2011). Diversity within canyons may deviate from the general parabolic pattern with depth, showing either increased species richness at depth (Cunha et al. 2011) or depressed diversity throughout (Vetter & Dayton 1998). An increase in productivity from low to moderate levels is thought to increase diversity (Rosenzweig 1995), but the funnelling of organic material in canyons may favour opportunistic species (Paterson et al. 2011), and thereby act to depress diversity if levels are too high (Curdia et al. 2004).

Submarine canyons are believed to be sites of enhanced species turnover (beta diversity), leading to an increase in regional diversity on continental margins. High levels of beta diversity within the megafauna (Vetter et al. 2010) and macrofauna, particularly the polychaetes (De Leo et al. 2014), were recorded in canyons in the Hawaiian archipelago. Vetter et al. (2010) recorded enhanced diversity of mobile megafauna, especially fish, inside canyons compared with the adjacent open slope. High inter- and intra-canyon species turnover of sponges was observed in five canyons on the continental margin off southeastern Australia from depths of 114 to 612 m (Schlacher et al. 2007). Seventy-six percent of sponge species were found only at a single site and 79 % occurred in a single canyon, suggesting that sponges had very compressed geographic ranges. McClain and Barry (2010) observed a high species turnover for macrofauna at scales of < 100 m and < 10 m in the Monterey Canyon (Northeast Pacific Ocean, 595 - 2500 m depth).

1.5 Thesis Aims and Objectives

The general aim of this thesis is to further understand the patterns and drivers of benthic abundance, diversity and composition in submarine canyons. The study area for this thesis is the Whittard Submarine Canyon, situated on the Celtic Margin in the northern Bay of Biscay (Northeast Atlantic). It is a large dendritic canyon, which extends from the shelf edge around 200 m to 4100 m water depth at the canyon mouth, where it opens out onto the Whittard Sea Fan (Reid & Hamilton 1990) and the Porcupine Abyssal Plain. The Whittard Canyon is a relatively large canyon. It spans a distance of 110 km (www.eu- hermione.net) and the global mean length of canyons is 41 km (Harris et al. 2014). It is a shelf-incising canyon, cutting into the shelf at the canyon head but not directly connected to a modern day river system. The formation of the Whittard Canyon began in the Plio-Pleistocene (5 mya). The canyon was cut into the continental shelf and slope by headward erosion and retrogressive slope failure during sea level low stands related to periodic glaciations (Bourillet et al. 2003, Stewart et al. 2014). The main branches deeply incise the upper slope, in their upper regions these branches have steep vertical walls with a topographic height up to 800 m (Hunter et al. 2013a). The three main branches converge at around 3800 m water depth to form one single channel, which at 4100 m continues as the Whittard Channel. The channel follows a sinuous course in the South to Southeastern direction, where it then joins the Shamrock Channel at about 4600 m (Amaro et al. 2015). A review of the Whittard Canyon physical, geological and biological attributes is in progress (Teresa Amaro pers. comm.). The macrofaunal organisms retained on a > 300 μm sieve will be the main faunal component investigated. An increased understanding of fauna associated with these complex topographical features can be achieved through the completion of a number of objectives addressed in this thesis. I focus specifically on four sites, the Western, Central and Eastern branches of the Whittard Canyon and the adjacent slope to the west of the canyon. All sites were located at a common water depth of around 3500 m. The main theme of this thesis concerns patterns of macrofaunal density, assemblage composition and diversity in three branches of the Whittard Canyon and on the adjacent slope.

In Chapter 2, the composition of macrofaunal higher taxa in the different branches of the Whittard Canyon is described and compared with macrofaunal assemblages on the adjacent open slope to the west of the canyon. Multivariate statistics are used to identify which environmental variables impact the faunal assemblages in the Whittard Canyon. This chapter is published as Gunton et al. (2015a).

In Chapter 3, polychaete species-level assemblages in the Whittard Canyon and on the adjacent slope are identified and compred with polychaete species-level data from the Iberian Margin canyons. This chapter is published as Gunton et al. (2015b).

In Chapter 4, nematode assemblages are identified and compared with polychaete assemblages in the Whittard Canyon. This is to understand if nematodes and polychaetes have different functional responses both inside and outside the canyon setting

In Chapter 5, our knowledge of canyon faunas is synthesised and new hypotheses are created to guide future research.

1.6 Thesis Hypotheses

This thesis will focus on a number of hypotheses including:

- The Whittard Canyon is an area of increased faunal abundance compared with the adjacent slope as a result of suspected organic matter trapping and channelling inside the canyon.
- The Whittard Canyon harbours a distinct macrofaunal assemblage compared with the adjacent continental slope as a result of suspected variant physical environmental conditions inside the canyon and canyon endemism.

- The Whittard Canyon is an area of depressed alpha diversity compared with the adjacent slope as a result of suspected increased physical disturbance levels inside the canyon.
- The Whittard Canyon acts to increase macrofaunal regional diversity along the continental margin by increased species turnover as a result of suspected enhanced habitat variation and potential canyon endemics.
- Polychaete and nematode assemblages exhibit different trends in composition and structure inside the Whittard Canyon and on the adjacent slope as a result of their different ecologies.

1.7 Candidate's Contribution to the Published Papers

Chapter 2: I was the first author on "*Macrofaunal abundance and community composition at lower bathyal depths in different branches of the Whittard Canyon and on the adjacent slope (3500m; NE Atlantic)*". This paper was published in the journal *Deep-Sea Research Part I* in 2015 (Appendix D). I identified the macrofauna to higher taxon level with help from Prof. Andrew Gooday. Dr. Brian Bett advised me on the statistics. Prof. Andrew Gooday, Dr. Brian Bett and Dr. Adrian Glover helped me with the writing of the manuscript.

Chapter 3: I am the first author of the manuscript "*Benthic polychaete diversity patterns and community structure in the Whittard Canyons system and adjacent slope (NE Atlantic)*". This paper was published in the journal *Deep-Sea Research Part I* in 2015 (Appendix D). Lenka Neal, Dr. Adrian Glover, Dr. Gordon Paterson and Dr. Claire Laguionie-Marchais helped me with the identification of the polychaetes to species level. Dr. Brian Bett helped with the statistics. Prof. Andrew Gooday, Dr. Brian Bett, Dr. Adrian Glover and Lenka Neal helped with the writing of the manuscript.

Chapter 2: Macrofaunal abundance and community composition at lower bathyal depths in different branches of the Whittard Canyon and on the adjacent slope (3500m; NE Atlantic)

2.1 Abstract

We studied benthic macrofaunal abundance and community composition in replicate Megacorer samples obtained from three sites in different branches of the Whittard Canyon (NE Atlantic) and one site on the adjacent slope to the west of the canyon system. All sites were located at a depth of ~ 3500 m. Abundance (macrobenthos sensu stricto, > 300 μm) varied significantly ($p < 0.001$) among sites, and decreased from east to west; highest in the Eastern branch (6249 ± standard deviation 1363 ind. m^{-2}) and lowest on the slope (2744 ± SD 269 ind. m^{-2}). Polychaetes were the dominant taxon, making up 53 % of the macrofauna, followed by isopods (11 %), tanaids (10 %), bivalves (7 %) and sipunculans (7 %). Among the polychaetes, the Amphinomidae was the dominant family (27 %), followed by the Spionidae (22 %). Assemblage composition changed across the sites. From east to west, the proportion of polychaetes and isopods decreased (by 6 % in each case), while sipunculans and tanaids increased (by 13 % and 8 %, respectively). The ranking of the two dominant polychaete families reversed from east to west (Eastern branch - Amphinomidae 36 %, Spionidae 21 %; Slope - Spionidae 30 %, Amphinomidae 10 %). Ordination of faunal groups (macrofaunal higher taxa, and polychaete families) revealed that the Central and Eastern branches were substantially similar, while the Western branch and slope sites were relatively distinct. A similar pattern was evident in a corresponding ordination of environmental variables across the sites. An analysis of faunal similarities (ANOSIM) indicated that the Western branch/slope and Central branch/Eastern branch groups displayed the highest similarity. The clearest separation was between the slope and the Eastern branch. We conclude that, when compared at the same water depth, macrofaunal abundance and composition varies between open slope and canyon location, as well as among canyon branches. These differences probably reflect the influence of organic enrichment together with hydrodynamic activity, both of which are influenced by the topographic profile of individual canyon branches.

2.2 Introduction

Submarine canyons are major topographic features on continental margins. They play an important role as fast-track conduits for the transport of material from the shelf to abyssal depths (Vetter and Dayton, 1998). Organic carbon in the form of macrophyte detritus (Rowe et al., 1982; Vetter and Dayton, 1999), sediment (Arzola et al., 2008) and even pollutants (Palanques et al., 2008) are transported through canyons out onto the adjacent abyssal plain. Active canyons are believed to be very unstable environments that are subject to tidal currents, episodic slumps, sediment gravity flows, turbidity flows and periodic flushing events (Gardner, 1989; Canals et al., 2006; de Stigter et al., 2007). Topography (Shepard and Dill, 1966) and proximity to a fluvial source will also influence the disturbance regime. Although they have been known for over a century and a half (Dana, 1863), the rugged topography of canyons and the difficulty of sampling within them have limited multidisciplinary studies to the last twenty years (Ramirez-Llodra et al., 2010a). As a result, current knowledge of canyon benthic biology is poor.

Deep-sea macrofauna abundance decreases with depth (Rowe, 1983; Rex et al., 2006). However, this decline in abundance is far from uniform (Gage, 2003) and regions of high productivity can show elevated benthic abundance regardless of depth (Rex and Etter, 2010). In this regard, submarine canyons have been referred to as biomass and productivity 'hotspots' (De Leo et al., 2010; Vetter et al., 2010). Canyon sediments are reported to be richer in fresh organic carbon, total nitrogen, phytopigments (Garcia et al., 2007) and lithogenic (Romano et al., 2013) material than sediments on the adjacent slope. High organic enrichment inside canyons compared with the open slope has been linked to increased megafaunal (Vetter and Dayton, 1999; Ramirez-Llodra et al., 2010b; Vetter et al., 2010; De Leo et al., 2010), macrofaunal (Rowe et al., 1982; Vetter and Dayton, 1998; Tyler et al., 2009; Duineveld et al., 2001; Paterson et al., 2011), meiofaunal (Ingels et al., 2009; Soetaert et al., 1991) and foraminiferal (Duros et al., 2011) densities. On the other hand, depressed faunal abundance inside canyons may be linked to frequent physical disturbance and high sedimentation rates (Gage et al., 1995; Koho et al., 2007).

As with faunal abundance, benthic community composition and diversity is influenced by the quality and quantity of food inputs (Gooday and Turley, 1990; Ruhl and Smith, 2004) and hydrodynamic disturbance (Thistle et al., 1985; Grassle and Morse-Porteous, 1987), as well as by water depth (Jumars and Gallagher, 1982; Flach et al., 2002), sediment grain size (Etter and Grassle, 1992; Leduc et al., 2012b), sediment mobility (Levin et al., 1994a) and bottom-water oxygen concentration (Levin et al., 2000). Many of these factors are thought to interact, regulating biological communities within canyons (McClain and Barry, 2010).

Evidence from the High Energy Benthic Boundary Layer Experiment (HEBBLE) site (Thistle and Sherman, 1985; Thistle and Wilson, 1987, 1996; Thistle et al., 1991, 1999) suggests that elevated levels of disturbance inside canyons, such as those caused by currents, will structure the faunal assemblage differently compared with more quiescent slope environments. Taxa such as tanaids that are able to burrow into the sediment and hide from disturbance (Reidenauer & Thistle, 1985) gain an advantage, while suspension-feeding organisms (sponges and corals) benefit from enhanced bottom currents inside canyons (Rowe, 1971) and deposit-feeding organisms can benefit from the increased levels of macrophyte detritus (Okey, 1997). Opportunistic species will also be favoured in areas of high disturbance (Paterson et al., 2011). The diverse current regimes, varying substratum types, and detrital funneling from the continental shelf, will combine to enhance habitat heterogeneity within canyons (Levin et al., 2010). Large sessile megafauna add to the habitat complexity, and cold-water corals provide habitats and refuges from predators for a variety of taxa (Buhl-Mortensen et al., 2010). Thus, a greater diversity of microhabitats is available to canyon inhabitants compared with those living on the open slope. Such factors may explain differences in community composition between canyons and adjacent slopes sites located at similar depths (Vetter and Dayton, 1998; Duineveld et al., 2001; Garcia et al., 2007).

The Whittard Canyon is a dendritic submarine canyon system on the NW European continental margin. Previous studies have shown that this feature hosts increased foraminiferal (Duros et al., 2011) and nematode (Ingels et al., 2011c) abundances compared with the open slope. Hunter et al. (2013a) reported high macrofaunal abundances inside the canyon. Duineveld et al. (2001) reported a significantly higher macro- and mega-faunal biomass inside the canyon compared with the slope, but no significant difference in macrofaunal abundance. Increased taxon richness and abundance in the Whittard Canyon have also been reported for cold-water corals (Morris et al., 2013). There are no previous studies, however, of macrofaunal abundance and community composition across the canyon system. With this in mind, the present study investigates these faunal parameters at the higher taxon level for the macrofauna as a whole, and at the family level for the dominant macrofaunal group (polychaetes) at the same water depth within different branches of the Whittard Canyon and on the adjacent slope. We aim to test whether (1) macrofaunal abundance is enhanced inside the Whittard Canyon relative to the adjacent slope, (2) community composition inside the canyon is distinct from that on the adjacent slope, and (3) canyon assemblages are distinct on an intra-canyon scale.

2.3 Materials and methods

2.3.1 Study area

The Whittard Canyon is located on the Irish margin, southwest of the British Isles and southeast of the Goban Spur, and is not directly connected to any rivers. It starts around the shelf break at about 200 m water depth and extends to a depth of 4000 m over a distance of about 110 km. Three main branches, the Western, Central and Eastern, are recognised within the canyon system (Fig. 2.1). These branches coalesce around 3700 m to form a single canyon that opens out on to the Porcupine Abyssal Plain. The upper part is very steep-sided with walls reaching a height of up to 800 m, but at depths of around 3600 m the walls are lower (Hunter et al., 2013a). The mouth of the canyon discharges into a large fan, 148 km long by 111 km wide (Reid and Hamilton, 1990).

The sediments in the upper part of the canyon are coarse compared with those further down (Hunter et al., 2013a). The sediment is characterised by silty clay and fine sand in the Western branch (~ 3000 m), whereas sandy silt and fine sand predominate in the Eastern branch (~ 3000 m). The slope to the west of the canyon system is characterised by sand and silt (Duros et al., 2012). Some of the canyon sediments are derived from the shelf, which presumably provides a significant proportion of the material that passes down the canyon system at present (Reid and Hamilton, 1990; Cunningham et al., 2005).

Evidence about the levels of activity within the Whittard Canyon is ambiguous. Reid and Hamilton (1990) report small slope failures and a semi-diurnal tidal current only strong enough to transport fine-grained material. However, there is also evidence for active down-slope sediment transport in the form of turbidity currents, as well as mud-rich flows large enough to overspill the canyon system and form overbank deposits (Cunningham et al., 2005). Near-bottom currents reaching a maximum speed of 16 cm s^{-1} have been reported at 3752 m depth inside the canyon (Reid and Hamilton, 1990). Tidal currents with speeds up to 40 cm s^{-1} at 1000 m and up to 20 cm s^{-1} at 2000 m were recorded in the Eastern and Western branches (de Stigter in Duros et al., 2011). Sediment fluxes down the Whittard Canyon have not been well quantified and how they vary between the different branches remains unknown.

The present study focuses on sites located at the same depth (~ 3500 m) in the Western, Central and Eastern branches. Previous studies reported differences in environmental parameters between the Western and Eastern branches at similar depths. These data are summarised in (Table S2.1).

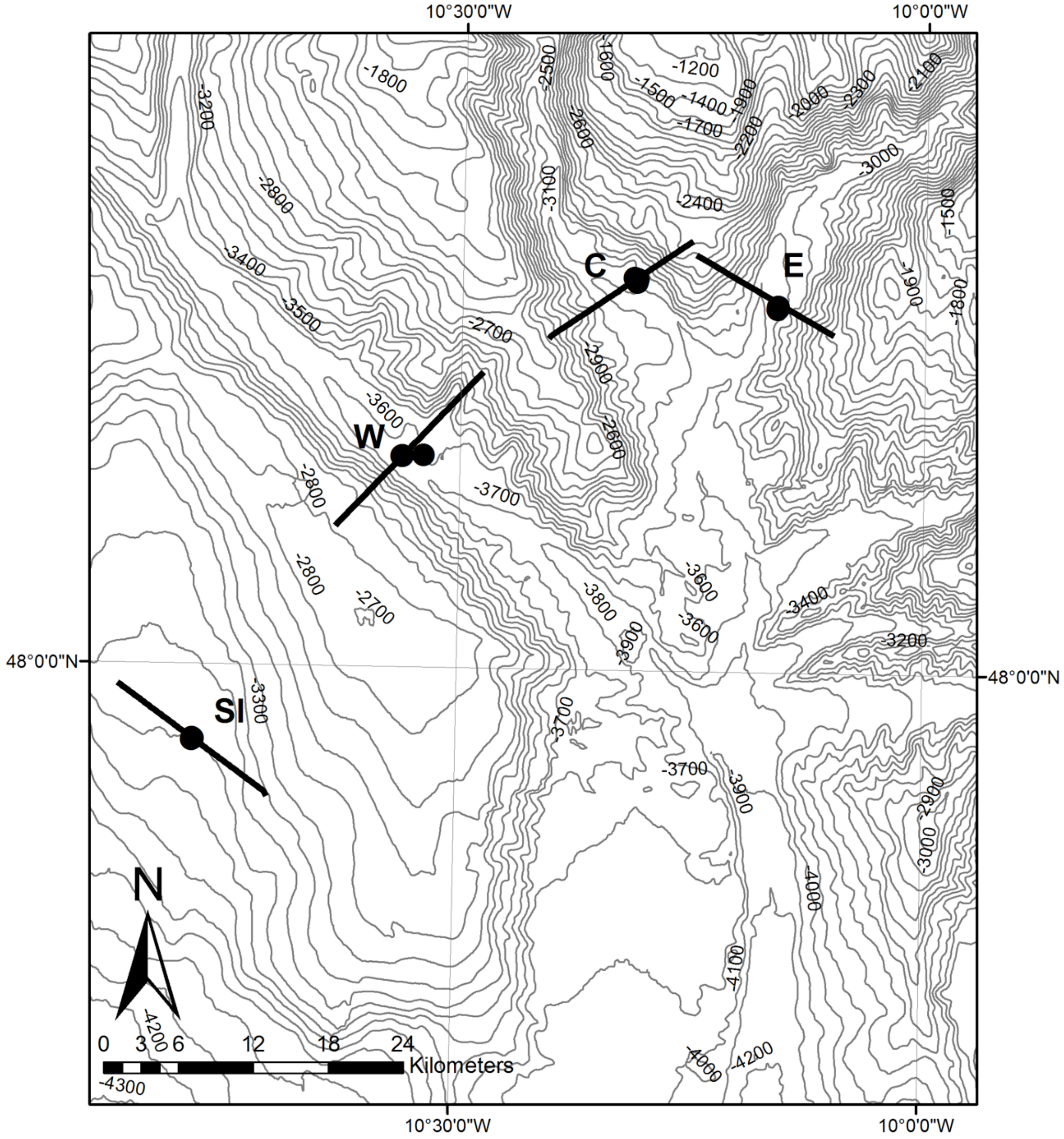


Figure 2.1 Bathymetric chart of Whittard Canyon.

Map based on data provided by the Geological Survey of Ireland (www.gsiseabed.ie). The four study sites are indicated: Western Branch (W), Central Branch (C) and Eastern Branch (E) of the canyon and one site on the adjacent slope (Sl). Contour lines are given in metres. Solid lines represent transverse bathymetric profiles shown in Fig. 2.2.

Table 2.1 Station list.

Megacore deployments on RRS *James Cook* cruise 36, Whittard Canyon and adjacent slope. W, Western branch; Sl, Slope site; C, Central branch; E, Eastern branch. MGS, mean grain size. Percentage clay, silt and sand (Wentworth, 1922).

Deploy.	Date (dd/mm/09)	Lat. North	Long. West	Depth (m)	Area (m^{-2})	Slope (°)	Rugosity ($x10^{-6}$)	Fine-scale BPI	MGS (µm)	Clay (%)	Silt (%)	Sand (%)
Sl016	24/06	47°56.79	10°46.85	3511	0.063	0.93	14	-20				
Sl017	24/06	47°56.78	10°46.85	3512	0.055	0.93	15	-20				
Sl018	24/06	47°56.81	10°46.91	3514	0.047	0.93	6	-20				
Sl019	24/06	47°56.74	10°46.94	3505	0.063	0.93	11	-17	71.8	16.5	56.7	26.8
Sl020	25/06	47°56.78	10°46.85	3514	0.055	0.93	14	-20				
W002	20/06	48°09.18	10°33.70	3670	0.063	2.36	161	3				
W003	21/06	48°09.17	10°33.70	3661	0.055	2.36	165	3				
W011	23/06	48°09.22	10°32.36	3582	0.047	0.20	6	30				
W026	27/06	48°09.18	10°33.73	3670	0.039	2.36	138	-10				
W043	08/07	48°09.15	10°33.76	3657	0.047	2.36	113	-10	28.8	13.3	74.2	12.5
C063	13/07	48°16.89	10°18.74	3375	0.047	2.49	140	-81				
C064	13/07	48°16.97	10°18.65	3382	0.063	2.49	610	-109				
C065	13/07	48°17.04	10°18.89	3373	0.055	3.35	239	-118	26.9	12.0	77.9	10.1
C067	13/07	48°16.98	10°18.72	3376	0.055	3.88	448	-106				
C066	13/07	48°16.83	10°18.72	3381	0.063	2.75	187	-91.5				
C068	13/07	48°17.01	10°18.83	3375								
E093	21/07	48°15.89	10°09.56	3424	0.063	3.15	92	-27	32.7	10.6	75.5	13.9
E094	21/07	48°15.78	10°09.57	3429	0.053	3.36	92	-23				
E095	21/07	48°15.78	10°09.58	3429	0.063	3.35	1150	-23				
E096	22/07	48°15.76	10°09.60	3424								
E097	22/07	48°15.89	10°09.54	3425	0.039	3.15	88	-28				
E098	22/07	48°15.76	10°09.60	3432	0.031	3.35	131	-23				

2.3.2 Field sampling

Macrofauna were collected from three sites in different branches of the canyon and one site on the adjacent slope (Fig. 2.1) using a Megacorer (Gage & Bett, 2005) during the RRS *James Cook* cruise 036 in June and July 2009. Samples were taken from 22 deployments (Table 2.1), between 3373 and 3670 m depth. In general, the Megacorer was fitted with eight large (100 mm internal diameter) core tubes. However, for one deployment at each site, one of the large tubes was replaced with a single smaller (59 mm internal diameter) tube. This collected a core that was used for sediment grain-size analysis.

Five replicate deployments were conducted in the Western branch, six in the Central branch, six in the Eastern branch and five at the slope site. The additional deployment in the Central and Eastern branches was made to compensate for the failure to recover enough cores during earlier deployments. On deck, the individual cores from each deployment were sliced into five sediment layers (0-1, 1-3, 3-5, 5-10 and 10-15 cm). Core slices from the same layer of the different cores from one deployment were placed in the same 20 litre bucket. The contents of the bucket were then homogenised to produce one combined sample for each layer (i.e. 5 combined samples for each deployment). The overlying water was added to the 0-1 cm layer. The combined samples (one for each sediment layer) were then carefully washed with filtered (mesh size 125 μm) seawater on 500 and 300 μm sieves. The > 500 μm residues from each combined sediment layer from one deployment were placed in one 5 litre plastic tub and fixed with 4 % borax-buffered formaldehyde and seawater solution. The same was done for the 300-500 μm residues. Thus each deployment yielded two combined sieve fractions for each of the five sediment layers.

2.3.3 Environmental data

A post-processed bathymetry map of the Whittard Canyon (cell size 10 x 10 m) was downloaded from the INFOMAR website (www.gsiseabed.ie/). The steepness of the terrain at each Megacore deployment station was calculated using the ArcMap 10 (ESRI) Spatial Analyst geoprocessing tool ‘Slope’ applied to the bathymetry map. The Slope tool calculates the maximum rate of change between each cell and its immediate neighbours in a 3 x 3 cell window. The Benthic Terrain Modeler ArcGIS Desktop Extension alpha version (Wright et al., 2005) was used to calculate the fine-scale Bathymetric Position Index (BPI) and Vector Ruggedness Measure (VRM) from the bathymetry data. BPI is a scale-dependent index representing a grid cell’s topographic location within a benthic landscape relative to its local surroundings; the fine-scale BPI allows the identification of smaller features within the benthic landscape (Wright et al., 2005). VRM is the variation in three-dimensional orientation of grid cells within a neighbourhood (3 x 3 window). Transverse bathymetric profiles of the canyon branches and the slope were derived using the ArcMap profile view tool.

Cores for sediment particle-size analysis (Table 2.1) were sliced on deck into 12 layers (0.5 cm layers between 0-2 cm depth and 1 cm layers between 2 and 10 cm). Each layer was placed in a 500 ml bottle and fixed in 10 % buffered formalin. Only the 0-0.5, 1-1.5, 2-3 and 4-5 cm sediment layers were analysed as other layers were used for meiofaunal analysis. Each layer was first homogenised (particles > 2mm removed), dispersed using a 0.05 % $(NaPO_3)_6$ solution and mechanically agitated before being analysed using a Malvern Mastersizer 2000 laser diffraction particle size analyser (Abbireddy & Clayton, 2009).

2.3.4 Macrobenthos processing

The top three sediment layers (0-1, 1-3, 3-5 cm) were analysed for this study. The samples were transferred from the formalin onto a 300-µm-mesh sieve, rinsed with 70 % ethanol to remove the formalin and then sorted for macrofauna, also in 70 % ethanol. The 300-500 µm and > 500 µm fractions were processed separately. All specimens were sorted to major taxa (phylum or class) under a Leica MZ9.5 stereomicroscope. We followed common practice in deep-sea studies by considering only the macrofauna sensu stricto (Gage & Tyler, 1991; Bett, 2014), i.e. meiofaunal taxa (foraminifera, copepods, nematodes, and ostracods) were excluded.

The polychaetes were identified to family level based on morphological characters visible under a light microscope and identified by reference to taxonomic keys (Hayward and Ryland, 1996; Beesley et al., 2000). Where fragmented specimens were encountered, only head fragments were counted.

2.3.5 Data analysis

Macrofaunal counts from the three sediment layers (0-1, 1-3, 3-5 cm) were pooled together, standardised to unit seafloor area sampled (i.e. density, ind. m^{-2}), and subject to a log (x + 1) transformation prior to analysis. The transformation log (x + 1) was to account for the likely aggregation of faunal abundance data. Before analyses were performed, the ANOVA assumptions of normality and homogeneity of variance were evaluated using Anderson-Darling and Levene's tests respectively. Density data satisfied tests of ANOVA assumptions. Thus, ANOVA and Tukey Pairwise tests were performed on density data. Mood's Median tests were used to test for significance of slope, rugosity and fine-scale BPI (bathymetric position index). These univariate tests were carried out using the Minitab statistical software package (v16, LEAD Technologies, 2010).

Multivariate analyses were executed using the PRIMER software package (Clarke and Gorley, 2006; v6, PRIMER-E Ltd). Macrobenthos data were assessed via non-metric multidimensional scaling (MDS) based on Bray Curtis similarity of log transformed density. Global and pair-wise analysis of similarities (ANOSIM) was employed to assess the distinctiveness of canyon and slope study sites. Environmental data were assessed via principal components analysis (PCA) of normalised data (i.e. transformed to zero mean, and unit variance). In the absence of direct measurement, macrofaunal abundance was used as a proxy for organic matter input, in order to examine the relationship between productivity and macrofaunal assemblage patterns. Global macrofaunal abundance in the deep sea has been predicted from the incoming flux of organic matter (Rex et al., 2006; Wei et al., 2010b). Similarly, the Metabolic Theory of Ecology (Brown et al., 2004) predicts that carrying capacity (faunal abundance) is directly related to resource supply where temperature is constant. Organic matter supply to the seafloor is normally estimated from surface primary productivity and water depth (e.g. Lutz et al., 2007), but this would fail to account for the funnelling action of the canyon system.

2.4 Results

2.4.1 Environmental characteristics

2.4.1.1 Bathymetry and derivatives

The slope angle of the seafloor at sites sampled inside the canyon branches was fairly uniform, ranging from means of 2.36° (Western branch) to 3.27° (Eastern branch) (Table 2.1). The angle on the adjacent slope was much lower (mean 0.93°). There was a statistically significant difference in slope between all four sites (Mood's Median Test: Slope versus Location $p < 0.001$). Bathymetric Position Index (BPI) values were higher in the Western branch and on the slope (representing higher points/crests in terrain compared with the surroundings) than in the Eastern and Central branches, and statistically different between all four sites (Mood's Median Test: BPI versus location $p < 0.001$). Rugosity was highest in the Central branch and lowest on the slope (Table 2.1); again the differences were significant between all four sites (Mood's Median Test: rugosity versus location $p = 0.015$). Canyon profiles are approximately "U" shaped (Fig. 2.2), most clearly so in the case of the Eastern branch, which has the narrowest branch width. The Western branch is wider with a flatter floor than the Eastern and Central branches. The flat slope profile in Fig. 2.2 is included for comparison.

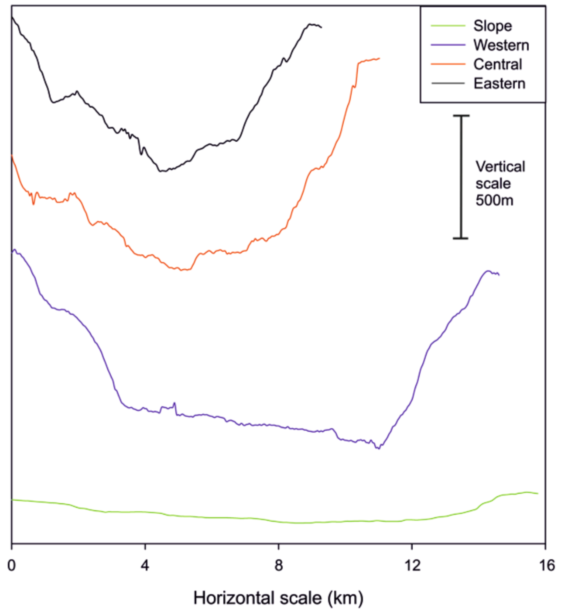


Figure 2.2 Slope–normal bathymetric profiles through the study sites
Eastern, Central and Western canyon branches, and on the adjacent open slope.

2.4.1.2 Sedimentology

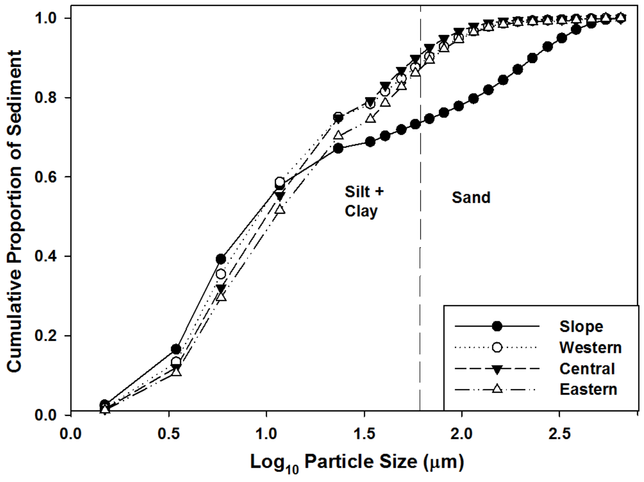


Figure 2.3 Cumulative sediment particle size distribution
Three canyon branch sites and adjacent open slope site.

The three canyons sites (Western, Central and Eastern branches) had similar mean particle sizes (28.8, 26.9 and 32.7 µm respectively) (Table 2.1). The slope site had a significantly coarser sediment (mean particle size 71.8 µm) (Fig. 2.3). At all four sites the sediment was composed predominantly (> 56 %) of silt (grain size 4 - 63µm). The Central branch sediment had a slightly higher percentage of silt (77.9 %), than the Eastern (75.5 %) and the Western (74.2 %)

branches, while the slope sediment had a much lower silt content (56.7 %) (Table 2.1). Clay content (grain size < 4 μm) was highest on the slope (16.5 %) and decreased inside the canyon from the Western (13.3 %) to the Eastern (10.6 %) branches. The slope sediment had a distinctly higher percentage of sand (26.8 %) compared with the canyon sites (< 13.9 %), where the percentage was lowest in the Central branch (10.1 %).

2.4.1.3 Principal Component Analysis

A PCA was performed on the following environmental variables (Fig. 2.4): sediment grain size, slope angle, fine-scale BPI, VRM and station depth (Table 2.1), with macrofaunal density used as a proxy for organic matter (OM) input. The four study sites were quite discrete in the ordination space formed by the first two axes. The differentiation of canyon and slope sites appeared to align with the environmental vectors of sediment grain size, rugosity, slope angle and fine-scale BPI. Differentiation of the Western from the Central and Eastern branches appeared to align with water depth and proxy organic matter supply (macrofaunal density).

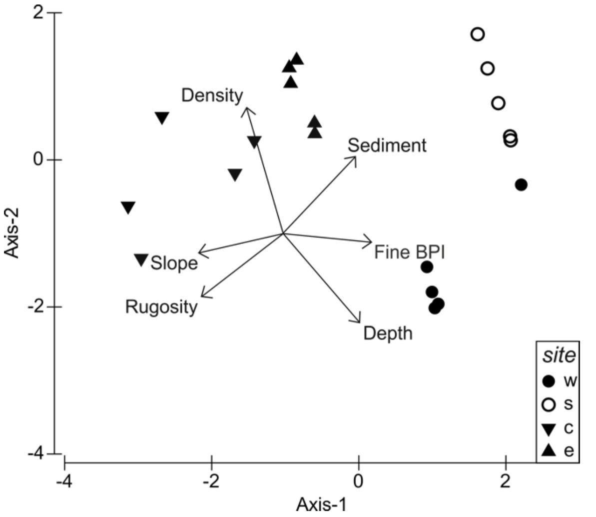


Figure 2.4 Principal components analysis of normalized environmental variables at canyon and slope sites.
The variables are depth, mean grain size (sediment), slope angle, rugosity, fine-scale Bathymetric Position Index (BPI) and macrofaunal density (as a proxy for organic matter supply).

2.4.2 Macrobenthos

2.4.2.1 Total abundance

In total, 4444 macrofauna individuals were picked from the samples. Fifty-three percent of the fauna was retained on the 500 μm sieve. There was a significant difference in abundance between sites (One-way ANOVA, $p < 0.001$, R2 (adj) = 76.32 %). Pairwise comparison revealed that the Central and Eastern branches were significantly different ($p < 0.05$) from the Western branch and slope. The Eastern branch had the highest abundance of macrofauna (6249 ± SD 1363 ind. m^{-2}). Values were intermediate in the Central branch (4461 ± SD 856 ind. m^{-2}) and lowest in the Western branch (2900 ± SD 538 ind. m^{-2}) (Table 2.2). The abundance decreased across all sites from east to west, with the slope site having the lowest value (2744 ± SD 269 ind. m^{-2}) (Table 2.2).

Table 2.2 Density of macrofaunal taxa at three canyon sites and on the adjacent slope. Values are mean densities (n = 5) for the 0 - 5 cm sediment layer, based on the > 300 µm sieve size fraction.

	Abundance (ind. m^{-2})			
Taxon	Slope	West	Central	East
Amphipoda	14.9	96.7	291.8	241.3
Aplacophora	18.5	21.3	37.9	18.3
Ascidiacea	0.0	0.0	0.0	5.1
Bivalvia	58.5	246.2	309.0	538.7
Cumacea	35.2	10.6	23.7	26.8
Echinoidea	0.0	5.1	7.3	8.3
Gastropoda	0.0	5.1	0.0	0.0
Holothuroidea	0.0	0.0	0.0	5.1
Isopoda	136.4	197.2	723.8	670.0
Nemertea	0.0	3.6	3.6	0.0
Ophiuroidea	70.2	111.7	83.2	164.8
Polychaeta	1386.9	1468.7	2236.6	3557.4
Scaphopoda	0.0	0.0	45.3	227.2
Sipuncula	329.0	362.2	233.8	263.2
Tanaidacea	562.5	235.6	326.1	461.8
Indet. worm	62.6	50.1	112.8	49.4
Unknown	69.7	85.6	26.4	16.6
Total	2744	2900	4461	6249

2.4.2.2 Major taxon composition

Sixteen higher taxa were recognised in the canyon and slope samples (Table 2). Polychaeta was always the most abundant taxon, making up just over 50 % of the macrofauna with 2255 individuals in total and an average density of 2191 ind. m^{-2} for the 0-5 cm layer. The tanaids (10 %; 397 ind. m^{-2}), isopods (11 %; 432 ind. m^{-2}), sipunculans (7 %; 297 ind. m^{-2}) and bivalves (7 %; 288 ind. m^{-2}) were also important faunal components.

Although polychaetes always represented > 50 % of the assemblage in each branch, the proportion of other taxa varied between branches (Fig. 2.5A). The percentage of sipunculans (13 %) was higher in the Western branch compared with Eastern (4 %) and Central (5 %) branches. The Eastern and Central branches had higher percentages of isopods (11 % and 16 % respectively) than the Western branch (6 %). The tanaids maintained fairly similar percentages throughout the branches, as did the bivalves. The slope fauna was more similar to the Western branch than to the Central and Eastern branch fauna and in this sense it fitted in with a gradient of change of macrofauna composition across the four sites. The slope had a high percentage of sipunculans (12 %) and tanaids (20 %) but a low percentage of isopods (5 %) and bivalves (2 %). These percentages were similar to the Western branch values: sipunculans (13 %), tanaids (10 %), isopods (6 %) and bivalves (7 %).

The numerical abundance of macrofauna displayed some of the same trends as the percentage abundance data (summarised in Table 2.2). Isopods had a high abundance in the Central and Eastern branches, but a much lower abundance in the Western branch, whereas sipunculans had a higher abundance in the Western branch compared with the Eastern and Central branches. Different trends were seen in other higher taxa. Tanaids were most abundant in the Eastern branch and less abundant in the Central and Western branches. Bivalves exhibited a similar east to west decline.

Numbers at the slope and Western branch sites were fairly similar for the sipunculans and isopods (summarised in Table 2.2). For other taxa there were larger differences. The tanaids were almost twice as abundant on the slope compared with the Western branch. Bivalves were four times more abundant in the Western branch than on the slope.

2.4.2.3 Multidimensional scaling analysis of major taxa

Differences between canyon branches in the major macrofaunal taxon composition are reflected in the corresponding MDS plot (Fig. 2.6A), which shows samples from the Central and Eastern sites intermingled and quite distinct from the Western branch and slope site samples. Two macrofaunal samples (Sl019 and Sl020) from the slope were distinct from the rest of the slope samples. The Western branch and remaining slope sites formed separate but adjacent grouping. ANOSIM global assessment indicated statistically significant ($p = 0.001$) variation among the sites. Significant ($p < 0.05$) pairwise differences were detected between Western/Central branches, Western/Eastern branches, slope/Central branch and slope/Eastern branch (Table 2.4).

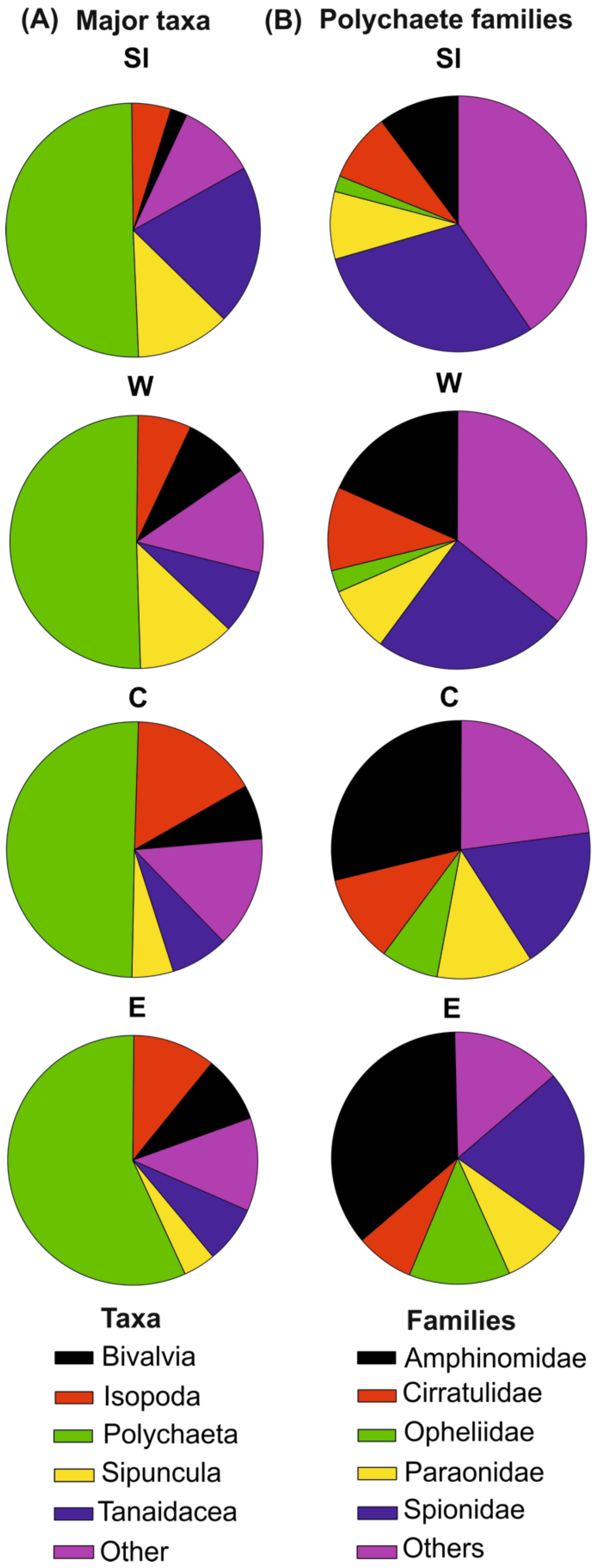


Figure 2.5 Relative abundance of top five taxa at the three canyon branch sites (W, E, C) and adjacent slope site (Sl).
A) Macrofaunal major taxa, (B) Polychaete families.

2.4.2.4 Polychaete family composition

In total, 2225 individual polychaetes were picked from the samples. Their abundance showed significant differences between sites (One-way ANOVA: $p < 0.001$, R^2 (adj) = 70.92 %) and followed the same patterns as the macrofauna. A Tukey pairwise test revealed that the Eastern and Central branches were significantly ($p < 0.05$) different from the Western branch and slope. The polychaetes represented 26 families (Table 2.3). The most abundant were the Amphinomidae, with an overall average density of 582 ind. m^{-2} (27 %), followed by the Spionidae (480 ind. m^{-2}; 22 %), Paraonidae (202 ind. m^{-2}; 9 %), Cirratulidae (196 ind. m^{-2}; 9 %) and Opheliidae (172 ind. m^{-2}; 8 %).

Polychaete composition differed between branches (Fig. 2.5B). The Eastern branch had the highest numbers of Amphinomidae (1270 ind. m^{-2}) compared with the other sites. This family represented 36 % of the polychaetes compared with 29 % in the Central branch and 18 % in the Western branch. The same pattern was seen in the Ophellidae; 13 % in the Eastern branch and 3 % in the Western branch. The Cirratulidae displayed the opposite pattern. The Western branch had the highest percentage (12 %), the Eastern branch the lowest (7 %) with intermediate values in the Central branch (11 %). The Spionidae exhibited a similar pattern (Western 24 %, Central 18 % and Eastern branch 21 %).

The slope site followed cross-canyon trends in polychaete family composition in being more similar to the Western branch than to the Central and Eastern branches. The slope assemblage was dominated by Spionidae (30 %), Amphinomidae (10 %) and Syllidae (10 %). These percentages were similar to those from the Western branch; Spionidae (24 %), Amphinomidae (18 %) and Syllidae (11 %). The ranking of the two dominant families on the slope was reversed in the Central (Amphinomidae 29 %, Spionidae 18 %) and Eastern branches (Amphinomidae 36 %, Spionidae 21 %).

The actual family abundance values followed the same trends between branches, except for the Spionidae, which reached their highest abundance in the Eastern and their lowest in the Western branch (summarised in Table 2.3). The slope site was generally more similar to the Western branch than to the other canyon branches in terms of the absolute abundance of the families Amphinomidae, Cirratulidae and Paraonidae. This was not true for all families; in particular the abundance of Spionidae on the slope was more similar to the Central branch values than to that of the Western branch.

Table 2.3 Density of polychaete families at three canyon sites and on the adjacent slope. Values are mean densities (n = 5) for the 0 - 5 cm sediment layer, based on the > 300 µm sieve size fraction.

	Abundance (ind m^{-2})			
Family	Slope	West	Central	East
Acrocirridae	99.6	57.7	41.7	57.6
Ampharetidae	93.5	22.1	10.0	9.6
Amphinomidae	140.4	265.2	651.1	1269.5
Capitellidae	7.9	0.0	12.7	0.0
Cirratulidae	120.7	169.3	239.1	262.5
Chrysopetalidae	0.0	0.0	11.5	3.2
Dorvilleidae	6.4	0.0	4.2	0.0
Glyceridae	49.1	40.6	48.7	74.4
Hesionidae	0.0	4.2	0.0	0.0
Lumbrineridae	21.7	21.1	26.4	48.4
Maldanidae	7.4	43.6	51.4	54.3
Nephtyidae	3.2	23.1	46.4	82.9
Onuphidae	6.8	0.0	0.0	0.0
Opheliidae	27.3	39.9	161.3	458.6
Orbiniidae	20.5	44.8	41.8	47.6
Paraonidae	118.9	120.5	272.3	298.3
Phyllodocidae	3.2	0.0	0.0	0.0
Pilargidae	0.0	0.0	3.6	0.0
Scalibregmatidae	23.2	19.0	16.8	27.8
Sigalionidae	33.8	69.5	25.0	17.3
Sphaerodoridae	3.2	0.0	91.0	0.0
Spionidae	417.1	351.6	405.2	746.8
Sternaspidae	0.0	3.6	6.4	3.2
Syllidae	139.5	161.9	30.6	67.9
Terebellidae	7.4	0.0	0.0	0.0
Poly. indet.	36.2	7.4	0.0	15.6
Larval poly. indet.	0.0	0.0	30.8	18.5
Total	1387	1469	2237	3557

2.4.2.5 Multidimensional scaling analysis of polychaete families

Polychaete family data revealed significant differences in assemblages between the sites. An MDS plot (Fig. 2.6B) grouped the Central and Eastern branch assemblages together, whereas the Western branch and slope sites were quite distinct. ANOSIM global assessment indicated statistically significant ($p = 0.001$) variation among the sites. Significant ($p < 0.05$) pairwise differences were detected between the slope site and all canyon branches (Table 2.4).

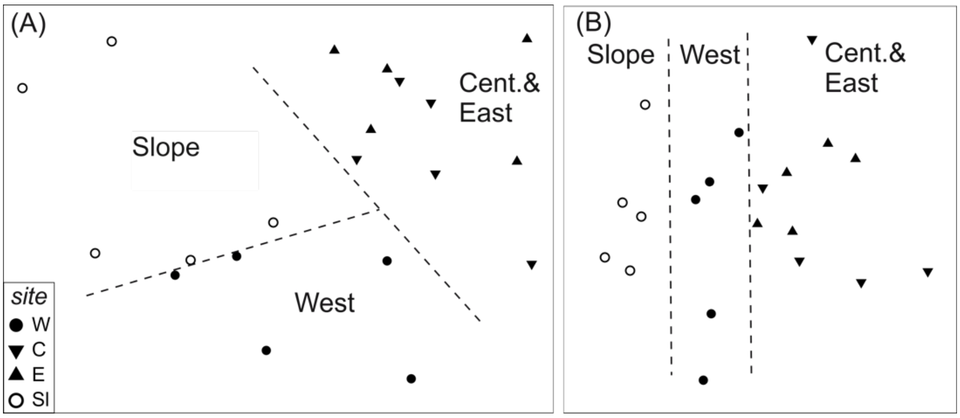


Figure 2.6 Non-metric multidimensional scaling ordinations.
(A) macrofaunal major taxa, and (B) polychaete families, for five replicate samples at each of the three canyon branch sites (W, E, C) and adjacent slope site (Sl).

Table 2.4 ANOSIM pairwise tests of macrofauna major taxa and polychaete families across four sites.
Western branch (W), Central branch (C), Eastern branch (E) and adjacent slope (Sl). n/s, not significant.

	Major Taxa		Polychaete Families	
Groups	R statistic	p value	R statistic	p value
W, Sl	0.240	n/s	0.276	0.048
W, C	0.576	0.008	0.204	n/s
W, E	0.724	0.008	0.248	n/s
Sl, C	0.784	0.008	0.684	0.008
Sl, E	0.868	0.008	0.864	0.008
C, E	0.032	n/s	0.048	n/s

2.5 Discussion

2.5.1 Comparison with earlier studies

2.5.1.1 Macrofaunal Abundance

Macrofaunal abundance decreased across the Whittard Canyon from the Eastern branch to the Western branch and was lowest on the adjacent slope. This pattern is consistent with the data of Hunter et al. (2013a). At similar depths (3500 m) in the Whittard Canyon, they observed a higher abundance of macrofauna in the Eastern branch (5352 ± SD 2583 ind. m^{-2}) compared with the Western branch (3416 ± SD 2069 ind. m^{-2}). An earlier study by Duineveld et al. (2001), however, reported a much lower abundance in the Western branch (1339 ind. m^{-2} at 3760 m) compared with the present study (2900 ± SD 538 ind. m^{-2}). At larger spatial scales, our macrofaunal densities can be compared with those in the extensively studied canyons on the Portuguese Margin (Tyler et al., 2009). Values from around 3500 m depth in the Setúbal

Canyon (2241 ind. m^{-2}), and particularly in the Nazaré Canyon (4600 ind. m^{-2}) (Cunha et al., 2011), are comparable to those reported in the present study (average 4536 ± SD 1676 ind. m^{-2}). On the slope, macrofaunal densities are higher (2744 ± SD 269 ind. m^{-2}) at our site to the west of the Whittard Canyon than on the nearby Goban Spur (500 ind. m^{-2} at 3700 m; Flach et al., 2002) and Porcupine Abyssal Plain (1465 ind. m^{-2} at 4850 m depth; Galeron et al. 2001), but comparable to those from 3600 m depth on the Goban Spur (2420 ind. m^{-2}) reported by Duineveld et al. (2001). These differences may reflect sampling and sample processing techniques. Flach et al. (2002), Galeron et al. (2001) and Duineveld et al. (2001) used box corers and 500, 250 and 500 µm sieves respectively, whereas a Megacorer and a 300 µm sieve were used in the present study. Densities in the Western branch based on our 500 µm sieve fractions were far lower (1777 ± SD 220 ind. m^{-2}) and more comparable to those of Duineveld et al. (2001) from the same area (1339 ind. m^{-2}). Box corers collect samples that are more disturbed than those obtained by hydraulically dampened multiple corers, leading to the loss of some meiofaunal and macrofaunal animals (Bett et al., 1994; Gage & Bett, 2005), while a larger sieve size would retain fewer animals.

Our macrofaunal densities from the canyon site considerably exceed the value (369 ind. m^{-2}) predicted by the regression equation of Rex et al. (2006) (Fig. 2.7); which was derived by plotting published global macrofaunal abundances against depth. The values in the present study are likewise far higher than the predicted 657 ind. m^{-2} derived from the formula in Wei et al. (2010b) (Fig. 2.7). Wei et al. (2010b) used a machine-learning algorithm, Random Forests, to model the relationship between oceanic properties and seafloor macrofaunal standing stock. They caution that the predicted values should be considered as conservative estimates for soft-bottomed communities relying solely on sinking phytodetritus. Wei et al. (2010b) also warn that their model may not hold true for submarine canyons. They argue that organic matter originating from the continental shelf accumulates inside canyons leading, to higher concentrations compared with non-canyon areas. Indeed, when canyon sites and non-canyon sites at similar depths in the NE Atlantic are compared, the Whittard Canyon sites yield some of the highest macrofaunal abundances (Fig. 2.7). To account for gear bias, as detailed by Bett et al., (1994) and Gage & Bett (2005), box core densities estimates have been increased by a factor of two to improve comparability with multiple corer estimates. The full list of original data is given in Table S2.2.

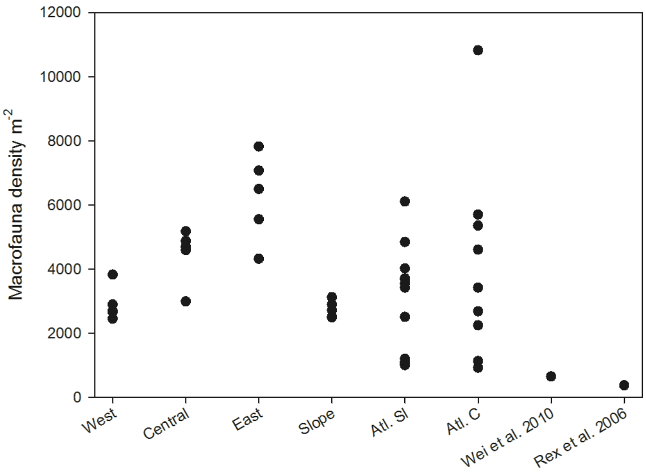


Figure 2.7 Benthic abundance comparison of macrofaunal densities
Values among present study sites (Western, Central and Eastern canyon branches and adjacent slope) and published Atlantic slope (Sl) and canyon (C) sites (Table S2.2). Global predictions for water depth 3500 m of Wei et al. (2010) and Rex et al. (2006) are also included. Data have been approximately corrected for sampling gear bias (see text for details).

2.5.1.2 Higher taxon composition

An important finding of our study was the clear shift in community composition, even at higher taxonomic levels, between the canyon branches and between the canyon and the adjacent slope. Polychaetes made up more than half of the macrofaunal assemblage at all sites. A lower percentage of polychaetes was reported by Hunter et al. (2013b) (Western branch 30 %, Eastern branch 20 %). However, Hunter et al. (2013a) included nematodes in the macrobenthos and, when these are excluded, polychaetes accounted for ~ 50 % of the macrofauna sensu stricto. Our Eastern branch samples were characterised by high abundances of polychaetes, bivalves and isopods whereas the Western branch and adjacent slope yielded high abundances of polychaetes, sipunculans and tanaids. Differences in macrofaunal assemblage composition between branches were also noted by Hunter et al. (2013a); polychaetes, crustaceans and macrofaunal-sized nematodes were equally abundant in the Western branch, whereas nematodes were dominant (> 50 %) in the Eastern branch.

Our results, and those of previous studies, suggest that there is a remarkable degree of heterogeneity between canyons in terms of their faunal composition, even at higher taxonomic levels. In the Setúbal Canyon, polychaetes were ranked first, crustaceans second and molluscs third (Cunha et al., 2011). In the Nazaré Canyon molluscs were the most abundant higher taxon, representing just under 50 % (2500 ind. m^{-2} at ~ 3400 m) of the total macrofaunal community (Cunha et al., 2011). Polychaetes were ranked second, followed by arthropods and echinoderms. In the Cascais Canyon (~ 3400 m depth), 45.9 % of total abundance was made up of crustaceans, polychaetes were ranked second (~ 40 %), and molluscs were the least abundant taxon (~ 5 %) (Cunha et al., 2011). In contrast, in the Whittard Canyon, polychaetes always made up > 50 % of the macrofaunal assemblages, crustaceans were ranked second (25 % total across all sites) and molluscs third (9 % total across all sites). Potential reasons for these differences in faunal composition are discussed in section 2.5.1.4.

2.5.1.3 Polychaete family composition

Polychaete family composition differed between the canyon branches. Particularly high numbers of Amphinomidae were observed in the Eastern branch. In contrast, Hunter et al. (2013) reported a high abundance of Amphinomidae in the Western branch and Cirratulidae and Spionidae in the Eastern branch. Duineveld et al.'s (2001) report of numerous small tubiculous Sabellidae in the Western branch is particularly interesting. Sabellidae are filter feeders, which strain food from passing water currents (Fauchald and Jumars, 1979). Duineveld et al. (2001) suggest their high abundance in the Western branch was caused by a high load of suspended organic particles passing over the canyon floor at that site, providing food for the sabellids. The absence of sabellids in our samples may indicate a reduced load of suspended organic particles in the water column when the samples were taken, or an absence of a suitable substrate for their tubes, or simply the heterogeneity of the canyon system.

Canyons cannot be characterised by one particular polychaete family. For example, the three most abundant families at depths around 3400 m in the Portuguese canyons were: Nazaré Canyon - Spionidae, Fauveliopsidae and Paraonidae; Cascais Canyon - Siboglinidae, Spionidae and Capitellidae; Setúbal Canyon - Spionidae, Ampharetidae and Nephytidae (Cunha et al., 2011). In the present study, the three top-ranked families were the Amphinomidae, Spionidae and Cirratulidae. However, it appears that Spionidae are often common in canyons. They were the top-ranked family overall in the Portuguese canyons (Paterson et al. 2011), second-ranked in the Whittard Canyon (this study) as well as the Cap-Ferret Canyon (Gerino et al. 1999). The Spionidae contain species thought to be opportunistic, such as those within the genus *Prionospio* (Paterson et al., 2011), which may be favoured in disturbed environments such as canyons where they are able exploit new patches of recently disturbed seafloor. Further investigations of species-level data are required to fully understand functional shifts in community composition.

2.5.1.4 Environmental controls on macrofaunal community structure and composition

2.5.1.4.1 Organic matter quantity and quality

The higher abundance of macrofauna in the Eastern branch of the Whittard Canyon compared with that in the other branches may reflect the quality and quantity of organic matter. Duineveld et al. (2001) observed higher concentrations of phytodetritus in cores from stations in the Eastern branch compared with those from the Western branch. Sediment analyses revealed a higher percentage of sedimentary POC in the Eastern (0.7 %) compared with the Western (0.5 %) branch, although this result was not statistically significant (Hunter et al., 2013). The composition of sedimentary particulate organic matter (POM) was also reported to vary between branches of the Whittard Canyon (Huvenne et al., 2011). Huvenne et al. (2011) record higher total lipid concentration in sediments from the Eastern (26 μgg^{-1}) compared with the Western (15 μgg^{-1}) branch. In the Eastern branch, the lipids included essential fatty acids thought to be derived from phytoplankton or zooplankton sources. In contrast, in the Western branch, sediment POM contained a high proportion of monounsaturated fatty acids (Huvenne et al., 2011), which are associated with mesozooplankton (Kiriakoulakis et al., 2005) and more degraded detritus compared with the "fresher" polyunsaturated fatty acids (Kiriakoulakis et al., 2004). Significantly higher values of sediment total nitrogen (TN) were recorded in the Eastern branch sediment (TN % 0.098 ± 0.006) of the Whittard Canyon compared with the Western branch sediment (TN % 0.076 ± 0.007) (Hunter et al., 2013). Cunha et al. (2011) argued that macrofaunal abundance in the Portuguese canyons (at 3500 m) was positively correlated with sediment TN concentration. Higher sediment TN values indicate better food quality, which Cunha et al. (2011) suggested was the driver for increased macrofaunal abundance. These data suggest that more and higher quality food may be available in the Eastern branch.

The Whittard Canyon stations appear to experience higher levels of organic matter input than the adjacent slope, probably derived from the channeling of organic matter from the shelf through the canyon branches via downslope processes such as turbidity currents. Possibly, channeling is more active through the Eastern branch than the Central and Western branches, although there is no direct evidence for this. The Eastern branch may also be a more efficient trap of material from along-slope currents. The northerly and north-westerly flow of the NE Atlantic slope current will be topographically steered to flow essentially east to west across our study site (Pingree and Le Cann, 1989). The similarity between the slope and the Western branch and between the Eastern branch and the Central branch may reflect similar organic matter availability and composition at each site given their geographical proximity. Unfortunately, no organic matter data exists for the slope and Central branch.

By comparison with Rex et al. (2006) and Wei et al. (2010b), the slope site also exhibited an elevated macrofaunal density for its depth. A possible factor explaining this high abundance is proximity to the canyon system. Cunningham et al. (2005) noted that mud-rich turbidity flows within the Whittard Canyon (<1500 m depth) have been of sufficient magnitude to overspill the canyon walls, depositing fine sediments on the adjacent slope. This could lead to some organic matter enrichment of the area surrounding the canyon.

2.5.1.4.2 Disturbance

The higher abundance of macrofauna at 3500 m inside the Whittard Canyon than on the adjacent slope could also reflect disturbance. A high frequency from bottom-currents within canyons is thought to depress infaunal abundance, as suggested for the Nazaré Canyon (Gage et al., 1995; Koho et al., 2007). On the other hand, physical disturbance has been shown to increase macrofaunal abundance at the HEBBLE site, located at 4820 m depth on the Nova Scotia Rise (western North Atlantic). Several times per year, this area experiences intense currents that are strong enough to transport sediment (Thistle et al., 1985, 1991). These “benthic storms” are thought to deliver more nutrients for the fauna. At the HEBBLE site, abundances of macrofaunal polychaetes, bivalves, tanaids and isopods were significantly higher than expected for their depth (Thistle et al., 1991). These macrofaunal groups were also abundant inside the Whittard Canyon. Similarly, the Cascadia Channel in the northeast Pacific Ocean experiences a high frequency of turbidity currents that deliver a significant amount of organic matter. As a result, this area has a benthic macrofaunal density four times that on the adjacent plain (Griggs et al., 1969). Thus, the influence of bottom currents on macrofauna abundance remains ambiguous.

Physical disturbance may also influence the taxonomic composition of the macrofauna. Composition of fauna differs between disturbed and quiescent sites in canyons (Gage et al., 1995) and in the HEBBLE area (Thistle et al., 1991; Thistle and Wilson, 1996). Disturbance events can suspend soft-bottom fauna making them vulnerable to predators and physical damage. “Exposed” isopods (exposed on the sediment surface) were less abundant at disturbed sites in the HEBBLE area than at nearby quiescent sites (Thistle and Wilson, 1996). In this study the abundance of isopods was highest in the Central branch and lowest on the slope, although we have no evidence that the intensity of current flow differed between these sites.

There may be a difference in disturbance regimes between the Western and Eastern branches of the Whittard Canyon. A higher abundance of disturbance-tolerant taxa led Hunter et al. (2013a) to conclude that disturbance events were more frequent in the Eastern branch. However, the magnitude and frequency of disturbance inside the Whittard Canyon is poorly understood (section 2.3.1) and there is no clear basis for linking macrofaunal patterns to disturbance levels.

2.5.1.4.3 Sediment grain size

Mean sediment grain size is higher on the slope than at our three canyon sites. The slope site had a larger proportion of sand and clay, whereas the canyon site sediments were composed predominantly of silt (Table 2.3.1). It is possible this difference may be caused by the slope site being more exposed to along-slope currents (Pingree and Le Cann, 1989). Sediment mobility and reworking is a critical factor in explaining the effect of physical disturbance on community structure (Thistle and Levin, 1998). On the summit of a high-energy seamount off the coast of California, areas with stable, coarse-grained sediments supported relatively immobile assemblages whose feeding activities were focused at the sediment-water interface. In contrast, areas of unstable coarse-grained sediments that moved daily supported highly mobile assemblages with well-developed burrowing abilities (Levin et al., 1994a). The different characteristics of canyon and slope sediments suggest that they may react differently to current activity, influencing the benthic community.

2.5.1.4.4 Other factors

A variety of other factors could influence the density and composition of macrofaunal assemblages. Differences in slope angle at the Whittard Canyon and slope sites are probably too slight (~ 2°) to have much effect on sediment stability. On the other hand, the bottom profiles of the canyon branches varied substantially. The Eastern branch has a much narrower, steeper-sided channel than the Western branch, which may suggest that sediment and organic matter pass along it more quickly. Steep and V- shaped canyons are thought to experience stronger and more frequent along-canyon currents than their more U-shaped counterparts (Shepard and Dill, 1966), and canyons with low topographic relief are more likely to resemble open-slope environments (Hecker et al., 1983). De Leo et al. (2014) reported that variability in canyon profiles partially explained variations in macrofaunal community structure among Hawaiian canyons.

Preferential predation by megafauna may affect macrofaunal taxonomic composition. Canyons generally have higher abundances of megafauna (De Leo et al., 2010; Vetter et al., 2010) than the surrounding slope and bottom-feeding fish may also exploit the high abundance of invertebrate macrobenthic communities (De Leo et al., 2010). Reduced oxygen availability has a strong effect on community composition by eliminating hypoxia-intolerant species (Levin, 2003). Ingels et al. (2011c) reported signs of oxygen limitation in the upper part of the Whittard Canyon. This was believed to reduce densities of nematodes. However, there is no evidence of reducing environments in deeper parts of the canyon. Similarly, water depth (hydrostatic pressure) is not considered to be an important discriminating factor in this study as all samples were taken from similar depths (~ 3500m).

2.6 Conclusions and future directions

Our results support all three hypotheses posed in the introduction. In summary, at 3500 m water depth the Whittard Canyon (1) has high macrofaunal abundance compared to the adjacent slope (2) contains a distinct community composition and (3) contains distinct within-canyon heterogeneity. These results are similar to those obtained for previous studies of the metazoan meiofauna and foraminifera. Within-canyon heterogeneity is probably explained by a combination of variable organic enrichment and hydrodynamic activity, both of which can be influenced by the topographic profile of individual canyon branches. Canyons are natural deep-sea laboratories for benthic sediment resuspension, disturbance and organic enrichment. As such these may be important future locations to investigate fundamental biological processes of relevance to future human impacts in the deep sea, such as those likely to occur through deep-water trawling or mining.

2.7 Supplementary Information

Table S 2.1 Summary of published biochemical data from the Whittard Canyon. Stations at a similar depth (c. 3500 m) to those in the present study are compared. WC: Whittard canyon. POC: particulate organic carbon. TN: total nitrogen. TOC: total organic carbon. ROV PC: Remotely Operated Vehicle push core. SAP: stand-alone pump. ± Standard deviations of mean values. [Ref. 1. Huvenne et al. (2011); 2. Duineveld et al. (2001); 3. Brigitte M. Crowe (pers. comm.); 4. Hunter et al. (2013a)]

					Sediments							Bottom waters			
Canyon branch	StationNo.	Depth,m	Lat. N Long. W	Apparatus	POC, %	TN, %	TOC,mmolg^{-1}	Lipids,ngg^{-1} (µg gTOC^{-1})	Molar C/N	Grain size,modal µm	Pigments, ug g^{-1}	POC, µM	Lipids,µgm^{-3} (µggTOC^{-1})	Molar C/N	Ref.
Western	JC036-004	3646	48°08.71 10°34.13	ROV PC			0.6	14660.4 (2375.9)	8.3						1.
Western	JC036-008	3586	48°09.18 10°32.35	SAP								0.5	35.4 (6620.7)	5.2	1.
Western	W1	3760	48°06.97 10°25.97	Box core							0.47±0.17				2.
Western	JC036-007	3595	48°10.86 10°33.07	ROV PC						10.489					3.
Western	West	3595	48°09.34 10°32.45	ROV PC	0.526 ±0.046	0.076 ±0.007			6.889 ±0.132						4.
Central	JC036-055	3347	48°17.01 10°18.84	SAP								0.3	22.3 (6766.9)	4.6	1.
Central	JC036-054	3372	48°17.01 10°18.84	ROV PC						11.912					3.
Central	JC036-062	3371	48°17.01 10°18.84	ROV PC						12.114					3.
Eastern	JC036-100	3411	48°16.00 10°09.46	ROV PC			0.6	25792.0 (2820.5)	9.5						1.
Eastern	JC036-058	3507	48°15.92 10°10.92	SAP								0.3	46.0 (1488.2)	4.1	1.
Eastern	M5	3699	48°09.20 10°15.00	Box core											2.
Eastern	East	3410	48°15.99 10°09.47	ROV PC	0.696 ±0.047	0.098 ±0.006			7.102 ±0.166						4.

Table S2.2 Macrofaunal abundance data for NE Atlantic canyon and slope sites. (Nr, near; WC, Whittard Canyon; PAP, Porcupine Abyssal Plain; BC, box core; MgC, Megacore; PC, push core).

Slope Sites	Depth (m)	Macrofaunal (ind. m^{-2})	Sieve (µm)	Sampling gear	Reference
Nr Setubal Canyon	1001	189	500	NIOZ BC	Cunha et al., 2011
Nr Nazare Canyon	1030	191	500	NIOZ BC	Cunha et al., 2011
Nr WC	3509	2744	300	MgC	This study
Nr WC	3509	1409	500	MgC	This study
Goban Spur	3600	2420	500	BC	Duineveld et al., 2001
Goban Spur	3600	500	500	NIOZ BC	Flach et al., 1999
Goban Spur	3673	550	500	NIOZ BC	Flach and Heip, 1996
Goban Spur	3648	600	500	NIOZ BC	Flach and Heip, 1996
Goban Spur	3650	528	500	NIOZ BC	Flach et al., 2002
Bay of Biscay	3000	2008	500	Reineck BC	Laubier & Sibuet 1979
Rockall Trough	2900	1856	420	USNEL BC	Gage 1978
Rockall Trough	2875	1853	420	USNEL BC	Gage 1977
BIOTRANS	4195	1836	500	USNEL BC	Pfannkucke 1992
Iberian margin	3750	1250	500	NIOZ BC	Flach et al., 2002
PAP (1996)	4850	1095	250	USNEL BC	Galeron et al., 2001
PAP (1997)	4850	1314	250	USNEL BC	Galeron et al., 2001
PAP (1997)	4850	1634	250	USNEL BC	Galeron et al., 2001
PAP (1998)	4850	1902	250	USNEL BC	Galeron et al., 2001
PAP (1998)	4850	1379	250	USNEL BC	Galeron et al., 2001
Prediction	3500	657	-	-	Wei et al., 2010b
Prediction	3500	369	-	-	Rex et al., 2006
Cape Verde Rise	3110	1841	250	USNEL BC	Galeron et al., 2000
Cape Verde Rise	3110	1708	250	USNEL BC	Galeron et al., 2000
Cape Verde Rise	3110	1772	250	USNEL BC	Galeron et al., 2000
Canyon Sites					
Nazaré Canyon	3517	4600	500	MgC	Cunha et al., 2011
Nazaré Canyon	3461	2849	500	USNEL BC	Cunha et al., 2011
Nazaré Canyon	3514	5409	500	USNEL BC	Curdia et al., 2004
Setúbal Canyon	3224	2241	500	MgC	Cunha et al., 2011
Setúbal Canyon	3400	459	300	USNEL BC	Gage et al., 1995
Cascais Canyon	3199	1126	500	MgC	Cunha et al., 2011
WC average	3500	4536	300	MgC	This study
WC average	3500	2483	500	MgC	This study
WC Western branch	3648	2900	300	MgC	This study
WC Western branch	3648	1777	500	MgC	This study
WC Western branch	3595	3416	250	ROV PC	Hunter et al., 2013b
WC Western branch	3760	1339	500	BC	Duineveld et al., 2001
WC Central branch	3377	4461	300	MgC	This study
WC Central branch	3377	2376	500	MgC	This study
WC Eastern branch	3427	6249	300	MgC	This study
WC Eastern branch	3427	3296	500	MgC	This study
WC Eastern branch	3410	5352	250	ROV PC	Hunter et al., 2013b

Chapter 3: Local and regional variation in deep-sea polychaete diversity; canyon influence

3.1 Abstract

We examined deep-sea macrofaunal polychaete species assemblage composition, diversity and turnover in the Whittard Canyon system (NE Atlantic; 3500 m water depth). Replicate Megacore samples were collected from three of the canyon branches and one site on the continental slope to the west of the canyon, all at c. 3500 m water depth. A total of 110 polychaete species were recorded. *Paramphinome jeffreysii* was the most abundant species (2326 ind m^{-2}) followed by *Aurospio* sp. B (646 ind m^{-2}), Opheliidae sp. A (393 ind m^{-2}), *Prionospio* sp. I (380 ind m^{-2}), and *Ophelina abranchiata* (227 ind m^{-2}). Species composition varied significantly across all sites. From west to east, the dominance of *Paramphinome jeffreysii* increased from 12.9 % on the slope to 39.6 % in the Eastern branch. Ordination of species composition revealed that the Central and Eastern branches were most similar, whereas the Western branch and slope sites were more distinct. High abundances of *P. jeffreysii* and Opheliidae sp. A characterised the Eastern branch of the canyon and may indicate an opportunistic response to a possible recent input of organic matter inside the canyon. Species diversity indices were higher on the slope than inside the canyon, and the slope site had higher species evenness. Within the canyon, species diversity between branches was broadly similar. Forty-six of the ninety-nine polychaete species found in the Whittard Canyon were not present on the adjacent slope, suggesting that this feature may make a substantial contribution to the regional diversity of soft-bottom benthic polychaetes.

3.2 Introduction

Describing and understanding patterns of biodiversity on our planet is a fundamental aim in biology (Gaston 2000). The deep-sea floor may harbour some of the highest levels of local (alpha) species diversity on Earth (Hessler & Sanders 1967, Sanders 1968, Sanders & Hessler 1969, Grassle & Maciolek 1992). Local diversity is thought to generally exhibit a parabolic distribution with depth. This pattern is particularly pronounced in the North Atlantic, with peaks at intermediate (i.e. bathyal) depths and reduced levels of diversity at upper bathyal and abyssal depths (Rex 1981, Rex 1983). Submarine canyons, major deep-sea topographic features incising the continental shelf and slope, are potential exceptions to this general pattern. They may show either increased species richness in their deeper parts (Cunha et al. 2011) or depressed diversity throughout (Vetter & Dayton 1998). Faunal diversity is also reported to vary down the canyon axis and over the adjacent canyon fan (Tyler et al. 2009); e.g. foraminifera (Duros et al. 2011) and polychaetes (Paterson et al. 2011). There is also no general agreement on whether alpha diversity is typically higher inside canyons (Vetter & Dayton 1998, 1999, Vetter et al. 2010, De Leo et al. 2012) or higher on the adjacent slope outside canyons (Gage et al. 1995, Curdia et al. 2004, Garcia et al. 2007, Koho et al. 2007). Indeed, there are many different diversity patterns in canyons as they are highly variable in both space and time.

The drivers that influence marine diversity at regional and local scales are not well understood (Levin et al. 2001, Snelgrove & Smith 2002). In the case of submarine canyons, a complex interplay of numerous factors is likely to regulate the diversity of biological communities (McClain & Barry 2010). These topographic features are typically associated with high surface water productivity, high levels of physical disturbance and a considerable degree of habitat heterogeneity, all of which could influence species diversity. Canyons have also been described as benthic biomass ‘hotspots’ (De Leo et al. 2010), reflecting an enhanced food supply compared with the surrounding continental slope and abyssal plain. They can act as conduits for the delivery of sediment and organic matter to the abyssal plains (Vetter & Dayton 1998). This enhanced supply of organic matter could increase diversity. Conversely, if enrichment is excessive, it may favour opportunistic species (Paterson et al. 2011) and act to depress species diversity (Stuart et al. 2003, Whittaker 1965) as reported, for example, from the Nazaré Canyon (Curdia et al. 2004). Diversity may also be influenced by physical disturbance, for example, steep topography may focus internal tides in the upper reaches of canyons (Gardner 1989), while tidal currents, episodic slumps, turbidity flows and dense shelf water cascading may periodically transport sediments into the deeper parts (Canals et al. 2006). These processes act on different time scales and will dynamically disturb the physical characteristics of the sediment.

Factors such as extreme topography, diverse current regimes, varying substratum types, and detrital funnelling from the continental shelf serve to increase habitat heterogeneity within canyons (Levin et al. 2010). For example, currents may distribute organic matter and sediment in a patchy manner (McClain & Barry 2010). Similarly, sediment granulometry can be expected to vary throughout a canyon, with potential impact on macrofaunal (Etter & Grassle 1992) and meiofaunal (Leduc et al. 2012a) diversity. Sessile megafauna add to the habitat complexity inside canyons; for example, deep-water corals can be found throughout canyon systems, providing refuge for diverse associated faunal communities (Mortensen & Buhl-Mortensen 2005, Buhl-Mortensen et al. 2010, Huvenne et al. 2011). All of these factors may increase small and medium-scale environmental heterogeneity, particularly within active canyons, and thereby enhance diversity compared with the adjacent slope (Tews et al. 2004). Indeed, increased macrohabitat heterogeneity inside canyons has been linked to the high beta diversity of nematode assemblages within canyons (Vanreusel et al. 2010).

On a larger scale, it is unclear whether canyons act to enhance regional diversity across continental margins. Species turnover (beta diversity) links local and regional scales of diversity and has been understudied in the deep sea (Paterson et al. 1998, Glover et al. 2002, Ellingsen et al. 2007a). In deep-sea, soft-sediment habitats, variation in beta diversity is expected to be gradual except when interrupted by topography, hard substratum, intense bottom currents, nutrient depo-centres, abrupt shifts in water masses, or other extreme environmental circumstances (Rex & Etter 2010). Many of these factors operate inside canyons. Thus, as in continental shelf settings (Ellingsen & Gray 2002), it seems likely that changes in environmental variables within canyons will have a stronger effect on beta diversity than spatial distance between sites. The bathymetric and geographical ranges of species, and hence beta diversity, are influenced by the interplay between adaptive traits and environmental drivers. Adaptive traits include feeding type, metabolic and locomotory capacity, morphological specialisation, larval dispersal, adult mobility, body size and shape, and enzymatic pressure sensitivity (reviewed by Rex and Etter 2010). Those traits typical of canyon settings will depend on the species present, which in turn will reflect the environmental conditions. Thus the interaction of species traits and environmental influences that determine the bathymetric and geographical ranges of species will be complex (Rex & Etter 2010). Since the environmental conditions inside canyons are often very different from those on the open slope, the faunal assemblages may differ correspondingly. This would act to increase faunal turnover across the continental margin and lead to enhanced regional diversity.

Much less quantitative data on species richness is available from deep-sea soft sediments than from comparable shallow-water settings (Gray 2002). As a result of their rugged terrain and inaccessibility, submarine canyons are particularly hard to sample. Thus, relatively little is known about the patterns and drivers of canyon diversity. This study will investigate diversity at different spatial scales inside the Whittard Canyon system (NE Atlantic), focussing on sites at a common water depth (3500 m). A previous study, on the same samples from the Whittard Canyon, reported macrofaunal abundance and community composition at the higher taxon level (Gunton et al. 2015a).

In the present study, a species-level assessment of polychaete assemblages, the dominant deep-sea macrofauna taxon, will be used to address the following hypotheses: 1) Species composition and diversity are consistent between Whittard Canyon branches 2) Species composition is distinct and species diversity is depressed inside the Whittard Canyon compared with the adjacent open slope. 3) Regional diversity is impacted by the Whittard Canyon system.

3.3 Methods

3.3.1 Sample collection and processing

Sediment samples were collected using a Megacorer (Gage and Bett, 2005) at three sites inside the Whittard Canyon system (NE Atlantic) and one on the adjacent continental slope to the west of the canyon during RRS *James Cook* cruise 036 in June and July 2009 (Table 3.1; Fig. 3.1). All sites were located at c. 3500 m depth. The Megacorer was fitted with eight large (100 mm internal diameter) core tubes. Five deployments were conducted in the Western branch, six in the Central and Eastern branches and five on the slope site. One extra deployment was made in the Central and Eastern branches to compensate for the failure to recover sufficient cores. Full details of macrofaunal sample processing are given in Gunton et al. (2015a). In the present study, the top three sediment horizons (i.e. 0-1, 1-3 and 3-5 cm) were analysed *in toto*.

3.3.2 Faunal analyses

In the laboratory, polychaetes were transferred from the formalin onto a 300 μm mesh sieve, rinsed with fresh water and sorted in 70 % ethanol. A Leica MZ9.5 stereomicroscope and a DM5000 compound microscope were used to identify polychaete specimens to species level. Polychaetes were assigned a Latin binomial name where possible using published identification keys. Where specimens could not be assigned to a described species they were recorded as an informal morphospecies in a genus (e.g. *Prionospio* sp. A) or family (e.g. Spionidae sp. A). Fragmented specimens were only counted if they included a head. The full species list, including abundance counts, is given in the appendix (Appendix B, Table B.3).

3.3.3 Data analysis

3.3.3.1 Diversity measures

Simple polychaete species dominance was calculated as the Berger-Parker index (i.e. Rank 1 Dominance; Magurran 2004) via Microsoft Excel. K-dominance plots (Lambshead et al. 1983) were drawn in SigmaPlot V12.5. The software package PRIMER V6 (Clarke & Gorley 2006) was used to calculate conventional diversity indices from the polychaete count data: Shannon index (Pielou 1966), Simpson's index (Simpson 1949) and Pielou's evenness (Pielou 1975).

Polychaete species richness was also estimated using individual based rarefaction curve (Gotelli & Colwell 2001, 2011). Rarefaction curves based on polychaete count data were constructed using the EstimateS software package (Colwell 2009). This approach was also applied to comparative polychaete species level data available from canyons on the Iberian Margin (Paterson et al., 2011).

In order to assess beta diversity across the canyon system, Whittaker's measure $\beta_W = \gamma / \overline{\alpha}$ (Whittaker 1960, 1972) was calculated, where γ is the diversity of the complete system, and $\overline{\alpha}$ is average sample diversity, where each sample is a standard (rarefied) size. Beta diversity was calculated using the number equivalents (Hill numbers) of species richness, ${}^0D = S$, Shannon index, ${}^1D = \exp(-\Sigma\, p_i \log p_i)$ and Simpson index, ${}^2D = 1 / \Sigma\, p_i^2$ (See Chao et al, 2012, 2014a; Jost 2007), derived from the output of EstimateS, after individual samples had been rarefied to 47 individuals, and pooled samples (the γ value) rarefied to 235 individuals (i.e. 5 replicate samples of 47 individuals). We adopted this approach following the rationale of Chao et al. (2014b), where the use of Hill number diversity values simplifies the calculation of reasonable beta diversity values. Similarly, we assess ${}^OD$, ${}^1D$ and ${}^2D$ to examine the potential variation in richness, heterogeneity and dominance aspects of beta diversity, according to the general framework proposed by Chao et al. (2014b).

3.3.3.2 Composition assessment

Polychaete species density data were transformed to square root, and the Bray-Curtis similarity calculated between samples. The resultant similarity matrix was visualised using non-metric multidimensional scaling plots (nMDS plots), and further assessed using the Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER) methods given in PRIMER V6.

A canonical correspondence analysis (CCA) on untransformed polychaete density was performed to examine the potential relationships between assemblages and environmental variables. The CCA was performed using R statistical software (RCoreTeam 2014) with the Vegan: Community Ecology package (Oksanen et al. 2013). Details of the available environmental factors are given in Gunton et al. (2015a). Briefly - a post-processed bathymetry map of the Whittard Canyon was downloaded from the INFROMAR website (www.gsiseabed.ie). Using the software ArcMap10 (ESRI)and the Benthic Terrain Modeler ArcGIS Desktop Extension alpha version (Wright et al.,2005), the following environmental descriptors were derived from the bathymetry map; 'Slope', bathymetric position index (BPI) and vector ruggedness measure (VRM). Sediment particle-size was obtained from the smaller cores collected at each site (see Section 2.1). Subsamples from the 0–0.5, 1–1.5, 2–3 and 4–5 cm sediment layers from each core were analysed using a Malvern Mastersizer 2000 laser diffraction particle size analyser (Abbireddy and Clayton, 2009).

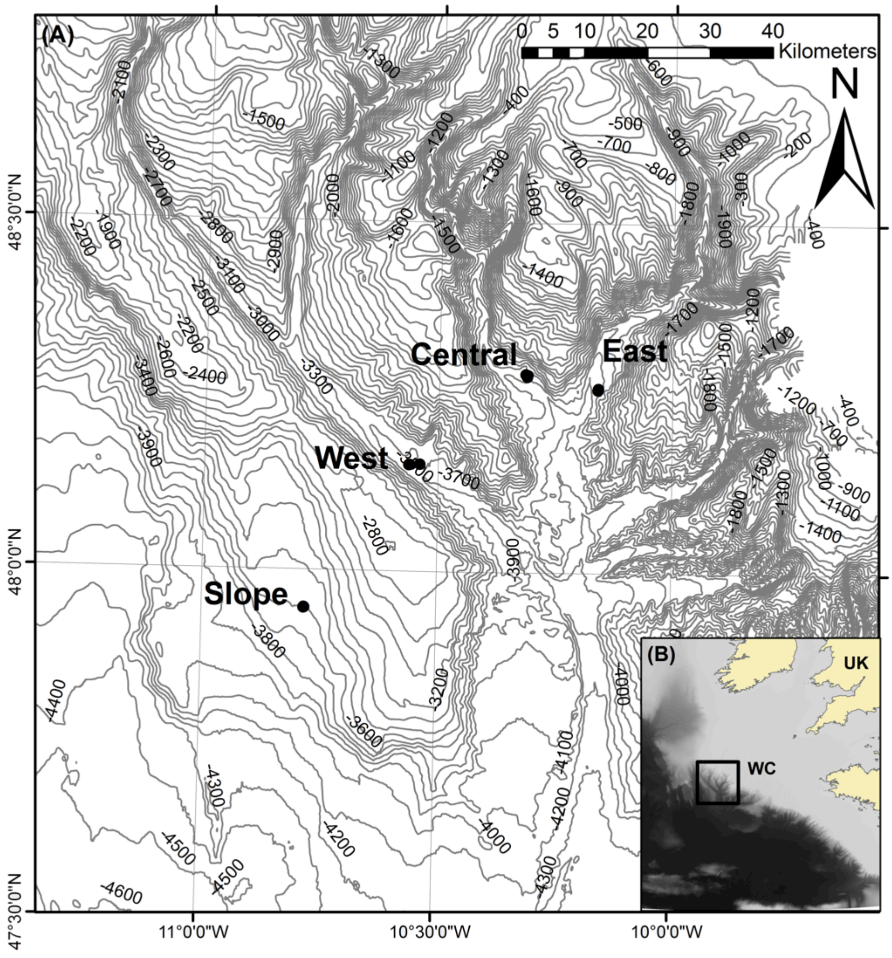


Figure 3.1 (A) Bathymetric chart of Whittard Canyon.
Data provided by the Geological Survey of Ireland (www.gsiseabed.ie). The four study sites are indicated: Western Branch (W), Central Branch (C) and Eastern Branch (E) of the canyon and one site on the adjacent slope (Sl). (B) Locality map of Whittard Canyon in NE Atlantic, based on GEBCO data (www.gebco.net).

Table 3.1 Sites and diversity summary.
*deployment where sample for sediment grain-size analysis was collected. Average = mean of five deployments. J′, Pielou’s evenness; H′ (log2), Shannon index; 1-λ′, Simpson index; Chao 1 values rarefied to 47 individuals.Results

Deploy.	Lat. (N)	Long. (W)	Depth (m)	Cores recovered	Area (m^{-2})	Density (ind. m^{-2})	Total species	J′	H′ (log2)	1-λ′	Rank 1 dom. (%)	Chao 1
Sl016	47°56.79′	10°46.85′	3511	8	0.063	939	21	0.876	3.848	0.902	22.6	38.81
Sl017	47°56.78′	10°46.85′	3512	7	0.055	982	23	0.923	4.175	0.932	13.7	35.91
Sl018	47°56.81′	10°46.91′	3514	6	0.047	1358	28	0.885	4.253	0.927	15.9	64.80
Sl019*	47°56.74′	10°46.94′	3505	8	0.063	1337	30	0.857	4.207	0.920	18.5	50.10
Sl020	47°56.78′	10°46.85′	3514	7	0.055	1364	25	0.870	4.039	0.910	23.0	32.68
Ave. Sl							**25.4**	**0.882**	**4.104**	**0.918**	**18.7**	**44.46**
W002*	48°09.18′	10°33.70′	3670	8	0.063	1226	22	0.800	3.567	0.870	26.7	34.18
W003	48°09.17′	10°33.70′	3661	7	0.055	1328	22	0.818	3.646	0.875	27.9	39.03
W011	48°09.22′	10°32.36′	3582	6	0.047	1422	24	0.861	3.949	0.905	20.3	37.58
W026	48°09.18′	10°33.73′	3670	5	0.039	1223	19	0.891	3.784	0.904	19.1	24.87
W043	48°09.15′	10°33.76′	3657	6	0.047	1443	23	0.792	3.582	0.848	34.4	47.59
Ave. W							**22.0**	**0.832**	**3.706**	**0.880**	**25.8**	**36.65**
C063*	48°16.89′	10°18.74′	3375	6	0.047	1995	25	0.748	3.474	0.799	42.7	29.67
C064	48°16.97′	10°18.65′	3382	8	0.063	2388	34	0.762	3.877	0.850	35.6	33.71
C065	48°17.04′	10°18.89′	3373	7	0.055	2165	36	0.810	4.187	0.887	29.8	42.41
C067	48°16.98′	10°18.72′	3376	7	0.055	1528	27	0.791	3.761	0.854	34.2	39.35
C066	48°16.83′	10°18.72′	3381	3	}0.063	2308	37	0.798	4.155	0.891	27.1	33.28
C068	48°17.01′	10°18.83′	3375	5								
Ave. C							**31.8**	**0.782**	**3.891**	**0.856**	**33.9**	**35.68**
E093*	48°15.89′	10°09.56′	3424	8	0.063	1942	35	0.723	3.709	0.797	43.6	42.06
E094	48°15.78′	10°09.57′	3429	7	0.055	2583	33	0.762	3.842	0.845	36.2	35.91
E095	48°15.78′	10°09.58′	3429	4	}0.063	3184	43	0.712	3.866	0.821	40.1	40.22
E096	48°15.76′	10°09.60′	3424	4								
E097	48°15.89′	10°09.54′	3425	5	0.039	4304	29	0.662	3.214	0.764	45.2	28.93
E098	48°15.76′	10°09.60′	3432	4	0.031	4330	32	0.730	3.652	0.843	33.6	39.78
Ave. E							**34.4**	**0.718**	**3.656**	**0.814**	**39.7**	**37.38**

3.4 Results

3.4.1 The polychaete assemblage

A total of 2225 polychaetes was examined; 1959 (88%) of these were assigned to species-level taxa. Across all sites, we recognised 110 species, of which 35 were described, and 75 could not be assigned to a known species and were possibly new to science. The Eastern branch yielded the highest number of species (68), followed by Central branch (65), the slope (64) and the Western branch (53) sites. Overall, 46 species were found only in the canyon branches, and 11 were found only at the slope site. Between site variation in species composition is illustrated in Fig. 3.2. By far the most abundant species was the amphinomid *Paramphinome jeffreysii* with a total of 2326 ind m^{-2}. *Aurospio* sp. B was ranked second (646 ind m^{-2}), Opheliidae sp. A third (393 ind m^{-2}, represented by juvenile individuals), *Prionospio* sp. I fourth (380 ind m^{-2}) and *Ophelina abranchiata* fifth (277 ind m^{-2}). *Paramphinome jeffreysii* increased in relative abundance from 21 % in the Western branch to 34 % and 40 % in the Central and Eastern branches, respectively (Table 3.2). It was less common at the slope site, where the most abundant species was *Aurospio* sp. B (Table 3.2). In contrast to *P. jeffreysii, Aurospio.* sp. B decreased in relative abundance from west to east (slope 14 %, Eastern branch 6 %).

There were notable differences in species composition with depth in the sediment profile. The percentage abundance of *Paramphinome jeffreysii* increased into the sediment across all of the sites (Fig. 3.3). At the Eastern branch, where it was most abundant, *P. jeffreysii* constituted 50 % of the polychaete species in the 1-3 and 3-5 cm sediment layers. Juvenile opheliids (Opheliidae sp. A) were particularly abundant (c. 20%) in the 0-1 cm layer of the Eastern branch.

Table 3.2 Top ten most abundant species at each site.
Relative abundance shown in brackets.* species observed only in the canyon

Slope	Western branch
Aurospio sp. B (14.3%)	*Paramphinome jeffreysii* (21.2%)
Paramphinome jeffreysii (12.9%)	*Aurospio* sp. B (11.2%)
Anguillosyllis capensis (9.3%)	*Ancistrosyllis* sp. A* (10.2%)
Prionospio sp. I (7.1%)	*Levinsenia gracilis* (6.5%)
Aurospio dibranchiata (6.3%)	*Prionospio* sp. I (6.0%)
Flabelligella cf. biscayensis (5.4%)	*Leanira hystricis* (3.9%)
Ampharetidae sp. A (4.7%)	*Ophelina abranchiata* (3.8%)
Glycera capitata (3.4%)	*Chaetozone* sp. F (3.1%)
Chaetozone sp. F (3.4%)	*Chaetozone* sp. C (1.8%)
Levinsenia gracilis (2.8%)	*Chaetozone* sp. A* (1.7%)

Central branch	Eastern branch
Paramphinome jeffreysii (33.6%)	*Paramphinome jeffreysii* (39.6%)
Aurospio sp. B (8.3%)	Opheliidae sp. A* (11.0%)
Ophelina abranchiata (4.9%)	*Prionospio* sp. I (5.5%)
*Levinsenia gracili*s (3.8%)	*Aurospio* sp. B (5.5%)
Chaetozone sp. F (3.4%)	*Leitoscoloplos* sp. B* (2.2%)
Ophelina cylindricaudata (3.3%)	*Ophelina abranchiata* (2.1%)
Polychaetae larva sp. A* (3.0%)	*Glycera capitata* (2.0%)
Aurospio dibranchiata (2.8%)	*Aricidea simplex* (1.8%)
Chaetozone sp. A* (2.5%)	*Prionospio* sp. B (1.7%)
*Leitoscoloplo*s sp. B*(2.5%)	*Ophelina cylindricaudata* (1.4%)

Table 3.3 SIMPER analysis.

Displaying the percentage contribution of the most important species responsible for within site similarity and between site dissimilarity. W - Western branch, C - Central branch, E - Eastern branch, Sl - Slope site.

Similarity between samples within sites (%)			
Sl - average 51.9	**W - average 49.0**	**C - average 61.0**	**E - average 56.1**
Paramphinome jeffreysii - 6.7	*Paramphinome jeffreysii* - 9.2	*Paramphinome jeffreysii* - 11.4	*Paramphinome jeffreysii* - 12.0
Aurospio sp. B - 6.7	*Aurospio* sp. B - 6.8	*Aurospio* sp. B - 4.9	Opheliidae sp. A - 4.4
Anguillosyllis capensis - 5.8	*Ancistrosyllis* sp. A - 4.1	*Levinsenia gracilis* - 3.5	*Aurospio* sp. B - 4.1
Aurospio dibranchiata - 4.6	*Chaetozone* sp. F - 3.9	*Ophelina cylindricaudata* - 3.5	*Prionospio* sp. I - 3.7
Flabelligella cf. biscayensis - 4.4	*Prionospio* sp. I - 3.1	*Chaetozone* sp. F - 3.0	*Leitoscoloplos* sp. B - 2.9
Dissimilarity between sites (%)			
C&E - average 45.2	**C&Sl - average 57.5**	**C&W - average 55.4**	**Sl&W - average 57.5**
Opheliidae sp. A - 2.6	*Paramphinome jefreysii* - 3.8	*Paramphinome jeffreysii* - 2.7	*Ancistrosyllis* sp. A - 3.3
Paramphinome jeffreysii - 2.0	*Anguillosyllos capensis* - 2.8	*Ancistrosyllis* sp. A - 2.5	*Anguillosyllis capensis* - 2.4
Prionospio sp. I - 1.4	*Ophelina cylindricaudata* - 2.0	*Ophelina cylindricaudata* - 2.2	Ampharetidae sp. A - 2.1
Sl&E - average 61.8	**E&W - average 61.7**		
Paramphinome jefreysii - 5.5	*Paramphinome jefreysii* - 4.6		
Opheliidae sp. A - 3.6	Opheliidae sp. A - 4.1		
Leitoscoloplos sp. B - 2.0	*Ancistrosyllis* sp. A - 2.5		

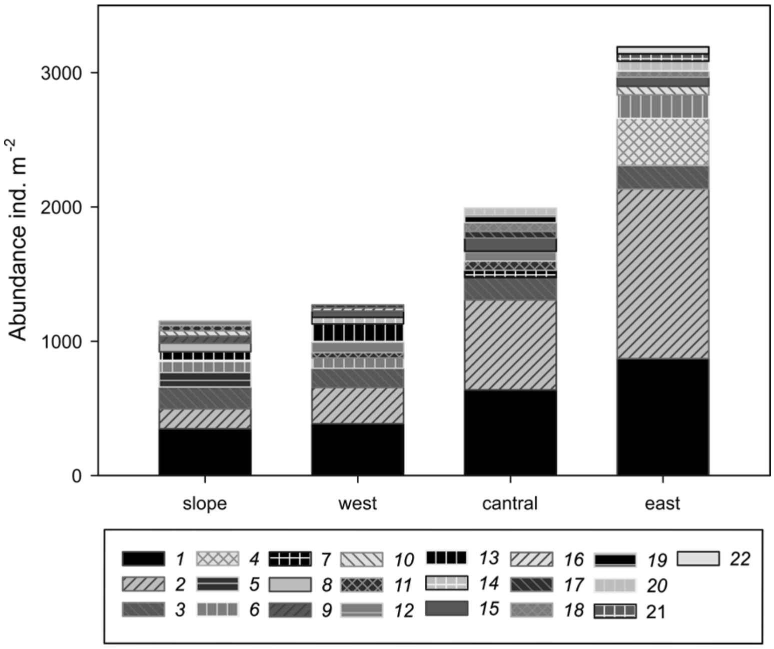


Figure 3.2 Composition of the most abundant polychaete species at each of the four study sites.

1, Others; 2, *Paramphinome jeffreysii*; 3, *Aurospio* sp. B; 4, Opheliidae sp. A; 5, *Anguillosyllis capensis*; 6, *Prionospio* sp. I; 7, *Aurospio dibranchiata* 8, *Flabelligella cf. biscayensis*; 9, Ampharetidae Genus A; 10, *Glycera capitata*; 11, *Chaetozone* sp. F; 12, *Levinsenia gracilis*; 13, *Ancistrosyllis* sp. A;14, *Leanira hystricis*;15, *Ophelina abranchiata*;16, *Chaetozone* sp. C;17, *Chaetozone* sp. A; 18, *Ophelina cylindricaudata*; 19, Polychaete larva sp. A; 20, *Leitoscoloplos* sp. B; 21, *Aricidea simplex*; 22, *Prionospio* sp. B

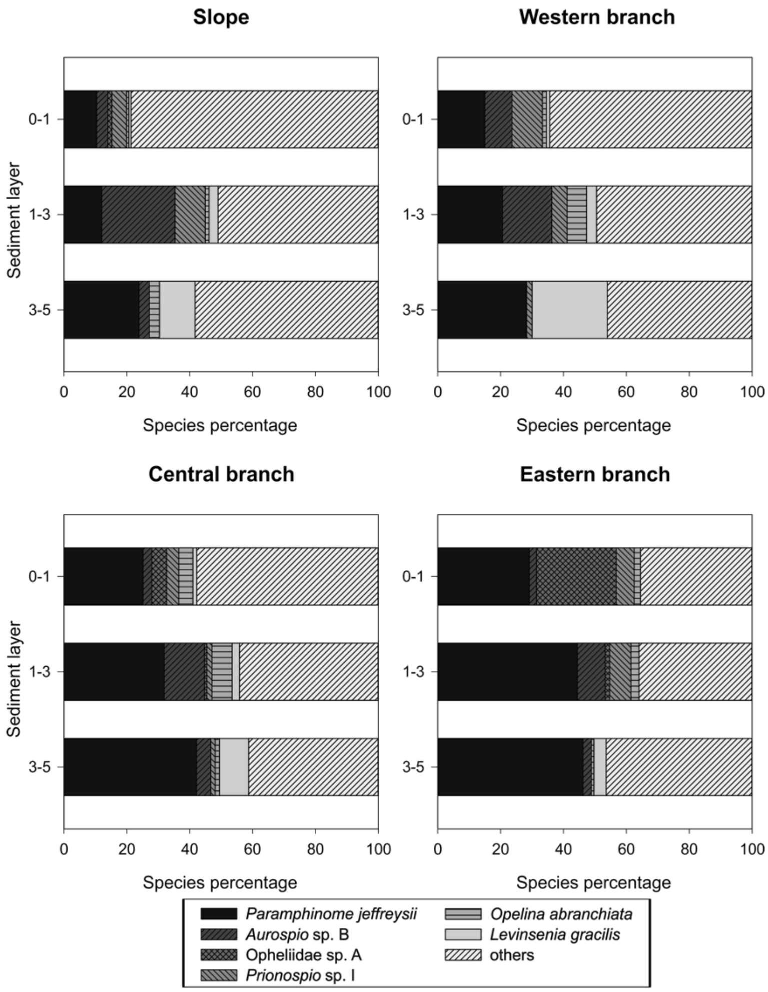


Figure 3.3 Vertical distribution of polychaetes in sediments.
(0-1, 1-3 and 3-5 cm) at each site represented as percentage abundance.

3.4.2 Species diversity

Rank 1 dominance differed between sites (Table 3.1). The Eastern branch had the highest rank 1 dominance (39 %) and the slope the lowest (14 %). The *k*-dominance plot (Fig. 3.4) revealed a similar trend in dominance, highest at the Eastern branch site and lowest at the slope site, with the Western and Central branches having intermediate values.

Simple alpha diversity measures indicated that diversity varied between sites. The average Simpson index (1-λ′) was highest at the slope site (0.92), intermediate in the Western and Central branches (0.88 and 0.86 respectively) and lowest in the Eastern branch (0.80)(Table 3.1). The average Shannon index (H′ (log2)) was likewise highest at the slope site (4.10) and lowest in the Eastern branch (3.66). Species evenness decreased from west to east across the sites. The average evenness index (*J'*) was highest on the slope and lowest in the canyon branches (Table 3.1).

Rarefied polychaete species richness was highest on the slope, intermediate in the Western and Central branches and lowest in the Eastern branch (Fig. 3.5a). None of the rarefaction curves reached an asymptote, suggesting that the local diversity was undersampled even when the results were pooled. The higher richness at the slope site was evident from the individual based (Fig. 3.5a) rarefaction curves, although confidence intervals overlapped, indicating that the differences were not statistically significant. When all sites were rarefied to 47 individuals, the slope site had the highest species richness (21 species). All three canyon sites had similar predicted numbers of species with $E[S_{47}]$ values decreasing only very slightly (from 20 to 18) from west to east (Table 3.4).

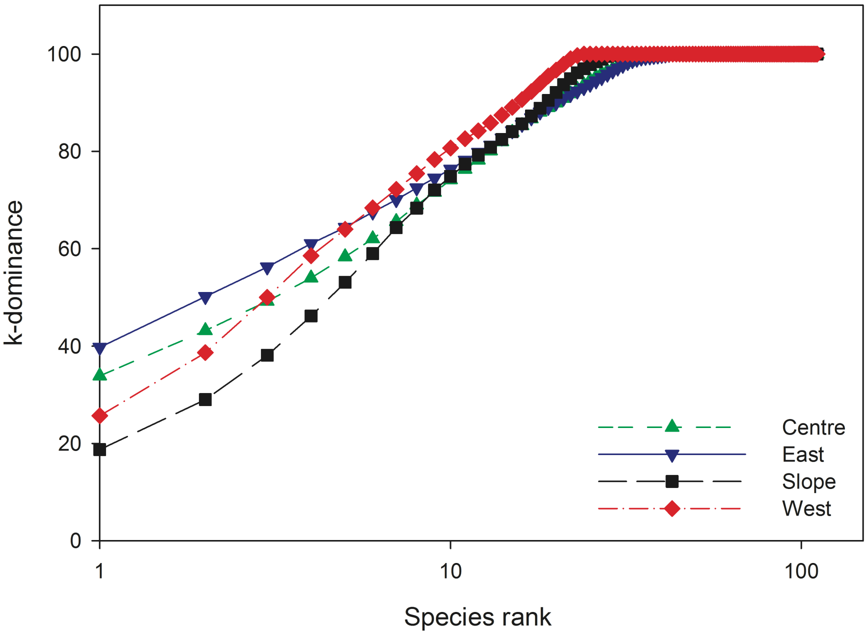


Figure 3.4 k-dominance plot for Whittard Canyon and slope sites.
Pooled data from five samples at each of the four sites.

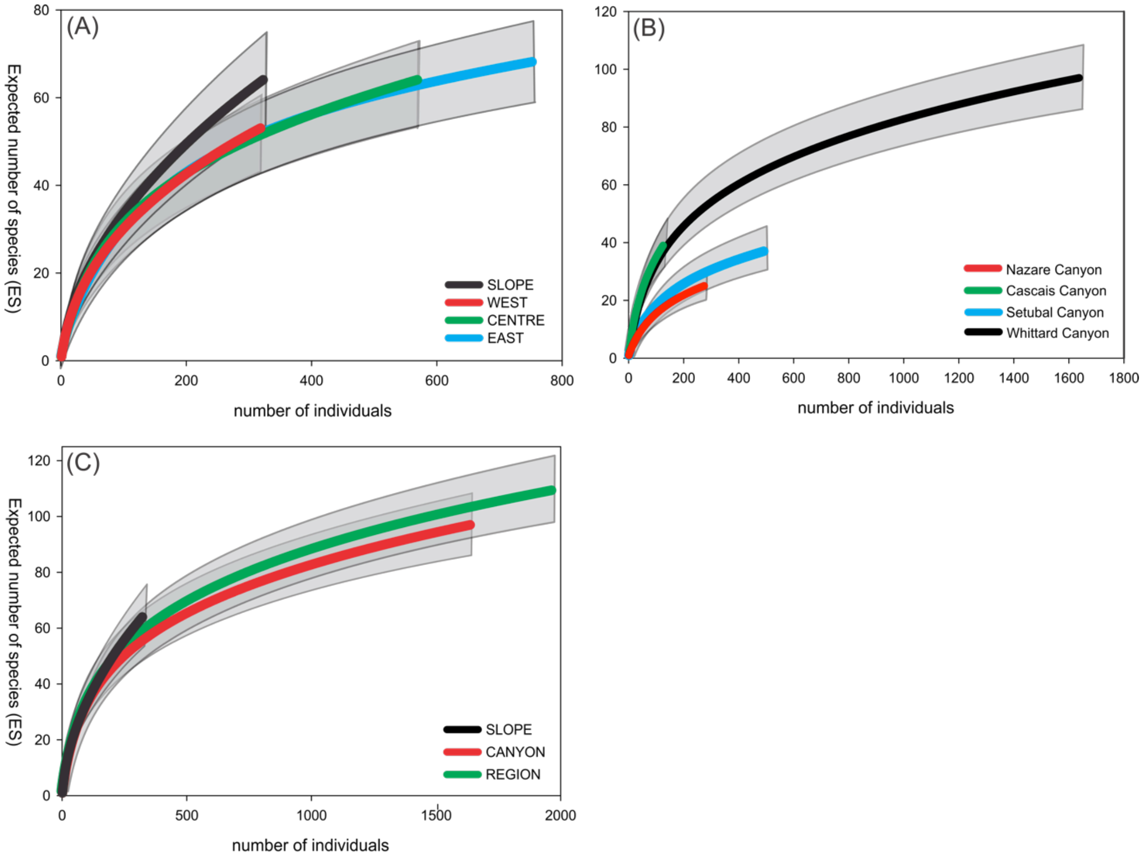


Figure 3.5 Polychaete diversity estimated using rarefaction, 95% confidence intervals shown as grey shading.
(A) Slope site, Western, Central and Eastern branches. (B) Combined Whittard Canyon branches (Western, Central and Eastern branches) and Iberian Margin canyons (Nazaré, Setúbal and Cascais Canyons) at 3400 m. (C) Combined Whittard Canyon branches, slope site and Whittard Canyon region (Slope site, Western, Central and Eastern branches).

3.4.3 Beta diversity

There is little if any variation in beta diversity within or among the sites studies, whether assessed as Hill number 0, 1 or 2 (Table 3.4). However, rarefied average α diversity, and rarefied γ diversity are uniformly maximal at the slope site. Similarly, rarefied average α diversity, and rarefied γ diversity are uniformly enhanced from canyon-level to regional-level assessments. The degree of enhancement appears to be related to the Hill number, with a lesser enhancement of richness, and greater enhancement of inverse Simpson. Taken together these results suggest both increased richness and reduced dominance at the slope site relative to the canyon sites.

Table 3.4 Assessment of beta diversity via rarefaction with Hill numbers.

(^{0}D, richness; ^{1}D, exponential Shannon; ^{2}D, inverse Simpson), α rarefied to 47 individuals, and γ rarefied to 235 individuals. $\boldsymbol{\beta}$ = beta diversity = γ / $\boldsymbol{\overline{\alpha}}$. Canyon = all canyon sites. Region = all canyon sites + slope site.

Site	^{0}D			^{1}D			^{2}D		
	$\overline{\alpha}$	β	γ	$\overline{\alpha}$	β	γ	$\overline{\alpha}$	β	γ
West	18.5	2.5	46.1	12.2	1.7	20.2	8.4	1.4	11.5
Centre	19.9	2.3	45.7	11.8	1.5	18.1	7.0	1.1	7.6
East	18.4	2.5	45.9	8.8	1.5	14.5	5.4	1.0	5.6
Slope	21.2	2.6	54.0	15.7	1.6	24.8	11.9	1.3	15.0
Canyon	18.9	2.6	49.0	11.3	1.7	18.7	6.9	1.1	7.5
Region	19.5	2.7	51.8	12.4	1.7	21.1	8.2	1.1	8.7

3.4.4 Species composition

A multidimensional scaling ordination of polychaete species data (Fig. 3.6) illustrated appreciable differences in community composition between all four study sites. The Eastern and Central branch sites were most similar to each other. Western branch samples formed a looser grouping, nonetheless distinct from those of the other canyon sites. The slope samples grouped together and were distinct from the canyon sites. Global ANOSIM indicated significant variation ($p < 0.001$), with all pair-wise site comparisons significant at $p < 0.01$, except slope and Western branch, which was significant at $p < 0.02$. SIMPER analysis indicated that *P. jeffreysii* abundance was responsible for most of the observed similarity within sites. *Aurospio* sp. B abundance was second or third most important at all sites. Between site dissimilarity was mostly driven by the abundance of *P. jeffreysii,* Opheliidae sp. A and *Ancistrosyllis sp.* A.

A CCA (Fig. 3.7) showed the potential interactions between environmental factors and the distribution of polychaete species. Axis 1 was positively correlated with water depth and negatively correlated with macrofaunal density (a potential proxy of organic matter supply, Gunton et al. 2015a). Axis 2 was correlated with sediment characteristics, including grain size and slope angle. Species such as *Leanira hystricis, Ancistrosyllis* sp. A, *Sternaspis* sp. A and *Chaetozone* sp. C were characteristic of the deeper and lower density macrofaunal sites in the Western branch (supplementary Fig. S3.1). Opheliidae sp. B, *Anguillosyllis capensis* and Scalibregmatidae sp. B were characteristic of the coarser-grained sediment with a higher clay percentage on the slope. Opheliidae sp. A (juveniles), *Paramphinome jeffreysii* and *Leitoscoloplos* sp. B were characteristic of the Eastern and Central branches, which shared similar environmental characteristics.

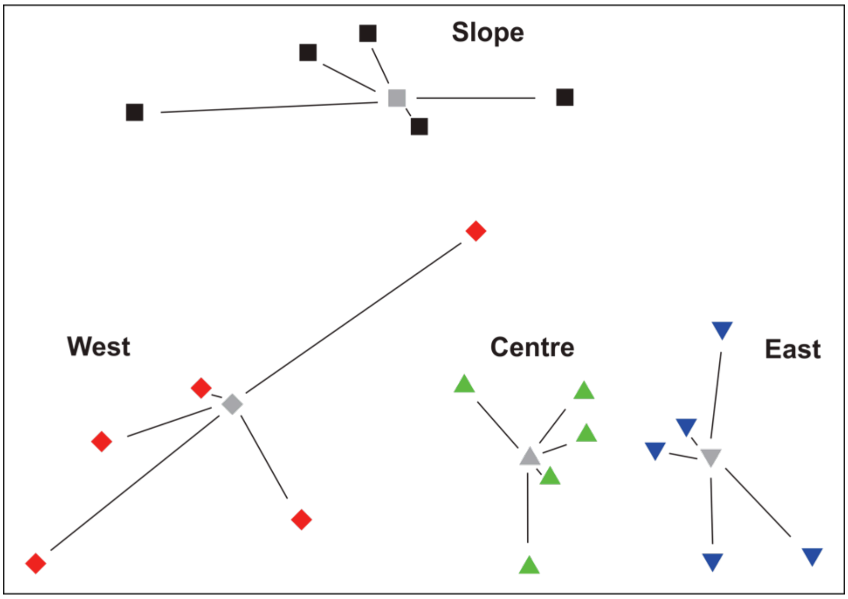


Figure 3.6 nMDS ordination plot of polychaete species composition at four study sites (grey symbols represent centroids)

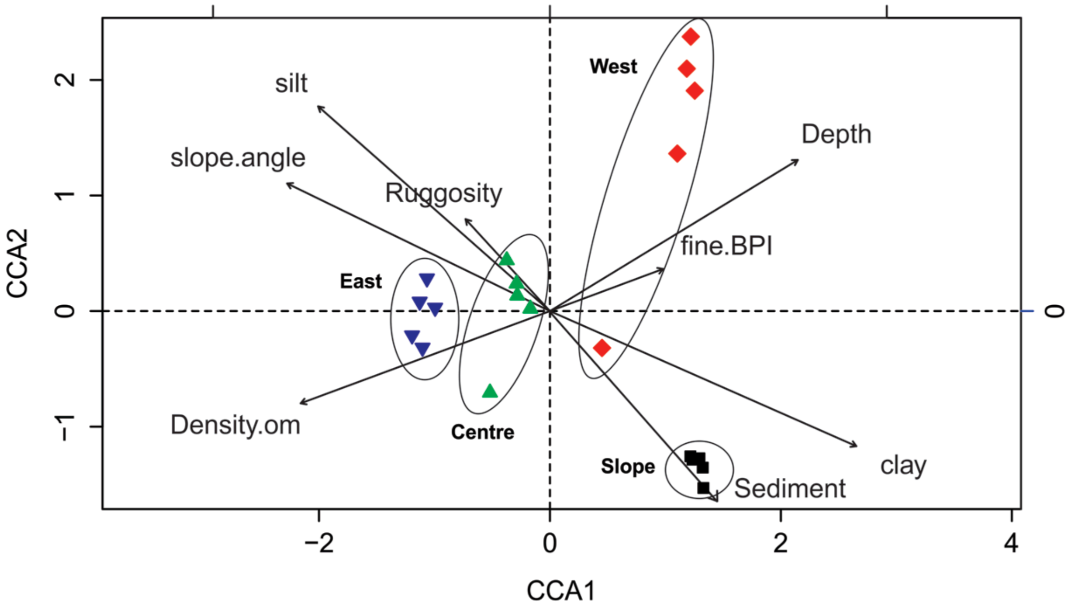


Figure 3.7 Canonical correspondence analysis of polychaete species composition at four study sites.

Depth, water depth; fine BPI, fine-scale bathymetry position index; clay, percentage clay; Density.om macrofaunal density as a proxy for organic matter input; slope.angle, slope angle ; Ruggosity; silt, silt percentage; Sediment, sediment grain size.

3.5 Discussion

3.5.1 Polychaete assemblage

The species composition of the polychaete assemblages differed between branches of the Whittard Canyon. This is consistent with previous family-level studies of polychaetes in the same canyon system (Hunter et al., 2013a; Gunton et al., 2015a). Multidimensional scaling and a CCA revealed that the Eastern and Central branch species assemblages were closely related (Figs. 3.6 & 3.7); again, this pattern was also observed at the family level (Gunton et al. 2015a). This faunal similarity may reflect a combination of similar environmental conditions and geographical proximity (Gunton et al., 2015a). The Western branch samples yielded a more distinct assemblage, characterised by *Ancistrosyllis* sp. A (a member of the family Pilargidae), which made up 10% of the polychaete species in the Western branch but was not present in other canyon branches. Pilargids are motile active burrowers and are 'presumably carnivores' (Jumars et al., 2015). A predatory pilargid (*Sigambra* sp.) was abundant at sites at the Porcupine Abyssal Plain, Tagus Abyssal Plain and Madeira Abyssal Plain in the northeast Atlantic (Glover et al., 2001). However, it was not clear why this species was abundant inthese areas. The high abundance of *Ancistrosyllis* sp. A in the Western branch of the Whittard Canyon may indicate a higher availability of suitable food.

In addition to these intra-canyon patterns, polychaete assemblage composition differed between the canyon branches and the adjacent open slope. The CCA suggested that these species-level differences might be linked to the different sediment characteristics (e.g. coarser-grained sediments on the slope than in the canyon) and increased organic matter input into the canyon branches (Fig. 3.7). Duros et al. (2011) attributed differences in the benthic foraminiferal species composition between the branches and the slope, at depths comparable to those of the present study, to the preferential deposition of organic detritus in canyon branches.

Paramphinome jeffreysii was the top-ranked species at all sites (Table 3.2). A SIMPER analysis suggests it was also responsible for much of the similarity between stations inside the canyon and between the canyon and the slope (Table 3.3). The relative abundance of *P. jeffreysii* increased from west to east, reaching almost 40 % of the assemblage in the Eastern branch. It was also more common in the deeper sediment layers (1-3, 3-5 cm) than in the upper 1 cm horizon (Fig. 3.3). The abundance of this small, omnivorous polychaete (Fauchald & Jumars 1979) throughout the canyon may indicate an opportunistic response to organic matter being transported down the canyon. Significant increases in the abundance of the same species in the North Sea have been linked to an increase in food availability (Kroncke et al. 2011). High abundances of *P. jeffreysii* were also associated with organically-enriched sediments near fish farms along the Norwegian coastline (Bannister et al., 2014) and a trough (100 m depth) off the Swedish west coast (Rosenberg 1995).

Juvenile polychaetes in the family Opheliidae (Opheliidae sp. A) were common in the top sediment layer (0-1 cm) of samples from the Eastern branch, where they accounted for 11% of the assemblage and were ranked second after *P. jeffreysii*. This too may indicate a recent input of organic matter onto the top sediment layer. During a time-series study at a deeper site (~ 4850 m), located 464 km to the west of our study area on the Porcupine Abyssal Plain (PAP), morphologically very similar juvenile opheliids were found in high densities in the upper 2 cm layer of multicore samples (Vanreusel et al., 2001). Over the two year study period, a stable population of juvenile Opheliidae displayed a slow increase in the body size (Vanreusel et al., 2001). These opheliids were interpreted as opportunists that had recently been recruited following the deposition of a pulsed input of phytodetritus. A separate contribution to the same time-series study (Soto et al. 2010) also recorded a large increase in the abundance of opheliid juveniles at PAP. Again, this was interpreted as a recruitment event linked to phytodetritus deposition. Studies of shallow-water opheliids suggest that they have an opportunistic life history (Hermans 1978). Experiments on the continental shelf off North Carolina showed opheliid and capitellid abundance increasing by 2 - 90 times in enriched sediment trays compared with unenriched trays (Renaud et al. 1999). Population densities of the opheliid *Armandia brevis* from waters off San Juan Island, Washington, fluctuate markedly throughout the year as a result of reproductive events (Woodin 1974). The opheliids may be opportunists waiting for optimal conditions before converting their energy resources into a reproductive effort (Vanreusel et al. 2001).

It is interesting to note the large depth range (3500 – 4850 m) of Opheliidae sp. A, which spans both the lower bathyal and abyssal zones in the NE Atlantic. It has been suggested that depth zonation amongst macrofauna is closely related to their dispersal abilities during their early development (Grassle et al. 1979). Assuming they all represent the same species, larvae of the opheliid recognised in the present study may be well adapted to dispersal, allowing them to span a large depth range. All juvenile opheliids in Vanreusel et al. (2001) were presumed to belong to the same species. This species could not be determined as adult opheliids found at the PAP site in previous studies were new to science and not formally identified. The most abundant identified opheliid in our material was *Ophelina abranchiata.* It is not clear whether the juveniles represent this species or a complex of several species. Further work using genetic methods may elucidate this problem.

3.5.2 Polychaete diversity

3.5.2.1 Alpha diversity

Polychaete species diversity was similar in the Western, Central and Eastern branches of the Whittard Canyon, with the Western branch samples yielding slightly higher values of H' than the other two branches (Table 3.1). Total species numbers (species richness) were highest in the Eastern branch, followed by the Central, and Western branches, consistent with the higher abundances in the Eastern branch.

Compared with the canyon, polychaete diversity was higher at the slope site and dominance also lower, while species richness values lay between those of the Western and Central branches. Depressed species richness and low evenness inside canyons has been noted in the case of macrobenthos in the Nazaré Canyon (Curdia et al. 2004) and polychaetes in the Portuguese canyons (Patterson et al 2011).

A number of ecological studies have suggested a unimodal relationship between diversity and productivity (Rosenzweig 1995). In oligotrophic settings, diversity increases with increasing food availability to reach maximal values at intermediate levels of productivity. Where levels of food availability are excessive, diversity may be depressed (Levin et al., 2001). In coastal marine systems, increased organic enrichment resulting from pollution can lead to higher infaunal standing stocks. However, it can also lead to oxygen depletion and hence dominance by a few hypoxia-tolerant species leading to low evenness (Pearson & Rosenberg 1978). This has also been observed in upper bathyal oxygen minimum zones where dense, high-dominance, low-diversity benthic assemblages are associated with natural organic enrichment (Levin et al. 1994b; Levin 2003; Gooday et al., 2010). However, there is no evidence for comparably high levels of organic enrichment and associated oxygen depletion at our study sites.

High levels of physical disturbance inside the canyon may also suppress polychaete diversity, in accordance with the Intermediate Disturbance Hypothesis (Connell 1978, Huston 1979), which predicts maximal levels of local species diversity when disturbance is neither too rare nor too frequent. At the High Energy Benthic Boundary Layer Experiment (HEBBLE) site in the North Atlantic, disturbance generated by episodic strong currents ('benthic storms') was linked to high species dominance in polychaetes and bivalves (Thistle et al. 1985). Disturbance in the form of high-energy currents was considered important in the structuring of polychaete diversity on the Hebridean Slope in the Rockall Trough (Paterson & Lambshead 1995). It has been suggested that community disturbance resulting from strong currents, high sedimentation rates and re-suspension explains the depressed diversity and increased dominance of certain species in the Nazaré (Gage et al. 1995, Curdia et al. 2004, Koho et al. 2007, Ingels et al. 2009) and Setúbal

(Gage et al. 1995) canyons. Paterson et al. (2011) attributed the dominance of a *Prionospio* species in the Nazaré Canyon to an opportunistic response to a disturbance event. The disturbance could have been caused by the periodic deposition of organically enriched sediment, but a spring-tide mediated turbidite event or increased bioturbation of larger macro/megafauna were also thought possible (Paterson et al 2011). The lower diversity of sessile and sedentary megafauna in Hawaiian canyons was believed to have been caused by periodic disturbances, such as sediment slumps and turbidity currents (Vetter et al. 2010).

Polychaete diversity in the Whittard Canyon system is relatively high compared with that in Iberian Margin canyons (Fig. 3.5b). Paterson et al. (2011) analysed polychaete diversity in the Nazaré, Setúbal and Cascais canyons on the Iberian Margin, in each case at depths of 1000, 3400, and 4300 m. Considering only the data from their 3400 m sites, i.e. closest in depth to our samples, rarefied species richness in the Whittard Canyon is generally higher than that in the Iberian canyons (Fig. 3.5b). Among the latter, rarefied species richness was lower in the Nazaré and Setúbal Canyons than that in the Cascais Canyon. Paterson et al. (2011) attributed differences in polychaete rarefied species richness between Iberian Margin canyons to different environmental characteristics (Paterson et al., 2011). The Nazaré Canyon is active with periodic disturbances and relatively high current speeds particularly in the upper and middle canyon (de Stigter et al. 2007, Garcia et al. 2007). Lower productivity characterised the mid-Setúbal Canyon leading to reduced diversity. The higher diversity in the Cascais Canyon suggested that it is a more quiescent canyon, where disturbance and productivity effects are balanced (Paterson et al., 2011). If correct, these inferences suggest that the Whittard Canyon may be less disturbed/ more quiescent than the Iberian canyons, at least around 3400 m in the middle section.

3.5.2.2 Beta diversity

Levels of beta diversity on the ocean floor are poorly understood and appear to vary between taxa (Ellingsen et al 2007a). Paterson et al. (1998) reported a difference in the species composition of polychaete assemblages at sites on NE Atlantic and equatorial Pacific abyssal plains separated by 500 -1000 km. They suggested that faunal turnover occurred across scales of 1000 + km on abyssal plains. Similarly, Glover et al. (2001) report differences in polychaete species assemblages at four sites in the NE Atlantic (Porcupine, Tagus and Cape Verde Abyssal Plains) that were separated by distances of up to 3300 km. However, our data suggest there is a change in polychaete species composition across the 60 km spanned by our four study sites. It seems likely, therefore, that rates of beta diversity are considerably higher on continental margins dissected by canyons than they are on abyssal plains, which are topographically much less complex and offer fewer barriers to dispersal than the ocean margins.

Another way to assess the change in species composition across the study sites is provided by Whittaker's beta diversity (β_W). There was no clear variation in beta diversity in the present study, though we should note that the sample size limitations (minimum number of specimens per sample) may have restricted our ability to detect a change. Our beta diversity assessment (Table 3.4) nevertheless makes clear the enhanced α and γ diversity levels of the slope site over the canyon sites. This consequently meant that all aspects of diversity (^{0}D, ^{1}D, ^{2}D) were reduced when canyon data were added to the slope data.

There was surprisingly little difference in the species composition of assemblages between the slope and the Western canyon branch (Fig. 3.8). Our canyon samples are all from soft-bottom areas that are not too dissimilar in terms of sediment characteristics from the open slope. However, the Whittard Canyon as a whole encompasses a wide range of different habitats. The head of the canyon is characterised by turbidity currents and oxygen-limited, possibly sulphidic conditions (Ingels et al. 2011c). Vertical cliffs (Huvenne et al. 2011) and cold-water corals (Morris et al. 2013, Huvenne et al. 2011, Robert et al. 2014) are present in the upper to mid reaches, flat areas of soft sediment in the thalweg (Robert et al. 2014) and deeper parts of the canyon. Analysis of polychaete assemblages from these different areas inside the canyon would almost certainly increase species-level differences in the assemblages both between canyon and slope and within the canyon and thereby enhance species turnover. McClain and Barry (2010) observed that the highest rate of faunal turnover in the Monterey Canyon off the central Californian coast, USA, was closest to the canyon wall. The authors concluded that the canyon walls enhanced the input of organic debris, which significantly altered the benthic assemblages. Our canyon samples were all collected from or next to the thalweg, so the effect of the canyon wall would be negligible.

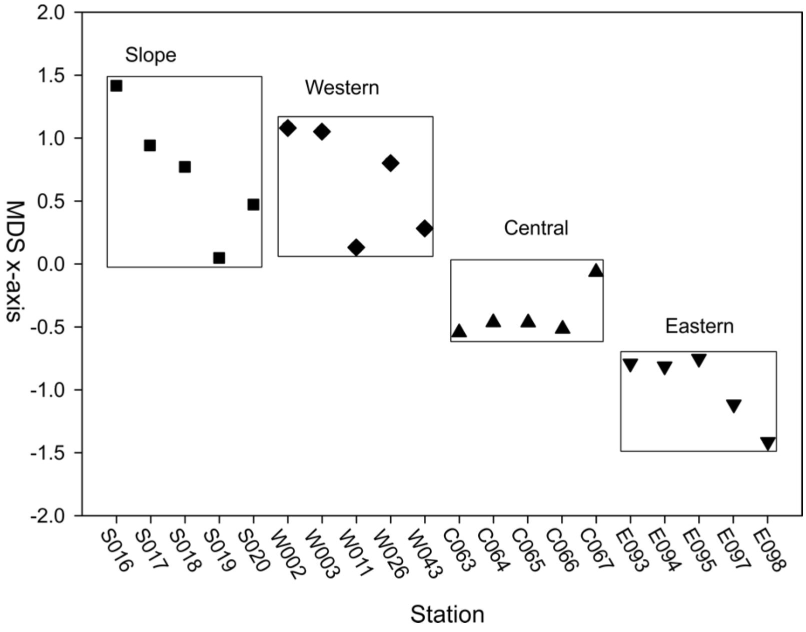


Figure 3.8 Plot of nMDS ordination x-value against sampling identity for polychaete species composition at four study sites.

3.5.2.3 Regional species diversity

Continental margins are characterised by high species diversity (Hessler & Sanders 1967, Levin et al. 2010), related in part to the considerable habitat heterogeneity that characterises these regions of the deep sea (Levin & Dayton 2009, Levin et al. 2010). By virtue of their extreme topography, complex current regimes, and tendency to concentrate organic matter and sediment, submarine canyons make a substantial contribution to this heterogeneity (Vetter & Dayton 1999, McClain & Barry 2010). Canyons in the Hawaiian Archipelago were thought to enhance the regional diversity of megafauna, with 41 species being only found inside the canyon and not on the slope (Vetter et al. 2010). In the present study, as noted above, diversity was reduced compared with the slope site when canyon and slope data were combined (Fig. 3.5c; Table 3.4). Nevertheless, 46 polychaete species were only recorded from the canyon branches, which tends to support the hypothesis that canyons increase regional diversity in soft-sediments by harbouring species that are not found on the adjacent slope.

3.5.3 Polychaete biogeography

The 25 species that were found at all four study sites accounted for 72.3 % of polychaete specimens. The two most abundant species (*Paramphinome jeffreysii* and *Aurospio* sp. B), which were among those found at all sites, made up 39.4 % of the total number of identified polychaetes in our samples. The 43 species that occurred at a single site accounted for only

2.9 % of specimens. This pattern is consistent with the observations of Glover et al. (2001), who recognised a core group of polychaete species that were widely distributed at their four NE Atlantic abyssal plain sites. These species represented about 70 % of the fauna at the Madeira Abyssal Plain but around 50 % or less at three other sites. However, a large majority (81 %) of the species they recognised were unique to one of their sites. They attributed the large number of unique species to a vast regional species pool and inadequate sampling effort. Wide spatial distributions of the most abundant species and the apparent compressed range of the least common species were also noted in the case of polychaetes from the Southern Ocean (Ellingsen et al. 2007b). Indeed, this pattern is suggested for many groups of species, habitat types and spatial scales (Brown 1984).

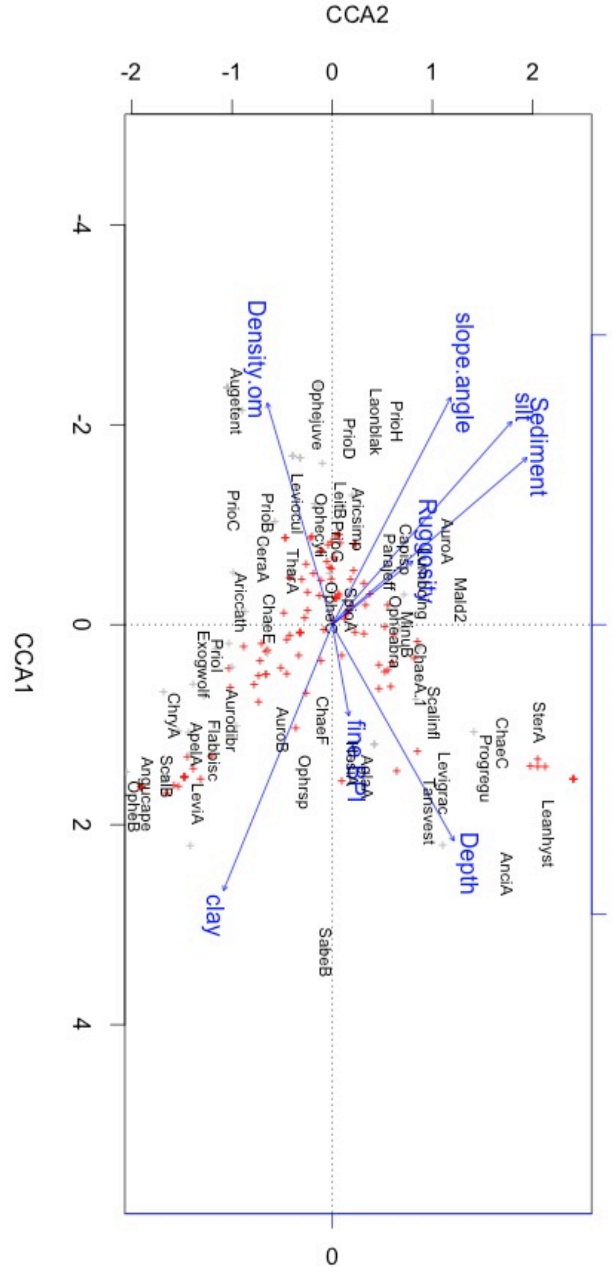
Some species found in the Whittard Canyon apparently have cosmopolitan distributions on a global scale. For example, there are records of *Aurospio dibranchiata,* which was found at all four of our sites and from the Atlantic, Pacific and Southern Oceans (Smith et al. 2006). With fewer barriers to dispersal in the deep sea, compared with shallow-water habitats, wide dispersal of species might be expected (Grassle and Morse-Porteous, 1987). However, barriers do exist and these are probably more common on continental margins than abyssal plains (McClain and Mincks Hardy, 2010). Despite these restrictions to dispersal, some species do appear to have cosmopolitan distributions in the deep sea, particularly at abyssal depths (Wilson and Hessler, 1987; McClain and Mincks Hardy, 2010). In the case of certain foraminifera, this is supported by molecular evidence (Pawlwoski et al., 2007; Lecroq et al., 2009). Conversely, some species identified morphologically as 'cosmopolitan' have proved to comprise a complex of cryptic species with smaller ranges when investigated with molecular methods (e.g.,Vrijenhoek et al. 1994; France and Kocher, 1966; Quattro et al., 2001).

Paterson et al. (2011) suggest that canyons may harbour endemic polychaete species. Forty-six polychaete species were found inside the Whittard Canyon branches but not on the adjacent slope. Of these 46 species, 34 could not be assigned a binomial Latin name. Out of the twelve species that could be given a Latin name, one was originally described from the Northeast Atlantic (*Exogone (Parexogone) campoyi*), two from the Northwest Atlantic (*Aglaophamus minusculus*, *Aricidea (Strelzovia) quadrilobata*), three from the Arctic Ocean (*Laonice blakei*, *Micronephthys minuta*, *Pseudoscalibregma parvum*), two from the Norwegian coast (*Ampharete finmarchica*, *Amphicteis gunneri*), two from the Californian coast (*Cenogenus fusca* and *Levinsenia oculata*), one from the Southern Ocean (*Augeneria tentaculata*) and one from off the Japanese islands (*Anobothrus patersoni*). None of these species is confined to the broader area around the canyon, although *E.(P.)campoyi* has been recorded only from the Bay of Biscay, the western Mediterranean, and the Aegean Sea. Interestingly, this species was first described from the Capbreton Canyon in the Bay of Biscay (San Martin et al. 1996), suggesting it may be common in canyons.

It is estimated that up to 90 percent of deep-sea species have not been formally described (Smith et al. 2006) and consequently species distributions are very poorly understood (Glover et al. 2001, McClain & Mincks Hardy 2010). This applies as much to polychaetes as it does to other deep-sea taxa (Paterson et al. 2011). The prevalence of undescribed species in our samples makes it difficult to determine whether there are any polychaete species endemic to the Whittard Canyon. Two species found in this study, *Aurospio* sp. B and *Prionospio* sp I., were also recorded in the Iberian Margin canyons and are currently under description (Paterson et al. submitted). These new species appear to be closely associated with canyons. *Prionospio* sp. I has only been found in canyons (L. Neal unpublished observations). *Aurospio* sp. B has been recorded in a non-canyon environment on the Porcupine Abyssal Plain, but only in very low densities (G. Paterson unpublished observations). Both may be opportunists adapted to canyon environments. Endemics species of deep-water hydromedusea are found in Mediterranean canyons (Gili et al., 2000; Bouillon et al., 2000). The life cycles of these endemic hydromedusea are closely linked to factors specific to the canyon environment, such as topography, sedimentation and hydrographic conditions. Similarly, Paterson et al. (2011) suggested that some polychaete species are adapted to the disturbed conditions typical of some canyons rather than being restricted to one particular canyon. Further research on the taxonomy of deep-sea canyon polychaetes using both morphological characteristics and genetic methods is required to understand endemics in canyons and connectively between different canyons.

Figure S3.1 **Canonical correspondence analysis of most abundant polychaete species in the Whittard Canyon and adjacent slope site**

Depth, water depth; fine BPI, fine-scale bathymetry position index; clay, percentage clay; Density.om macrofaunal density as a proxy for organic matter input; slope.angle, slope angle; Ruggosity; silt, silt percentage; Sediment, inverse of sediment grain size;



AglaA, *Aglaophamus sp. A*; **AnciA**, *Ancistrosyllis sp. A;* **Angucape**, *Anguillosyllis capensis*; **ApelA**, *Apelochaeta sp. A;* **Arcsimp**, *Aricidea simplex;* **Ariccath**, *Aricidae catherinae*; **Augetent**, *Augeneria cf. tentaculata;* **AuroA**, *Aurospio sp. A;* **AuroB**, *Aurospio sp. B* ;**Aurodibr**, *Aurospio dibranchiate;* **Capisp**, *Capitellidae sp. A*; **ChaeA.1**, *Chaetozone sp. A*; **ChaeC**, *Chaetozone sp. C*;**ChaeE**, *Chaetozone sp. E;* **ChaeF**, *Chaetozone sp. F;***ChryA**, *Chrysopetalidae sp. A;* **Exogwolf**, *Exogone (Parexogone) wolfi*; **Flabbisc**, *Flabelligella cf. biscayensis*; **HesiA**, *Hesionidae sp. A;* **Laonblak**, *Laonice blakei;* **Leanhyst**, *Leanira hystricis*; **LeitB**, *Leitoscoloplos sp. B;***LeviA**, *Levinsenia sp. A;***LeviA**, *Levinsenia sp. B*; **Levigrac**, *Levinsenia gracilis*; **Leviocul**, *Levinsenia oculata*; **Lumbcing**, *Lumbrineris cf. cingulate*; **Mal2**, *Maldanidae sp. B;* **MinuB**, *Minuspio sp. B*; **Opheabra**, *Ophelina abranchiata*; **OpheB**, *Ophelina sp. B;* **OpheC**, *Ophelina sp. C*; **Ophejuve**, Ophelidae sp. A (juvenile); **Ophrsp**, *Ophryotrocha sp.;***Parajeff**, *Paramphinome jeffreysii*; **PrioB**, *Prionospio sp. B*; **PrioC**, *Prionospio sp. C;* **PrioD**, *Prionospio sp. D*; **PrioG**, *Prionospio sp. G;* **PrioH**, *Prionospio sp. H***;** **PrioI**, *Prionospio sp. I;* **Progregu**, *Progoniada regularis*; **SabeB**, *Sabellidae sp. B;* **ScaliB**, *Scalibregmatidae sp. B;* **Scalinfl**, *Scalibregma inflatum*; **SpioA**, *Spiophanes sp. A*; **SterA**, *Sternapsis sp. A*;**Tansvest**, *Tanseimaruana vastis*; **TharA**, *Tharyx sp. A*;

Chapter 4: Macrofaunal nematodes from the lower bathyal Whittard Canyon (NE Atlantic): assemblage characteristics and comparison with polychaete assemblages.

4.1 Abstract

Macrofaunal nematode assemblage composition, diversity and functional traits were analysed at lower bathyal depths within the Whittard Canyon (NE Atlantic) and on the nearby continental slope. Four sites were sampled with a Megacorer, three in the canyon branches and one on the slope to the west of the canyon, all at a depth of ~3500 m. We analysed nematode genera retained on a 500-µm mesh and compared these results with those for polychaete genera from the same sieve fraction of the same sediment samples. *Paramesacanthion* was the most abundant nematode genus overall (33 ind. 0.1 m^{-2}, 21 % total abundance), *Metacylicolaimus* (31 ind. 0.1 m^{-2}, 20 %), *Cylicolaimus* (13 ind. 0.1 m^{-2}, 9 %) and *Phanodermopsis* (9 ind. 0.1 m^{-2}, 6 %) were also abundant. Nematode diversity was similar between canyon branches but lower inside the canyon compared with the open slope. An MDS analysis based on nematode genera revealed that all three canyon sites grouped together, while the slope site was distinct; this pattern was reflected in the pair-wise ANOSIM. Nematode feeding group 1A (selective deposit feeders) represented 40 % of individuals at the slope site, while type 2B (predators/scavengers/omnivores) represented 44 % inside the canyon. Polychaete diversity showed the same pattern as nematode diversity. Polychaete functional guilds also displayed a similar across-site shift to that of the nematodes, suggesting that the two taxa were responding in a similar fashion to environmental factors. However, in contrast to the nematodes, an MDS analysis of polychaete genera distinguished the Western branch from the other canyon sites, whilst a pair-wise ANOSIM revealed a statistical difference between all sites. These differences may reflect different life history traits of nematodes and polychaetes and the closer association of nematodes with the sediment.

4.2 Introduction

Nematoda is generally the most abundant and species-rich metazoan phylum living in deep-sea sediments (Vincx et al. 1994), since nematodes make up about 90 % of total metazoan meiofaunal numbers in most samples (Thiel 1975). As part of the meiobenthos, their patterns of abundance and distribution are relatively well documented (Thiel 1975, Thiel 1983, Vanreusel et al. 2010, Pape et al. 2013). However, nematodes are not only found in the meiobenthic size fraction, i.e. organisms that pass through a 500 µm (or 1000 µm) mesh sieve and are retained on a 44 µm (or 63 µm) mesh sieve (Giere 2009), but also span the macrobenthos, which in a deep-sea context is defined as organisms retained on a > 300 µm mesh sieve (Thiel 1983). Since nematodes are considered to be meiobenthic animals, they are often omitted from macrobenthic studies. Nevertheless, they have been recorded in high densities in some deep-sea macrobenthic studies (Lambshead in Giere, 2009). Specimens measuring up to 1 cm in length were found in epibenthic sled samples down to 2.9 km depth in the Rockall Trough, NE Atlantic (Gage & Tyler 1991). At this site, they made up about half of the total number of macrofaunal-sized taxa (Gage 1979). On the nearby Goban Spur, nematodes within the macrofaunal size fraction became relatively more important with increasing water depth and made up to 20 % of total macrofaunal numbers at the deepest station (4460 m) (Flach et al. 1999). In the abyssal Pacific, nematodes comprised around half of the total metazoan fauna retained on a 297 µm (Hessler & Jumars 1974) or a 300 µm (Hecker & Paul 1979) mesh sieve. However, these large nematodes are very rarely identified taxonomically. One of the few such studies is that of Sharma et al. (2011), who compared meio- and macrobenthic nematode assemblages from the deep Arctic (Canada Basin), Gulf of Mexico (GOM) and the Bermuda slope (640-3961 m, 212 - 3000 m, 1535 - 2200 m water depth, respectively). They concluded that the meio- and macrobenthic nematodes were distinct assemblages in terms of community structure, body size and functional grouping and that large nematodes should be included in macrobenthic studies. The study by Baldrighi & Manini (2011) of meio- and macrobenthic nematodes and polychaetes from six sites in the deep Mediterranean Sea (1200 - 2800 m depth) reached a similar conclusion. Other studies of macrobenthos that have identified macrofaunal nematodes to the species level are those of Pavithran et al. (2009), Henry & Roberts (2007) and Netto et al. (1999).

Distinct meiofaunal and macrofaunal size peaks are thought to characterise deep-sea sediment communities. From the upper intertidal to 5850 m, when biomass is plotted against equivalent spherical diameter, a trough in size distribution between these two groups is apparent (Schwinghamer 1985). The existence of this trough has been supported by quantitative studies (Schwinghamer 1981, Warwick & Clarke 1984, Schwinghamer 1985, Warwick 2014) that concluded that marine meiofauna represent a separate group of animals that is biologically and ecologically distinct from the macrofauna. Thus, the meio- and macrobenthos are generally thought to represent distinct functional groups (Gage and Tyler 1991). It has been suggested that this distinction is related to the physical nature of the benthic habitat, which varies with spatial scale and imposes an optimal size for each functional group (Schwinghamer 1983). In general, the meiofauna live in the fluid-filled spaces between the particles, while the macrofauna burrow into the sediment or live on the surface (Schwinghamer 1983). However, different ecological types of meiobenthic nematode prefer different grain sizes (Wieser 1959). Some nematodes, “sliders”, live in the interstitial spaces between coarse sand grains. Below 200 μm grain size the interstitial space becomes too small, and in fine sand and mud, burrowing nematodes predominate (Giere 2009). It has been proposed recently that the size-distribution of meio- and macrofauna, may be the result of a sampling artefact, and that best practise is to study the macrobenthos in toto (macrobenthos *sensu lato*), i.e. to include all taxa retained by the chosen sieve (Bett 2013, 2014).

In previous papers (Gunton et al., 2015a,b), we described the polychaete family and species-level assemblage composition and structure at around 3500 m depth in the Whittard Canyon (NE Atlantic) and on the adjacent slope to the west of the canyon. In the present study, we focus on the community structure and functional traits of large nematodes from the 500-μm sieve fraction of the same samples. Submarine canyons are conduits for organic matter and sediment transport and often harbour an increased density of macrofauna (Vetter & Dayton 1998) and meiofauna (Ingels et al. 2011c). There are differences in environmental conditions between the Whittard Canyon and the adjacent continental slope, and between branches of the canyon. Sediments inside the canyon are organically enriched compared with the adjacent slope (Duineveld et al. 2001). Bathymetry derivatives (e.g. Bathymetric Position Index, slope angle and ruggosity) (Gunton et al. 2015a) and current activity differ between branches (Amaro et al. in prep). As a result, the benthic community composition also differs between the branches of the Whittard Canyon and the adjacent continental slope (Duineveld et al. 2001, Duros et al. 2011, Gunton et al. 2015a). This makes the Whittard Canyon an interesting setting in which to study the comparative community-level responses of nematodes and polychaetes. The objectives, therefore, are to 1) describe the assemblage composition, diversity and feeding types of macrofaunal nematodes and 2) compare the across-site trends in macrofaunal nematode assemblage structure and diversity with those of polychaetes, based on the same samples collected inside the canyon and on the adjacent slope.

4.3 Methods

4.3.1 Sampling

Macrofauna were collected from three sites inside the Whittard Canyon and one site on the adjacent slope using a Megacorer during the RRS *James Cook* cruise 036 in June and July 2009. Samples were taken from 22 deployments of the Megacorer (Table 4.1, Figure 4.1), all located at a depth of around 3500 m. In general, the Megacorer was fitted with eight large (100 mm internal diameter, 78.5 cm cross-sectional area) core tubes. Five deployments were conducted in the Western branch, six in the Central branch and six in the Eastern branch of the canyon and five on the adjacent slope. One additional deployment was made in the Central and Eastern branches to compensate for the failure to recover enough cores on earlier deployments. On deck, all the cores from one Megacorer deployment were cut into five sediment layers (0-1, 1-3, 3-5, 5-10 and 10-15 cm) and each layer sieved using filtered seawater on 500 and 300-µm meshes. For each deployment, all of the > 500-µm sieve residues from one layer were combined into a single residue and the same procedure performed for the 300-500-µm fraction. Thus, each deployment yielded ten sieve residues (five > 500 µm and five 300-500 µm). Samples were fixed with 10 % borax-buffered formalin. See Gunton et al. (2015a) for further details of Megacore sample processing and preservation. For this study, only the pooled top 3 layers (0-5 cm) and the 500-µm sieve size fractions were analysed. The use of the 500-µm fraction is based on one of the conventional sieve mesh sizes used for macrobenthos studies.

Table 4.1 Megacorer sampling sites in the three branches of the Whittard Canyon and on the adjacent slope.

Site	Deploy.	Lat. (N)	Long. (W)	Depth (m)	Area (m^{-2})
Slope	S016	47°56.79"	10°46.85"	3511	0.063
	S017	47°56.78"	10°46.85"	3512	0.055
	S018	47°56.81"	10°46.91"	3514	0.047
	S019	47°56.74"	10°46.94"	3505	0.063
	S020	47°56.78"	10°46.85"	3514	0.055
Western branch	W002	48°09.18"	10°33.70"	3670	0.063
	W003	48°09.17"	10°33.70"	3661	0.055
	W011	48°09.22"	10°32.36"	3582	0.047
	W026	48°09.18"	10°33.73"	3670	0.039
	W043	48°09.15"	10°33.76"	3657	0.047
Central branch	C063	48°16.89"	10°18.74"	3375	0.047
	C064	48°16.97"	10°18.65"	3382	0.063
	C065	48°17.04"	10°18.89"	3373	0.055
	C067	48°16.98"	10°18.72"	3376	0.055
	C066	48°16.83"	10°18.72"	3381	}0.063
	C068	48°17.01"	10°18.83"	3375	
Eastern branch	E093	48°15.89"	10°09.56"	3424	0.063
	E094	48°15.78"	10°09.57"	3429	0.053
	E095	48°15.78"	10°09.58"	3429	}0.063
	E096	48°15.76"	10°09.60"	3424	
	E097	48°15.89"	10°09.54"	3425	0.039
	E098	48°15.76"	10°09.60"	3432	0.031

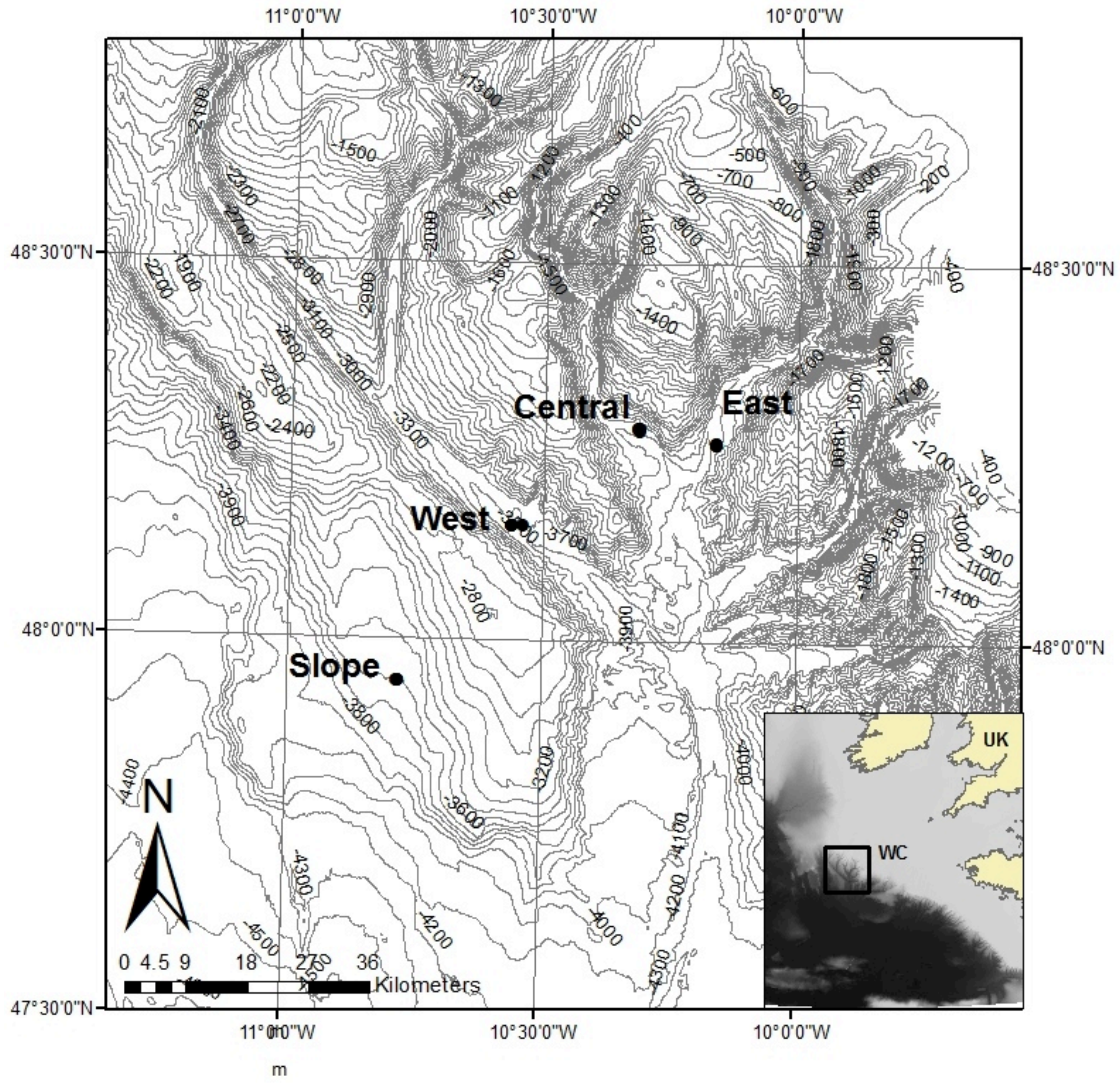


Figure 4.1 Bathymetry and location map of Whittard Canyon and adjacent slope study sites

4.3.2 Macrofaunal nematode and polychaete identification

In the laboratory, the large nematodes were transferred from the formalin onto a 300-μm mesh sieve, rinsed with fresh water and sorted in 70 % ethanol. The large nematodes were picked out under a stereomicroscope, transferred to glycerine (Seinhorst 1959) and mounted on glass slides under cover slips sealed with paraffin wax. Macrofaunal nematodes were identified to genus level using the pictorial key of Warwick et al. (1998). For polychaetes, we combined species level data from Gunton et al. (2015b) to generate generic abundances.

4.3.3 Nematode and polychaete community structure

The software program EstimateS V9 (Colwell 2013) was used to construct rarefaction curves to predict genus richness. Rarefied diversity indices were also calculated using EstimatesS (Fisher's alpha, Shannon index, Shannon exponential, Simpson's inverse). Abundance data were standardised to account for the number of Megacore tubes obtained during each deployment and then transformed by log ($x + 1$). Results were analysed using Primer V6 and used to create multidimensional scaling plots (MDS plots) based on Bray Curtis similarity to understand assemblage similarity. The lengths of the nematodes (excluding the filiform tail) and their maximal widths were measured using an Olympus BX 51 microscope, a Nixon Coolpix 500 camera and ImageJ software (Schneider et al. 2012). Biomass, as mg wet weight, was estimated using a standard formula (Andrassy 1956).

4.3.4 Nematode trophic analysis

Individuals were assigned to the following four feeding groups based on buccal morphology (Wieser 1953): buccal cavity either absent or minimal - selective deposit feeders (1A); large but unarmed buccal cavity - non-selective deposit feeders (1B); buccal cavity with scraping tooth or teeth - epigrowth feeders (2A); buccal cavity with large jaws - predators/omnivores/scavenges (2B). The index of trophic diversity (ITD) was calculated as ITD = $\Sigma Ø^2$, where Ø is the relative contribution of each trophic group to the total nematode density (Heip et al. 1998). Given four trophic groups, ITD ranges from 0.25, the highest trophic diversity where the four groups each account for 25 % of the assemblage, to 1.0, the lowest trophic diversity where one group accounts for 100 % of the assemblage.

The relative importance of colonisers compared with persisters (c-p values) was calculated following Bongers et al. (1991), and Bongers et al. (1995). According to this scheme, marine nematode taxa are placed on an arbitrary c-p scale, which ranges from 2 for colonisers (short life-cycle, high reproduction rates, high colonisation ability and disturbance tolerant) to 5 for persisters (long life-cycles, low colonisation ability and sensitive to disturbance). The maturity index (MI) was calculated from the weighted mean of individual genus scores:

MI=$\Sigma\, v(i)f(i)$, where $v(i)$ is the c-p value of the taxon, $f(i)$ is the frequency of the taxon.

Nematode tail shapes were assigned to four groups based on the scheme of Thistle et al. (1995). These were type 1, "rounded" tails with a blunt end; type 2, "clavate-conicocylindrical" tails, initially conical with an extension to the tip; type 3, "conical" tails with a pointed tip and tail length less than five body widths and type 4, "long", a tail longer than five body widths.

4.3.5 Polychaete trophic analysis

Polychaete trophic groupings were determined using the scheme proposed by Jumars et al. (2015) in which each family is assigned to a functional guild based on a number of attributes (feeding mode, motility and feeding apparatus). We considered motility and feeding mode for the present analysis. To analyse motility, polychaetes were grouped according to whether they were motile (burrowing, crawling, swimming) discretely motile (burrow constructing, tube dwelling, able to rebuild or extend tube, portable tube) or sessile (unlikely to survive if removed from attachment site, tube or burrow). To analyse feeding mode, polychaetes were grouped according to whether they were microphagous (feeding on small particles), macrophagous (feeding on larger items), omnivorous (simultaneously feeding on more than one type of food) or osmotrophic (individuals that take up dissolved organic compounds by osmosis for nutrition) (Jumars et al. 2015).

4.3.6 Univariate statistical analyses

To test for statistical significance of results, ANOVA and Tukey Pairwise tests were performed on nematode density data. Non-parametric Mood's Median tests were performed on nematode tail length data. Mood's Median tests were also performed on percentage data for nematode feeding group, tail shape and on polychaete feeding and motility mode. These univariate tests were carried out using the Minitab statistical software package (v17).

4.4 Results

4.4.1 Nematodes Assemblages

4.4.1.1 Nematode abundance and biomass

In total, 410 macrofaunal nematodes were picked from the samples and identified to genus level (supplementary Table 4.1). There was a significant difference in abundance between sites (One-way ANOVA, $p = 0.041$, R^2 (adj) = 28.16 %). Pairwise comparison revealed that the Eastern branch was significantly different ($p < 0.05$) from the slope site. The Eastern branch had the highest abundance of nematodes (51.7 ± standard deviation 24.8 ind. 0.1 m^{-2}), the Western and Central branches had lower and very similar abundances (42.2 ± SD 21.7 ind. 0.1m^{-2} and 44.3 ± SD 16.1 ind. 0.1 m^{-2}, respectively), while the slope site had the lowest abundance (16.4 ± SD 3.3 ind. 0.1 m^{-2}). The highest nematode wet weight biomass was recorded in the Central branch (9.4 ± SD 0.4 ng wwt 0.1 m^{-2}). The slope site had the lowest biomass (0.7 ± SD 0.1 ng wwt 0.1

m^{-2}), while the Western and Eastern branches yielded intermediate values (5.5. ± SD 0.2, 7.5 ± SD 0.2 ng wwt 0.1 m^{-2}, respectively) (Table 4.2).

Table 4.2 Feeding types at each site according to Wieser (1953).

Sl, Slope. W, Western branch. C, Central branch. E, Eastern branch.1A: selective deposit feeders, 1B: non-selective deposit feeders, 2A: epigrowth feeders, 2B: predators/scavengers. Trophic diversity, maturity index and biomass estimates. Bracketed values represent standard deviations between replicates at the same site.

Site	Feeding type (%)				Trophic diversity index	Maturity Index	Bmass 0.1m^{-2} (ng wwt)
	1A	1B	2A	2B			
Sl	39.8	4.9	20.0	35.3	0.42 (0.14)	3.36 (0.41)	0.7
W	13.2	6.6	45.1	35.2	0.40 (0.13)	3.27(0.18)	5.5
C	14.8	8.8	34.1	42.4	0.34 (0.02)	3.03 (0.25)	9.4
E	7.7	4.6	34.3	53.4	0.44 (0.10)	3.23 (0.24)	7.5

4.4.1.2 Nematode composition

Nineteen nematode families and 48 genera were identified. *Paramesacanthion* was the most abundant genus overall (33 ind. 0.1 m^{-2}, 21 % total abundance) followed by *Metacylicolaimus* (31 ind. 0.1 m^{-2}, 20 % total abundance); *Cylicolaimus* (13 ind. 0.1 m^{-2}, 9 %) and *Phanodermopsis* (9 ind. 0.1 m^{-2}, 6 %) were also common. *Paramesacanthion* (3.1 ind. 0.1 m^{-2}) was the most abundant genus at the slope site, *Metacylicolaimus* at the Western (12.3 ind. 0.1 m^{-2}) and Central branch (11.8 ind. 0.1 m^{-2}) and *Cylicolaimus* (10.8 ind. 0.1 m^{-2}) at the Eastern branch (Table 4.2). Juveniles were the most abundant life-stage across all stations (> 35 %)(Fig. 4.2), apart from the Central branch, where females were most abundant (39 %). Males were consistently the least abundant component. There was a significant difference in body length between all four sites (Mood's Median Test body length versus site p = 0.04). Nematodes were, on average, longest in the Eastern branch (5.3 ± SD 2.9 mm), shorter in the Central and Western branches (5.2 ± SD 2.8 and 4.5 ± SD 2.3 mm, respectively) and shortest at the slope site (4.2 ± SD 2.0 mm).

Samples from the Central, Eastern and Western branches were intermingled in an MSD plot (Fig. 4.3A) based on nematode genera, indicating that the three canyon branch assemblages were similar in composition. The slope samples formed a distinct group apart from the canyon samples. A global ANOSIM indicated significant variation; in all pair-wise comparisons, canyon branches were significantly different from the slope site ($p < 0.01$); however, canyon branches were not significantly different from each other ($p > 0.3$).

Table 4.3 Density per 0.1 m^{-2} of top five most abundant nematode genera at three Whittard Canyon sites (Western, Central and Eastern branch) and one slope site.

Slope	Western branch	Central branch	Eastern branch
Paramesacanthion - 3.1	*Metacylicolaimus* - 12.3	*Metacylicolaimus* - 11.8	*Cylicolaimus* - 10.8
Micoletzkyia - 2.2	*Paramesacanthion* - 7.8	*Paramesacanthion* - 11.2	*Paramesacanthion* - 10.3
Oxystomina - 2.2	*Synonchus* - 3.8	*Anticoma* - 2.9	*Metacylicolaimus* - 6.8
Phanodermopsis -1.6	*Phanodermopsis* - 3.4	*Sphaerolaimus* - 2.6	*Phanodermopsis* - 3.5
Phanoderma - 1.1	*Micoletzkyia* - 1.9	*Synonchus* - 2.2	*Cephalanticoma* - 3.3
Cephalanticoma - 0.8	*Anticoma* - 1.3	*Cylicolaimus* - 1.5	Genus indet 1 - 1.9
Metalinhomoeus - 0.8	*Pierrickia* - 1.1	*Micoletzkyia* - 1.0	*Sphaerolaimus* - 1.9
Anticoma - 0.7	*Oncholaimus* - 1.0	*Paralinhomoeus* - 0.8	Genus indet. 4 - 1.8
Oncholaimellus - 0.4	*Eurystomina* - 0.9	*Pierrickia* - 0.8	*Micoletzkyia* - 1.5
Rhabdodemania - 0.4	*Cylicolaimus* - 0.9	Genus indet. 4 - 0.8	*Oxystomina* - 1.4

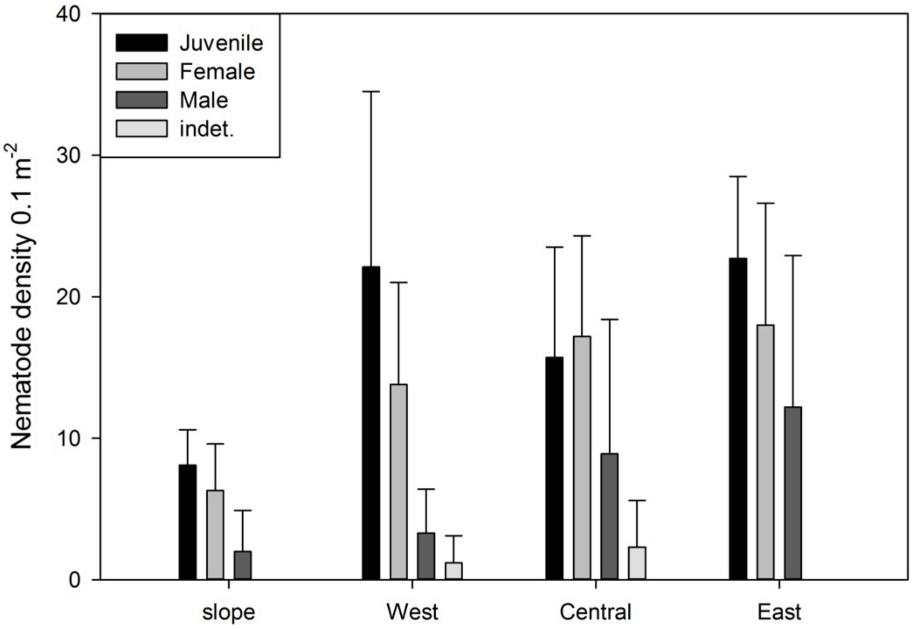


Figure 4.2 Nematode density and life stage at three canyon sites (Western, Central and Eastern branch) and slope site.
Error bars represent standard deviations.

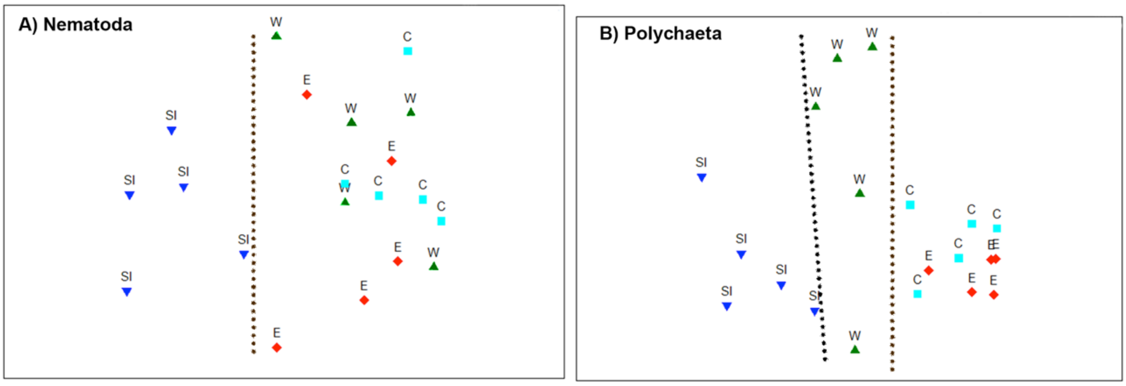


Figure 4.3 (A) Nematode and (B) polychaete genus MDS analysis from three canyon sites and slope site.

4.4.1.3 Nematode feeding types

There was a significant difference in percentage composition of feeding group 1A between sites (Moods Median test p = 0.015), all other feeding groups showed no significant difference across site. Nematodes in the canyon branches were predominantly (77 – 88 %) either epigrowth feeders (2A) or predators/scavengers/omnivores (2B) (Table 4.2). Group 2B were the most abundant group in the Central and Eastern branches, although their proportion decreased from the Eastern branch (> 50 % of all nematodes) to the Central (42 %) and Western (35 %) branch. Group 2A the most abundant group in the Western branch (45 % of large nematodes). Group 2B included *Cylicolaimus*, *Paramesacanthion* and *Metacylicolaimus,* all of which have a prominent buccal armature (Fig. 4.4). The slope fauna was characterised by relatively high numbers (40 %) of selective deposit feeders. Group 2B was also abundant (35%) at the slope site. Non-selective deposit feeders (1B), which included the genera *Pierrickia* and *Paralinhomoeus,* were consistently the least common group across all sites.

The MI, derived from c-p values, was highest at the slope and Western branch sites and lowest in the Central and Eastern branches (Table 4.2). The trophic diversity index indicated a higher trophic complexity on the Central branch compared with that on the slope site and in the Western and Eastern branches (Table 4.2). Trophic complexity was lowest at the Eastern branch site. This shift in trophic structure reflected an increased dominance of group 2B and a decrease in 1A (selective deposit feeders) in the Eastern branch.

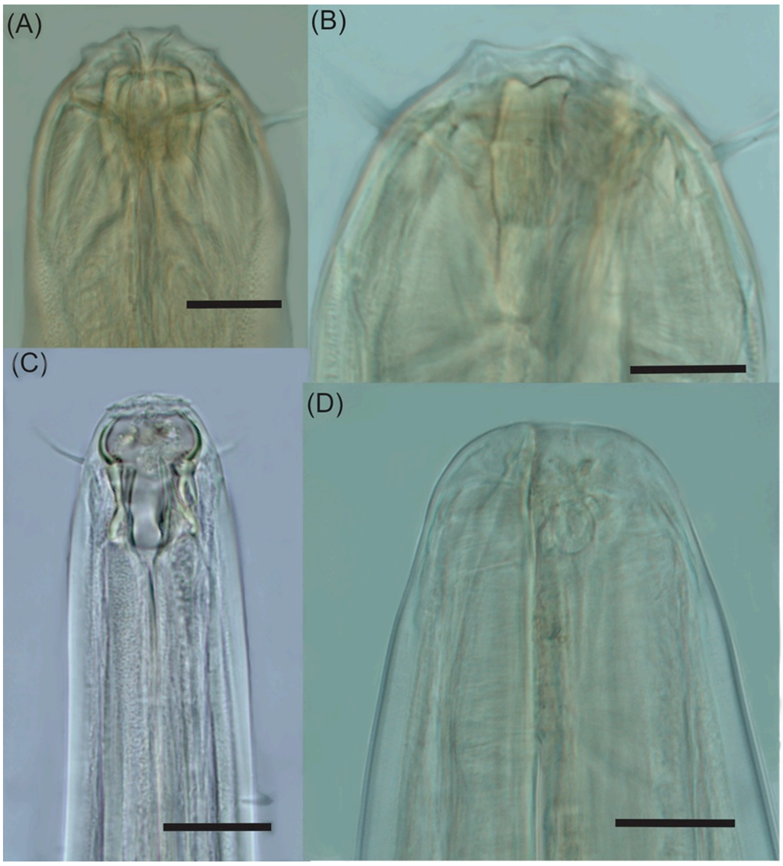


Figure 4.4 Nematodes with buccal armature. Scale bar 20 µm. (A) ***Mesacanthoides,*** **(B)** ***Cylicolaimus,*** **(C)** ***Eurystomina,*** **(D)** ***Synonchus*****.**

4.4.1.4 Nematode tail shape

There was a significant difference in the percentage composition of tail shape type 4, between sites (Moods Median Test, p = 0.034), all other tail shapes showed no significant difference between sites. Nematode tail-shape type 2 (clavate-conicocylindrical) was the most abundant, and type 4 (long) was the second most abundant, at all of the sites (Fig. 4.5). Within the canyon, the percentage of tail shape 4 (39 %) was higher in the Eastern branch than in the Central and Western branches (19 % in both cases). The slope site had a higher percentage of tail shape 3 (conical, 24 %) compared with that in the branch sites (average 10 %). Nematodes with tail-shape type 1 (rounded) were rare at all sites.

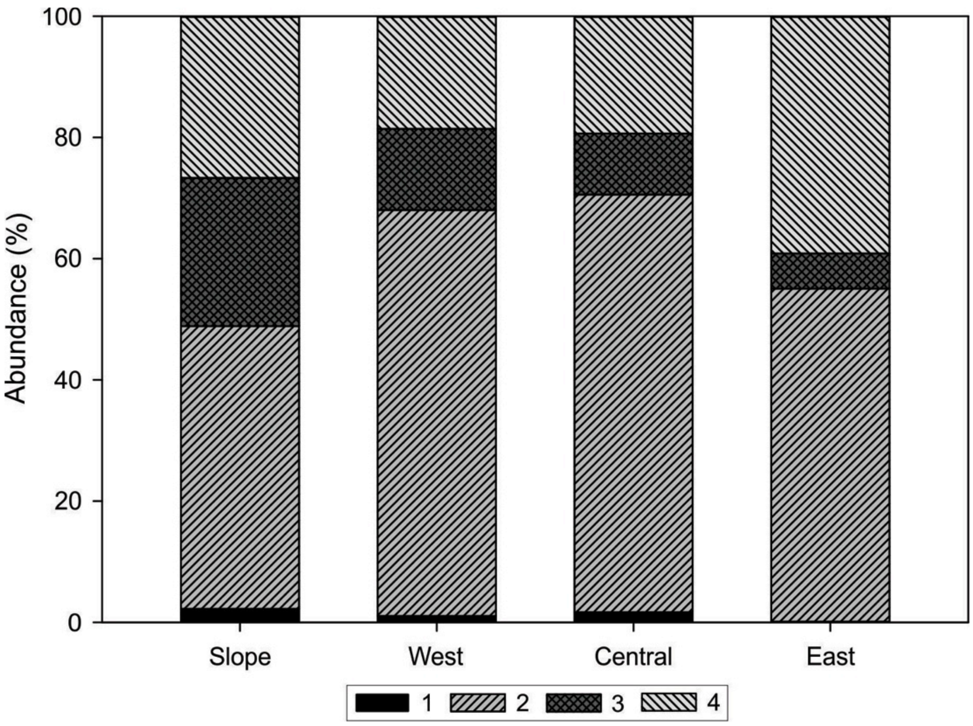


Figure 4.5 Percentage abundance of nematode tail shape.
According to Thistle et al.'s (1995) scheme at each of the four sites (three branch sites and one adjacent slope site). Type 1, "rounded"; type 2, "clavate-conicocylindrical"; type 3, "conical" and type 4, "long".

4.4.1.5 Nematode diversity

Within the canyon, the total number of genera recorded was similar in each branch (27, 28 and 25 for Western, Central and Eastern branches, respectively). When the number of individuals was rarefied, the slope had a higher number of expected genera than the canyon sites (Slope $E(G_{46}) = 19$, West $E(G_{46}) = 17$, Centre $E(G_{46}) = 16$ and East $E(G_{46}) = 15$) (Fig. 4.6A). The diversity indices show a similar trend, except for the Central branch site, which yielded the lowest values (Table 4.4).

Table 4.4 Nematode and polychaete genus diversity measures.
Nematode diversity measures rarefied to 46 individuals, polychaete measures rarefied to 318 individuals. G, number of genera. N, number of individuals. E(G), expected number of genera. F, Fisher's alpha. H´(log2) Shannon diversity index.

	G	N	$E(G_{46})$	F	H´(log2)	Shannon exp.	Simpson's inverse
Nematode							
Sl	19	46	19	12.1	2.59	13.4	10.1
W	27	100	17.2	10.2	2.34	10.5	7.0
C	28	124	16.4	9.1	2.21	9.3	6.0
E	25	140	15.4	8.4	2.32	10.3	7.6
Polychaete			$E(G_{318})$				
Sl	45	322	44.7	14.2	2.89	18.0	11.0

W	35	318	35.0	10.0	2.67	14.5	9.6
C	41	568	33.3	9.4	2.47	11.8	6.6
E	40	751	30.4	8.2	2.30	10.0	5.2

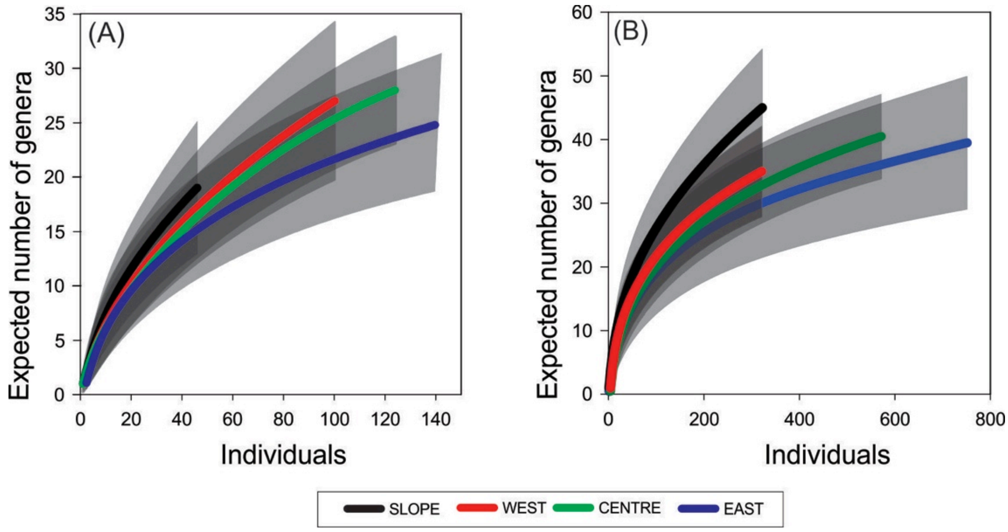


Figure 4.6 (A) Nematode genus richness and (B) polychaete genus richness at three canyon sites and one slope site.
95% confidence interval shown in grey.

4.4.2 Comparison of macrofaunal nematode and polychaete assemblages

An MDS analysis of polychaete genus-level data (Fig 4.3B) groups the Central and Eastern branches together, whereas the slope and Western branch sites were more distinct. A global ANOSIM based on polychaete genera revealed statistically significant differences between sites; all pair-wise tests were significant (p = 0.008). In terms of generic diversity, canyon branches had similar levels of rarefied polychaete genus richness (Fig. 4.6B). The Western branch samples yielded the highest diversity indices and the Eastern branch yielded the lowest (Table 4.4). The slope site had a slightly higher level of rarefied richness compared with the canyon sites. This pattern was also reflected in the polychaete diversity indices. Polychaete feeding modes changed across the study sites (Fig. 4.7A). The feeding mode ‘omnivorous’ changed significantly between sites (Mood’s Median test p = 0.015), feeding groups ‘microphage’ and ‘macrophage’ did not change significantly. The microphages were consistently the most abundant trophic group (> 50 % at each site), although their abundance slightly decreased from the slope (62%) to the Eastern branch (56 %). The omnivores increased slightly across site (slope 11 % to Eastern branch 19 %). The macrophage group were relatively consistent across site (25- 26 %). There was also a shift in polychaete motility modes (Fig. 4.7B). The motility mode ‘motile’ changed significantly between sites (Mood’s Median test p=

0.004), the motility groups 'discretely motile' and 'sessile' did not vary significantly. 'Motile' taxa were most abundant, increasing from the slope site (54 %) to the Eastern branch (78 %). The slope site had the highest relative abundance of 'discretely motile' polychaetes (32 %), a proportion that decreased to < 25 % inside the canyon branches.

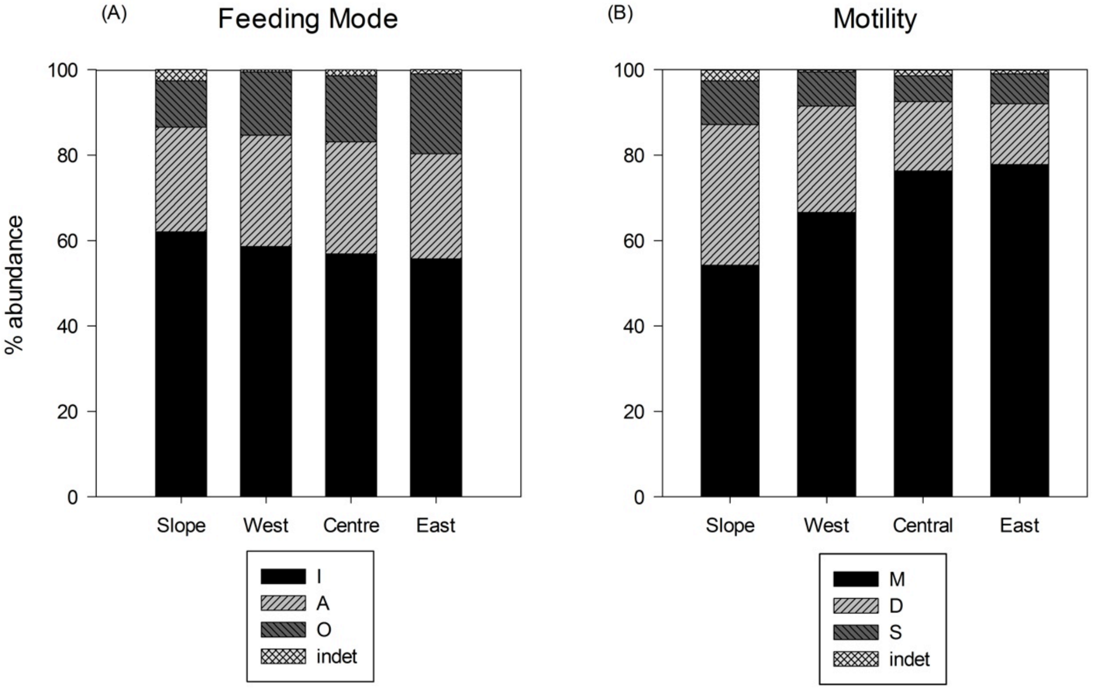


Figure 4.7 (A) Polychaete feeding mode (I = micro, A = macro, O = omnivore) and (B) polychaete motility (M = motile, D = discretely motile, S = sessile)

Across-site trends in generic diversity were similar for polychaetes and nematodes (Fig. 4.6). The Western branch had the highest diversity within the canyon, the Eastern branch the lowest, and the slope site had a higher diversity than any of the canyon branches. Polychaete feeding guilds and nematode feeding types displayed similar changes across the sites. Polychaete motility increased from the slope to the Eastern branch. A similar shift was seen in nematode tail shape, with the "long" tail shape being more abundant in the Eastern branch and the "rounded" shape more abundant on the slope. Patterns of generic composition were slightly different for polychaetes and nematodes. In the case of polychaetes, an MDS plot showed that the Western branch samples were distinct from those of the other canyon branches; whereas the canyon samples were intermingled for the nematode assemblages.

4.5 Discussion

4.5.1 Comparison with previous nematode studies

Although the occurrence of macrofaunal nematodes in deep-sea samples is fairly well documented, less is known about their taxonomic composition. Perhaps the most relevant genus-level study is that of Sharma et al. (2011), who described meio- and macrobenthic nematodes from the deep Arctic (Canada Basin), Gulf of Mexico (GOM) and Bermuda slope (212 - 3961 m depth). In the GOM, Sharma et al. (2011) concluded that the meio- and macrobenthic nematode assemblages were taxonomically distinct. In all three areas, the macrobenthic assemblages were dominated by *Enoploides*, *Crenopharynx*, *Micoletzkyia* and *Phanodermella*. In our material, *Enoploides* was absent while the other three genera were present only in relatively low numbers. The dominant genera in the Whittard Canyon, *Paramesacanthion* and *Metacylicolaimus,* were not abundant in Sharma et al.'s (2011) samples. *Sabatieria* and *Viscosia* were the dominant genera in a related study on macrobenthic nematodes from the Arctic deep sea (Canada Basin; 640-3848 m depth) (Sharma & Bluhm 2011). Again, these two genera were observed in the present study but were not abundant, while *Paramesacanthion* and *Metacylicolaimus* were not reported by Sharma & Bluhm (2011). These authors used a 250-μm mesh size, smaller than the mesh size used in the present study (500 μm). *Sabatieria* and *Viscosia* are generally smaller in size than *Paramesacanthion* and *Metacylicolaimus* and may have slipped through the larger mesh size used in the present study. Furthermore, *Sabateria* is often associated with fine (i.e. organic-rich) muddy sediments that are anoxic just below the surface (Vanreusel 1991; Vincx et al. 1990), however, sediment oxygen concentration was not measured in the present study, thus there is no evidence of anoxia in the case of sediments from 3500 m depth in the Whittard Canyon.

A few other studies have recognised macrofaunal nematode species, although in most cases these are undescribed. Dense aggregates of *Metacholaimus* sp. 1 were observed in a South Atlantic atoll by Netto et al. (1999). In the abyssal Indian Ocean (4500 - 5500 m depth), *Viscosia* sp. was the most abundant macrofaunal nematode species, followed by *Halalaimus* sp., *Dicholaimus* sp., *Polygastrophora* sp. and *Phanoderma* sp. (Pavithran et al. 2009). Two large nematodes, *Synonchus* cf *acuticaudata* and *Cylicolaimus* cf *magnus,* were abundant among macrofaunal species in coarse sediments adjacent to cold-water coral mounds in the Porcupine Seabight (NE Atlantic, ~ 900 m depth) (Henry & Roberts 2007). Interestingly, *Synonchus* and *Cylicolaimus* were among the top 10 genera at our study sites (Table 4.2). Henry & Roberts (2007) also list a species (*Metacylicolaimus* sp. 1) belonging to one of the dominant genera in our samples.

The macrofaunal nematode genera identified in the present study are different from those that are generally common in meiofaunal assemblages. Only four of the genera (*Sabatieria, Aegialoalaimus, Sphaerolaimus, Oxystomina*) listed by Pape et al. (2013) as dominant (> 3 %) at sites around the southern European Margin (Mediterranean and Iberian) are present in our collections. The most relevant comparative study is that of Ingels et al. (2011c) who analysed meiofaunal nematodes from 1160 and 762 m depth in the Whittard Canyon and at similar depths in the nearby Gollum Channel. Only three of the genera (*Syringolaimus, Sabateria* and *Cervonema*) reported as abundant in the Whittard Canyon by Ingels et al. (2011c) were found in our samples, and these were relatively uncommon. Conversely, Ingels et al. (2011c) recorded our two top-ranked genera, *Metacylicolaimus* and *Paramesacanthion,* but they were not abundant. The use of completely different sieve fractions (> 500 µm vs. > 32 µm) probably accounts for these faunal differences, but different sampling depths (3500 m this study vs. 762 and 1160 m Ingels et al. 2011b) may be an additional factor.

Similar size-related taxonomic differences occur in the case of Southern European canyons. The most abundant nematode genus found among the meiofauna in a group of Mediterranean canyons was *Sabatieria* (18 % mean abundance), with *Sphaerolaimus* ranked second (4.1 %) and *Synonchiella* (2.9 %) third (Soetaert & Heip 1995). *Paramesacanthion* was uncommon (0.6 %) and *Metacylicolaimus* was not reported. *Paramesacanthion* and *Metacylicolaimus,* are not listed among the dominant genera (> 3 %) between 3200 and 4500 m in the Cascais and Sebútal canyons (Ingels et al. 2011a), the dominant genus at all sites was *Acantholaimus* (> 13 %). *Metalinhomoeus* and *Sabatieria* were the dominant meiofaunal nematode genera in the Nazaré Canyon on the Iberian Margin (300 - 4970 m depth), *Paramesacanthion* and *Metacylicolaimus* were also present but were not among the most common genera (Garcia et al. 2007). Again, these differences most likely result from the use of much finer mesh size fractions compared with the present study. Most free-living meiobenthic marine nematodes span a body length range of 0.5 – 3 mm (Giere 2009), whereas in this study nematodes reached lengths of up to 13 mm. Mesh size is therefore likely to have a strong influence on the species that are recorded.

Little is known about the ecology of our two dominant genera, *Paramesacanthion* and *Metacylicolaimus.* As mentioned above, they are not among the common macrofaunal nematode genera listed by Sharma et al. (2011). The former was a moderately common component of the meiofaunal nematode assemblage at 4969 m in the Nazaré Canyon (Garcia et al. 2007) and, as also mentioned above, both genera occur occasionally in the meiofaunal material of Ingels at al. (2011b). A link to canyon environments is therefore possible. Soetaert and Heip (1995) note that some Mediterranean canyons are characterised by predatory nematodes, including *Paramesacanthion.*

4.5.2 Controls on densities of macrofauna-sized nematodes

Hunter et al. (2013b) counted, but did not identify, macrofaunal-sized nematodes at sites close to ours in the Eastern (3410 m depth) and Western (3595 m) branches of the Whittard Canyon, where they represented a higher proportion of the macrofauna in the Eastern (55 %, 487.2 ind. 0.1 m^{-2}) than in the Western (35 %, 164.6 ind. 0.1 m^{-2})(Hunter et al. 2013a). We also found that the Eastern branch had the highest relative and absolute abundances of macrofaunal-sized nematodes (15 %, 51.7 ind. 0.1 m^{-2}). The much lower abundances reported in the present study must reflect, to a large extent, the use of a 500-µm-mesh sieve compared with the 250-µm sieve used by Hunter et al. (2013a). These authors concluded that the high densities of nematodes and cirratulid and spionid polychaetes in the Eastern branch may indicate either organic-matter enrichment, oxygen limitation or disturbance of the sedimentary environment. They point out that this may be linked to the rocky substrata in the Eastern branch, which also hosted rich coral communities that were not evident in the Western branch. A link between large nematodes and organic enrichment is consistent with the conclusion of Vanreusel et al. (1995) that mean nematode body size is linked to food availability. They compared two abyssal sites in the NE Atlantic and found that the more eutrophic site on the Porcupine Abyssal Plain yielded a higher number of large nematodes than the oligotrophic site on the Madeira Abyssal Plain. Furthermore, nematodes made up 71% of the macrofaunal assemblage at a eutrophic site (5256 m) compared with 36 % at an oligotrophic site (4277 m) in the western North Pacific (Alevs et al. 2015). Bett and Moore (1988) reported high abundances of a very large (up to 20 mm), free-living nematode (*Pontonema alaeospicula)* at organically polluted sublittoral habitats off the Scottish coast (82 m depth). Fresh-water macrobenthic nematodes in an Italian river showed a strong preference for sediment with a small particle size enriched with organic matter (Bazzanti 2000). High numbers of macrofaunal nematodes (> 300 µm) were observed in the Baltimore Canyon (west Atlantic), this was linked to increased food availability inside the canyon (Bourque et al. 2015). More generally, high levels of organic enrichment are thought to result in dramatic increases in abundance of the largest species of meiobenthos, mainly nematodes in the family Oncholaimidae and harpacticoid copepods (Warwick et al. 1986).

4.5.3 Macrobenthic nematode morphological adaptions to canyon environments

Feeding type 2B (predators/omnivores/scavengers) nematodes, which were most abundant in the Whittard Canyon, are generally rare in deep-sea, meiobenthic assemblages (Jensen 1988, Thistle et al. 1995, Pape et al. 2013). The high abundance of group 2B in the present study reflected the relative abundance of the genus *Paramesacanthion.* This genus is most likely a predator feeding on nematodes, oligochaetes and other meiofauna (Moens & Vincx 1997). Pavithran et al. (2009) reported that predatory omnivores, dominated by *Viscosia* sp., *Polygastrophora* sp., and *Dolicholaimus* sp., made up 62 % of the macrobenthic nematode assemblage in the abyssal Indian Ocean. Omnivores/predators were also dominant among macrobenthic nematodes from an atoll in the South Atlantic (Netto et al. 1999). Sharma et al. (2011) noted a non-significant increase with depth in members of feeding group 2B, as well as group 1A (selective deposit feeders), as a proportion of the macrofaunal nematode assemblage. Feeding group 2B was represented by the families Oncholaimidae and Enchelidiidae in Sharma et al.'s (2011) study. These authors proposed that the increase with depth could be linked to decreased competition from other macrobenthic predators. This is unlikely to explain the trend observed in the present study as density of total macrofauna (Gunton et al. 2015a) and the polychaete feeding groups of macrophage and omnivores increased in parallel with nematode density across the sites.

Nematode feeding group 2B encompasses a range of feeding methods and possible food sources (Moens and Vincx, 1997). Warwick et al. (1986) suggested that in organically enriched settings, larger meiofaunal organisms that are generalist feeders will be more successful than smaller species with highly specialised feeding behaviours. The high abundance of group 2B in the Whittard Canyon is consistent with this idea. As mentioned above, predatory and scavenging nematodes were abundant in Mediterranean canyons. A relatively high abundance of meiobenthic group 2B nematodes was recorded inside the Nazaré Canyon compared with the open slope (Ingels et al. 2009), the large predatory nematodes also had high biomass values (Ingels et al. 2011b). Furthermore, Soetaert & Heip (1995) noted that more than 20 % of all meiobenthic nematodes in Mediterranean canyons belonged to group 2B. They linked the resulting increase in the density of higher trophic level nematodes (i.e., predators/omnivores/scavengers) inside the Mediterranean canyons, compared with the shelf, slope and abyssal regions, to an increased supply of organic matter in canyons and therefore an increased number of smaller nematodes on which the predatory species fed (Soetaert and Heip, 1995). Indeed, the relative proportion of nematode feeding groups depends on the type of available food (Danovaro & Gambi 2002) and a positive relationship exists between the biomass of predatory nematodes and of other nematode feeding groups (Danovaro & Gambi 2002). Thus, the abundance of predatory nematodes may be higher in organically enriched settings, such as canyon with higher densities of nematodes.

'Clavate-conicocylindrical' and 'long' were the most abundant tail shapes in the Whittard Canyon region. The Eastern branch samples yielded the highest proportion of long tail shapes. It has been suggested that long-tailed nematodes are disproportionately abundant in high-energy settings (Thistle & Sherman 1985). These authors speculated that individuals may use their tails to escape into deeper sediment layers in order to avoid resuspension by non-catastrophic erosive flows in hydrodynamically-active regions. Riemann (1974) observed that individuals with long flagelliform tails were able to anchor the tip of the tail with mucus from the caudal gland to sediment particles. This allowed them to move forward from the anchor by extending their tails, or to quickly pull the body into the sediment by coiling the tails. Long tails might also allow tube-dwelling nematodes to quickly retreat into their tubes if disturbed (Riemann 1974). Ingels et al. (2011b), suggested that large nematodes have a greater manoeuvrability than smaller ones, this may enhance their survival rate in disturbed environments such as canyons. Since the four tail shapes were designated by Thistle et al. (1995), only a handful of studies (Tita et al. 1999, Fleeger et al. 2006, Armenteros et al. 2009, Fleeger et al. 2010, Alves et al. 2014) have reported the presence of clavate-conicocylindrical tails in nematode assemblages, but none of these has linked this tail type to a particular ecological function. As in the case of the ‘long’ tail shape, the 'clavate-conicocylindrical’ tail shape may be used for anchorage in the sediment.

4.5.4 Macrofaunal nematode and polychaete assemblage trends

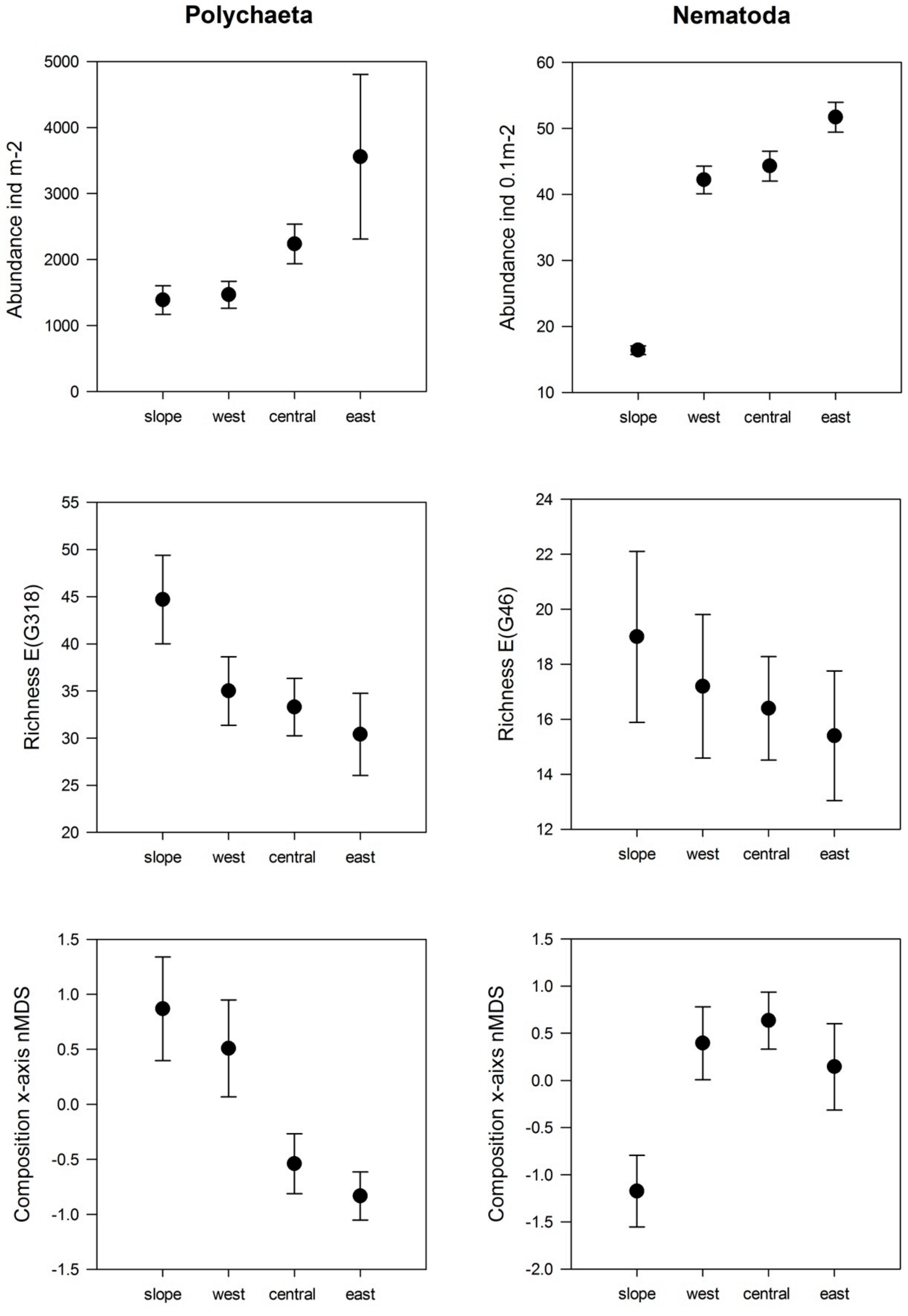


Figure 4.8 Relative variation in abundance, genus richness and faunal composition across site (adjacent slope, Western branch, Central branch, Eastern branch) between polychaete and nematode assemblages.

4.5.4.1 Life history traits

Polychaetes and nematodes display many biological and ecological differences (Table 4.5). Nematodes are generally small in size, have low mobility and undergo direct benthic development without a planktonic larval stage. Polychaetes are generally larger, more mobile than nematodes, and may have planktonic larvae leading to a high dispersal potential. Nematodes have a closer association with the sediment, as their motility is tightly coupled with the interstitial spaces in the sediment. They squirm through these spaces by pushing their body against the sediment particles (Gerlach 1954). Nematodes are considered to be poor swimmers, although passive transport of juvenile and adult nematodes via sediment resuspension and current flow events could play an important role in their dispersal (Thomas & Lana, 2011). Benthic polychaetes fall into several motility categories - motile, discretely motile or sessile (Jumars et al. 2015). Motile polychaetes either burrow through sediment, crawl over the sediment surface or swim. Sediment grain size has been shown to significantly affect nematode community composition (Heip et al. 1990, Vincx et al. 1990, Vanaverbeke et al. 2011). Grain size was significantly coarser at the slope site (mean particle size 71.8 μm) compared with the Whittard Canyon branches (Western 28.8 μm, Central 26.9 μm, Eastern 32.7 μm) (Gunton et al. 2015a). This factor may have a strong influence on the assemblage composition of nematodes.

4.5.4.2 Composition

The composition of the nematode assemblages inside the canyon was more consistent between sites than the polychaete assemblages, as is evident from the MDS analysis (Fig 4.3a) and ANOSIM pair-wise comparisons. Studies comparing meiofauna with macrofauna often report differences between the two size compartments. Meiofaunal nematode and macrofaunal assemblages both exhibited distinct changes in assemblage composition along an estuarine gradient in Portugal (Patricio et al. 2012). However, the meiofaunal nematode assemblages were more distinct between stations and were thought to be more affected by within-habitat physical variability than the macrofaunal assemblages. Schratzberger et al. (2008) report that macrofaunal polychaete assemblages displayed higher similarity than meiofaunal nematode assemblages between two sites, one in the Celtic Deep (c. 100 m) and one in the NW Irish Sea (c. 78 m). These authors concluded that species distribution patterns were likely to be strongly influenced by the dispersal and recruitment of species. Both macrofaunal polychaetes and meiofaunal nematodes displayed differences in community composition between fine- and coarse-grained sediment in the Belgian part of the North Sea (~ 20 m depth) (Vanaverbeke et al. 2011). Polychaete assemblages were more similar than nematode assemblages in coarser-grained sediments. Interestingly, the assemblage composition of polychaetes was more similar to that of nematodes than to any other macrofaunal taxon or to total macrofauna (Vanaverbeke et al. 2011). This may suggest that vermiform organisms respond in the same way to environmental changes.

Physical disturbance can influence the taxonomic composition of meio- and macrofauna to different extents (Austen & Widdicombe 2006). Meiofauna may be more resiliant to physical disturbance and sediment reworking than macrofauna. Macrofauna and meiofauna (total metazoan meiofauna and nematode) assemblages displayed distinct community composition patterns between sites in Hamilton Harbour, Bermuda (water depth 10 ± 1m)(Warwick et al. 1990). The macrofaunal assemblages exhibited depressed diversity at two stations close to a major shipping lane whereas the meiofaunal assemblages did not show a depression in diversity. These authors concluded that physical disturbance of sediment particles impacted the macrofaunal assemblages more than the meiofaunal assemblages. Along a pollution gradient in Portugal, the meiofaunal community displayed a gradient in community composition, however, the macrofaunal community did not (Austen et al. 1989). These authors concluded that macrofauna were influenced more by sediment disturbance than the pollution gradient. The fact that polychaete community composition differed more than nematode composition between the Whittard Canyon branches may reflect sediment instability inside the canyon. However, the magnitude and frequency of disturbance between branches of the Whittard Canyon is poorly understood and further information is needed to support this speculation.

Table 4.5 Comparison life history for free living marine nematodes and polychaetes

Life History Trait	Nematodes	Polychaetes
Body plan	Long and slender. Simple structure consisting of two concentric tubes (Heip et al 1986) a surrounding cuticle, setae and a tail.	Diverse reflecting habits and habitat.
Motility	Move through interstitial spaces of sediment particles in a snake-like, writhing motion performed at relatively high speed (Cullen 1973). Tails can be used as anchors enabling them to extend into the sediment and then quickly retract (Riemann 1974)	Burrowers in mud and sand, some dig continuously through sediment others live in permanent burrows or tubes (Beesley et al 2000). Fleshy protrusions (parapoida) on side of body act as locomotion and anchorage.
Feeding mode	Selective feeders, which are able to selectively differentiate between prey organisms as small as bacteria (Moens et al 1997). Bacteria appear to be the main nutritive source in the deep sea for nematodes (Giere,	An array of feeding methods: raptorial feeding, non-selective deposit-feeders, selective deposit-feeders, filter- feeders (Beesley et al. 2000).

	2009).	
Reproduction	Bisexual amphimixis. Adult females produce 10- 50 eggs (Giere, 2009).	Sexual and asexual (Beesley et al. 2000). Typically dioecious but many species are hermaphroditic (Beesley et al. 2000). Polychaetes spawn after fertilization.
Development	Direct development. Juveniles undergo four moults before reaching maturity (Giere, 2009).	Free-swimming larval trochophore stage may be produced or a brooded larval stage, which develops directly into a juvenile
Generation time	Short, 13- 60 days or less (Giere, 2009)	Few weeks to several years

4.5.4.3 Density

Despite differences in the life-history characteristics of polychaetes and nematodes, this study shows that these taxa display many of the same across-site trends (Figure 4.8). For both taxa, density increased from the adjacent continental slope to inside the canyon, consistent with the trend in total macrofaunal density in the same samples (Gunton et al. 2015a). As far as we are aware, faunal trends between macrobenthic nematodes and polychaetes have never been compared directly, although there are some previous studies comparing macrofauna and meiofauna in which nematodes were included in both size fractions (Netto et al. 1999, Renaud et al. 2006, Sharma et al. 2011, Baldrighi & Manini 2015). In one such study, Baldrighi & Manini (2015) reported a significant eastward decrease in the density of both meio- and macrofauna from six continental slope areas in the Mediterranean Sea (1200 – 2800 m water depth). They suggested that this reflected a similar response to decreasing food inputs. The abundance of these two groups was believed to be influenced by different environmental factors; the macrofauna (polychaetes and nematodes) by organic matter quality and sediment grain size and the meiofauna (nematodes) by Particulate Organic Carbon (POC) flux (Baldrighi & Manini 2015). The POC flux derived from surface production is unlikely to have an effect on nematode density at the relatively small spatial scale of the present study. Instead, enhanced organic matter enrichment inside the Whittard Canyon environment is the most likely explanation for the increased density for both polychaetes and nematodes (Duineveld et al. 2001, Gunton et al. 2015a).

4.5.4.4 Diversity

Macrofaunal nematodes and polychaetes displayed similar diversity patterns, in contrast to previous studies in which environmental factors controlling diversity patterns are considered to be both locality and taxon specific (Wei et al. 2010a, Carvalho et al. 2013). In agreement with the present study, however, Baldrighi and Manini (2015) report a positive relationship between the diversity of macrofauna and meiofauna, as well as between macro- and meiofaunal nematodes, and between meiofaunal nematodes and macrofaunal polychaetes. Deep-sea benthic nematode diversity is thought to be linked to the diversity of other benthic components including the macrofauna (Levin et al 2001) and foraminifera (Gooday et al. 1998). Benthic macrofauna affects the meiobenthos through direct predation, non-selective feeding, competition for food sources and biological disturbance (Olafsson 2003, Nascimento et al. 2011). Macrobenthic polychaetes have been shown to influence the species diversity of meiofauna, both positively and negatively, through the formation of burrows, mud balls and sediment disturbance (Olafsson et al, 1990; Olafsson 2003). Ingels et al. (2014) observed a change in nematode community structure after manipulation of macrofaunal density and composition in a mesocosm experiment. The effect on nematode structure was generally a result of the reduction in the abundance of a few dominant nematode species. This was dependent on the macrofaunal species included in the experiment and on whether low or high density macrofaunal treatments were considered (Ingels et al. 2014). In a similar mesocosm experiment, nematode alpha and beta diversity were affected differently by differing disturbance intensities (low, medium and high) caused by the bivalves *Nuculoma tenuis* and *Abra alba* and the urchin *Brissopsis lyrifera* (Austen et al. 1998). Additionally, the meiofauna may affect the macrofaunal diversity through predation on macrofaunal larvae (Watzin 1983). These kinds of interaction may take place between macrofaunal nematodes and polychaetes inside the Whittard Canyon; although the precise mechanisms by which these taxa influence each other are not known. There is present study yielded insufficient data to determine whether diversity is influenced more by taxa present or by environmental factors.

4.5.4.5 Trophic structure

Macrobenthic nematodes and polychaetes exhibited a similar shift in trophic structure across sites (Fig 4.9). The increase in predator/omnivore (group 2B) nematodes coincided with the increase in macrophage and omnivore polychaetes inside the canyon. Baldrighi & Manini (2015) reported that the trophic structure of macrobenthic nematodes and polychaetes, exhibited a significant change on the continental slope across the west and east Mediterranean basins, the change of polychaete trophic structure mirrored that of the macrofauna as a whole, whilst the change of the nematode trophic structure was more variable and did not follow the same pattern. Nevertheless, similar to the present study, the percentage of carnivores/scavengers/predators increased for both groups in the central-eastern basin. This may indicate that macrofaunal polychaetes and nematodes display similar functional shifts to certain environmental conditions.

In summary, the present study suggests that macrofaunal nematodes may be an important part of the macrofaunal assemblage and the role of these nematodes in deep-sea benthic communities should not be overlooked.

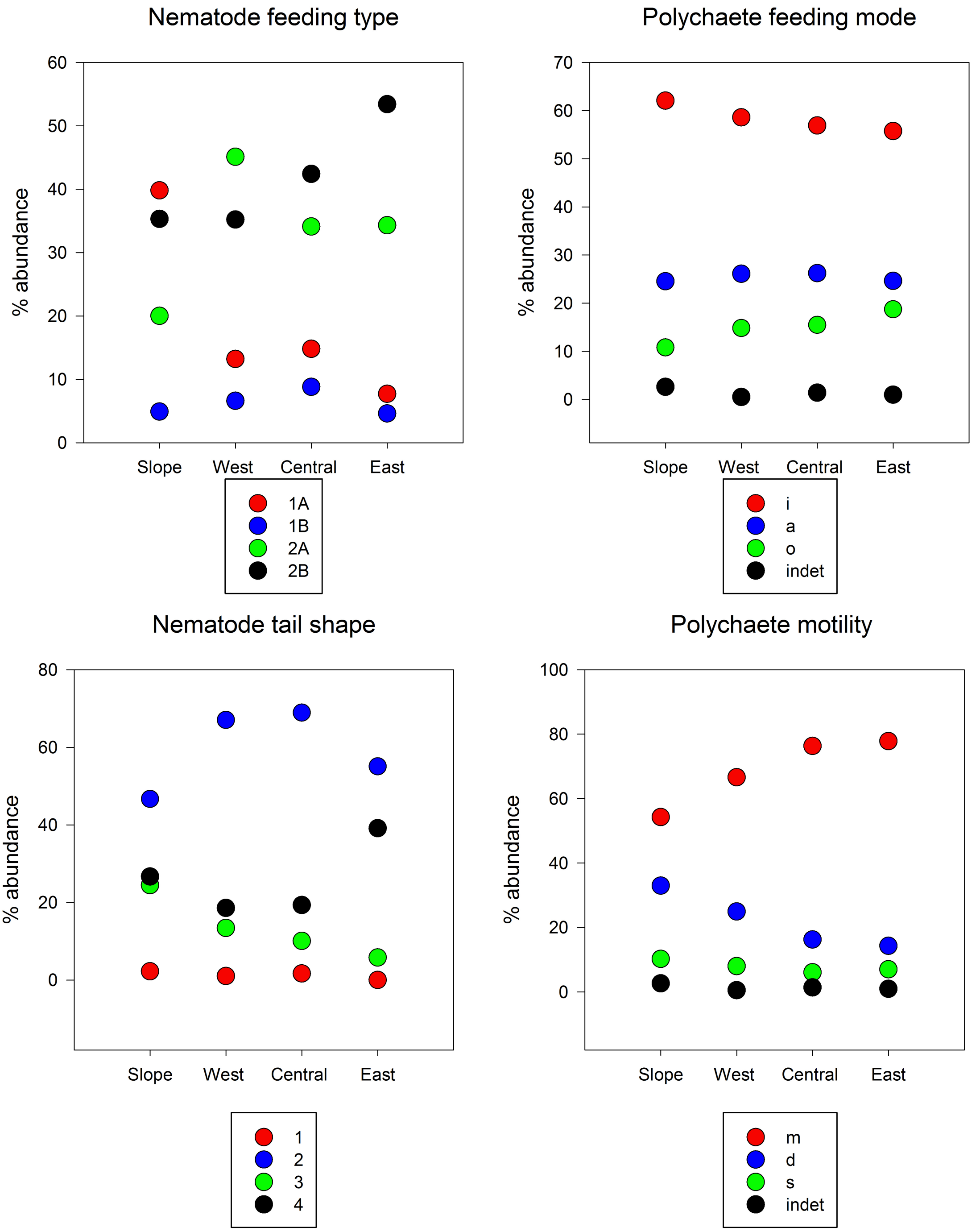


Figure 4.9 Macrofaunal nematode and polychaete functional group assemblage trends
Nematode feeding type (1A = selective deposit feeder, 1B = non-selective deposit feeder, 2A = epigrowth feeder, 2B= predator/scavenger). Nematode tail shape (1 = rounded, 2= clavate-conicocylinfrical, 3= conical, 4 = long). Polychaete feeding mode (i = micro, a = macro, o = omnivore). Polychaete motility (m = motile, d = discretely motile, s = sessile)

Chapter 5: Conclusions and future directions

5.1 Limitations of study

This study provided new information on the ecology of macrofauna inside the Whittard Canyon, and in particular on faunal differences between the different branches of this topographically complex feature. However, many gaps remain in our knowledge of submarine canyon ecosystems, reflecting the inaccessibility of deep-sea canyon habitats and the difficulty of sampling their faunas. One major limitation in the present study was that only soft-sediment environments were sampled within a narrow depth range (3373-3670 m). The Whittard Canyon as a whole spans a total depth range of 200 to > 4000 m and encompasses many different habitats such as rocky outcrops, steep vertical walls and cold-water corals (Huvenne et al. 2011, Robert et al. 2014). The macrofauna inhabiting these hard-substrate habitats were not studied, which inevitably resulted in an underestimation of faunal diversity within the canyon.

With regard to sample design, three canyon sites were sampled compared with one slope site. It may have been better to have sampled an additional two slope sites to the west of the canyon and three slope sites to the east of the canyon. The slope site was relatively close to the canyon and possibly influenced by canyon-related processes, such as sediment deposition from mud-rich flows spilling over the canyon walls (Cunningham et al. 2005). There was limited environmental data available from the study sites, especially the open slope site. Previous studies on the Whittard Canyon have only reported environmental data for the shallower regions (Ingels et al. 2011c) or different parts of the canyon (Duineveld et al. 2001, Duros et al. 2011, Huvenne et al. 2011, Amaro et al. 2015). In order to interpret the macrofaunal patterns it would have been helpful to have had sediment data, such as pore water oxygen concentrations, total nitrogen content, total organic carbon content, phytopigments (e.g. chlorophyll-a), and lipid concentration and composition, as well as more samples for grain size analyses, bottom current speed data and seafloor photographs of the areas where Megacorer samples were taken.

The molecular analysis (Appendix II) was limited by the number of specimens and the sites that they were collected from. Megacore samples recovered on JC036 were preserved in formalin, which prevented any molecular analyses being carried out on them. For this reason, samples for the molecular analysis were collected opportunistically on four different sampling campaigns to the Whittard Canyon and nearby Goban Spur (RV *Belgica* cruise ST1217, RRS *Discovery* cruise 377, RRS *James Cook* cruise 076T and RV *Celtic Explorer* cruise 12006). As there was no opportunity to return to the main sampling area (~ 3500 m), the molecular samples were recovered from shallower regions in the canyon (375 - 1670 m). As a result a comparison of morphological and molecular diversity could not be carried out. This prevented investigation, for example, of cryptic speciation among the polychaetes, similar to that reported by e.g. Wiklund et al. (2009) from a whale-fall in Sweden and sediment samples beneath a fish farm in Norway, where a new cryptic species of chrysopetalid was recorded. In addition, the lack of species overlap between the limited molecular samples and the large sample set from deeper water precluded studies of genetic connectivity between the Whittard Canyon branches.

5.2 Main Conclusions

The overall purpose of this project was to investigate differences in macrofaunal abundance, composition and diversity between different branches of the Whittard Canyon and the adjacent slope.

In Chapter 2, I concluded that, at around 3500 m water depth, the Whittard Canyon (1) has relatively high macrofaunal abundance compared with the adjacent slope, (2) has a distinct macrofaunal assemblage composition at the higher taxon level, and (3) encompasses distinct within-canyon heterogeneity in the form of faunal differences between the canyon branches. These results are consistent with those obtained during previous studies of the metazoan meiofauna and foraminifera (Ingels et al. 2011c, Duros et al. 2012). Within-canyon heterogeneity is probably explained by a combination of variable organic enrichment and hydrodynamic activity, both of which can be influenced by the topographic profile of individual canyon branches.

In Chapter 3, I showed that polychaete species richness and diversity indices were higher on the slope compared with the canyon, and that the slope site had higher species evenness. Within the canyon, species diversity between branches was broadly similar. Despite depressed diversity within the canyon compared with the adjacent slope, the fact that 46 of the 99 polychaete species found in the Whittard Canyon were not present on the adjacent slope suggests that this feature may enhance the regional species pool. However, sampling effort on the adjacent slope was insufficient to fully test this observation.

In Chapter 4, I analysed the assemblage characteristics of macrofauna-sized nematodes (i.e. those retained on a 500-µm mesh) and compared them with those of polychaetes from the same sieve fractions. I concluded that nematode diversity was similar between canyon branches but lower inside the canyon compared with the open slope. An MDS ordination based on nematode genera revealed that all three canyon sites grouped together while the slope site was distinct. Nematode feeding group 1A (selective deposit feeders) represented 40 % of individuals at the slope site while type 2B (predators/scavengers/omnivores) represented 44 % inside the canyon. Polychaete diversity displayed the same pattern as nematode diversity. Polychaete functional guilds also displayed a similar across-site shift to that of the nematodes, suggesting that the two taxa were responding in a similar fashion to environmental factors. However, in contrast to the nematodes, an MDS plot of polychaete genera distinguished the Western branch from the other canyon sites. In the case of the nematodes, there were no significant differences in the branches. These contrasting patterns may reflect the different life history traits of nematodes and polychaetes and the potential closer association of nematodes with the sediment.

The overall conclusion of the project was that the benthic fauna varies not only between canyon and slope environments but also between branches of the Whittard Canyon. This is attributed to varied environmental conditions among the canyon branches.

5.3 Hypotheses revisited:

- The Whittard Canyon is an area of increased faunal abundance compared with the adjacent slope as a result of suspected organic matter trapping and channelling inside the canyon. **Hypothesis is supported.** *Significantly higher macrofaunal abundance was found in the canyon compared with the adjacent open slope, this is most likely the result of organic enrichment of sediments inside the canyon.*
- The Whittard Canyon harbours a distinct macrofaunal assemblage compared with the adjacent continental slope as a result of suspected variant physical environmental conditions inside the canyon. **Hypothesis is supported.** *Macrofauna higher taxa, polychaete species and nematode genera composition differed inside the canyon compared with the open slope. This likely resulted from differing environmental characteristics inside the canyon compared with the adjacent slope. Indeed, after performing a BIOENV test in Primer, the environmental variables, depth and clay % (correlation coefficient = 0.684, p = 0.01) best explained the patterns in the polychaete species community composition.*
- The Whittard Canyon is an area of depressed alpha diversity compared with the adjacent slope as a result of suspected increased ‘disturbance’ levels inside the canyon. **Hypothesis is partially supported.** *Polychaete species and nematode genus alpha diversity was lower inside the canyon compared with the open slope (and the slope site*

had a higher evenness). However, it could not be directly confirmed whether this was the result of increased levels of physical disturbance (insufficient environmental data).

- The Whittard Canyon acts to increase regional macrofaunal diversity along the continental margin by increased species turnover as a result of suspected enhanced habitat variation and potential canyon endemics. **Hypothesis is partially supported.** *Although alpha diversity was depressed inside the canyon compared with the adjacent slope, forty-six polychaete species recorded in the canyon were not found on the open slope, suggesting that the canyon may add species to the regional species pool. However, limited sample size precludes identification of true canyon endemics.*
- Polychaete and nematode assemblages exhibit different trends in composition and structure inside the Whittard Canyon and on the adjacent slope as a result of their different ecologies. **Hypothesis partially supported.** *Abundance, diversity and functional group traits displayed the same patterns for both polychaetes and nematodes inside the Whittard Canyon and on the adjacent slope. However, community composition patterns differed between polychaete and nematodes. Differences may have resulted from the different life history traits of the two taxa.*

5.4 The Whittard Canyon in Context

5.4.1 Regional Scale

To compare Whittard Canyon species diversity with other sites in the NE Atlantic, I compiled published estimates of polychaete species richness at canyon and abyssal plain sites in the NE Atlantic (Table 5.1). Rarefaction analysis of these published results revealed a broad range in local diversity (species richness) at these sites, with ES(119) values ranging from 17 to 54 (Table 5.1, Fig. 5.1). The highest species richness was recorded at the EUMELI oligotrophic site (Cape Verde Abyssal Plain) and the lowest in the Nazaré Canyon (3400m). In general, polychaete species richness appears to be depressed at canyon sites compared with abyssal plain sites (Fig. 5.1). However, the Whittard Canyon branches (Western, Central and Eastern) have only slightly lower species richness than the Madeira Abyssal Plain (MAP) and Tagus Abyssal Plain (TAP) sites. This pattern of depressed diversity at bathyal canyons sites compared with abyssal plain sites in the NE Atlantic contradicts the parabolic relationship of alpha diversity with depth in deep-sea soft sediments, as reported in other studies (Rex 1981, Rex 1983, Etter & Grassle 1992, Levin et al. 2001, Rex & Etter 2010, Paterson & Lambshead 1995). This comparison must be treated with caution as different sampling apparatus were used for the different studies. Samples from abyssal plain sites were collected using a box corer whereas the canyon samples were collected using a Megacorer. A box core collects a larger surface area of sediment and also produces a bow wave (see chapter 2), which will influence the estimated species richness through the removal of surface-dwelling organisms.

Paterson et al. (2011) used a Dynamic Equilibrium Model (DEM) to understand patterns of polychaete species richness inside Iberian Margin canyons. The DEM predicts species richness based on the interaction of productivity and disturbance levels (Kondoh 2001, Kadmon & Benjamini 2006, Svensson et al. 2007). The 3400-m Whittard Canyon samples yielded similar levels of species richness to the Cascais Canyon ($E[S_{119}] = 33$ and 38, respectively) (Figure 5.1, Table 5.1). Paterson et al. (2011) suggested that species richness recorded from the middle section (3400 m) of the Cascais Canyon was high because disturbance and productivity were at optimal levels (i.e. quite high), which resulted in maximal species richness. This may also be true for the Whittard Canyon. Abyssal plain sites are characterised by low levels of disturbance (i.e. low current speeds) (Table 5.1). No comparable productivity data are available for the abyssal plain and canyon sites, however, according to the DEM at lower levels of disturbance, lower levels of productivity are needed to reach maximum species richness. Indeed, one would expect lower food availability at abyssal plain sites compared with canyons due to their greater depth and distance from land. The DEM predicts a positive relationship between disturbance and diversity when productivity is high (Kondoh 2001). Reduced richness at canyon sites suggests that productivity levels are not high enough to balance disturbance levels. Species richness does not always follow model predictions (Svensson et al. 2007) and this interpretation suffers from a lack of productivity data. Nevertheless, the DEM is useful for understanding patterns of polychaete assemblage structure at contrasting sites (Paterson et al. 2011).

Table 5.1 Comparison of polychaete species richness from different deep-sea sites.

MAP-Maderia Abyssal Plain, PAP-Porcupine Abyssal Plain, EUMELI- EUMELI oligotrophic site, TAP- Tagus Abyssal Plain, WWC-Western branch Whittard Canyon, CWC-Central branch Whittard Canyon, EWC-Eastern branch Whittard Canyon, WSl-Whittard Canyon adjacent slope, NC-Nazaré Canyon, CC-Cascais Canyon, SC-Setubal Canyon. BC-Box core, MC- Megacore. D- density individuals m^{-2}. Species diversity $E[S_{119}]$ estimated using EstimatesS.

Site	Area Atlantic	Sample No.	Location (centred on)	Depth (m)	Gear	$E[S_{119}]$	D	Current speed
MAP[a]	N	5	31°N 21°W	4900	BC	42.00	70	7.5 cm s^{-1}
PAP[a]	NE	5	48°N 16°W	4800	BC	51.31	342	3.5 cm s^{-1}[d]
EUMELI[a]	N	8	20°N 30°W	4600	BC	53.65	143	3 cm s^{-1}
TAP[a]	N	6	38°N 11°W	5035	BC	44.44	258	low
WSl[b]	NE	5	47°N 10°W	3500	MC	37.01	1148	-
WWC[b]	NE	5	48°N 10°W	3500	MC	32.93	1268	16 cm s^{-1}[e]
CWC[b]	NE	5	48°N 10°W	3500	MC	33.98	1990	16 cm s^{-1}[e]
EWC[b]	NE	5	48°N 10°W	3500	MC	33.19	3191	16 cm s^{-1}[e]
NC[c]	NE	5	39°N 09°W	3400	MC	17.00	1257	25-35 cm s^{-1}[f]
CC[c]	NE	4	38°N 09°W	3400	MC	38.08	422	-
SC[c]	NE	5	38°N 09°W	3400	MC	20.00	1558	Max 25 cm s^{-1}[g]

[a] Glover et al. (2002), [b] This study, [c] Paterson et al. (2011), [d] Reid and Hamilton (1990), [e] Vangriesheim et al. (2001), [f] de Stigter et al. (2007), [g] de Stigter original data in Paterson et al. (2011)

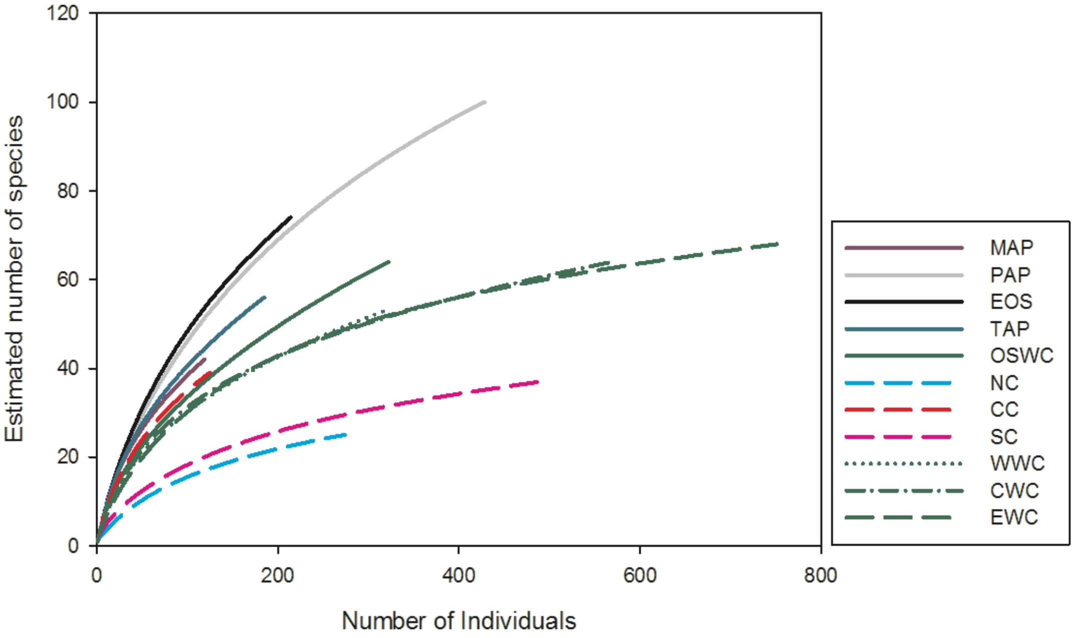


Figure 5.1 Polychaete species diversity in the NE Atlantic.
Rarefaction curves at abyssal plain sites; MAP- Maderia Abyssal Plain, PAP- Porcupine Abyssal Plain, EOS-EUMELI oligotrophic site and TAP- Tagus Abyssal Plain. Bathyal slope site; OSWC- open slope Whittard Canyon. Canyon sites; NC- Nazaré canyon, CC- Cascais Canyon, SC-Setúbal Canyon, WC- Whittard Canyon (W-western, C-central and E-eastern branches).

Based on a comparison of species lists from the Whittard Canyon and the adjacent abyssal plain site (PAP), *Aurospio dibranchiata* was the only species common to both areas. In addition, the unnamed opportunistic juvenile opheliid recorded at the PAP site (Vanreusel et al. 2001, Soto et al. 2010) was also observed in the Whittard Canyon (Chapter 2). These findings suggest that there is some connection between the bathyal Whittard Canyon and abyssal PAP populations. However, only three species (*Ceratocephale abyssorum, Aricidea* cf. *neosuecica* and *Aurospio dibranchiate*) at the PAP site could be assigned Latin binomial names, making it difficult to establish how many species are shared between the two sites.

5.4.2 Conservation

The Whittard Canyon is an area of potential importance in terms of conservation. Submarine canyons, in general, may be biodiversity "hotspots" (Vetter 1994, De Leo et al. 2010), harbour unique biological assemblages (Davies et al. 2014), act as nursery grounds for fish larvae (Stefanescu et al. 1994) and are important feeding areas for cetaceans and seabirds (Würtz 2012). Canyons may also encompass Vulnerable Marine Ecosystems (VME) that are vulnerable to fishing activity (FOA 2008). Adjacent to the Whittard Canyon, in the Explorer and Dangeard canyons, four megabenthic assemblages were classified by Davies et al. (2014) as VMEs according to the guidelines put forward by FAO (FOA 2008) and OSPAR (OSPAR (Agreement 2008-6)). Three of these assemblages were cold-water coral reefs and one was a 'sea pen and burrowing megafauna community'. Cold-water coral mini-mounds, which are of ecological and conservation interest, have also been observed in these canyons (Stewart et al. 2014). Cold-water corals have been well documented in the Whittard Canyon (Huvenne et al. 2011, Morris et al. 2013, Robert et al. 2014). Mapping these megabenthic assemblages inside canyons is critical for designing effective Marine Protected Areas (Schlacher et al. 2007, Davies et al. 2014, Robert et al. 2014). Although the main canyon study sites in this thesis were all areas of soft-sediment and did not have any characteristics of VMEs, some macrofaunal species found inside the canyon were not present on the adjacent slope. Deeper canyon areas do appear to harbour macrofaunal assemblages distinct from the open slope, this should be taken into account when planning Marine Protected Areas.

5.5 Future Challenges

This research builds on the HERMES and HERMIONE projects, but there is still much more to learn about the Whittard Canyon, and submarine canyon habitats generally. The Whittard Canyon is a relatively well-studied canyon compared with other canyons in the wider region

(Table 5.2). Out of the 116 named canyons on the Iberian Peninsula, Celtic Sea and Western Mediterranean only 21 have been locations for benthic faunal studies. This highlights the lack of benthic sampling inside canyons.

Table 5.2 Benthic faunal ecological studies on submarine canyons in the NE Atlantic and western Mediterranean, using canyons listed in De Leo et al. (2014).

Canyon	Area	Faunal component studied	References
Nazaré	Iberian Peninsula	Foraminifera Metazoan meiofauna, Macrofauna, Megafauna	(Garcia et al. 2007, King et al. 2008, Danovaro et al. 2009, Ingels et al. 2009, Amaro et al. 2010, Bianchelli et al. 2010, Nardelli et al. 2010, Cunha et al. 2011, Gooday et al. 2011, Ingels et al. 2011b, Paterson et al. 2011, Duffy et al. 2012, Ingels & Vanreusel 2013, Ramalho et al. 2014)
Setúbal	Iberian Peninsula	Meiofauna, Macrofauna	(Cunha et al. 2011, Ingels et al. 2011a, Paterson et al. 2011, Duffy et al. 2012)
Cascais	Iberian Peninsula	Foraminifera, Macrofauna, Metazoan meiofauna	(Danovaro et al. 2009, Bianchelli et al. 2010, Nardelli et al. 2010, Cunha et al. 2011, Ingels et al. 2011a, Paterson et al. 2011, Duffy et al. 2012)
Cap-Breton	Iberian Peninsula	Foraminifera, Meiofauna	(Rallo et al. 1994, Pascual et al. 2008, Bolliet et al. 2014)
Cap-Ferret	Iberian Peninsula	Foraminifera, Macrofauna	(Dauvin et al. 1996, Sorbe 1999, Fontanier et al. 2005, Duros et al. 2014)
26 named canyons [a]	Iberian Peninsula	None studied	
Whittard	Celtic Sea	Foraminifera, Metazoan meiofauna, Macrofauna, Megafauna	(Duineveld et al. 2001, Duros et al. 2011, Ingels et al. 2011c, Duros et al. 2012, Tchesunov et al. 2012, Morris et al. 2013, Gunton et al. 2015a) (Huvenne et al. 2011, Hunter et al. 2013a, Robert et al. 2014, Amaro et al. 2015) (Ingels & Vanreusel 2013, Johnson et al. 2013)
4 named canyons [b]	Celtic Sea	None studied	
Cap de Creus/Sete	Catalan Margin,	Foraminifera,	(Danovaro et al. 2009,

	Mediterranean Sea	Metazoan meiofauna, Megafauna	Orejas et al. 2009, Bianchelli et al. 2010, Company et al. 2012, Contreras-Rosales et al. 2012, Gori et al. 2013, Pusceddu et al. 2013)
Blanes	West Mediterranean	megafauna	(Ramirez-Llodra et al. 2010b)
Palamos (La Fonera)	West Mediterranean	megafauna	(Pagès et al. 2007, Company et al. 2012)
Lacaze-Duthiers	West Mediterranean	Metazoan meiofauna, Megafauna,	(Danovaro et al. 2009, Bianchelli et al. 2010, Gori et al. 2013, Pusceddu et al. 2013, Fabri et al. 2014)
Marti	West Mediterranean	megafauna	(Fabri et al. 2014)
Se`te	West Mediterranean	megafauna	(Fabri et al. 2014)
Montpellier	West Mediterranean	megafauna	(Fabri et al. 2014)
Petit Rhone	West Mediterranean	Foraminifera, Metazoan meiofauna Megafauna	(de Bovée et al. 1990, Fontanier et al. 2008b, Fabri et al. 2014)
Grand Rhone	West Mediterranean	Foraminifera	(Fontanier et al. 2008b, Fabri et al. 2014)
Marseille	West Mediterranean	Megafauna	(Fabri et al. 2014)
Cassis	West Mediterranean	Foraminifera, Metazoan meiofauna, Megafauna	(Soetaert & Heip 1995, Fontanier et al. 2012, Fabri et al. 2014)
Stoechades	West Mediterranean	Megafauna	(Fabri et al. 2014)
Saint-Tropez	West Mediterranean	Foraminifera, Megafauna	(Fontanier et al. 2008a, Fabri et al. 2014)
Var	West Mediterranean	Metazoan meiofauna, Megafauna	(Fabri et al. 2014, Guidi-Guilvard & Dallot 2014)
Calvi	West Mediterranean	Metazoan meiofauna	(Soetaert et al. 1991)
64 named canyons [c]	West Mediterranean	None studied	

5.5.1 Total Canyon Diversity

Concerning the Whittard Canyon itself, it would be valuable to sample additional sites on the slope to the east of the canyon. This would provide a clearer picture of the apparent west to east gradient of change in fauna abundance, composition and diversity discussed in chapters 2-4. Analysis of samples from additional slope sites would result in a better understanding of polychaete diversity and species turnover at lower bathyal depths across the Whittard Canyon region. An improved understanding of macrofaunal diversity inside the Whittard Canyon as a whole would be obtained by sampling macrofauna communities from different depths and habitats inside the canyon, including the rocky canyon walls and cold-water corals.

5.5.2 Polychaete biogeography

A comparison of polychaete species from the shallower (375 - 1670 m, Appendix A) and deeper (~ 3500 m, Chapter 3) parts of the Whittard Canyon and the nearby Goban Spur revealed that only *Paramphinome jeffreysii* (1335 m, Whittard Canyon) and *Aurospio dibranchiata* (992 m, Goban Spur; 1335 m, Whittard Canyon) were found in both shallow and deep areas. This suggests that the polychaete assemblages in the shallower regions of the canyon are somewhat different from the deeper assemblages. Similarly, species composition of benthic foraminifera changed with depth (300 – 3000 m) inside the Whittard Canyon (Duros et al. 2011). Foraminiferal species abundant in the shallower regions of the canyon were associated with organically-enriched sediments, whereas those in the deeper part of the canyon were associated with recolonisation after a gravity flow event (Duros et al. 2011). Species in the canyon could also be compared with those found at greater depths (~4800 m) on the neighbouring Porcupine Abyssal Plain (PAP) (Glover et al. 2001). Based on those that have been described, only one of the polychaete species (*Aurospio dibranchiata*) occurs at 992 m on the Goban Spur, 1335 m and 3500 m in the Whittard Canyon and 4850 m at PAP. As noted in Chapter 3, there are records of *Aurospio dibranchiata* from the Atlantic, Pacific and Southern Oceans (Smith et al. 2006). Species of other taxa are zoned by depth on the Celtic Margin. Seastars in the Porcupine Seabight (PS) and Porcupine Abyssal Plain (PAP) often had narrow depth ranges (200 - 300 m) but some had ranges exceeding 1000 m (Howell et al. 2002). Six distinct faunal zones were recorded from the upper slope (~150 m) to the abyssal zone, which started at 2800 m. In the same region, the depth distributions of holothurian species ranged from ~ 360 m (1430 - 1794 m, *Paroriza pallens*) to just over 3300 m in the case of the opportunistic species *Kolga hyalina,* found between 1484 and 4815 m (Billett 1991). Holothurians were distributed in three depth zones, upper and mid-slope zone, mid- and lower slope zone and abyssal zone. Holothurians and seastars also had similar patterns of species turnover with depth at the PS and PAP sites (Wagstaff et al. 2014). It would be of value to test whether polychaetes exhibit similar depth zonation and species turnover patterns to those of seastars and holothurians.

5.5.3 Source - Sink Hypothesis

Increased knowledge of polychaete species distributions at the Whittard Canyons and PAP site will help us to determine if the continental margin acts as a source for abyssal populations, as suggested by the 'source-sink' hypothesis of Rex et al. (2005). This hypothesis predicts that abyssal faunas exist at densities that are too low to sustain reproductively successful populations and thus they depend on immigration from bathyal sources. If the Whittard Canyon species' distributions extend into the abyss this would lend some support to the source-sink hypothesis.

5.4.4 Cryptic speciation

The preliminary results presented in Appendix A suggest that further molecular analyses would be worthwhile. Suitably fixed polychaete material from the same sites as the Megacore samples used for faunal analyses could provide a basis for comparing diversity based on morphological and molecular criteria. This could, for example, reveal if the Whittard Canyon harbours endemic or cryptic species. The abundant opportunistic juvenile opheliid (Opheliidae sp. A) found at the Whittard Canyon and the PAP site (Chapter 3) could be identified to confirm whether it was the common opheliid (*Ophelina abranchiata*) recorded at the Whittard Canyon site or a complex of multiple species, as seen from studies on other juvenile polychaetes (Neal et al. 2014). Further molecular analyses to barcode the polychaetes in the Iberian Margin canyons would be valuable. How many genetically similar polychaetes are shared between these canyons? For example, the spionidae morphospecies *Aurospio* sp. B and *Prionospio* sp. I, which were recorded in both the Whittard Canyon and the Iberian Margin canyons (Chapter 3), could be investigated to see if they are genetically the same species. Similarly, is the apparently cosmopolitan *Aurospio dibranchiata,* one species or a complex of many species?

5.5.4 Canyons in a wider setting

In a broader context, it would be useful to gain a better understanding of how the Whittard Canyon compares with other submarine canyons in terms of activity. Although we know that canyons are a common feature of continental margins around the globe (de Leo et al., 2010, Harris and Whiteway, 2011, Harris et al. 2014), there is no overall understanding of the proportion that are currently active in terms of sediment transport processes and the extent of this activity. Is there a relationship between the activity of a canyon and the faunal diversity inside it? Do canyons endemics, or even species endemic to a particular canyon, exist? Do canyon environments select for species that are more resilient to disturbance? It would be interesting to compare canyons with other major topographic features such as trenches, ocean ridges, seamounts and hydrothermal vents. How do canyons compare with these features in terms of species diversity, endemicity and turnover?

5.5.5 Functional ecology of macrofaunal nematodes

Little is known about the functional role of macrofaunal nematodes. It is unclear whether they perform the same roles as polychaetes of the same size or of smaller meiofaunal-sized nematodes. According to the feeding group scheme proposed by Wieser (1953), most of the nematodes in the present study were group (2B) predators/omnivores/scavengers. However, group 2B is a very broad group containing nematodes with diverse feeding habits and food sources (Moens & Vincx 1997). *In-situ* pulse-chase experiments such as Ingels et al. (2011), and laboratory based experiments and observations such as Moens & Vincx (1997), would provide valuable information about the functional role of large nematodes. Meiofaunal nematodes play an important role in deep-sea ecosystem functioning (Danovaro et al. 2008), macrofaunal nematodes may enhance the importance of nematodes even further as Sharma et al. (2011) reported that macrofaunal nematodes perform a different ecological role from meiofaunal nematodes. Furthermore, macrofaunal nematodes appear to be abundant in canyon settings (This study, Hunter et al. 2013a, Bourque et al. 2015). Why is this? Are large nematodes adapted to the high productivity or high disturbance regimes?

Appendices

Appendix A Molecular barcoding of polychaetes from the Whittard Canyon and Goban Spur - preliminary analysis

A.1 Rationale

DNA barcoding is increasingly used to confirm the identification of deep-sea species (e.g. Janssen et al. 2015). Unfortunately, the Megacore samples collected during RRS *James Cook* cruise 036, on which this thesis is based, were preserved in formalin, making molecular analysis extremely difficult. An opportunity arose for me to collect samples suitable for molecular analysis during a cruise to the Whittard Canyon on RV *Belgica* (Cruise ST1217, summer 2012) with scientists from the University of Ghent. Due to bad weather conditions, very few samples were obtained during this cruise. However, during RRS *Discovery* cruise 377 (summer 2012) to the Porcupine Abyssal Plain (PAP), samples were collected from the nearby Goban Spur. Later that year, two further cruises to the Whittard Canyon took place during which Dr. Lucy Woodall from the Natural History Museum, London (RRS *James Cook* 76T) and Dr. Louise Allcock from the the National University of Ireland, Galway (RV *Celtic Explorer* 12006) collected additional samples for this project. Unfortunately, despite these efforts, insufficient polychaete specimens on which to base a thesis chapter were obtained from the Whittard Canyon and Goban Spur. Furthermore, all sampling depths were much shallower (375 - 1670 m) than the main sampling sites (~3500 m). The following appendix presents some preliminary molecular analysis based on these samples. The original intention was to compare polychaete diversity inside the Whittard Canyon based on molecular and morphological criteria. However, for reasons mentioned above, it was necessary to focus instead on the molecular biodiversity and species distributions of polychaetes in the shallower regions of the Whittard Canyon and the Goban Spur.

A.2 Methods

A.2.1 Field Sampling

Samples were collected opportunistically during four different sampling campaigns around the Whittard Canyon and Goban Spur (NE Atlantic) in 2012. The cruises were those of the RV *Belgica* (ST1217), RRS *James Cook* (076T; ROV *ISIS* test cruise), RV *Celtic Explorer* (12006) and RRS *Discovery* (377). During the *Belgica* and *Discovery* cruises, polychaetes were picked out from sieved residues (300 μm mesh size) of the sediment samples and held on ice as soon as possible after collection. Specimens were then transferred to 90 % ethanol for preservation. For sample processing on JC076T and CE12006, in which I did not take part, please see respective cruise reports (Allcock 2012, Woodall 2012). Locations, sampling gear and preservation methods are given in Table A.1 and the sampling sites are shown in Figure A.1.

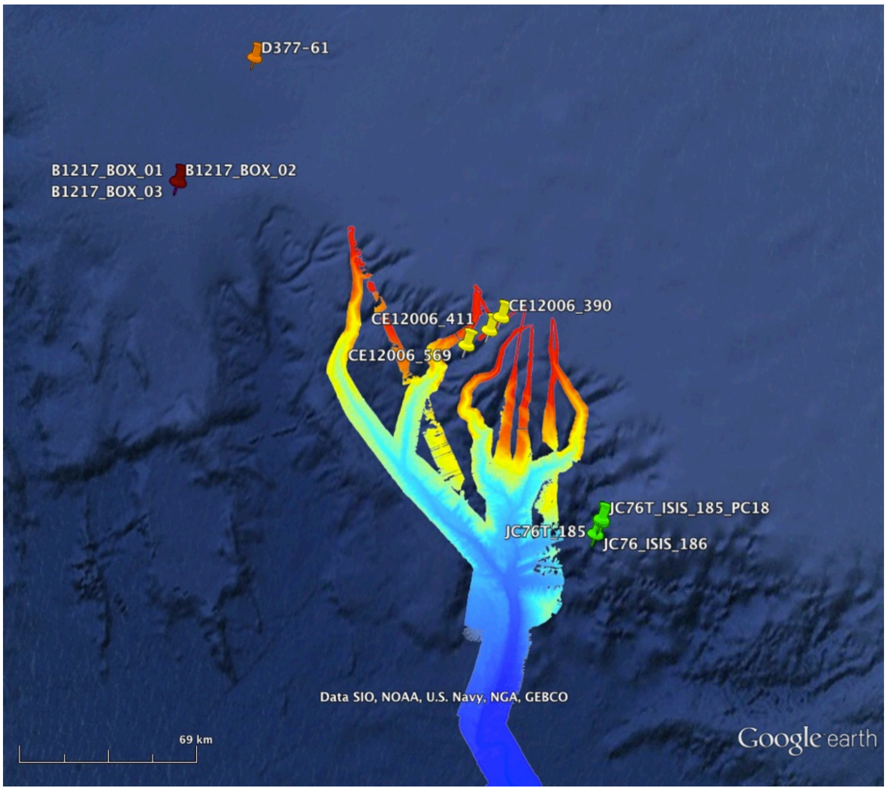


Figure A.1 Bathymetry map of Whittard Canyon and nearby Goban Spur.
Elven stations from four cruises are displayed. Goban Spur: Orange placemark RRS *Discovery* (377), Red placemarks RV *Belgica* (ST1217).Whittard Canyon: Green placemarks RRS *James Cook* (076T; ROV *ISIS* test cruise). Yellow placemarks RV *Celtic Explorer* (12006).

Table A.1 Details of cruise and sampling stations used in this study.
Goban Spur (GS), Whittard Canyon (WC). [1] piece of coral.

Cruise	Date (dd/mm/yy)	Loc.	Station	Depth (m)	Latitude (N)	Longitude (W)	Gear	Preservation
ST1217	13/06/12	GS	B1217-BOX-01	1000	49°7’58.80”	12°9’22.20”	Boxcorer	ETOH
ST1217	13/06/12	GS	B1217-BOX-02	1000	49°7’59.40”	12°9’25.80”	Boxcorer	ETOH
ST1217	13/06/12	GS	B1217-BOX-03	1000	49°7’60.00”	12°9’26.40”	Boxcorer	ETOH
D377	27/07/12	GS	D377-061	992	49°35’28.56”	11°50’47.58”	Megacorer	ETOH
JC076T	22/08/12	WC	ISIS dive 185	1400	48°9’25.20”	9°47’11.40”	Suction sample[1]	RNAlater
JC076T	22/08/12	WC	ISIS dive 185-PC18	1371	48°9’51.12”	9°47’10.68”	Pushcore	RNAlater
JC076T	26/08/12	WC	ISIS dive 186	1670	48°6’45.72”	9°48’34.92”	Suction sample[1]	RNAlater
JC076T	26/08/12	WC	ISIS dive 186- PC27	1648	48°6’49.68”	9°48’16.92”	Pushcore	RNAlater
CE12006	15/04/12	WC	Event 2 ROV390	375	48°48’33.84”	10°24’29.52”	Pushcore	ETOH
CE12006	16/04/12	WC	Event 12 ROV411	750	48°45’38.52”	10°27’38.88”	Pushcore	ETOH
CE12006	22/04/12	WC	Event 64 ROV 569	1335	48°42’5.04”	10°34’10.92”	Pushcore	ETOH

Table A.2 List of primers used in this study

Primer	Sequence 5'-3'	References
LCO 1490	GGTCAACAAATCATAAAGATATTGG	(Folmer et al. 1994)
HCO 2198	TAMACTTCWGGGTGACCAAARAATCA	(Folmer et al. 1994)
PolyLCO	GAYTATWTTCAACAAATCATAAAGATATTGG	(Carr et al. 2011)
PolyHCO	TAMACTTCWGGGTGACCAAARAATCA	(Carr et al. 2011)
Ann16SF	GCGGTATCCTGACCGTRCWAAGGTA	(Sjölin et al. 2005)
16SBRH	CCGGTCTGAACTCAGATCACGT	(Palumbi et al. 2002)

A.2.2 Morphological investigation

A Leica MZ9.5 stereomicroscope and a DM5000 compound microscope were used to identify polychaete specimens to family level based on morphological characteristics and by reference to taxonomic keys (Hayward & Ryland 1996, Beesley et al. 2000). Fragmented specimens were included in the morphological and molecular analyses.

A.2.3 Molecular analyses

DNA was extracted from 138 specimens (Table A.3), from the parapodia when the specimen was large enough but otherwise from part of the tail end. Samples preserved in 90 % ethanol were first washed using a buffer solution made from 50 µl 1 M TRIS-HCL pH 7.5 dilution 1/1000, 100 µl 0.5 M EDTA pH 8 dilution 1/500 and 50 ml sterile H_2O. A DNAeasy Tissue Kit (Qiagen) was used according to the manufacturer's instructions.

Two genes were targeted for amplification, the 'barcoding' mitochondrial (mt) CO1 and 16S genes. The CO1 gene is the most commonly used part of the genome for animal barcoding studies and is an effective tool for polychaete species identification (Rice et al. 2008, Olson et al. 2009, Pleijel et al. 2009, Barroso et al. 2010, Carr et al. 2011, Nygren & Pleijel 2011, Janssen et al. 2015). The 16S gene has also been used as a barcoding gene for identifying polychaete species (Bastrop et al. 1998, Dahlgren et al. 2001, Wiklund et al. 2009a,b, Capa et al. 2010, Amon et al. 2014). PCR mixtures contained 1 µl of each primer (concentration 10 µM)(see Table A.2), 2 µl template DNA and 21 µl Red Taq DNA Polymerase 1.1X MasterMix (VWR) in a mixture totalling 25 µl. The temperature profile was as follows: 95°C for 180 s, followed by (94°C for 45 s, 48°C for 45 s then 72°C for 120 s)*40 cycles, and finally 72 °C for 600 s. Products of the PCR were confirmed by electrophoresis in a 1 % agarose gel. Purification was performed using a Millipore Multiscreen 96-well PCR Purification System. Sequencing was performed on an ABI 3730XL DNA Analyser (Applied Biosystems) at the Natural History Museum London Sequencing Facility, using the CO1 and 16S primers (Table A.2). Not all PCR products were successfully sequenced (Table A.3).

Overlapping sequence fragments were merged into consensus sequences using Geneious (Drummond et al. 2007). The nucleotide sequences were run in the Basic Local

Alignment Search Tool (BLAST) through Geneious to find the closest matching sequences from GenBank (Table A.3). The 16S sequences were aligned using the MAFFT (Katoh et al. 2002) plug-in and the CO1 sequences using the MUSCLE (Edgar, 2004) plug-in using the default settings. Bayesian phylogenetic analyses were conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). As this was only a preliminary study, analyses were run once for 1,000,000 generations and the first 250,000 generations were discarded. FigTree (http://tree.bio.ed.ac.uk/software/figtree) was used to visualise the final phylogenetic trees.

Table A.3 Individuals DNA extracted and genes sequenced

X indicates sequence obtained. GS- Goban Spur. WC- Whittard Canyon * error in sequencing, not all PCR products returned a successful sequence. NHMUK ANEA-Natural History Museum London voucher numbers. NCBI GenBank accession number

Morphology ID (Family)	Phylogeny ID	Extract. no.	Loc.	Station	CO1	16S	Top BLAST sequence result	NHMUK ANEA	GenBank Accession No.
Acrocirridae	LG23GS9Acrocirridae	23	GS	B1217-BOX-01	x	-	-		
Opheliidae	LG119GSOpheliidae	119	GS	B1217-BOX-01	-	x	*	2016.276	KT592243
Spionidae	-	24	GS	B1217-BOX-01	-	x	*		
Syllidae	-	120	GS	B1217-BOX-01	-	-	-		
Cirratulidae	-	121	GS	B1217-BOX-01	-	-	-		
Spionidae	-	122	GS	B1217-BOX-01	-	-	-		
Spionidae	-	124	GS	B1217-BOX-01	-	-	-		
Dorvilleidae	LG123GSDorvilleidae	123	GS	B1217-BOX-02	-	x	*Protodorvillea kefersteini*		
Glyceridae	LG125GSGlyceridae	125	GS	B1217-BOX-02	-	x	Glyceridae sp.	2016.277	
Opheliidae	LG126GSOpheliidae01	126	GS	B1217-BOX-02	-	x	*	2016.278	
Opheliidae	-	127	GS	B1217-BOX-02	-	x	*		
Paraonidae	-	128	GS	B1217-BOX-02	-	x	*		
Sigalionidae	-	129	GS	B1217-BOX-02	-	x	*		
Spionidae	-	25	GS	B1217-BOX-02	-	-	-		
Spionidae	LG26GSSpionidae02	26	GS	B1217-BOX-02	-	x	*Spiophanes kroeyeri*	2016.280	KT592250
Spionidae	-	27	GS	B1217-BOX-02	-	-	-		
Trichobranchidae	-	130	GS	B1217-BOX-02	-	-	-		
Opheliidae	-	131	GS	B1217-BOX-02	-	-	-		
Cirratulidae	LG132GSCirratulidae	132	GS	B1217-BOX-02	-	x	*Aglaophamus australiensis*		
Paraonidae	LG133GSParaonidae	133	GS	B1217-BOX-02	-	x	*Ophelina* sp.	2016.279	KT592246
Acrocirridae	-	134	GS	B1217-BOX-02	-	-	-		
Lumbrineridae	-	135	GS	B1217-BOX-03	-	-	-		
Spionidae	LG28GSSpionidae	28	GS	B1217-BOX-03	-	x	*Prionospio cirrifera*	2016.281	KT592248
Syllidae	-	135	GS	B1217-BOX-03	-	-	-		
Amphinomidae	-	138	GS	B1217-BOX-03	x	-	*		
Amphinomidae	-	137	GS	B1217-BOX-03	x	-	*		
Ampharctidae	LG4D7Ampharctidae	5	GS	D377-061	x	-	*Melinna albicincta*		KT592276
Amphinomidae	-	11	GS	D377-061	x	-	*		
Glyceridae	LG1D1Glyceridae01	1	GS	D377-061	x	-	Glyceridae sp.		
Glyceridae	LG06DCGlyceridae02	6	GS	D377-061	-	x	*Protodorvillea kefersteini*		
Glyceridae	LG07DCGlyceridae03	7	GS	D377-061	x	-	*		KT592271
Lumbrineridae	-	3	GS	D377-061	-	-	-		
Maldanidae	LG2D2Maldanidae	2	GS	D377-061	x	-	*		KT592266

Scalibregmatidae	LG3D6Scalibregmatidae	4	GS	D377-061	x	-	*	2016.325	KT592254
Glyceridae	LG14GS1Glyceridae04	14	GS	D377-061	x	-	*Hediste atoka*		
Maldanidae	LG09Maldanidae	9	GS	D377-061	-	-	-		KT592265
Opheliidae	LG15D3Opheliidae	15	GS	D377-061	-	x	*		KT592242
Spionidae	LG12GS3Spionidae01	12	GS	D377-061	x	-	*	2016.324	KT592253
Spionidae	LG10D3Spionidae02	10	GS	D377-061	-	x	*Aurospio dibranchiata*		KT592247
Syllidae	-	13	GS	D377-061	-	x	*		
Maldanidae	LG16WCLMaldanidae	16	WC	ISIS dive 185	x	-	*	2016.326	KT592263
Onuphidae	LG17WCQOnuphidae	17	WC	ISIS dive 185	x	-	*.		
poly indet.	LG18WCRPolyindet	18	WC	ISIS dive 185	x	-	*		
Onuphidae	LG19WCSOnuphidae	19	WC	ISIS dive 185	x	-	*		
Glyceridae	LG20WCTGlyceridae	20	WC	ISIS dive 185	x	-	*		
Poly indet.	LG21WCWPolyindet	21	WC	ISIS dive 186	x	-	*Harmothoe fragilis*		
Poly indet.	LG22WCYpolyindet	22	WC	ISIS dive 186	x	-	*Nereis pelagica*		
Hesionidae	LG51CEHesionidae	51	WC	CE12006-390	x	-	*Sige fusigera*	2016.283	KT592269
Lumbrineridae	LG49CELumbrineridae01	49	WC	CE12006-390	-	x	*Lumbrineris funchalensis*		
Lumbrineridae	LG50CELumbrineridae02	50	WC	CE12006-390	x	-	*		
Magelonidae	LG52Magelonidae	52	WC	CE12006-390	-	x	*		
Maldanidae	LG65CEMaldanidae01	65	WC	CE12006-390	x	-	*.		
Maldanidae	LG62CEMaldanidae02	62	WC	CE12006-390	x	-	*Axiothella constricta*	2016.284	
Maldanidae	LG64CEMaldanidae03	64	WC	CE12006-390	x	-	*Axiothella constricta*	2016.285	KT592268
Maldanidae	LG66CEMaldanidae04	66	WC	CE12006-390	x	-	*Euclymene santandarensis*	2016.286	
Maldanidae	LG63CEMaldanidae05	63	WC	CE12006-390	x	-	*Axiothella constricta*		
Nephtyidae	LG47CENephtyidae	47	WC	CE12006-390	-	x	*Nephtys hystricis*	2016.282	KT592241
Paraonidae	LG48CEParaonidae	48	WC	CE12006-390	x	-	*		
Eunicidae	LG29CE411Eunicidae	29	WC	CE12006-411	x	-	*Eunice norvegica*	2016.287	KT592274
Hesionidae	LG30CEHesionidae	30	WC	CE12006-411	x	-	Polychaeta sp.	2016.288	KT592270
Maldanidae	LG31CE411Maldanidae	31	WC	CE12006-411	x	-	*Axiothella rubrocincta*	2016.289	KT592264
Phyllodocidae	-	32	WC	CE12006-411	x	-	*		
Polynoidae	LG33CE411Polynoidae01	33	WC	CE12006-411	x	-	*	2016.290	
Polynoidae	LG34CE411Polynoidae02	34	WC	CE12006-411	x	-	*	2016.291	KT592255
Polynoidae	LG35CE411Polynoidae03	35	WC	CE12006-411	x	-	*	2016.292	KT592262
Polynoidae	LG36CE411Polynoidae04	36	WC	CE12006-411	x	-	*	2016.293	KT592257
Polynoidae	LG53CEPolynoidae05	53	WC	CE12006-411	x	-	*	2016.294	
Serpulidae	-	67	WC	CE12006-411	-	-	-		

Ampharetidae	-	38	WC	CE12006-569	-	-	-		
Ampharetidae	-	39	WC	CE12006-569	-	-	-		
Ampharetidae	LG40CEAmpharetidae03	40	WC	CE12006-569	x	-	*Anobothrus gracilis*	2016.299	KT592275
Ampharetidae	-	41	WC	CE12006-569	-	-	-		
Ampharetidae	-	42	WC	CE12006-569	-	-			
Ampharetidae	LG43CE569Ampharetidae	43	WC	CE12006-569	x	-	*Anobothrus gracilis*	2016.300	
Ampharetidae	LG44CEAmpharetidae07	44	WC	CE12006-569	x	-	*Anobothrus gracilis*	2016.301	
Ampharetidae	LG45CE569Ampharetidae08	45	WC	CE12006-569	x	-	*Anobothrus gracilis*	2016.302	
Ampharetidae	LG46CEAmpharetidae09	46	WC	CE12006-569	x	-	*Sabellides octocirrata*		KT592277
Ampharetidae	-	106	WC	CE12006-569	-	-	-		
Ampharetidae	-	107	WC	CE12006-569	-	-	-		
Ampharetidae	LG108CEAmpharetidae12	108	WC	CE12006-569	x	-	*	2016.295	KT592252
Ampharetidae	LG109CEAmpharetidae13	109	WC	CE12006-569	-	x	*		
Ampharetidae	-	110	WC	CE12006-569	-	-	-		
Ampharetidae	-	111	WC	CE12006-569	-	-	-		
Ampharetidae	LG112CEAmpharetidae16	112	WC	CE12006-569	-	x	*	2016.296	KT592239
Ampharetidae	-	113	WC	CE12006-569	-	-	-		
Ampharetidae	LG114CEAmpharetidae114	114	WC	CE12006-569	x	-	*		
Ampharetidae	LG115CEAmpharetidae19	115	WC	CE12006-569	x	-	*		
Ampharetidae	LG116CEAmpharetidae20	116	WC	CE12006-569	-	x	*	2016.297	
Ampharetidae	LG117CEAmpharetidae21	117	WC	CE12006-569	-	x	*	2016.298	KT592240
Amphinomidae	-	54	WC	CE12006-569	x	-	*		
Amphinomidae	LG55CEAmphinomidae03	55	WC	CE12006-569	x	-	*Paramphinome jeffreysii*		KT592260
Amphinomidae	LG56CEAmphinomidae03	56	WC	CE12006-569	-	x	*Paramphinome jeffreysii*		
Amphinomidae	-	101	WC	CE12006-569	x	-	*		
Amphinomidae	-	57	WC	CE12006-569	-	-	-		
Amphinomidae	LG58CEAmphinomidae06	58	WC	CE12006-569	-	x	*Paramphinome jeffreysii*	2016.303	KT592244
Amphinomidae	LG59CEAmphinomidae07	59	WC	CE12006-569	-	x	*Paramphinome jeffreysii*	2016.304	
Amphinomidae	LG60CEAmphinomidae08	60	WC	CE12006-569	-	x	*Paramphinome jeffreysii*	2016.305	
Amphinomidae	-	61	WC	CE12006-569	x	-	*		
Flabelligeridae	LG68CEFlabelligeridae01	68	WC	CE12006-569	x	-	*	2016.306	KT592259
Flabelligeridae	LG69CEFlabelligeridae02	69	WC	CE12006-569	x	-	*	2016.307	
Flabelligeridae	LG70CEFlabelligeridae04	70	WC	CE12006-569	x	-	*	2016.308	KT592273
Flabelligeridae	LG71CEFlabelligeridae05	71	WC	CE12006-569	x	-	*	2016.309	KT592272
Flabelligeridae	LG72CEFlabelligeridae06	72	WC	CE12006-569	-	x	*		

Hesionidae	LG118CEHesionidae02	118	WC	CE12006-569	x	-	*Nereimyra woodsholea*		
Hesionidae	LG86CEHesionidae03	86	WC	CE12006-569	x	-	*Nereimyra woodsholea*	2016.316	
Hesionidae	LG87CEHesionidae04	87	WC	CE12006-569	x	-	*Nereimyra woodsholea*	2016.317	
Hesionidae	LG88CEHesionidae05	88	WC	CE12006-569	x	-	*Nereimyra woodsholea*		
Hesionidae	LG89CE569Hesionidae06	89	WC	CE12006-569	x	-	*Nereimyra woodsholea*		
Hesionidae	LG90CE569Hesionidae07	90	WC	CE12006-569	x	-	*Nereimyra woodsholea*	2016.318	KT592261
Hesionidae	LG91CE560Hesionidae08	91	WC	CE12006-569	x	-	*Melaenis loveni*		
Glyceridae	-	103	WC	CE12006-569	-	-	-		
Lumbrineridae	LG75CELumbrineridae01	75	WC	CE12006-569	x	-	Polychaeta sp.		
Maldanidae	LG92CE569Maldanidae01	92	WC	CE12006-569	x	-	*	2016.319	KT592267
Maldanidae	LG104CEMaldanidae02	104	WC	CE12006-569	x	-	*Amynthas* sp.		
Maldanidae	-	94	WC	CE12006-569	-	-	-		
Maldanidae	LG95CEMaldanidae04	95	WC	CE12006-569	x	-	*	2016.321	
Maldanidae	LG96CE569Maldanidae05	96	WC	CE12006-569	x	-	*	2016.322	
Maldanidae	LG97CE569Maldanidae06	97	WC	CE12006-569	x	-	*	2016.323	
Maldanidae	LG98CE569Maldanidae07	98	WC	CE12006-569	x	-	*	2016.320	
Maldanidae	LG99CE569Maldanidae08	99	WC	CE12006-569	x	-	*		
Maldanidae	LG100CE569Maldanidae09	100	WC	CE12006-569	x	-	*		
Nereididae	-	105	WC	CE12006-569	-	-	-		
Paraonidae	LG73CEParaonidae01	73	WC	CE12006-569	x	-	Polychaeta sp		
Paraonidae	LG74CEParaonidae02	74	WC	CE12006-569	-	x	*Caulleriella* sp.		KT592245
Polynoidae	LG79CEPolynoidae02	79	WC	CE12006-569	x	-		2016.312	
Polynoidae	LG80CEPolynoidae02	80	WC	CE12006-569	x	-	*Eunoe oerstedi*		
Polynoidae	LG81CEPolynoidae03	81	WC	CE12006-569	x	-	*	2016.313	KT592256
Polynoidae	LG82CEPolynoidae04	82	WC	CE12006-569	x	-	*	2016.314	
Spionidae	-	83	WC	CE12006-569	x	-	*		
Sigalionidae	LG84CE569Sigalionidae	84	WC	CE12006-569	x	-	Polynoidae sp.		
Spionidae	LG102CESpionidae	102	WC	CE12006-569	-	x	*Spiophanes kroeyeri*		
Spionidae	LG76CESpionidae	76	WC	CE12006-569	-	x	*Aurospio dibranchiata*	2016.310	KT592249
Syllidae	LG78CESyllidae	78	WC	CE12006-569	-	x	*Lumbrineris inflata*		
Trichobranchidae	LG77CETrichobranchidae	77	WC	CE12006-569	x	-	*	2016.311	KT592251

A.3 Results

A.3.1 Morphological analysis

Analysed polychaete specimens belonged to twenty-three families; Ampharetidae, Acrocirridae, Amphinomidae, Cirratulidae, Dorvilleidae, Flabelligeridae, Glyceridae, Hesionidae, Lumbrineridae, Magelonidae, Maldanidae, Nephtyidae, Opheliidae, Onuphidae, Paraonidae, Phyllodocidae, Polynoidae, Scalibregmatidae, Serpulidae, Sigalionidae, Spionidae, Syllidae, Trichobranchidae. There were three unidentified specimens. Fragments, as well as specimens with heads, were identified if possible based on morphology. I cannot exclude the possibility that multiple fragments belonged to the same individual.

A.3.2 Molecular analysis

In total, 109 sequences were obtained, 77 for the CO1 gene and 32 for the 16S gene (Table A.3). If the CO1 gene could not be sequenced the 16S gene was sequenced; as a result, only one of these two genes was analysed for each specimen. The CO1 and 16S sequences returned 50 close matches in a BLAST analysis (Table A.3). Forty-one specimens returned a match with a full Latin binomial name, three specimens returned a family level name, three specimens returned a genus level name and three specimens were identified only as Polychaete sp.

Table A.4 Occurrence of species at sampling sites based on CO1 gene only. X indicates species present.

		Station										
		Goban Spur				Whittard Canyon						
		B1217-bx1	B1217-bx2	B1217-bx3	D377-61	ISIS dive 185	ISIS dive 186	ISIS dive 185-PC18	ISIS dive 186-PC27	CE12006- 390	CE12006- 411	CE12006- 569
	Depth (m)	1000	1000	1000	992	1400	1670	1317	1648	375	750	1335
Family	Species											
Acrocirridae	1	-	-	-	-	-	-	-	-	-	-	X
Ampharetidae	1	-	-	-	-	-	-	-	-	-	-	X
Ampharetidae	2	-	-	-	-	-	-	-	-	-	-	X
Ampharetidae	3	-	-	-	X	-	-	-	-	-	-	-
Amphinomidae	*Paramphinome jeffreysi*i	-	-	-	-	-	-	-	-	-	-	X
Eunicidae	*Eunice norvegica*										X	
Flabelligeridae	1	-	-	-	-	-	-	-	-	-	-	X
Flabelligeridae	2	-	-	-	-	-	-	-	-	-		X
Glyceridae	1		X		X							X
Hesionidae	1	-	-	-	-	-	-	-	-	-	-	X
Hesionidae	2	-	-	-	-	-	-	-	-	X	-	-
Hesionidae	*Nereimyra woodsholea*	-	-	-	-	-	-	-	-	-	X	-
Lumbrineridae	1	-	-	-	-	-	-	-	-	X	-	-
Maldanidae	1	-	-	-	-	X	-	-	-	-	-	-
Maldanidae	2	-	-	-	-	-	-	-	-	-	-	X

A.3.3 CO1 Phylogenetic trees

Thirty-three species from six different stations, (D377-61, JC76T ISIS dive 185, JC76T ISIS dive 186, CE12006-390, CE12006-411 and CE12006-569) were recognised using the CO1 gene (Table A.4). Six species belonged to the family Maldanidae (Figure A.2), two from D377-061 and one from each of stations JC76T Isis dive 185, CE12006-569, CE12006-390 and CE12006-411. Five species fall within the *Clymene* (*Euclymene*) clade and one (LG16WCLMaldanidae) lies outside this clade. Four species of Polynoidae were recorded (Figure A.3), three from station CE12006-411 and one from station CE12006-569. Two species from station CE12006-569 were assigned to the family Ampharetidae (Figure A.4). One species of Ampharetidae within the *Melinna* clade was recorded at station D377-061. Two species of Flabelligeridae were recognised at station CE12006-569 (Figure A.4). Three species of Hesionidae were recorded from three different stations; CE12006-569, CE12006-411 and CE12006-390 (Figure A.6).

Three species could be designated a Latin binomial name based on the phylogenetic analyses of the CO1 gene. One species of Polynoidae found at station CE12006-411 corresponded to *Neopolynoe paradoxa* (Figure A.3). The individual LG29CE411Eunicidae is most likely *Eunice norvegica* (Figure A.5), as indicated by the BLAST result (Table A.3). The specimens LG86CEHesionidae03, LG89CE569Hesionidae06, LG118CEHesionidae02, LG90CE569Hesionidae07, LG87CEHesionidae04 and LG85CE560Hesionidae clustered with *Nereimyra woodsholea* (Figure A.6) and returned a BLAST result consistent with this species.

Some specimens returned molecular results that were inconsistent with their morphological identifications. For example, a specimen identified morphologically as a member of the family Lumbrineridae (LG75CELumbrineridae01) did not cluster with other lumbrinerids (Figure A.5). Similarly, the specimen LG114CEAmpharetidae114 did not cluster with the ampharetids (Figure A.4). LG37CE411Syllidae had a very long branch length (Figure A.6) suggesting that it is not closely related to other syllids. LG91CE560Hesionidae08 fell outside the Hesionidae cluster and therefore is most likely not a member of this family. Whereas, the specimen designated LG07D7Glyceridae03 grouped within the Hesionidae. Two specimens, LG108CEAmpharetidae12 and LG115CEAmpharetidae19, represent the same species but fell within the Terebellidae clade (Figure A.4) and are probably not ampharetids. The specimen LG68CEFlabelligeridae01, identified as a member of the family Flabelligeridae, clusters with a species of the family Accrocirridae (*Swima bombiviridis*) and therefore may not be a flabelligerid (Figure A.4). The specimens LG17WCQOnuphidae and LG84CE569Sigalionidae represent distinct species, but neither the species nor the family assignment could be confirmed by molecular data (Figure A.7). Finally, three specimens (LG18WCRPolyindet, LG21WCWPolyindet, LG22WCYpolyindet) could not be identified either morphologically or by using molecular methods.

A.3.4 16S Phylogenetic trees

Four different species of Spionidae were recognised from the stations B1217-BOX-02, B1217-BOX-03, D377-061 and CE12006-569 based on the 16S gene (Figure A.8). Two specimens of the same species were found at different stations, specimen LG26GSSpionidae02 at station D377-061 (Goban Spur) and specimen LG102CESpionidae at station CE12006-569 (Whittard Canyon). The individuals LG10D3Spionidae02, LG28GSSpionidae and LG76CESpionidaa02 appeared to lie within the *Aurospio*/*Prionospio* complex; however, the bootstrap score is low for this branch (0.8), thus it is not safe to say which genus they belong to.

Two species of Paraonidae were recorded from different locations, LG133GSParaonidae at station B1217-BOX-02 (Goban Spur) and LG74CEParaonidae02 at station CE12006-569 (Whittard Canyon) (Figure A.9). Two species of Ampharetidae were recorded at station CE12006-569 (Figure A.10). Analysis of the 16S gene suggests that LG109CEAmpharetidae13 may be a member of the family Terebellidae, but the low support value (0.9) makes this assignment tentative. Two species of ophellid were recorded from three different stations, one from station D377-061 and the other from stations B1217-BOX-02 and B1217-BOX-01 (Figure A.11).

Two species could be assigned a Latin binomial based on the phylogenetic analyses of the 16S gene. From the Nephtyidae phylogeny (Figure A.12) the specimen LG47CENephtyidae appears to be closely related to *Nephtys hystricis*. All Amphinomidae clustered within *Paramphinome jeffreysii* (Figure A.13), supporting the BLAST result (Table A.3).

The 16S phylogenies also revealed differences between the morphological and the molecular identification. It is likely that LG06DCGlyceridae02 (D377-61) and LG123GSDorvilleidae (B1217-BOX-02) are the same species occurring at different stations (Figure A.13). Specimen LG06DCGlyeridae02 may also not be a glycerid (Figure A.12).

A.4 Limitations and implications of the analysis

These molecular analyses were based on a limited number of specimens obtained from sites that did not match the 5 sites located around 3500 m depth, which were the main focus of this thesis. Furthermore, deep-sea polychaetes are difficult to study using molecular methods as there are relatively few relevant sequences deposited in GenBank (Janssen et al. 2015). This makes it difficult to identify unknown specimens and to interpret phylogenies. Resolution of phylogenetic trees could have been improved by sequencing the CO1 and 16S gene for each specimen. However, as this was a preliminary analysis this was not possible due to cost and time restraints. Some specimens were identified as belonging to different families in the morphological and molecular investigation (Table A.3). For example, LG91CEHesionidae08 was identified as a Hesionidae based on morphology, but fell outside the Hesionidae clade in the molecular phylogeny of the CO1 gene (Fig. A.6). This may be because the CO1 gene is not particularly effective in resolving the Hesionidae family tree, more genes e.g. 18S, 28S and 16S may be needed in combination with CO1 to effectively resolve the phylogenetic tree for hesionids (Ruta et al. 2007). The discrepancy between morphological and molecular identification may also be due to morphological misidentification. In this analysis an attempt was made to morphologically identify polychaete fragments, without heads, this may have led to misidentification. In all previous chapters of this thesis only polychaetes with heads were morphologically identified.

From the 138 polychaete specimens analysed, the CO1 amplification and sequencing was successful for 56 % of the specimens (77 specimens). From the remaining 61 specimens where the CO1 gene could not be successfully amplified and sequenced, the 16S amplification and sequencing was successful for 52 % of the specimens (32 specimens). This success rate is similar to that of Janssen et al. (2015), who report a success of 44% for CO1 gene amplification and sequencing of deep-sea polychaetes from the Clarion and Clipperton Fracture Zones, abyssal central Pacific.

There is also evidence of contamination. The specimens LG19WCSOnuphidae and LG20WCTGlyceridae were morphologically different, but the molecular analysis suggests that they are the same species (Figure A.6). This was most likely due to contamination during the DNA extraction process.

The molecular analysis revealed higher levels of diversity than the morphological analysis. For example, based on morphology specimens could only be assigned to the family Maldanidae (Maldanidae sp.), whereas, the molecular analyses revealed six species of maldanid. Although the analyses were limited, a few polychaetes were identified to species level. Five species could be designated a Latin name from the phylogenetic analyses of the CO1 and 16S genes; these were *Neopolynoe paradoxa* (Anon, 1888)*, Eunice norvegica* (Linnaeus, 1767)*, Nereimyra woodsholea* (Hartman, 1965)*, Nephtys hystricis* McIntosh, 1900 and *Paramphinome jeffreysii* (McIntosh, 1868). The type locality of *N. paradoxa* is in unspecified Norwegian waters (Read, 2015). It is widely distributed in the NE Atlantic. *Eunice norvegica* was also first described from Norwegian waters and subsequently recorded in the Mediterranean Sea, NE Atlantic Ocean and the Gulf of Mexico (Read, 2015). *Nereimyra woodsholea* has a type locality at the upper end of Block Canyon, Middle Atlantic Bight, North Atlantic 300 m water depth (Pleijel et al. 2012) and has also been recorded in the waters of Trondheimsfjord, Norway and Gullmarsfjorden, Sweden. This species appears to span a wide depth range; the specimens for the present study were collected at 1335 m from the Whittard Canyon compared with the type locality at 300 m water depth. *Nephtys hystricis* has a type locality off Bergen, Norway (Ravara et al. 2010) and elsewhere has been recorded from the Mediterranean Sea, Eastern Basin to the Northeast Atlantic (Read, 2015). Finally, *Paramphinome jeffreysii* was first described from off the Shetland Islands (McIntosh, 1868) and has a wide distribution in North Atlantic waters as well as being found in the Gulf of Mexico (Read, 2015). This species is also known to occur in the deeper parts of the Whittard Canyon (~ 3500 m) in high densities, as noted in Chapter 3.

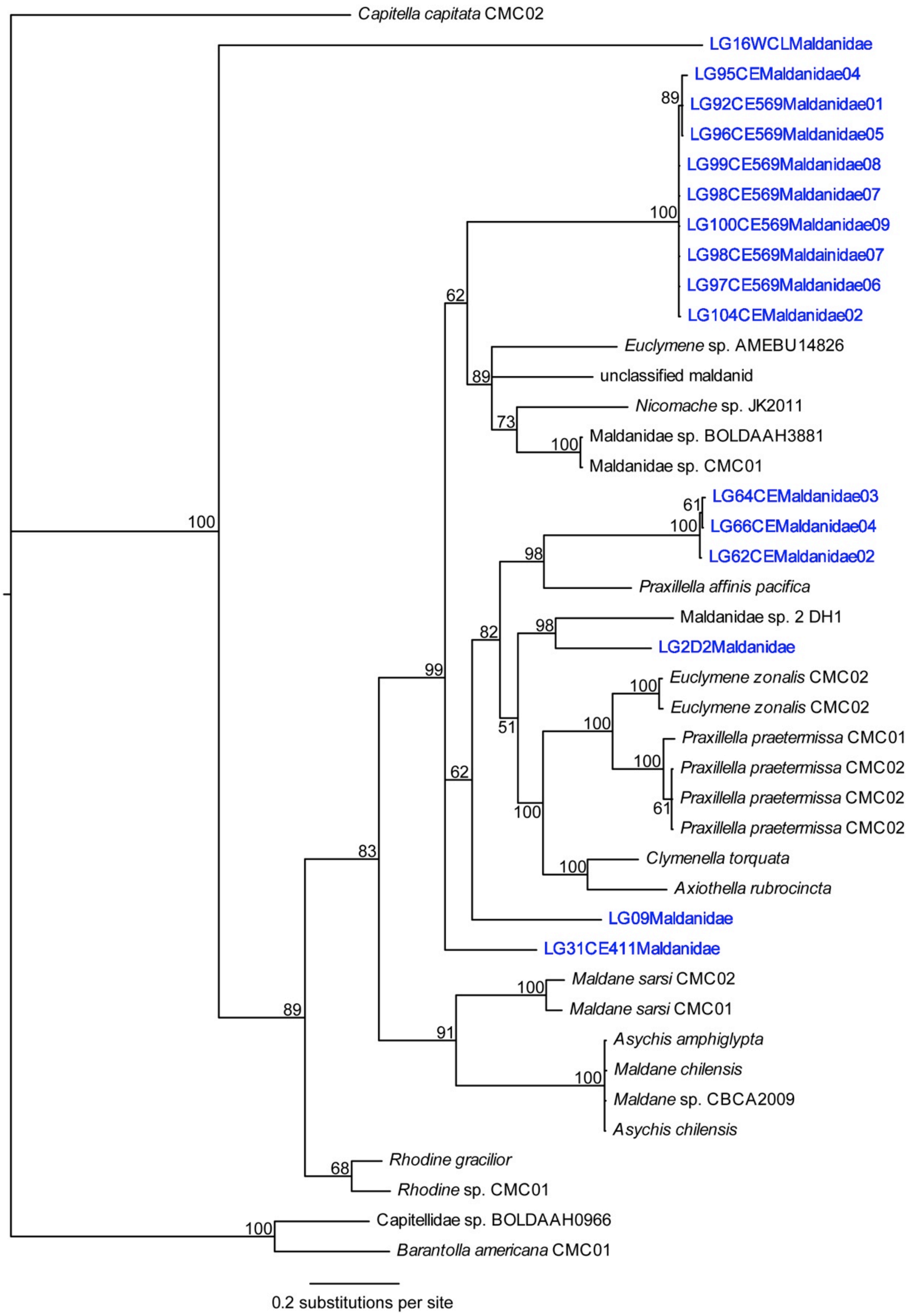


Figure A.2 Molecular phylogeny of the polychaete family Maldanidae, based on CO1 (mtDNA) gene sequences

Specimens from this study have the prefix “LG” and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

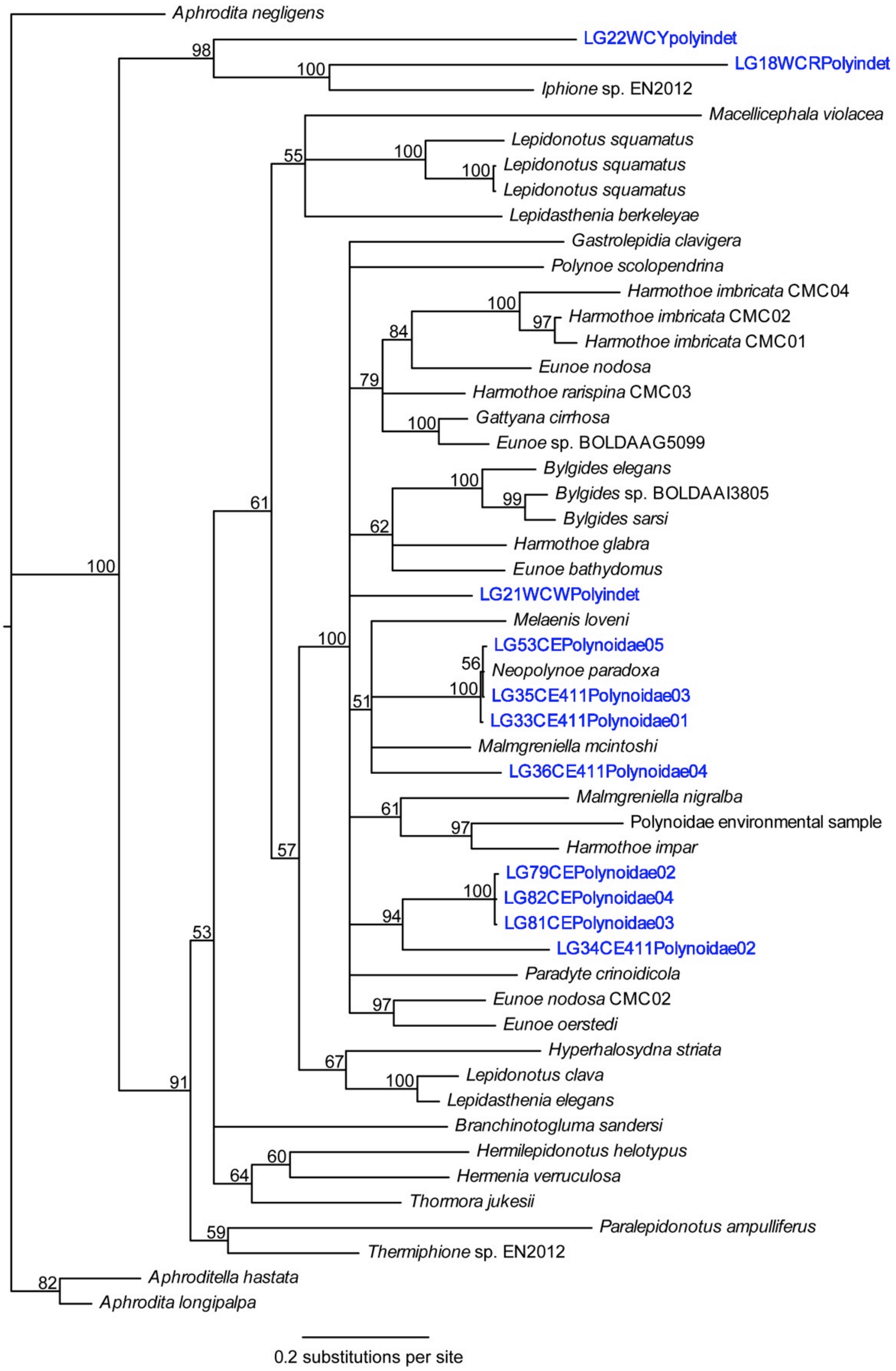


Figure A.3 Molecular phylogeny of the polychaete family Polynoidae, based on CO1 (mtDNA) gene sequences.

Specimens from this study have the prefix "LG" and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

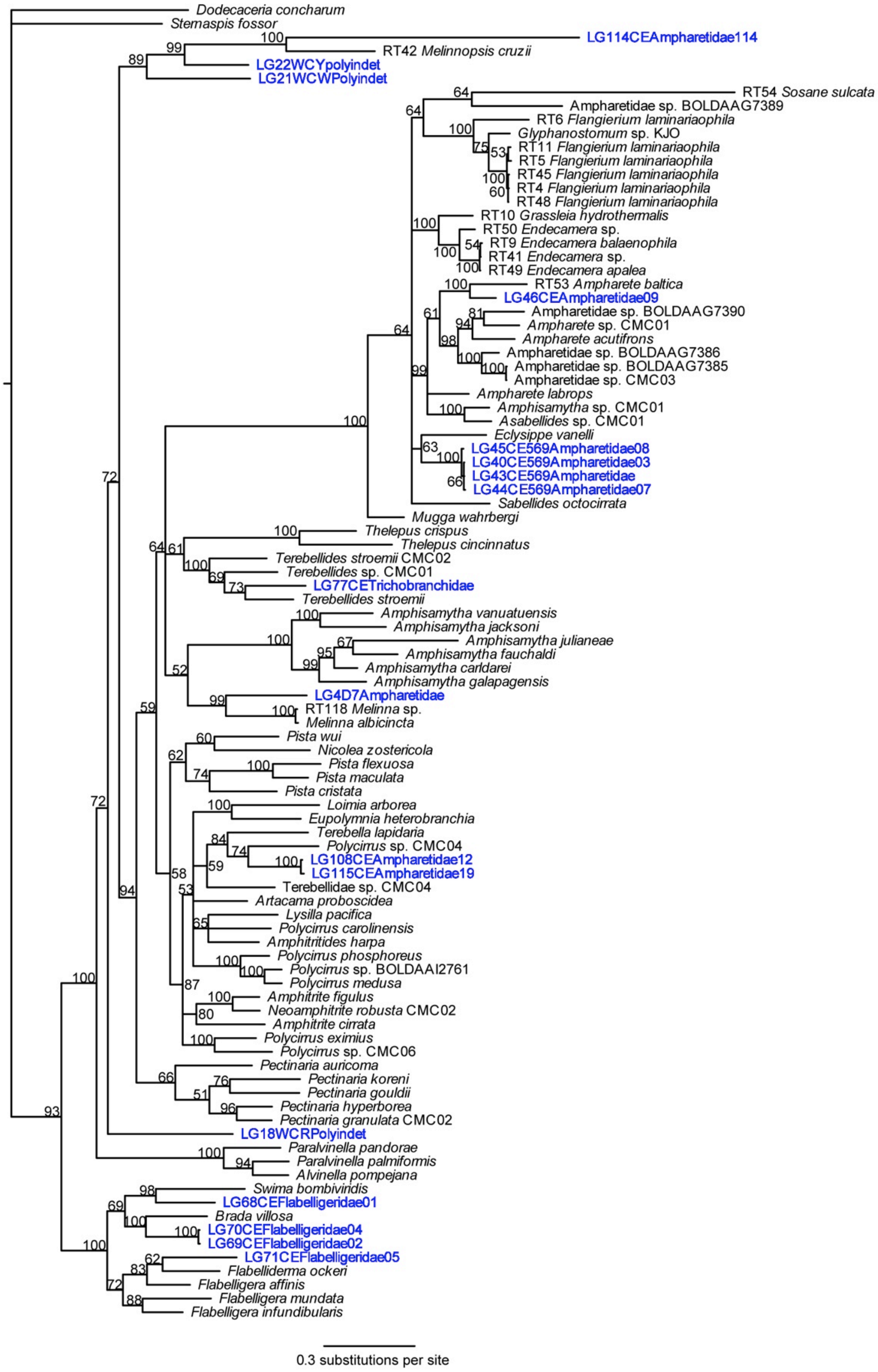


Figure A.4 Molecular phylogeny of the polychaete families Ampharetidae, Flabelligeridae, Terebellidae, Trichobranchidae and Acrocirridae based on CO1 (mtDNA) gene sequences.

Specimens from this study have the prefix "LG" and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

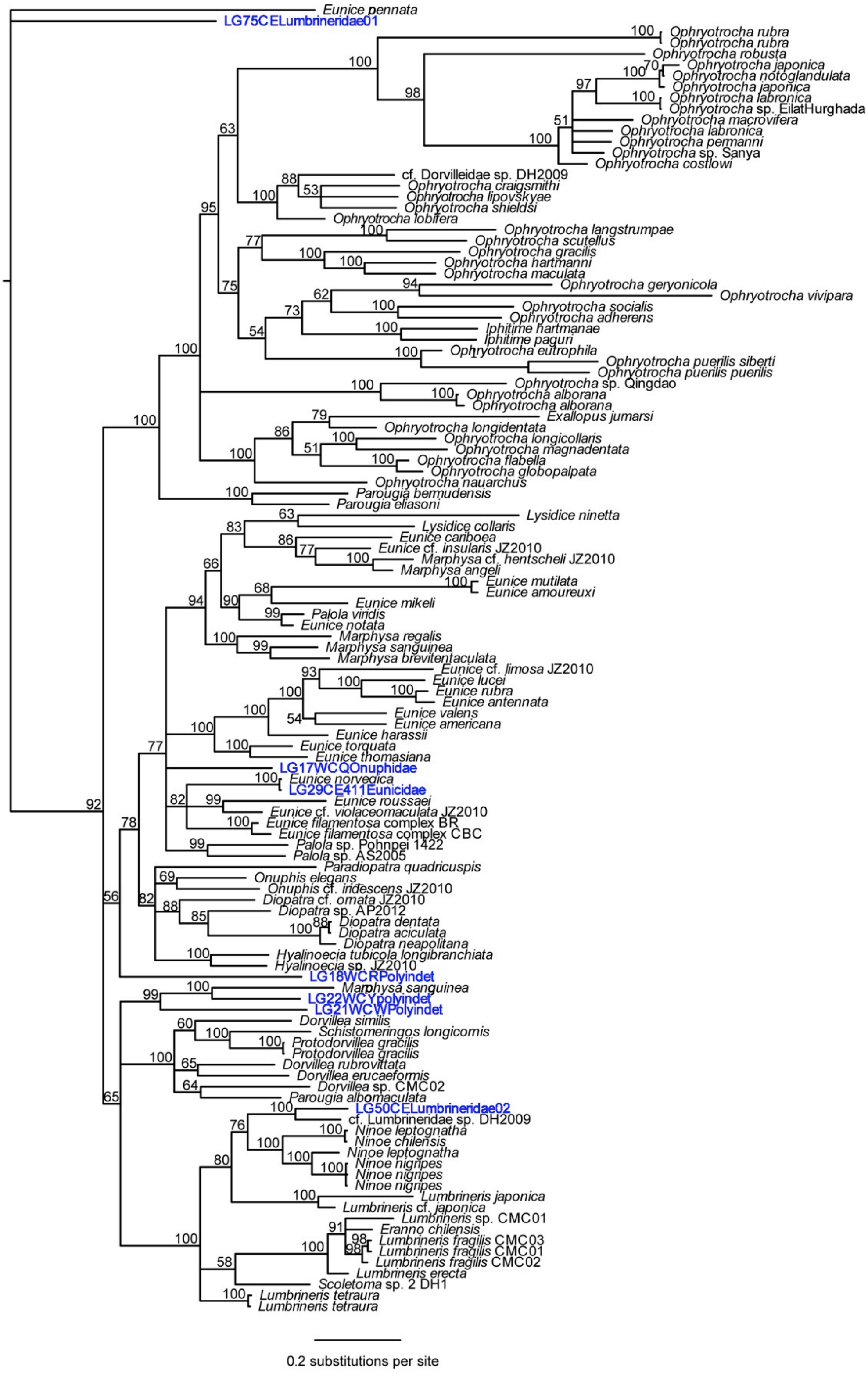


Figure A.5 Molecular phylogeny of the polychaete families Lumbrineridae and Dorvilleidae, based on CO1 (mtDNA) gene sequences.

Specimens from this study have the prefix "LG" and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant

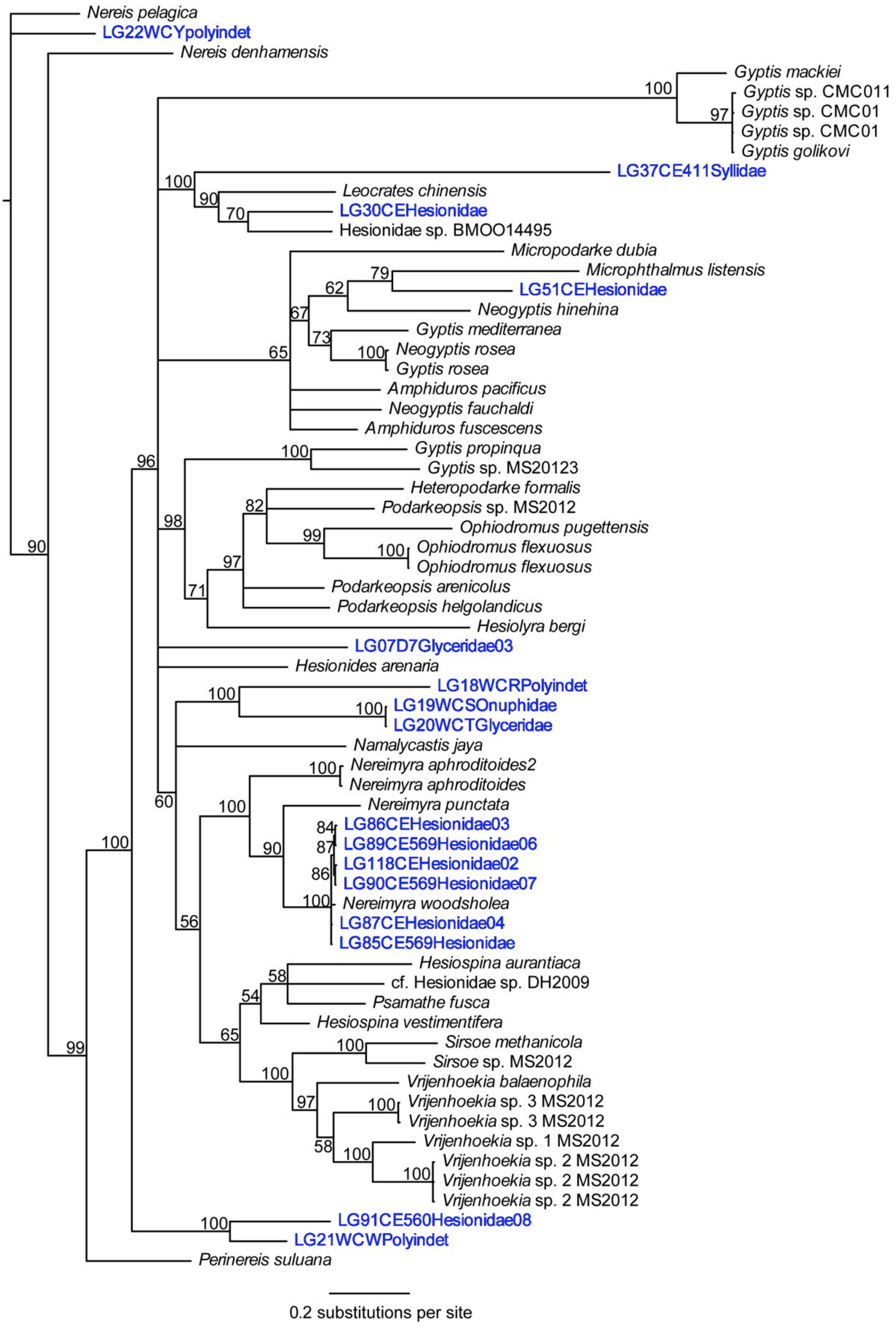


Figure A.6 Molecular phylogeny of the polychaete family Hesionidae, based on CO1 (mtDNA) gene sequences.

Specimens from this study have the prefix "LG" and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

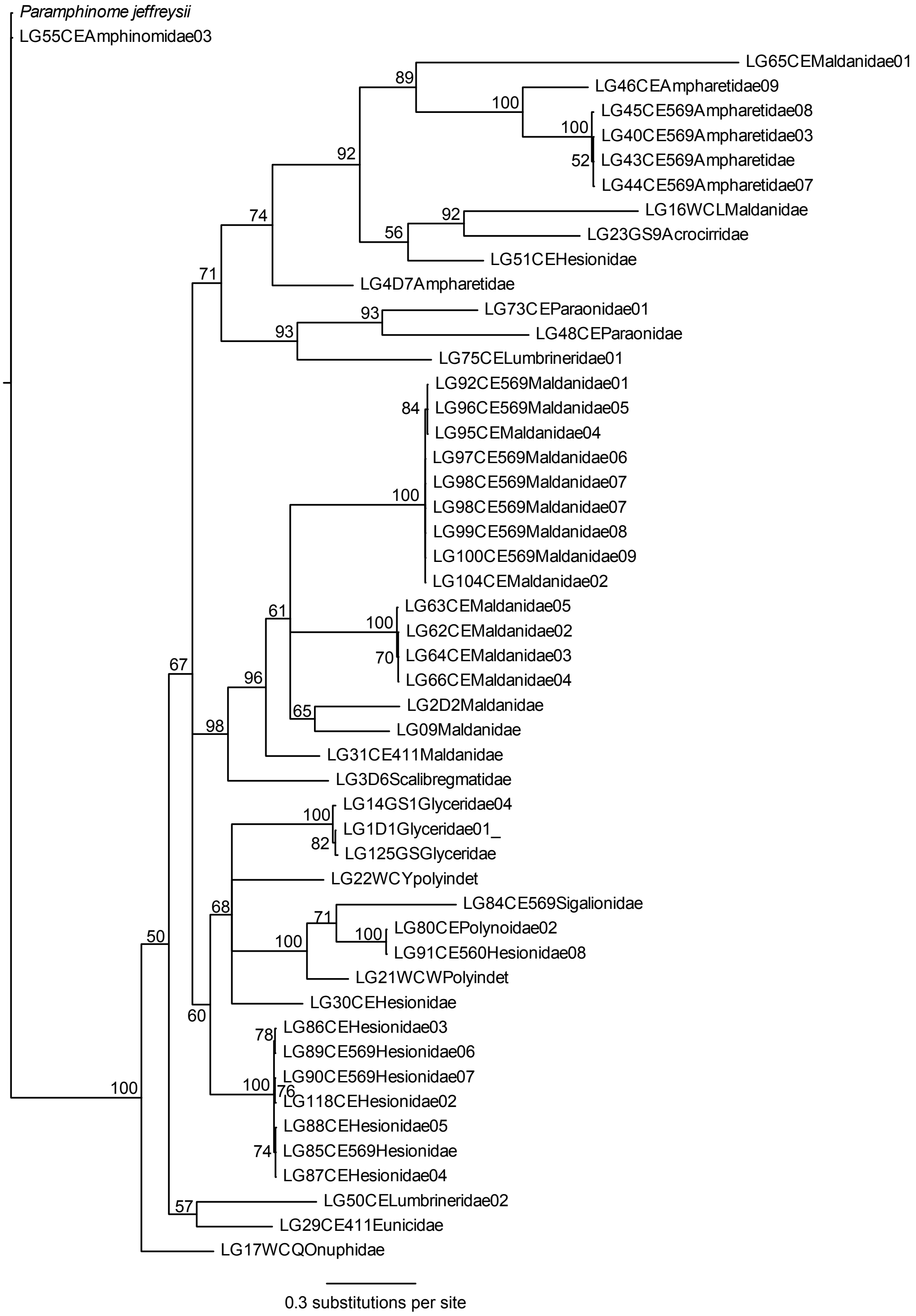


Figure A.7 Molecular phylogeny based on polychaete family CO1 (mtDNA) sequences from the present study.

Specimens from this study have the prefix “LG” and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

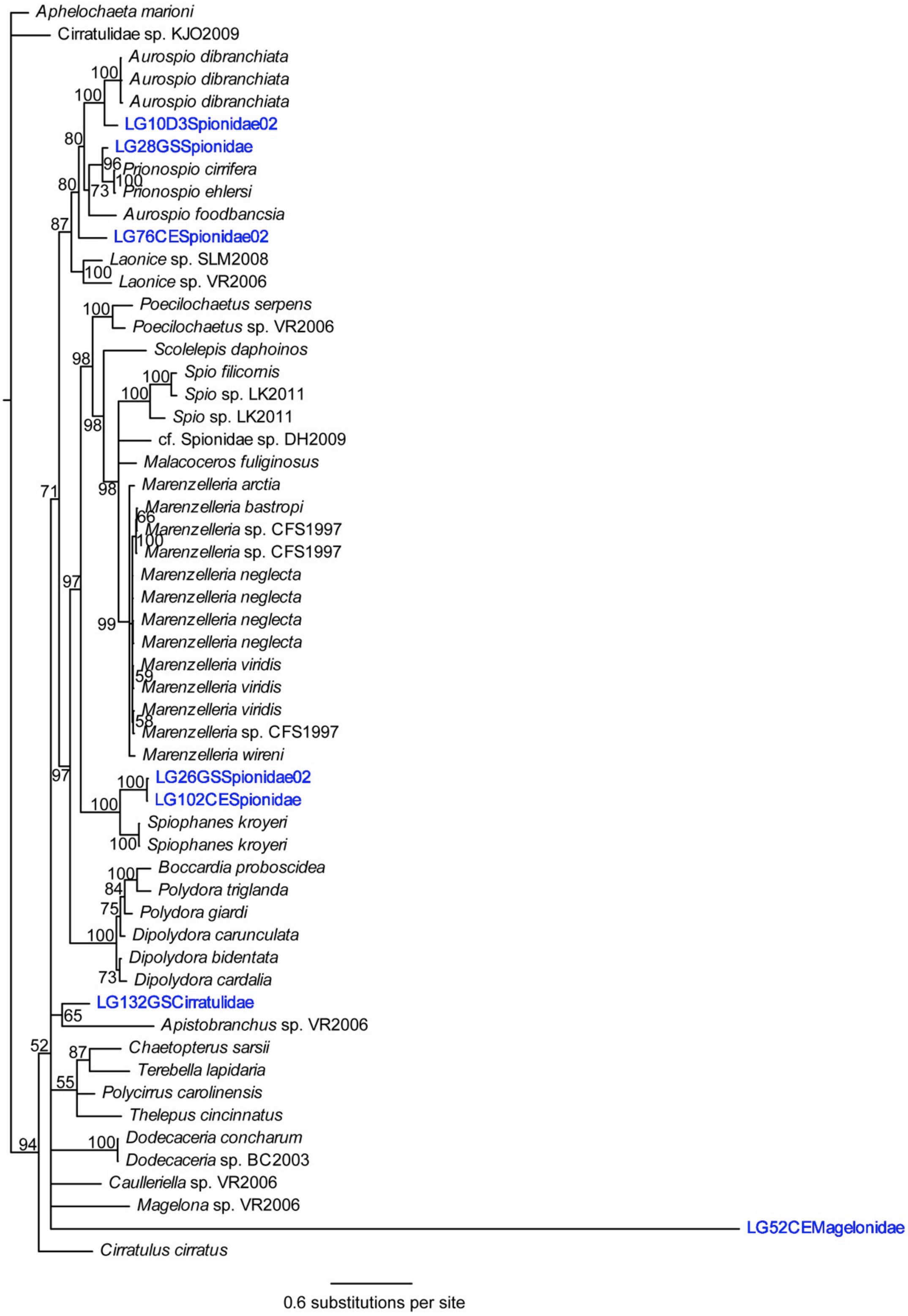


Figure A.8 Molecular phylogeny of the polychaete families Spionidae and Magelonidae, based on16S (mtDNA) gene sequences.

Specimens from this study have the prefix "LG" and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

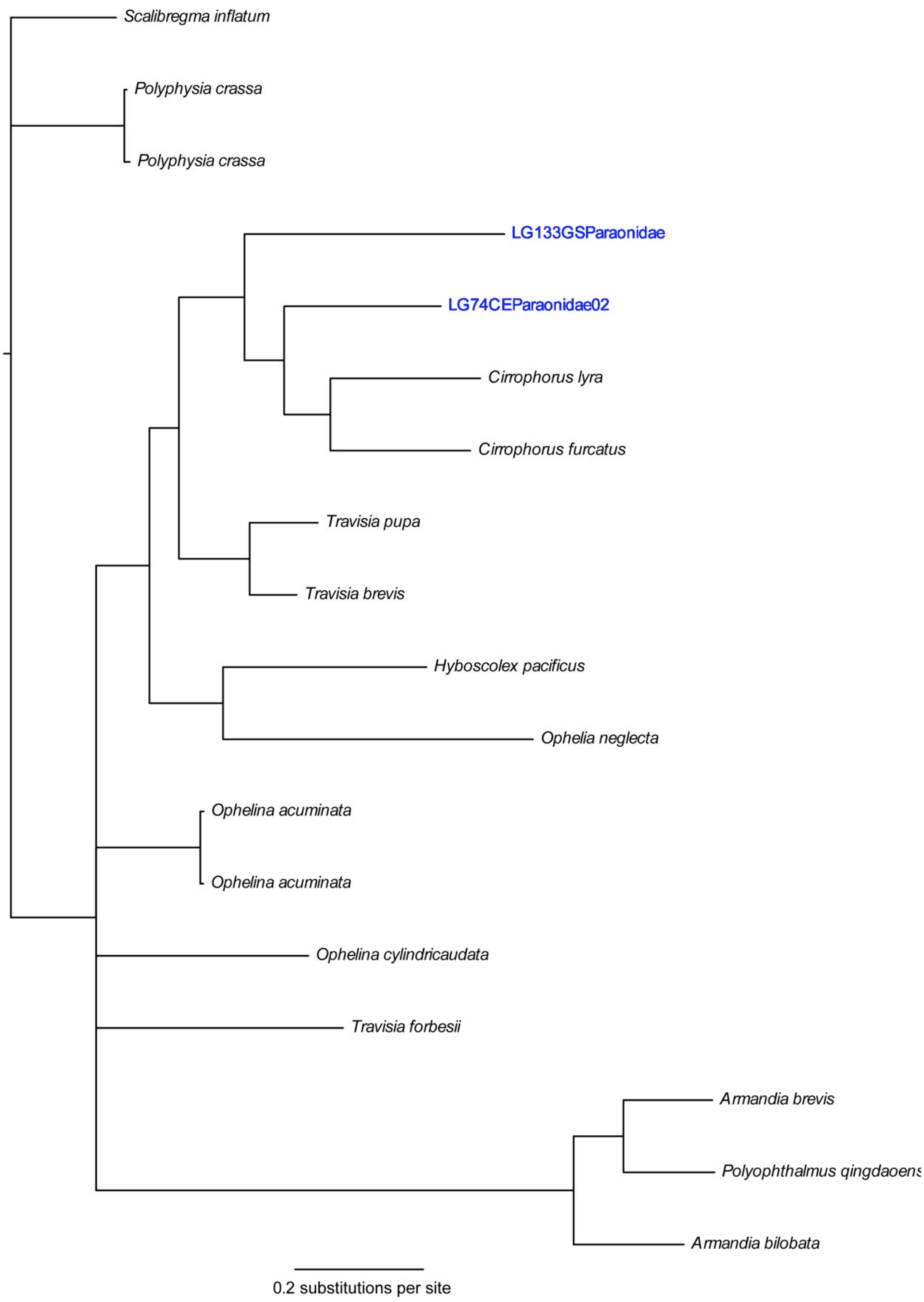


Figure A.9 Molecular phylogeny of the polychaete families Paraonidae and Opheliidae, based on16S (mtDNA) gene sequences.
Specimens from this study have the prefix "LG" and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

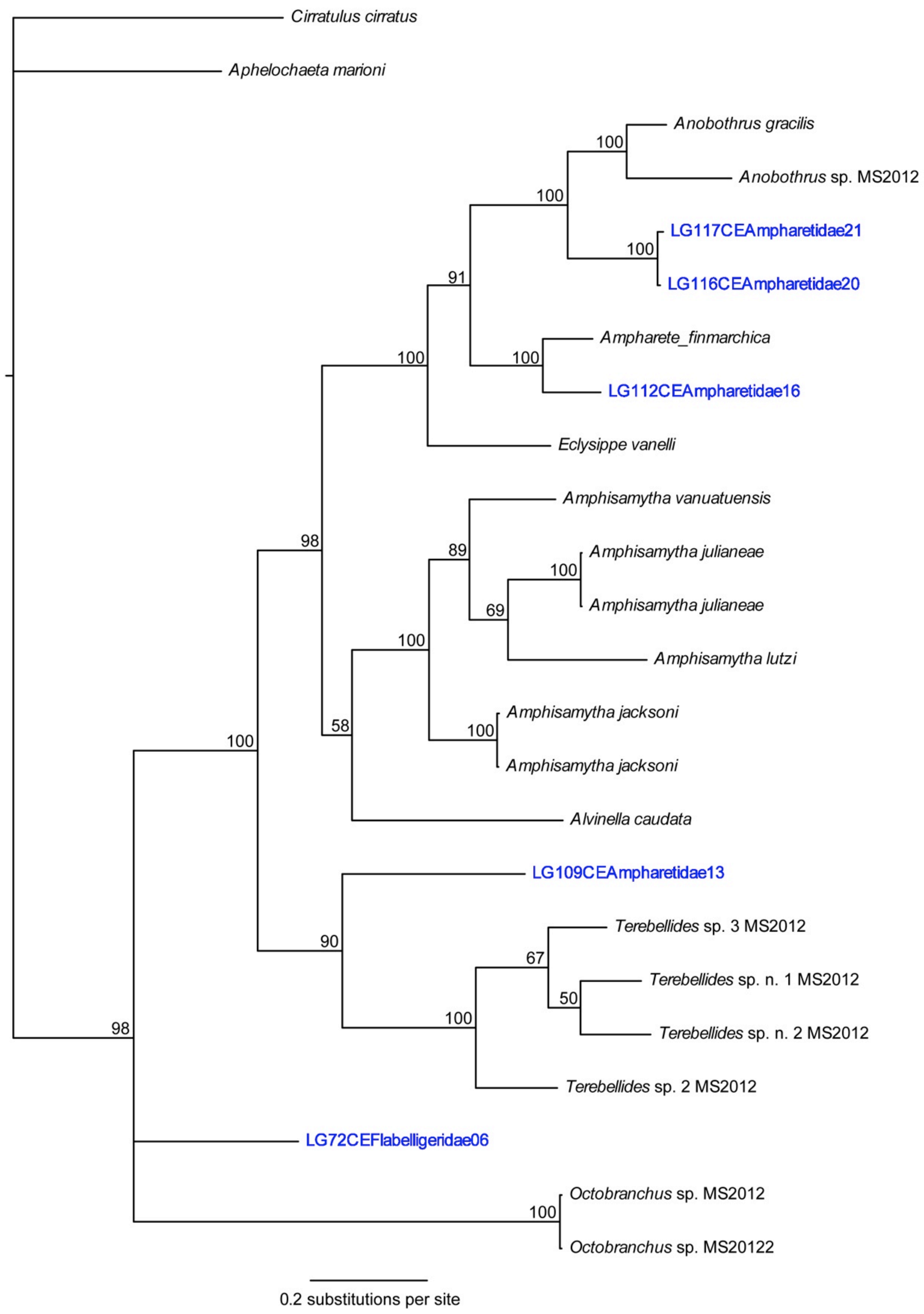


Figure A.10 Molecular phylogeny of the polychaete families Ampharetidae and Trichobranchidae, based on 16S (mtDNA) gene sequences.

Specimens from this study have the prefix “LG” and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

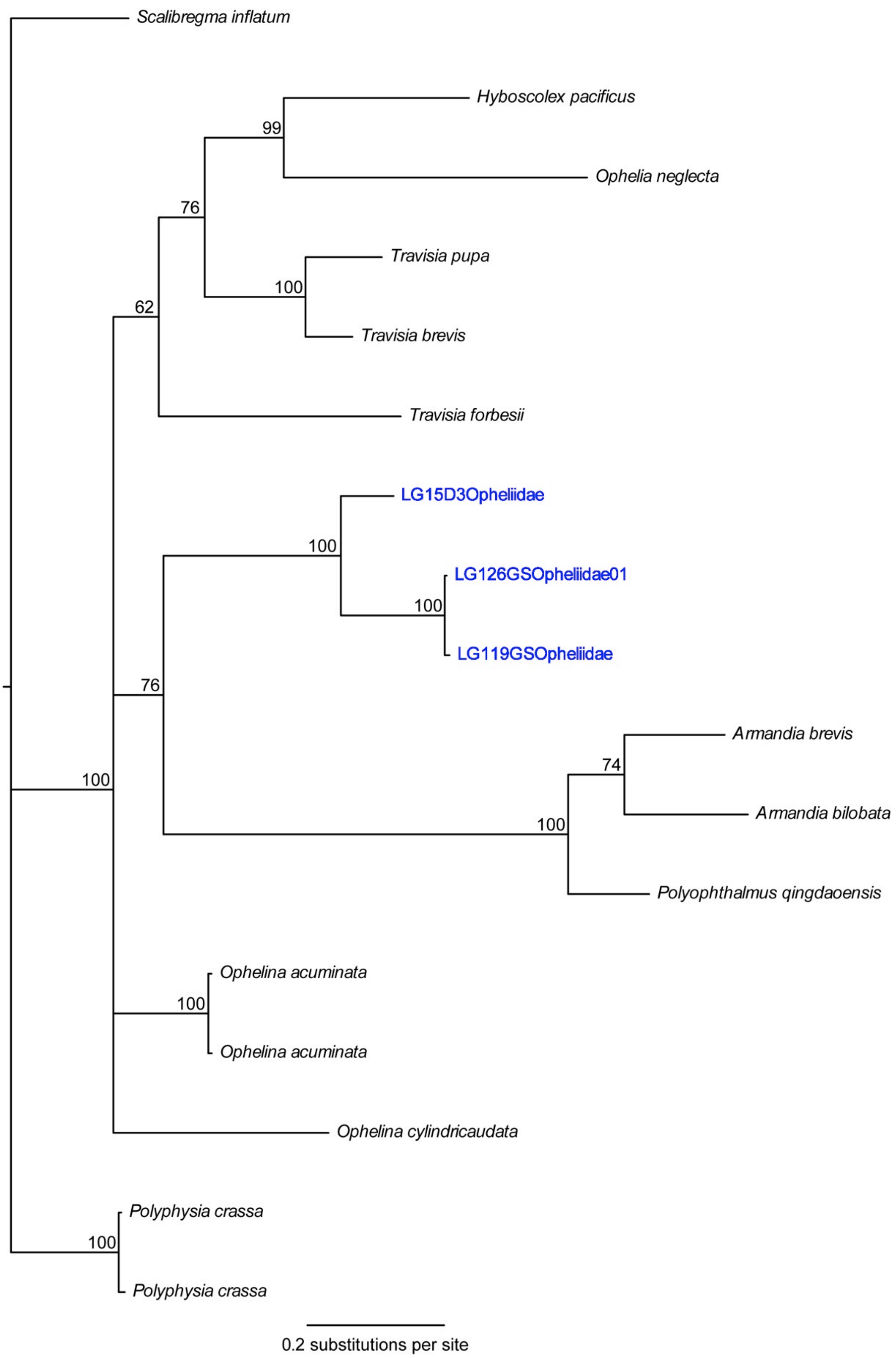


Figure A.11 Molecular phylogeny of the polychaete families Ampharetidae and Trichobranchidae, based on 16S (mtDNA) gene sequences.

Specimens from this study have the prefix “LG” and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

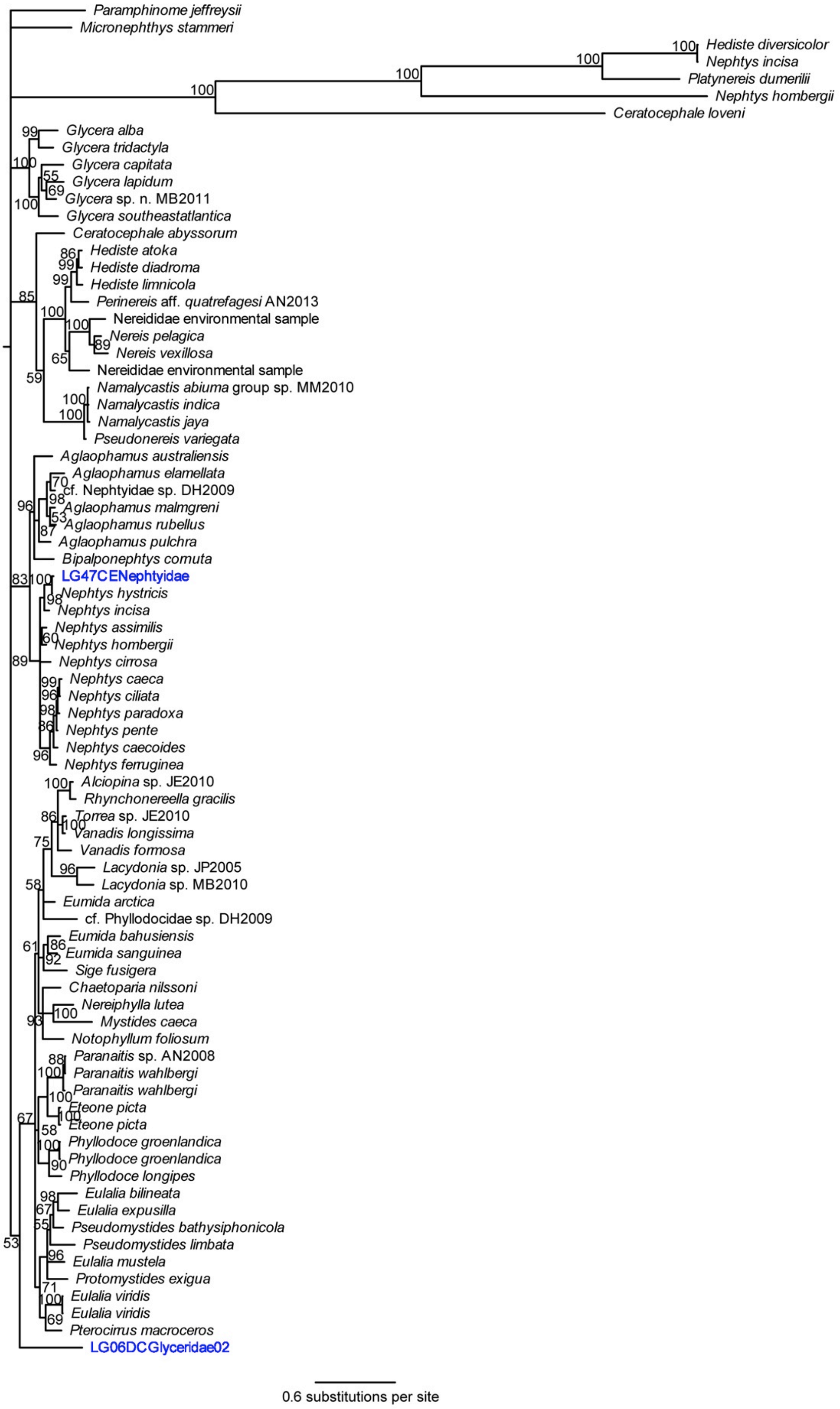


Figure A.12 Molecular phylogeny of the polychaete families Nephtyidae and Glyceridae, based on 16S (mtDNA) gene sequences.

Specimens from this study have the prefix “LG” and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

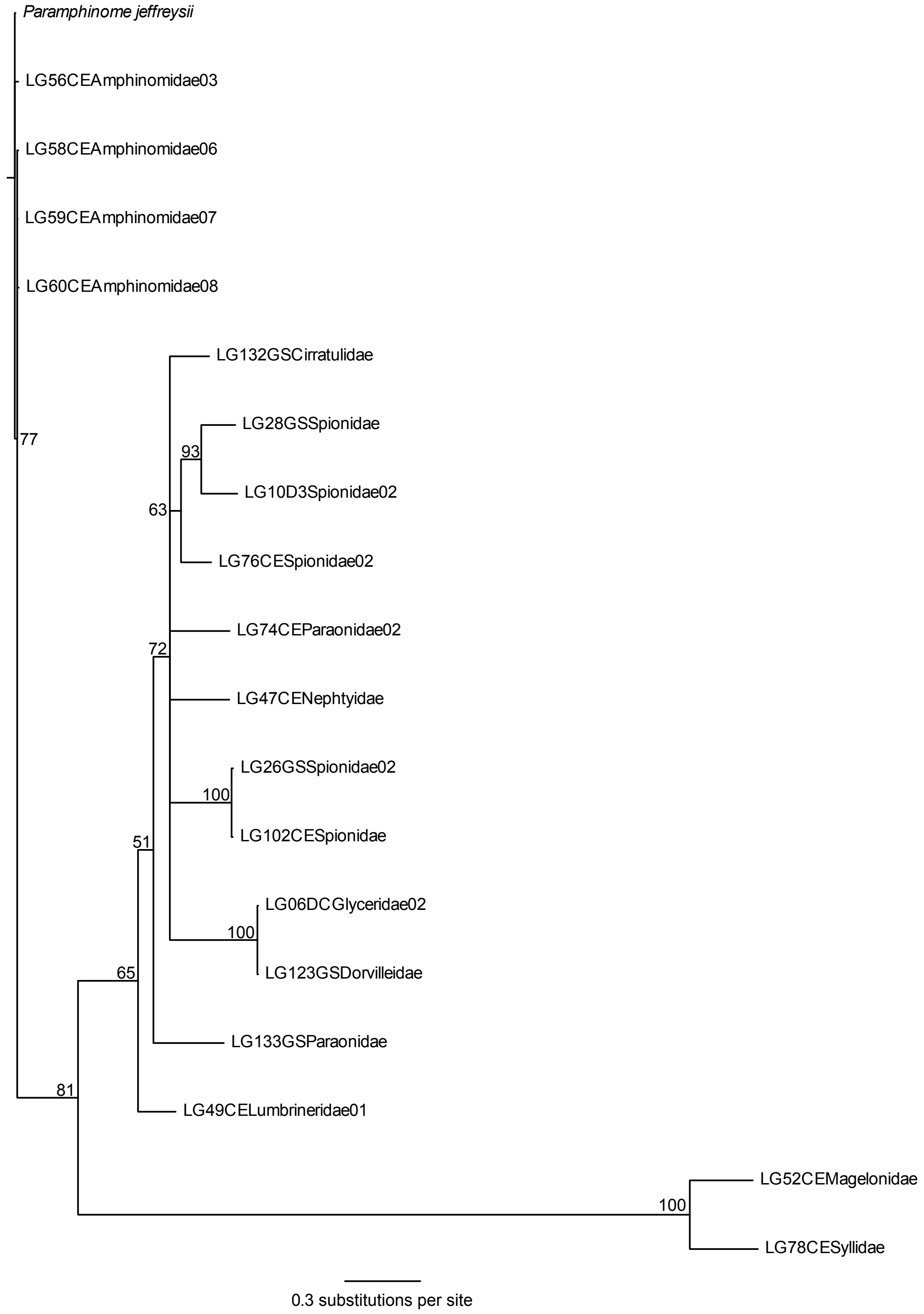


Figure A.13 Molecular phylogeny of all the polychaete families based on 16S (mtDNA) gene sequences.

Specimens from this study have the prefix "LG" and are shown in blue. Numbers indicate the posterior probability values out of 100. Values of 95 and over are regarded as significant.

Appendix B Supplementary tables

Appendix B

Table B.1 Macrofauna higher taxa count data

higher taxon raw data																				
Site	W	W	W	W	W	Sl	Sl	Sl	Sl	Sl	C	Cl	C	C	C	E	E	E	E	E
Station JC036	002	003	011	026	043	016	017	018	019	020	063	064	065	067	066/068	093	094	095/096	097	098
Area sampled m2	0.06	0.05	0.04	0.03	0.04	0.06	0.05	0.04	0.06	0.05	0.04	0.06	0.05	0.05	0.06	0.06	0.05	0.06	0.03	0.03
Higher Taxon																				
Amphipoda	4	3	2	1	14	2	0	2	0	0	11	21	10	11	32	14	14	19	8	7
Aplacophora	1	1	1	2	0	2	1	2	0	0	1	4	1	3	2	2	1	1	1	0
Ascidiacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Bivalvia	21	15	1	7	20	3	2	5	3	3	13	22	25	15	12	23	28	37	27	17
Cumacea	2	0	1	0	0	1	2	1	3	3	0	2	3	0	2	2	3	3	0	0
Echinoidea	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0
Gastropoda	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holothuroidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Isopoda	16	8	4	8	14	5	8	9	3	12	13	59	51	26	63	46	27	32	26	30
Nemertea	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ophiuroidea	7	8	4	1	9	8	4	1	7	1	6	2	6	2	7	9	4	13	12	3
Polychaeta	80	76	75	53	83	85	63	70	99	87	114	159	126	100	148	123	160	213	189	152
Scaphopoda	0	0	0	0	0	0	0	0	0	0	2	5	4	0	2	11	18	21	8	3
Sipuncula	21	17	32	10	11	20	11	16	22	24	18	19	14	3	11	13	20	24	13	1
Tanaidacea	10	14	11	5	19	38	36	29	36	20	30	27	12	5	16	26	27	43	17	9
Indet. worm	0	0	0	4	7	0	0	8	9	0	9	6	8	2	6	3	5	0	3	1
Macrofauna Indet.	8	3	5	3	3	4	11	4	0	0	0	0	2	0	6	1	0	1	2	0

Table B.2 Polychaete family count data

Polychaete family raw data																				
Site	W	W	W	W	W	Sl	Sl	Sl	Sl	Sl	C	C	C	C	C	E	E	E	E	E
Station JC036	002	003	011	026	043	016	017	018	019	020	063	064	065	067	066/068	093	094	095/096	097	098
Area Sampled m2	0.06	0.05	0.04	0.03	0.04	0.06	0.05	0.04	0.06	0.05	0.04	0.06	0.05	0.05	0.06	0.06	0.05	0.06	0.03	0.03
Family																				
Acrocirridae	0	0	2	3	8	5	5	3	12	4	5	2	3	0	1	0	2	5	3	3
Ampharetidae	0	0	3	1	1	8	6	5	1	6	0	2	0	1	0	1	0	0	0	1
Amphinomidae	11	19	7	9	21	12	5	5	14	5	38	53	31	24	38	43	50	79	76	48
Capitellidae	0	0	0	0	0	0	0	1	0	1	0	0	0	0	4	0	0	0	0	0
Cirratulidae	6	10	8	4	14	5	6	4	7	12	17	10	13	11	15	21	13	15	11	7
Chrysopetalidae	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0
Dorvilleidae	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0
Glyceridae	2	1	5	1	1	1	2	3	7	1	3	5	1	1	4	1	4	5	3	4
Hesionidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lumbrineridae	3	2	0	0	1	3	1	2	0	0	0	1	1	1	5	3	0	3	2	3
Maldanidae	1	2	1	4	2	0	0	1	1	0	3	3	3	5	0	4	6	3	2	0
Nephtyidae	3	0	1	1	1	0	0	0	1	0	3	5	1	3	1	3	3	4	1	7
Onuphidae	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Opheliidae	0	0	2	2	5	0	1	0	4	3	5	15	8	6	13	7	6	33	27	27
Orbiniidae	1	0	3	4	2	3	1	0	0	2	3	2	0	1	6	4	1	5	3	0
Paraonidae	15	6	3	5	3	5	6	7	7	8	11	20	18	16	12	8	23	11	19	9
Phyllodocidae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pilargidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Scalibregmatidae	1	2	2	0	0	0	1	3	1	1	0	2	1	1	1	1	1	1	1	2
Sigalionidae	3	9	4	2	0	6	0	1	1	2	0	1	4	2	0	0	3	2	0	0

Sphaerodoridae	0	0	0	0	0	0	0	0	1	0	0	0	1	24	0	0	0	0	0	0
Spionidae	12	18	32	12	12	19	21	24	24	28	15	31	30	0	42	19	39	37	35	39
Sternaspidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0
Syllidae	20	6	1	5	11	6	5	8	10	10	1	3	2	0	3	5	5	7	1	1
Terebellidae	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Polychaeta indet.	1	0	1	0	0	0	2	2	3	3	0	0	0	0	0	0	2	1	1	0
larva indet.	0	0	0	0	0	0	0	0	0	0	5	3	0	0	0	0	0	1	3	0

Table B.3 Polychaete species count data

			Slope					Western					Central					Eastern		
JC036-	016	017	018	019	020	002	003	011	026	043	063	064	065	066/068	067	093	094	095/096	097	098
no. core tubes	8	7	6	8	7	8	7	6	5	6	6	8	7	8	7	8	7	8	5	4
area sampled (m2)	0.06	0.05	0.04	0.06	0.05	0.06	0.05	0.04	0.03	0.04	0.04	0.06	0.05	0.06	0.05	0.06	0.05	0.06	0.03	0.03
Species																				
Aglaophamus cf. minusculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Aglaophamus sp. acirrate sunsu Hartman 1965	0	0	1	0	0	3	0	1	1	0	0	1	1	1	1	1	1	1	0	0
Ammotrypanella princessa	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	2	0	0	2	0
Ampharete cf. finmarchica	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Ampharetidae Genus A sp. A	5	2	4	1	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Amphicteis cf. gunneri	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Amphicteis sp. A	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0
Ancistrosyllis sp. A	0	0	0	0	0	20	7	0	3	6	1	0	0	1	0	0	0	0	0	0
Anguillosyllis capensis	4	4	7	9	6	0	0	1	1	1	0	0	0	0	0	1	0	1	0	1
Anobothrus patersoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Aphelochaeta sp. A	1	1	1	0	0	1	0	0	0	0	1	0	2	0	1	2	0	0	0	0
Aricidea (Acmira) catherinae	1	0	1	0	1	0	0	0	0	2	0	0	0	0	1	1	1	3	0	3
Aricidea (Acmira) simplex	2	0	0	1	0	0	0	1	0	0	1	2	2	0	1	2	4	3	5	0
Aricidea (Strelzovia) antennata	0	0	0	0	1	0	0	1	1	1	1	0	0	1	0	0	2	0	1	1
Aricidea (Strelzovia) quadrilobata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aricidea sp. A	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Augeneria cf. tentaculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Augeneria sp. A	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Aurospio dibranchiata	3	3	2	8	5	0	2	3	1	1	2	7	1	3	3	0	2	3	2	2
Aurospio sp. A	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	5	0

Appendix B

Aurospio sp. B	6	5	10	7	17	10	8	10	6	2	3	12	7	19	8	5	9	7	9	9
Capitella sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Capitellidae sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Cenogenus brevipes	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cenogenus fusca	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cenogenus sp. A	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ceratocephale sp. A	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Chaetopteridae sp. A	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Chaetozone sp. A	0	0	0	0	0	2	0	0	1	6	3	4	1	3	3	1	3	3	1	0
Chaetozone sp. B	0	0	0	5	1	0	0	2	0	0	2	1	2	1	1	3	0	1	0	0
Chaetozone sp. C	0	0	0	0	1	0	4	2	2	1	0	1	2	1	0	2	0	2	0	1
Chaetozone sp. D	0	0	0	0	1	0	0	0	0	0	0	0	3	2	0	1	0	0	0	1
Chaetozone sp. E	0	0	1	1	1	1	0	3	0	0	0	3	0	5	2	4	2	2	3	0
Chaetozone sp. F	3	3	1	0	4	3	2	1	2	2	6	4	4	1	3	1	0	1	3	3
Chaetozone sp. H	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Chrysopetalidae sp. A	0	1	0	0	2	0	0	0	0	0	1	0	2	0	0	1	0	0	0	0
Cirrophorus sp. A	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphrosinidae sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Exogone (Parexogone) cf. campoyi	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Exogone (Parexogone) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Exogone (Parexogone) wolfi	0	2	1	1	4	0	0	0	0	1	0	2	3	3	1	2	4	5	0	0
Flabelligella cf. biscayensis	2	4	4	3	4	0	0	1	3	4	2	0	2	1	0	0	1	1	2	3
Glycera capitata	0	2	3	5	1	1	0	4	0	1	3	5	1	4	1	1	2	4	3	4
Glycera cf. southeastatlantica	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyceridae sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glyphanostomum sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Hesionidae sp. A	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Laonice blakei	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0
Laonice sp. A	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
Laonice sp. B	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	2
Laonice sp. C	1	0	0	0	0	0	1	0	0	1	2	0	1	0	0	0	0	0	0	0
Leanira hystricis	4	0	1	1	0	3	7	1	2	0	0	1	0	0	1	0	0	0	0	0
Leitoscoloplos sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0
Leitoscoloplos sp. B	0	0	0	0	0	0	0	0	0	1	1	7	1	6	0	6	5	4	3	1
Levinsenia gracilis	1	2	1	1	4	9	4	1	7	0	4	4	6	5	2	0	1	1	1	1
Levinsenia oculata	0	0	0	0	0	0	0	0	0	0	2	3	0	1	1	0	0	1	0	2
Levinsenia sp. A	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0
Lumbrineridae sp. A	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Lumbrineris cf. cingulata	1	0	0	0	0	0	1	0	0	0	0	0	1	5	1	2	0	1	1	1
Maldanidae Genus 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Maldanidae Genus 2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	2	0	0
Maldanidae Genus 3	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Maldanidae Genus 4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Micronephthys minuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Myriochele sp. A	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nephtyidae sp. A	1	1	0	1	0	0	0	0	0	1	0	1	0	0	0	2	2	2	0	0
Notomastus sp.	0	0	2	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Opheliidae sp. A (juvenile)	1	0	0	1	0	0	0	0	0	0	2	3	4	1	0	2	9	16	25	21
Ophelina abranchiata	0	1	0	2	1	0	1	3	2	5	0	8	6	9	6	4	5	10	1	0
Ophelina cylindricaudata	0	0	0	1	0	0	0	0	0	0	4	3	4	4	3	2	3	7	0	1
Ophelina sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ophelina sp. B	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix B

Ophelina sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ophryotrocha sp. A	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Ophryotrocha sp. B	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Orbiniidae sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Paradiopatra cf. fragosa	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paradoneis abranchiata	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Paradoneis bathyilvana	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paramphinome jeffreysii	12	5	6	15	5	10	19	7	9	22	38	52	34	38	27	51	50	79	76	44
Polychaetae sp. A (larva)	0	0	0	0	0	0	0	0	0	0	4	3	9	0	0	0	0	7	3	0
Polynoidae sp. A (juvenile)	0	0	0	2	2	0	1	2	0	0	0	1	1	2	0	3	2	3	0	0
Prionospio sp. A	0	0	0	0	0	2	0	0	0	0	0	1	0	0	4	0	0	4	2	2
Prionospio sp. B	0	1	0	1	0	0	0	1	0	0	2	1	2	3	2	0	4	3	4	3
Prionospio sp. C	0	0	1	0	0	0	0	0	0	0	0	0	2	2	0	1	1	0	2	2
Prionospio sp. D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0
Prionospio sp. E	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	2	1	1	1
Prionospio sp. F	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Prionospio sp. G	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1
Prionospio sp. H	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Prionospio sp. I	0	7	6	4	5	1	1	13	2	1	1	6	1	5	1	4	11	5	6	12
Prionospio sp. J	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prionospio sp. K	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Prionospio sp. L	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	1	0	0
Progoniada regularis	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	2	1	0	0
Pseudoscalibregma parvum	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae sp. A	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sabellidae sp. B	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Scalibregma inflatum	0	0	1	0	0	1	2	0	0	0	0	1	1	2	1	0	2	1	1	0
Scalibregmatidae sp. B	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaerodoropsis sp. A	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Spiophanes sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Spiophanes sp. B	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Sternaspis sp. A	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0
Tanseimaruana vestis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebellinae sp. A	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tharyx sp. A	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Travisia sp. A	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grand Total	53	51	63	81	74	75	68	64	47	64	89	146	114	140	79	117	138	196	167	130

Appendix C Species identification sheets

C.1 Polychaete Identification Sheets

On CD-ROM. Polychaete species identification sheets for polychaetes recorded in the Whittard Canyon (also available at Figshare Part I: http://dx.doi.org/10.6084/m9.figshare.1561385 and Part II: http://dx.doi.org/10.6084/m9.figshare.1561384)

Appendix D Published papers

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Macrofaunal abundance and community composition at lower bathyal depths in different branches of the Whittard Canyon and on the adjacent slope (3500 m; NE Atlantic)

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ABSTRACT

We studied benthic macrofaunal abundance and community composition in replicate Megacorer samples obtained from three sites in different branches of the Whittard Canyon (NE Atlantic) and one site on the adjacent slope to the west of the canyon system. All sites were located at a depth of ~3500 m. Abundance (macrobenthos sensu stricto, $>300\ \mu m$) varied significantly ($p<0.001$) among sites, and decreased from east to west; highest in the Eastern branch (6249 ± standard deviation 1363 ind. m^{-2}) and lowest on the slope (2744 ± SD 269 ind. m^{-2}). Polychaetes were the dominant taxon, making up 53% of the macrofauna, followed by isopods (11%), tanaids (10%), bivalves (7%) and sipunculans (7%). Among the polychaetes, the Amphinomidae was the dominant family (27%), followed by the Spionidae (22%). Assemblage composition changed across the sites. From east to west, the proportion of polychaetes and isopods decreased (by 6% in each case), while sipunculans and tanaids increased (by 13% and 8%, respectively). The ranking of the two dominant polychaete families reversed from east to west (Eastern branch—Amphinomidae 36%, Spionidae 21%; Slope—Spionidae 30%, Amphinomidae 10%). Ordination of faunal groups (macrofaunal higher taxa, and polychaete families) revealed that the Central and Eastern branches were substantially similar, while the Western branch and slope sites were relatively distinct. A very similar pattern was evident in a corresponding ordination of environmental variables across the sites. An analysis of faunal similarities (ANOSIM) indicated that the Western branch/slope and Central branch/Eastern branch groups displayed the highest similarity. The clearest separation was between the slope and the Eastern branch. We conclude that, when compared at the same water depth, macrofaunal abundance and composition varies between open slope and canyon location, as well as among canyon branches. These differences probably reflect the influence of organic enrichment together with hydrodynamic activity, both of which are influenced by the topographic profile of individual canyon branches.

1. Introduction

Submarine canyons are major topographic features on continental margins. They play an important role as fast-track conduits for the transport of material from the shelf to abyssal depths (Vetter and Dayton, 1998). Organic carbon in the form of macrophyte detritus (Rowe et al., 1982; Vetter and Dayton, 1999), sediment (Arzola et al., 2008) and even pollutants (Palanques et al., 2008) are transported through canyons out onto the adjacent abyssal plain. Active canyons are believed to be very unstable environments that are subject to tidal currents, episodic slumps, sediment gravity flows, turbidity flows and periodic flushing events (Gardner, 1989; Canals et al., 2006; de Stigter et al., 2007). Topography (Shepard and Dill, 1966) and proximity to a fluvial source will also influence the disturbance regime. Although they have been known for over a century and a half (Dana, 1863), the rugged topography of canyons and the difficulty of sampling within them have limited multidisciplinary studies to the last 20 years (Ramirez-Llodra et al., 2010b). As a result, current knowledge of canyon benthic biology is poor.

Deep-sea macrofauna abundance decreases with depth (Rowe, 1983; Rex et al., 2006). However, this decline in abundance is far from uniform (Gage, 2003) and regions of high productivity can show elevated benthic abundance regardless of depth (Rex and Etter, 2010). In this regard, submarine canyons have been referred to as biomass and productivity 'hotspots' (De Leo et al., 2010; Vetter et al., 2010). Canyon sediments are reported to be richer in

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fresh organic carbon, total nitrogen, phytopigments (Garcia et al., 2007) and lithogenic (Romano et al., 2013) material than sediments on the adjacent slope. High organic enrichment inside canyons compared with the open slope has been linked to increased megafaunal (Vetter and Dayton, 1999; Ramirez-Llodra et al., 2010; Vetter et al., 2010; De Leo et al., 2010), macrofaunal (Rowe et al., 1982; Vetter and Dayton, 1998; Tyler et al., 2009; Duineveld et al., 2001; Paterson et al., 2011), meiofaunal (Ingels et al., 2009; Soetaert et al., 1991) and foraminiferal (Duros et al., 2011) densities. On the other hand, depressed faunal abundance inside canyons may be linked to frequent physical disturbance and high sedimentation rates (Gage et al., 1995; Koho et al., 2007).

As with faunal abundance, benthic community composition and diversity is influenced by the quality and quantity of food inputs (Gooday and Turley, 1990; Ruhl and Smith, 2004) and hydrodynamic disturbance (Thistle et al., 1985; Grassle and Morse-Porteous, 1987), as well as by water depth (Jumars and Gallagher, 1982; Flach et al., 2002), sediment grain size (Etter and Grassle, 1992; Leduc et al., 2012), sediment mobility (Levin et al., 1994) and bottom-water oxygen concentration (Levin et al., 2000). Many of these factors are thought to interact, regulating biological communities within canyons (McClain and Barry, 2010).

Evidence from the High Energy Benthic Boundary Layer Experiment (HEBBLE) site (Thistle and Sherman, 1985; Thistle and Wilson, 1987, 1996; Thistle et al., 1991, 1999) suggests that elevated levels of disturbance inside canyons, such as those caused by currents, will structure the faunal assemblage differently compared with more quiescent slope environments. Taxa such as tanaids that are able to burrow into the sediment and hide from disturbance (Reidenauer and Thistle, 1985) gain an advantage, while suspension-feeding organisms (sponges and corals) benefit from enhanced bottom currents inside canyons (Rowe, 1971) and deposit-feeding organisms can benefit from the increased levels of macrophyte detritus (Okey, 1997). Opportunistic species will also be favoured in areas of high disturbance (Paterson et al., 2011). The diverse current regimes, varying substratum types, and detrital funneling from the continental shelf, will combine to enhance habitat heterogeneity within canyons (Levin et al., 2010). Large sessile megafauna add to the habitat complexity, and cold-water corals provide habitats and refuges from predators for a variety of taxa (Buhl-Mortensen et al., 2010). Thus, a greater diversity of microhabitats is available to canyon inhabitants compared with those living on the open slope. Such factors may explain differences in community composition between canyons and adjacent slopes sites located at similar depths (Vetter and Dayton, 1998; Duineveld et al., 2001; Garcia et al., 2007).

The Whittard Canyon is a dendritic submarine canyon system on the NW European continental margin. Previous studies have shown that this feature hosts increased foraminiferal (Duros et al., 2011) and nematode (Ingels et al., 2011) abundances compared with the open slope. Hunter et al. (2013) reported high macrofaunal abundances inside the canyon. Duineveld et al. (2001) reported a significantly higher macro- and mega-faunal biomass inside the canyon compared with the slope, but no significant difference in macrofaunal abundance. Increased taxon richness and abundance in the Whittard Canyon have also been reported for cold-water corals (Morris et al., 2013). There are no previous studies, however, of macrofaunal abundance and community composition across the canyon system. With this in mind, the present study investigates these faunal parameters at the higher taxon level for the macrofauna as a whole, and at the family level for the dominant macrofaunal group (polychaetes) at the same water depth within different branches of the Whittard Canyon and on the adjacent slope. We aim to test whether (1) macrofaunal abundance is enhanced inside the Whittard Canyon relative to the adjacent slope, (2) community composition inside the canyon is distinct from that on the adjacent slope, and (3) canyon assemblages are distinct on an intra-canyon scale.

2. Material and methods

2.1. Study area

The Whittard Canyon is located on the Irish margin, southwest of the British Isles and southeast of the Goban Spur, and is not directly connected to any rivers. It starts around the shelf break at about 200 m water depth and extends to a depth of 4000 m over a distance of about 110 km. Three main branches, the Western, Central and Eastern, are recognised within the canyon system (Fig. 1). These branches coalesce around 3700 m to form a single canyon that opens out on to the Porcupine Abyssal Plain. The upper part is very steep-sided with walls reaching a height of up to 800 m, but at depths of around 3600 m the walls are lower (Hunter et al., 2013). The mouth of the canyon discharges into a large fan, 148 km long by 111 km wide (Reid and Hamilton, 1990).

The sediments in the upper part of the canyon are coarse compared with those further down (Hunter et al., 2013). The sediment is characterised by silty clay and fine sand in the Western branch (~3000 m), whereas sandy silt and fine sand predominate in the Eastern branch (~3000 m). The slope to the west of the canyon system is characterised by sand and silt (Duros et al., 2012). Some of the canyon sediments are derived from the shelf, which presumably provides a significant proportion of the material that passes down the canyon system at present (Reid and Hamilton, 1990; Cunningham et al., 2005).

Evidence about the levels of activity within the Whittard Canyon is ambiguous. Reid and Hamilton (1990) report small slope failures and a semi-diurnal tidal current only strong enough to transport fine-grained material. However, there is also evidence for active down-slope sediment transport in the form of turbidity currents, as well as mud-rich flows large enough to overspill the canyon system and form overbank deposits (Cunningham et al., 2005). Near-bottom currents reaching a maximum speed of 16 cm s^{-2} have been reported at 3752 m depth inside the canyon (Reid and Hamilton, 1990). Tidal currents with speeds up to 40 cm s^{-1} at 1000 m and up to 20 cm s^{-1} at 2000 m were recorded in the Eastern and Western branches (de Stigter in Duros et al., 2011). Sediment fluxes down the Whittard Canyon have not been well quantified and how they vary between the different branches remains unknown.

The present study focuses on sites located at the same depth (~3500 m) in the Western, Central and Eastern branches. Previous studies reported differences in environmental parameters between the Western and Eastern branches at similar depths. These published data are summarised in electronic Supplementary information (Table S1).

2.2. Field sampling

Macrofauna were collected from three sites in different branches of the canyon and one site on the adjacent slope (Fig. 1) using a Megacorer (Gage and Bett, 2005) during the RRS *James Cook* cruise 036 in June and July 2009. Samples were taken from 22 deployments (Table 1), between 3373 and 3670 m depth. In general, the Megacorer was fitted with eight large (100 mm internal diameter) core tubes. However, for one deployment at each site, one of the large tubes was replaced with a single smaller (59 mm internal diameter) tube. This collected a core that was used for sediment grain-size analysis.

Five replicate deployments were conducted in the Western branch, six in the Central branch, six in the Eastern branch and five

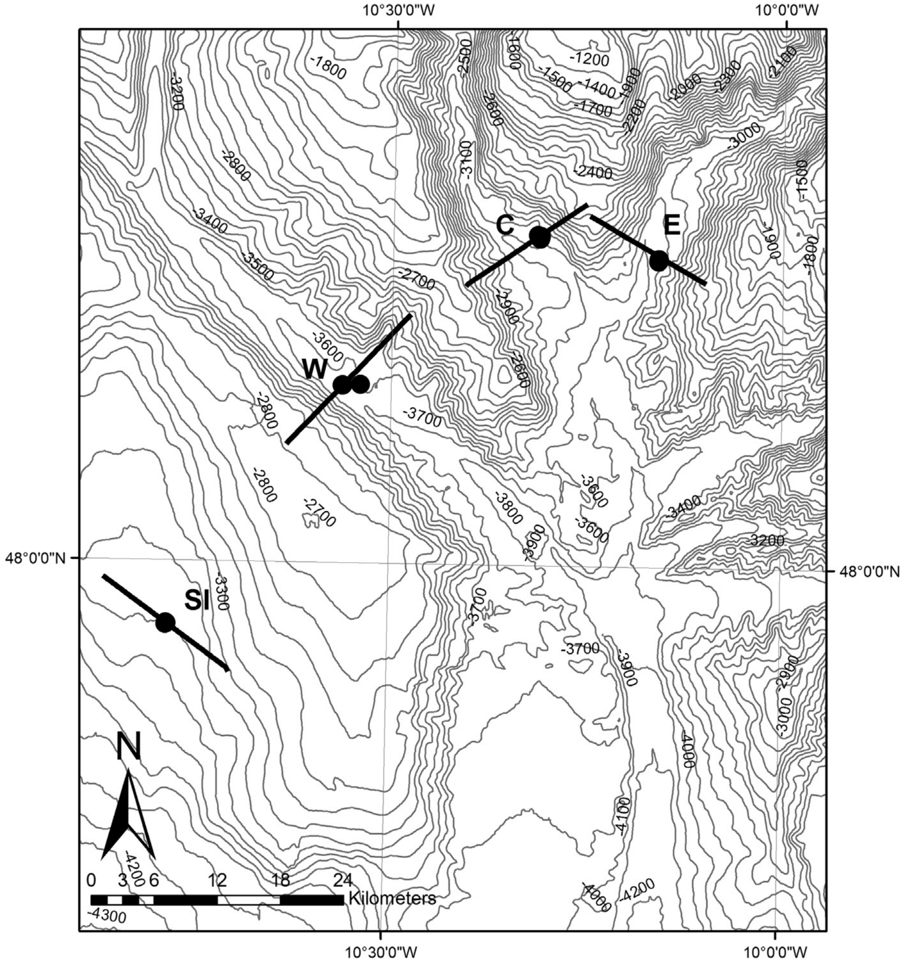

Fig. 1. Bathymetric chart of Whittard Canyon, based on data provided by the Geological Survey of Ireland (www.gsiseabed.ie). The four study sites are indicated: Western branch (W), Central branch (C) and Eastern branch (E) of the canyon and one site on the adjacent slope (Sl). Contour lines are given in metres. Solid lines represent transverse bathymetric profiles shown in Fig. 2.

Table 1
Station list. Megacore deployments on RRS *James Cook* cruise 36, Whittard Canyon and adjacent slope. W, Western branch; Sl, Slope site; C, Central branch; E, Eastern branch. MGS, mean grain size. Percentage clay, silt and sand (Wentworth, 1922).

Deployment	Date (dd/mm/09)	Latitude North	Longitude West	Depth (m)	Area sampled (m^{-2})	Slope angle (°)	Rugosity × 10^{-6})	Fine-scale BPI	MGS (μm)	Clay (%)	Silt (%)	Sand (%)
Sl016	24/06	47°56.79	10°46.85	3511	0.063	0.93	14	– 20				
Sl017	24/06	47°56.78	10°46.85	3512	0.055	0.93	15	– 20				
Sl018	24/06	47°56.81	10°46.91	3514	0.047	0.93	6	– 20				
Sl019	24/06	47°56.74	10°46.94	3505	0.063	0.93	11	– 17	71.8	16.5	56.7	26.8
Sl020	25/06	47°56.78	10°46.85	3514	0.055	0.93	14	– 20				
W002	20/06	48°09.18	10°33.70	3670	0.063	2.36	161	3	28.8	13.3	74.2	12.5
W003	21/06	48°09.17	10°33.70	3661	0.055	2.36	165	3				
W011	23/06	48°09.22	10°32.36	3582	0.047	0.20	6	30				
W026	27/06	48°09.18	10°33.73	3670	0.039	2.36	138	– 10				
W043	08/07	48°09.15	10°33.76	3657	0.047	2.36	113	– 10				
C063	13/07	48°16.89	10°18.74	3375	0.047	2.49	140	– 81	26.9	12.0	77.9	10.1
C064	13/07	48°16.97	10°18.65	3382	0.063	2.49	610	– 109				
C065	13/07	48°17.04	10°18.89	3373	0.055	3.35	239	– 118				
C067	13/07	48°16.98	10°18.72	3376	0.055	3.88	448	– 106				
C066	13/07	48°16.83	10°18.72	3381}	0.063	2.75	187	– 91.5				
C068	13/07	48°17.01	10°18.83	3375								
E093	21/07	48°15.89	10°09.56	3424	0.063	3.15	92	– 27	32.7	10.6	75.5	13.9
E094	21/07	48°15.78	10°09.57	3429	0.053	3.36	92	– 23				
E095	21/07	48°15.78	10°09.58	3429}	0.063	3.35	1150	– 23				
E096	22/07	48°15.76	10°09.60	3424								
E097	22/07	48°15.89	10°09.54	3425	0.039	3.15	88	– 28				
E098	22/07	48°15.76	10°09.60	3432	0.031	3.35	131	– 23				

at the slope site. The additional deployment in the Central and Eastern branches was made to compensate for the failure to recover enough cores during earlier deployments. On deck, the individual cores from each deployment were sliced into five sediment layers (0–1, 1–3, 3–5, 5–10 and 10–15 cm). Core slices from the same layer of the different cores from one deployment were placed in the same 20 l bucket. The contents of the bucket were then homogenised to produce one combined sample for each layer (i.e. five combined samples for each deployment). The overlying water was added to the 0–1 cm layer. The combined samples (one for each sediment layer) were then carefully washed with filtered (mesh size 125 μm) seawater on 500 and 300 μm sieves. The >500 μm residues from each combined sediment layer from one deployment were placed in one 5 l plastic tub and fixed with 10% borax-buffered formalin. The same was done for the 300–500 μm residues. Thus each deployment yielded two combined sieve fractions for each of the five sediment layers.

2.3. Environmental data

A post-processed bathymetry map of the Whittard Canyon (cell size 10×10 m) was downloaded from the INFOMAR website (www.gsiseabed.ie/). The steepness of the terrain at each site was calculated using the ArcMap 10 (ESRI) Spatial Analyst geoprocessing tool 'Slope' applied to the bathymetry map. The Slope tool calculates the maximum rate of change between each cell and its immediate neighbours in a 3×3 cell window. The Benthic Terrain Modeler ArcGIS Desktop Extension alpha version (Wright et al., 2005) was used to calculate the fine-scale bathymetric position index (BPI) and vector ruggedness measure (VRM) from the bathymetry data. BPI is a scale-dependent index representing a grid cell's topographic location within a benthic landscape relative to its local surroundings; the fine-scale BPI allows the identification of smaller features within the benthic landscape (Wright et al., 2005). VRM is the variation in three-dimensional orientation of grid cells within a neighbourhood (3×3 window). Transverse bathymetric profiles of the canyon branches and the slope were derived using the ArcMap profile view tool.

Cores for sediment particle-size analysis (Table 1) were sliced on deck into 12 layers (0.5 cm layers between 0 and 2 cm depth and 1 cm layers between 2 and 10 cm). Each layer was placed in a 500 ml bottle and fixed in 10% buffered formalin. Only the 0–0.5, 1–1.5, 2–3 and 4–5 cm sediment layers were analysed as other layers were not available. Each layer was first homogenised (particles >2 mm removed), dispersed using a 0.05% $(NaPO_3)_6$ solution and mechanically agitated before being analysed using a Malvern Mastersizer 2000 laser diffraction particle size analyser (Abbireddy and Clayton, 2009).

2.4. Macrobenthos processing

The top three sediment layers (0–1, 1–3, 3–5 cm) were analysed for this study. The samples were transferred from the formalin onto a 300-μm-mesh sieve, rinsed with 70% ethanol to remove the formalin and then sorted for macrofauna, also in 70% ethanol. The 300–500 μm and >500 μm fractions were processed separately. All specimens were sorted to major taxa (phylum or class) under a Leica MZ9.5 stereomicroscope. We followed common practice in deep-sea studies by considering only the macrofauna sensu stricto (Gage and Tyler, 1991; Bett, 2014), i.e. meiofaunal taxa (foraminifera, copepods, nematodes, and ostracods) were excluded.

The polychaetes were identified to family level based on morphological characters visible under a light microscope and identified by reference to taxonomic keys (Hayward and Ryland, 1996; Beesley et al., 2000). Where fragmented specimens were encountered, only head fragments were counted.

2.5. Data analyses

Macrofaunal counts were standardised to unit seafloor area sampled (i.e. density, ind. m^{-2}), and subject to a log $(x+1)$ transformation prior to analysis. Before analyses were performed, the ANOVA assumptions of normality and homogeneity of variance were evaluated using Anderson-Darling and Levene's tests, respectively. Density data satisfied tests of ANOVA assumptions. Thus, ANOVA and Tukey Pairwise tests were performed on density data. Mood's Median tests were used to test for significance of slope, rugosity and fine-scale BPI. These univariate tests were carried out using the Minitab statistical software package (v16, LEAD Technologies, 2010).

Multivariate analyses were executed using the PRIMER software package (Clarke and Gorley, 2006; v6, PRIMER-E Ltd). Macrobenthos data were assessed via non-metric multidimensional scaling (MDS) based on Bray Curtis similarity of log transformed density. Global and pair-wise analysis of similarities (ANOSIM) was employed to assess the distinctiveness of canyon and slope study sites. Environmental data were assessed via principal components analysis (PCA) of normalised data (i.e. transformed to zero mean, and unit variance). In the absence of direct measurement, macrofaunal abundance was used as a proxy for organic matter input. Global macrofaunal abundance in the deep sea has been predicted from the incoming flux of organic matter (Rex et al., 2006; Wei et al., 2010). Similarly, the metabolic theory of ecology (Brown et al., 2004) predicts that carrying capacity (faunal abundance) is directly related to resource supply where habitat and temperature are constant. Organic matter supply to the seafloor is normally estimated from surface primary productivity and water depth (e.g. Lutz et al., 2007), but this would fail to account for the funnelling action of the canyon system.

3. Results

3.1. Environmental characteristics

3.1.1. Bathymetry and derivatives

The slope angle of the seafloor at sites sampled inside the canyon branches was fairly uniform, ranging from means of 2.36° (Western branch) to 3.27° (Eastern branch) (Table 1). The angle on the adjacent slope was much lower (mean 0.93°). There was a statistically significant difference in slope between all four sites (Mood's Median Test: Slope versus Location $p<0.001$). Bathymetric position index (BPI) values were higher in the Western branch and on the slope (representing higher points/crests in terrain compared with the surroundings) than in the Eastern and Central branches, and statistically different between all four sites (Mood's Median Test: BPI versus location $p<0.001$). Rugosity was highest in the Central branch and lowest on the slope (Table 1); again the differences were significant between all four sites (Mood's Median Test: rugosity versus location $p=0.015$). Canyon profiles are approximately "U" shaped (Fig. 2), most clearly so in the case of the Eastern branch, which has the narrowest branch width. The Western branch is wider with a flatter floor than the Eastern and Central branches. The flat slope profile in Fig. 2 is included for comparison.

3.1.2. Sedimentology

The three canyons sites (Western, Central and Eastern branches) had similar mean particle sizes (28.8, 26.9 and 32.7 μm, respectively) (Table 1). The slope site had a significantly coarser sediment (mean particle size 71.8 μm) (Fig. 3). At all four sites the sediment was composed predominantly ($>56\%$) of silt (grain size 4–63 μm). The Central branch sediment had a slightly higher percentage of silt

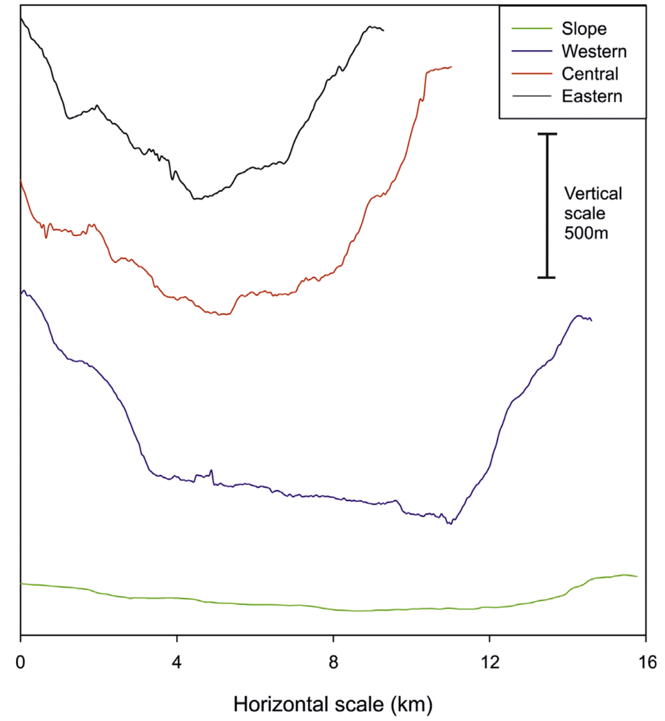

Fig. 2. Slope-normal bathymetric profiles through the study sites in the Eastern, Central and Western canyon branches, and on the adjacent open slope.

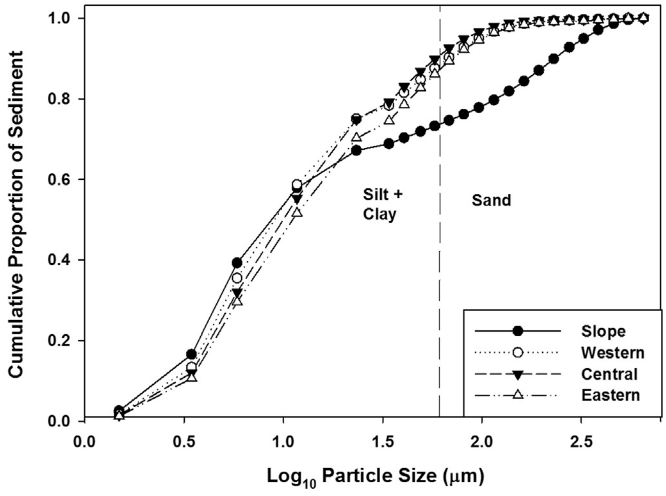

Fig. 3. Cumulative sediment particle size distribution at three canyon branch sites and adjacent open slope site.

(77.9%), than the Eastern (75.5%) and the Western (74.2%) branches, while the slope sediment had a much lower silt content (56.7%) (Table 1). Clay content (grain size < 4 μm) was highest on the slope (16.5%) and decreased inside the canyon from the Western (13.3%) to the Eastern (10.6%) branches. The slope sediment had a distinctly higher percentage of sand (26.8%) compared with the canyon sites (< 13.9%), where the percentage was lowest in the Central branch (10.1%).

3.1.3. *Principal component analysis*

A PCA was performed on the following environmental variables (Fig. 4): sediment grain size, slope angle, fine-scale BPI, VRM and station depth (Table 1), with macrofaunal density used as a proxy for organic matter (OM) input. The four study sites were quite discrete in the ordination space formed by the first two axes. The differentiation of canyon and slope sites appeared to align with the environmental vectors of sediment grain size, rugosity, slope angle and fine-scale BPI. Differentiation of the Western from the Central and Eastern branches appeared to align with water depth and proxy organic matter supply (macrofaunal density).

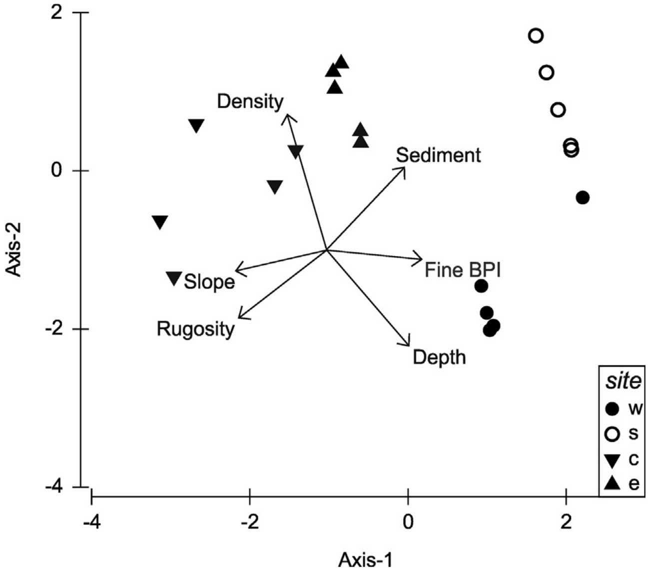

Fig. 4. Principal components analysis of normalized environmental variables at canyon and slope sites. The variables are depth, mean grain size (sediment), slope angle, rugosity, fine-scale Bathymetric Position Index (BPI) and macrofaunal density (as a proxy for organic matter supply).

3.2. *Macrobenthos*

3.2.1. *Total abundance*

In total, 4444 macrofauna individuals were picked from the samples. Fifty-three percent of the fauna was retained on the 500 μm sieve. There was a significant differences in abundance between sites (One-way ANOVA, $p < 0.001$, R^2 (adj)=76.32%). Pairwise comparison revealed that the Central and Eastern branches were significantly different ($p < 0.05$) from the Western branch and slope. The Eastern branch had the highest abundance of macrofauna (6249 ± SD 1363 ind. m^{-2}). Values were intermediate in the Central branch (4461 ± SD 856 ind. m^{-2}) and lowest in the Western branch (2900 ± SD 538 ind. m^{-2}) (Table 2). The abundance decreased across all sites from east to west, with the slope site having the lowest value (2744 ± SD 269 ind. m^{-2}) (Table 2).

3.2.2. *Major taxon composition*

Sixteen higher taxa were recognised in the canyon and slope samples (Table 2). Polychaeta was always the most abundant taxon, making up just over 50% of the macrofauna with 2255 individuals in total and an average density of 2191 ind. m^{-2} for the 0–5 cm layer. The tanaids (10%; 397 ind. m^{-2}), isopods (11%; 432 ind. m^{-2}), sipunculans (7%; 297 ind. m^{-2}) and bivalves (7%; 288 ind. m^{-2}) were also important faunal components.

Although polychaetes always represented > 50% of the assemblage in each branch, the proportion of other taxa varied between branches (Fig. 5A). The percentage of sipunculans (13%) was higher in the Western branch compared with Eastern (4%) and Central (5%) branches. The Eastern and Central branches had higher percentages of isopods (11% and 16% respectively) than the Western branch (6%). The tanaids maintained fairly similar percentages throughout the branches, as did the bivalves. The slope fauna was more similar to the

Table 2
Density of macrofaunal taxa at three canyon sites and on the adjacent slope. Values are mean densities ($n=5$) for the 0–5 cm sediment layer, based on the $>300\ \mu m$ sieve size fraction.

Taxon	Abundance (ind. m^{-2})			East
	Slope	West	Central	
Amphipoda	14.9	96.7	291.8	241.3
Aplacophora	18.5	21.3	37.9	18.3
Ascidiacea	0.0	0.0	0.0	5.1
Bivalvia	58.5	246.2	309.0	538.7
Cumacea	35.2	10.6	23.7	26.8
Echinoidea	0.0	5.1	7.3	8.3
Gastropoda	0.0	5.1	0.0	0.0
Holothuroidea	0.0	0.0	0.0	5.1
Isopoda	136.4	197.2	723.8	670.0
Nemertea	0.0	3.6	3.6	0.0
Ophiuroidea	70.2	111.7	83.2	164.8
Polychaeta	1386.9	1468.7	2236.6	3557.4
Scaphopoda	0.0	0.0	45.3	227.2
Sipuncula	329.0	362.2	233.8	263.2
Tanaidacea	562.5	235.6	326.1	461.8
Indet. worm	62.6	50.1	112.8	49.4
Unknown	69.7	85.6	26.4	16.6
Total	2744	2900	4461	6249

Western branch than to the Central and Eastern branch fauna and in this sense it fitted in with a gradient of change of macrofauna composition across the four sites. The slope had a high percentage of sipunculans (12%) and tanaids (20%) but a low percentage of isopods (5%) and bivalves (2%). These percentages were similar to the Western branch values: sipunculans (13%), tanaids (10%), isopods (6%) and bivalves (7%).

The numerical abundance of macrofauna displayed some of the same trends as the percentage abundance data (summarised in Table 2). Isopods had a high abundance in the Central and Eastern branches, but a much lower abundance in the Western branch, whereas sipunculans had a higher abundance in the Western branch compared with the Eastern and Central branches. Different trends were seen in other higher taxa. Tanaids were most abundant in the Eastern branch and less abundant in the Central and Western branches. Bivalves exhibited a similar east to west decline.

Numbers at the slope and Western branch sites were fairly similar for the sipunculans and isopods (summarised in Table 2). For other taxa there were larger differences. The tanaids were almost twice as abundant on the slope compared with the Western branch. Bivalves were four times more abundant in the Western branch than on the slope.

3.2.3. Multidimensional scaling analysis of major taxa

Differences between canyon branches in the major macrofaunal taxon composition are reflected in the corresponding MDS plot (Fig. 6A), which shows samples from the Central and Eastern sites intermingled and quite distinct from the Western branch and slope site samples. Two macrofaunal samples (Sl019 and Sl020) from the slope were distinct from the rest of the slope samples. The Western branch and remaining slope sites formed separate but adjacent grouping. ANOSIM global assessment indicated statistically significant ($p=0.001$) variation among the sites. Significant ($p<0.05$) pairwise differences were detected between Western/Central branches, Western/Eastern branches, slope/Central branch and slope/Eastern branch (Table 4).

3.2.4. Polychaete family composition

In total, 2225 individual polychaetes were picked from the samples. Their abundance showed significant differences between sites (One-way ANOVA: $p<0.001$, R^2 (adj)=70.92%) and followed the same patterns as the macrofauna. A Tukey pairwise test revealed that the Eastern and Central branches were significantly ($p<0.05$) different from the Western branch and slope. The polychaetes represented 26 families (Table 3). The most abundant were the Amphinomidae, with an overall average density of 582 ind. m^{-2} (27%), followed by the Spionidae (480 ind. m^{-2}; 22%), Paraonidae (202 ind. m^{-2}; 9%), Cirratulidae (196 ind. m^{-2}; 9%) and Opheliidae (172 ind. m^{-2}; 8%).

Polychaete composition differed between branches (Fig. 5B). The Eastern branch had the highest numbers of Amphinomidae (1270 ind. m^{-2}) compared with the other sites. This family represented 36% of the polychaetes compared with 29% in the Central branch and 18% in the Western branch. The same pattern was seen in the Ophellidae; 13% in the Eastern branch and 3% in the

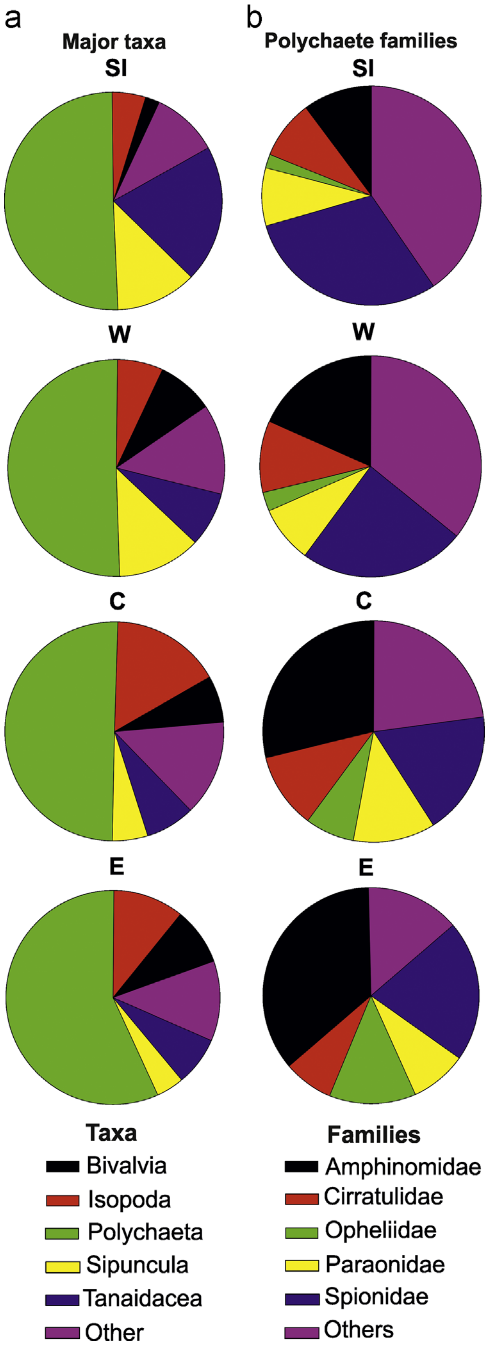

Fig. 5. Relative abundance of top five taxa at the three canyon branch sites (W, E, C) and adjacent slope site (Sl). (A) Macrofaunal major taxa, (B) polychaete families.

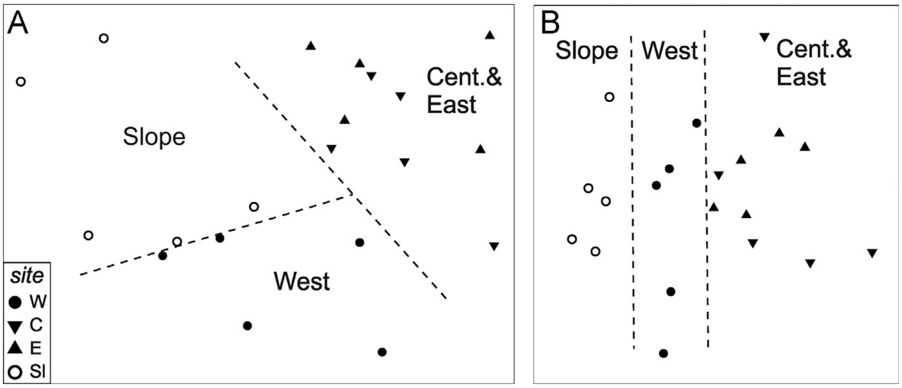

Fig. 6. Non-metric multidimensional scaling ordinations of (A) macrofaunal major taxa, and (B) polychaete families, for five replicate samples at each of the three canyon branch sites (W, E, C) and adjacent slope site (Sl).

Table 3
Density of polychaete families at three canyon sites and on the adjacent slope. Values are mean densities ($n=5$) for the 0–5 cm sediment layer, based on the > 300 μm sieve size fraction.

Family	Abundance (ind. m^{-2})			East
	Slope	West	Central	
Acrocirridae	99.6	57.7	41.7	57.6
Ampharetidae	93.5	22.1	10.0	9.6
Amphinomidae	140.4	265.2	651.1	1269.5
Capitellidae	7.9	0.0	12.7	0.0
Cirratulidae	120.7	169.3	239.1	262.5
Chrysopetalidae	0.0	0.0	11.5	3.2
Dorvilleidae	6.4	0.0	4.2	0.0
Glyceridae	49.1	40.6	48.7	74.4
Hesionidae	0.0	4.2	0.0	0.0
Lumbrineridae	21.7	21.1	26.4	48.4
Maldanidae	7.4	43.6	51.4	54.3
Nephtyidae	3.2	23.1	46.4	82.9
Onuphidae	6.8	0.0	0.0	0.0
Opheliidae	27.3	39.9	161.3	458.6
Orbiniidae	20.5	44.8	41.8	47.6
Paraonidae	118.9	120.5	272.3	298.3
Phyllodocidae	3.2	0.0	0.0	0.0
Pilargidae	0.0	0.0	3.6	0.0
Scalibregmatidae	23.2	19.0	16.8	27.8
Sigalionidae	33.8	69.5	25.0	17.3
Sphaerodoridae	3.2	0.0	91.0	0.0
Spionidae	417.1	351.6	405.2	746.8
Sternaspidae	0.0	3.6	6.4	3.2
Syllidae	139.5	161.9	30.6	67.9
Terebellidae	7.4	0.0	0.0	0.0
Poly. indet.	36.2	7.4	0.0	15.6
Larval poly. indet.	0.0	0.0	30.8	18.5
Total	1387	1469	2237	3557

Table 4
ANOSIM pairwise tests of macrofauna major taxa and polychaete families across four sites. Western branch (W), Central branch (C), Eastern branch (E) and adjacent slope (Sl). n/s, not significant.

Groups	Major taxa		Polychaete families	
	R statistic	*p* Value	*R* statistic	*p* Value
W, Sl	0.240	n/s	0.276	0.048
W, C	0.576	0.008	0.204	n/s
W, E	0.724	0.008	0.248	n/s
Sl, C	0.784	0.008	0.684	0.008
Sl, E	0.868	0.008	0.864	0.008
C, E	0.032	n/s	0.048	n/s

Western branch. The Cirratulidae displayed the opposite pattern. The Western branch had the highest percentage (12%), the Eastern branch the lowest (7%) with intermediate values in the Central branch (11%). The Spionidae exhibited a similar pattern (Western 24%, Central 18% and Eastern branch 21%).

The slope site followed cross-canyon trends in polychaete family composition in being more similar to the Western branch than to the Central and Eastern branches. The slope assemblage was dominated by Spionidae (30%), Amphinomidae (10%) and Syllidae (10%). These percentages were similar to those from the Western branch; Spionidae (24%), Amphinomidae (18%) and Syllidae (11%). The ranking of the two dominant families on the slope was reversed in the Central (Amphinomidae 29%, Spionidae 18%) and Eastern branches (Amphinomidae 36%, Spionidae 21%).

The actual family abundance values followed the same trends between branches, except for the Spionidae, which reached their highest abundance in the Eastern and their lowest in the Western branch (summarised in Table 3). The slope site was generally more similar to the Western branch than to the other canyon branches in terms of the absolute abundance of the families Amphinomidae, Cirratulidae and Paraonidae. This was not true for all families; in particular the abundance of Spionidae on the slope was more similar to the Central branch values than to that of the Western branch.

3.2.5. *Multidimensional scaling analysis of polychaete families*

Polychaete family data revealed significant differences in assemblages between the sites. An MDS plot (Fig. 6B) grouped the Central and Eastern branch assemblages together, whereas the Western branch and slope sites were quite distinct. ANOSIM global assessment indicated statistically significant ($p=0.001$) variation among the sites. Significant ($p < 0.05$) pairwise differences were detected between the slope site and all canyon branches (Table 4).

4. Discussion

4.1. *Comparison with earlier studies*

4.1.1. *Macrofaunal abundance*

Macrofaunal abundance decreased across the Whittard Canyon from the Eastern branch to the Western branch and was lowest on the adjacent slope. This pattern is consistent with the data of Hunter et al. (2013). At similar depths (3500 m) in the Whittard Canyon, they observed a higher abundance of macrofauna in the Eastern branch (5352 ± SD 2583 ind. m^{-2}) compared with the Western branch (3416 ± SD 2069 ind. m^{-2}). An earlier study by Duineveld et al. (2001), however, reported a much lower abundance in the Western branch (1339 ind. m^{-2} at 3760 m) compared with the present study (2900 ± SD 538 ind. m^{-2}). At larger spatial scales, our macrofaunal densities can be compared with those in the extensively studied canyons on the Portuguese Margin (Tyler et al., 2009). Values from around 3500 m depth in the Setúbal Canyon (2241 ind. m^{-2}), and particularly in the Nazaré Canyon (4600 ind. m^{-2}) (Cunha et al., 2011), are comparable to those reported in the present study (average 4536 ± SD 1676 ind. m^{-2}). On the slope, macrofaunal densities are higher (2744 ± SD 269 ind. m^{-2}) at our site to the west of the Whittard Canyon than on the nearby Goban Spur (500 ind. m^{-2} at 3700 m; Flach et al., 2002) and Porcupine Abyssal Plain (1465 ind. m^{-2} at 4850 m depth; Galeron et al., 2001), but comparable to those from 3600 m depth on the Goban Spur (2420 ind. m^{-2}) reported by Duineveld et al. (2001). These differences may reflect sampling and sample processing techniques. Flach et al. (2002), Galeron et al. (2001) and Duineveld et al. (2001) used box corers and 500, 250 and 500 µm sieves, respectively, whereas a Megacorer and a 300 µm sieve were used in the present study. Densities in the Western branch based on our 500 µm sieve fractions were far lower (1777 ± SD 220 ind. m^{-2}) and more comparable to those of Duineveld et al. (2001) from the same area (1339 ind. m^{-2}). Box corers collect samples that are more disturbed than those obtained by hydraulically dampened multiple corers, leading to the loss of some meiofaunal and macrofaunal animals (Bett et al., 1994; Gage and Bett, 2005), while a larger sieve size would retain fewer animals.

Our macrofaunal densities from the canyon site considerably exceed the value (369 ind. m^{-2}) predicted by the regression equation of Rex et al. (2006) (Fig. 7); which was derived by plotting published global macrofaunal abundances against depth. The values in the present study are likewise far higher than the predicted 657 ind. m^{-2} derived from the formula in Wei et al. (2010) (Fig. 7). Wei et al. (2010) used a machine-learning algorithm, Random Forests, to model the relationship between oceanic properties and seafloor macrofaunal standing stock. They caution that the predicted values should be considered as conservative estimates for soft-bottomed communities relying solely on sinking phytodetritus. Wei et al. (2010) also warn that their model may not hold true for submarine canyons. They argue that organic matter originating from the continental shelf accumulates inside canyons leading, to higher concentrations compared with non-canyon areas. Indeed, when canyon sites and non-canyon sites at similar depths in the NE Atlantic are compared, the Whittard Canyon sites yield some of the highest macrofaunal abundances (Fig. 7). To account for gear bias, as detailed by Bett et al. (1994) and Gage and Bett (2005), box core densities estimates have been increased by a factor of two to improve comparability with multiple corer estimates. The full list of original data is given in the electronic Supplementary information (Table S2).

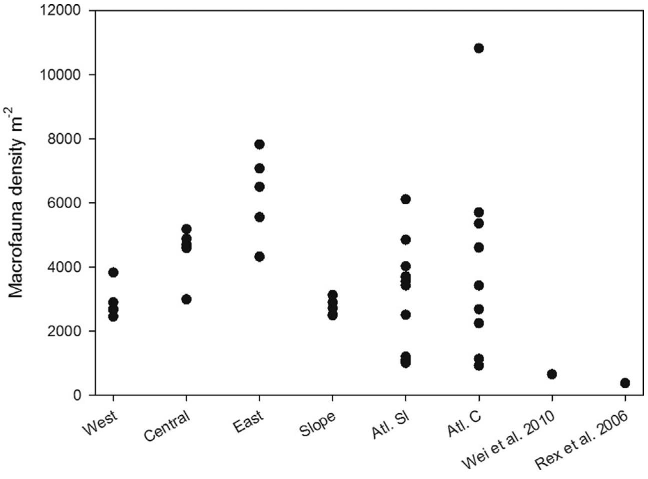

Fig. 7. Benthic abundance comparison of macrofaunal densities among present study sites (Western, Central and Eastern canyon branches and adjacent slope) and published Atlantic slope (Sl) and canyon (C) sites (Table S2). Global predictions for water depth 3500 m of Wei et al. (2010) and Rex et al. (2006) are also included. Data have been approximately corrected for sampling gear bias (see text for details).

4.1.2. Higher taxon composition

An important finding of our study was the clear shift in community composition, even at higher taxonomic levels, between the canyon branches and between the canyon and the adjacent slope. Polychaetes made up more than half of the macrofaunal assemblage at all sites. A lower percentage of polychaetes was reported by Hunter et al. (2013) (Western branch 30%, Eastern branch 20%). However, Hunter et al. (2013) included nematodes in the macrobenthos and, when these are excluded, polychaetes accounted for ~50% of the macrofauna sensu stricto. Our Eastern branch samples were characterised by high abundances of polychaetes, bivalves and isopods whereas the Western branch and adjacent slope yielded high abundances of polychaetes, sipunculans and tanaids. Differences in macrofaunal assemblage composition between branches were also noted by Hunter et al. (2013); polychaetes, crustaceans and macrofaunal-sized nematodes were equally abundant in the Western branch, whereas nematodes were dominant (> 50%) in the Eastern branch.

Our results, and those of previous studies, suggest that there is a remarkable degree of heterogeneity between canyons in terms of their faunal composition, even at higher taxonomic levels. In the Setúbal Canyon, polychaetes were ranked first, crustaceans second and molluscs third (Cunha et al., 2011). In the Nazaré Canyon molluscs were the most abundant higher taxon, representing just under 50% (2500 ind. m^{-2} at ~3400 m) of the total macrofaunal community (Cunha et al., 2011). Polychaetes were ranked second, followed by arthropods and echinoderms. In the Cascais Canyon (~3400 m depth), 45.9% of total abundance was made up of crustaceans, polychaetes were ranked second (~40%), and molluscs were the least abundant taxon (~5%) (Cunha et al., 2011). In contrast, in the Whittard Canyon, polychaetes always made up > 50% of the macrofaunal assemblages, crustaceans were ranked second (25% total across all sites) and molluscs third (9% total across all sites). Potential reasons for these differences in faunal composition are discussed in Section 4.2.

4.1.3. Polychaete family composition

Polychaete family composition differed between the canyon branches. Particularly high numbers of Amphinomidae were observed in the Eastern branch. In contrast, Hunter et al. (2013) reported a high abundance of Amphinomidae in the Western branch and Cirratulidae and Spionidae in the Eastern branch. Duineveld et al.'s (2001) report of numerous small tubiculous Sabellidae in the Western branch is particularly interesting. Sabellidae are filter feeders, which strain food from passing water currents (Fauchald and Jumars, 1979). Dunieveld et al. (2001) suggest their high abundance in the Western branch was caused by a high load of suspended organic particles passing over the canyon floor at that site, providing food for the sabellids. The absence of sabellids in our samples may indicate a reduced load of suspended organic particles in the water column when the samples were taken, or an absence of a suitable substrate for their tubes, or simply the heterogeneity of the canyon system.

Canyons cannot be characterised by one particular polychaete family. For example, the three most abundant families at depths around 3400 m in the Portuguese canyons were: Nazaré Canyon – Spionidae, Fauveliopsidae and Paraonidae; Cascais Canyon – Siboglinidae, Spionidae and Capitellidae; Setúbal Canyon – Spionidae, Ampharetidae and Nephytidae (Cunha et al., 2011). In the present study, the three top-ranked families were the Amphinomidae, Spionidae and Cirratulidae. However, it appears that Spionidae are often common in canyons. They were the top-ranked family overall in the Portuguese canyons (Paterson et al., 2011), second-ranked in the Whittard Canyon (this study) as well as the Cap-Ferret Canyon (Gerino et al., 1999). The Spionidae contain species thought to be opportunistic, such as those within the genus *Prionospio* (Paterson et al., 2011), which may be favoured in disturbed environments such as canyons where they are able exploit new patches of recently disturbed seafloor. Further investigations of species-level data are required to fully understand functional shifts in community composition.

4.2. Environmental controls on macrofauna community structure and composition

4.2.1. Organic matter quantity and quality

The higher abundance of macrofauna in the Eastern branch of the Whittard Canyon compared with that in the other branches may reflect the quality and quantity of organic matter. Duineveld et al. (2001) observed higher concentrations of phytodetritus in cores from stations in the Eastern branch compared with those from the Western branch. Sediment analyses revealed a higher percentage of sedimentary POC in the Eastern (0.7%) compared with the Western (0.5%) branch, although this result was not statistically significant (Hunter et al., 2013). The composition of sedimentary particulate organic matter (POM) was also reported to vary between branches of the Whittard Canyon (Huvenne et al., 2011). Huvenne et al. (2011) record higher total lipid concentration in sediments from the Eastern ($26\,\mu g\,g^{-1}$) compared with the Western ($15\,\mu g\,g^{-1}$) branch. In the Eastern branch, the lipids included essential fatty acids thought to be derived from phytoplankton or zooplankton sources. In contrast, in the Western branch, sediment POM contained a high proportion of monounsaturated fatty acids (Huvenne et al., 2011), which are associated with mesozooplankton (Kiriakoulakis et al., 2005) and more degraded detritus compared with the “fresher” polyunsaturated fatty acids (Kiriakoulakis et al., 2004). Significantly higher values of sediment total nitrogen (TN) were recorded in the Eastern branch sediment (TN % 0.098 ± 0.006) of the Whittard Canyon compared with the Western branch sediment (TN % 0.076 ± 0.007) (Hunter et al., 2013). Cunha et al. (2011) argued that macrofaunal abundance in the Portuguese canyons (at 3500 m) was positively correlated with sediment TN concentration. Higher sediment TN values indicate better food quality, which Cunha et al. (2011) suggested was the driver for increased macrofaunal abundance. These data suggest that more and higher quality food may be available in the Eastern branch.

The Whittard Canyon stations appear to experience higher levels of organic matter input than the adjacent slope, probably derived from the channeling of organic matter from the shelf through the canyon branches via downslope processes such as turbidity currents. Possibly, channeling is more active through the Eastern branch than the Central and Western branches, although there is no direct evidence for this suggestion. The Eastern branch may also be a more efficient trap of material from along-slope currents. The northerly and north-westerly flow of the NE Atlantic slope current will be topographically steered to flow essentially east to west across our study site (Pingree and Le Cann, 1989). The similarity between the slope and the Western branch and between the Eastern branch and the Central branch may reflect similar organic matter availability and composition at each site given their geographical proximity. Unfortunately, no organic matter data exists for the slope and Central branch.

By comparison with Rex et al. (2006) and Wei et al. (2010), the slope site also exhibited an elevated macrofaunal density for its depth. A possible factor explaining this high abundance is proximity to the canyon system. Cunningham et al. (2005) noted that mud-rich turbidity flows within the Whittard Canyon have been of sufficient magnitude to overspill the canyon walls, depositing fine sediments on the adjacent slope. This could lead to some organic matter enrichment of the area surrounding the canyon.

4.2.2. Disturbance

The higher abundance of macrofauna at 3500 m inside the Whittard Canyon than on the adjacent slope could also reflect disturbance. A high frequency from bottom-currents within canyons is thought to depress infaunal abundance, as suggested for the Nazaré Canyon (Gage et al., 1995; Koho et al., 2007). On the other hand, physical disturbance has been shown to increase macrofaunal abundance at the HEBBLE site, located at 4820 m depth on the Nova Scotia Rise (western North Atlantic). Several times per year, this area experiences intense currents that are strong enough to transport sediment (Thistle et al., 1985, 1991). These “benthic storms” are thought to deliver more nutrients for the fauna. At the HEBBLE site, abundances of macrofaunal polychaetes, bivalves, tanaids and isopods were significantly higher than expected for their depth (Thistle et al., 1991). These macrofaunal groups were also abundant inside the Whittard Canyon. Similarly, the Cascadia Channel in the northeast Pacific Ocean experiences a high frequency of turbidity currents that deliver a significant amount of organic matter. As a result, this area has a benthic macrofaunal density four times that on the adjacent plain (Griggs et al., 1969). Thus, the influence of bottom currents on macrofauna abundance remains ambiguous.

Physical disturbance may also influence the taxonomic composition of the macrofauna. Composition of fauna differs between disturbed and quiescent sites in canyons (Gage et al., 1995) and in the HEBBLE area (Thistle et al., 1991; Thistle and Wilson, 1996). Disturbance events can suspend soft-bottom fauna making them vulnerable to predators and physical damage. “Exposed” isopods (exposed on the sediment surface) were less abundant at disturbed sites in the HEBBLE area than at nearby quiescent sites (Thistle and Wilson, 1996). In this study the abundance of isopods was highest in the Central branch and lowest on the slope, although we have no evidence that the intensity of current flow differed between these sites.

There may be a difference in disturbance regimes between the Western and Eastern branches of the Whittard Canyon. A higher abundance of disturbance-tolerant taxa led Hunter et al. (2013) to conclude that disturbance events were more frequent in the Eastern branch. However, the magnitude and frequency of disturbance inside the Whittard Canyon is poorly understood (Section 2.1) and there is no clear basis for linking macrofaunal patterns to disturbance levels.

4.2.3. Sediment grain size

Mean sediment grain size is higher on the slope than at our three canyon sites. The slope site had a larger proportion of sand and clay, whereas the canyon site sediments were composed predominantly of silt (Table 1). It is possible this difference may be caused by the slope site being more exposed to along-slope currents (Pingree and Le Cann, 1989). Sediment mobility and reworking is a critical factor in explaining the effect of physical disturbance on community structure (Thistle and Levin, 1998). On the summit of a high-energy seamount off the coast of California, areas with stable, coarse-grained sediments supported relatively immobile assemblages whose feeding activities were focused at the sediment-water interface. In contrast, areas of unstable coarse-grained sediments that moved daily supported highly mobile assemblages with well-developed burrowing abilities (Levin et al., 1994). The different characteristics of canyon and slope sediments suggest that they may react differently to current activity, influencing the benthic community.

4.2.4. *Other factors*

A variety of other factors could influence the density and composition of macrofaunal assemblages. Differences in slope angle at the Whittard Canyon and slope sites are probably too slight (~2°) to have much effect on sediment stability. On the other hand, the bottom profiles of the canyon branches varied substantially. The Eastern branch has a much narrower, steeper-sided channel than the Western branch, which may suggest that sediment and organic matter pass along it more quickly. Steep and V-shaped canyons are thought to experience stronger and more frequent along-canyon currents than their more U-shaped counterparts (Shepard and Dill, 1966), and canyons with low topographic relief are more likely to resemble open-slope environments (Hecker et al., 1983). De Leo et al. (2014) reported that variability in canyon profiles partially explained variations in macrofaunal community structure among Hawaiian canyons.

Preferential predation by megafauna may affect macrofaunal taxonomic composition. Canyons generally have higher abundances of megafauna (De Leo et al., 2010; Vetter et al., 2010) than the surrounding slope and bottom-feeding fish may also exploit the high abundance of invertebrate macrobenthic communities (De Leo et al., 2010, 2012). Reduced oxygen availability has a strong effect on community composition by eliminating hypoxia-intolerant species (Levin, 2003). Ingels et al. (2011) reported signs of oxygen limitation in the upper part of the Whittard Canyon. This was believed to reduce densities of nematodes. However, there is no evidence of reducing environments in deeper parts of the canyon. Similarly, water depth (hydrostatic pressure) is not considered to be an important discriminating factor in this study as all samples were taken from similar depths (~3500 m).

5. Conclusions and future directions

Our results support all three hypotheses posed in the introduction. In summary, at 3500 m water depth the Whittard Canyon (1) has high macrofaunal abundance compared to the adjacent slope (2) contains a distinct community composition and (3) contains distinct within-canyon heterogeneity. These results are similar to those obtained for previous studies of the metazoan meiofauna and foraminifera. Within-canyon heterogeneity is probably explained by a combination of variable organic enrichment and hydrodynamic activity, both of which can be influenced by the topographic profile of individual canyon branches. Canyons are natural deep-sea laboratories for benthic sediment resuspension, disturbance and organic enrichment and as such may be important future locations to investigate fundamental biological processes of relevance to future human impacts in the deep sea, such as those likely to occur through deep-water trawling or mining.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2014.11.010.

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Benthic polychaete diversity patterns and community structure in the Whittard Canyon system and adjacent slope (NE Atlantic)

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ABSTRACT

We examined deep-sea macrofaunal polychaete species assemblage composition, diversity and turnover in the Whittard Canyon system (NE Atlantic) using replicate megacore samples from three of the canyon branches and one site on the continental slope to the west of the canyon, all at ~3500 m water depth. A total of 110 polychaete species were recorded. *Paramphinome jeffreysii* was the most abundant species (2326 ind. m^{-2}) followed by *Aurospio* sp. B (646 ind. m^{-2}), Opheliidae sp. A (393 ind. m^{-2}), *Prionospio* sp. I (380 ind. m^{-2}), and *Ophelina abranchiata* (227 ind. m^{-2}). Species composition varied significantly across all sites. From west to east, the dominance of *Paramphinome jeffreysii* increased from 12.9% on the slope to 39.6% in the Eastern branch. Ordination of species composition revealed that the Central and Eastern branches were most similar, whereas the Western branch and slope sites were more distinct. High abundances of *P. jeffreysii* and Opheliidae sp. A characterised the Eastern branch of the canyon and may indicate an opportunistic response to a possible recent input of organic matter inside the canyon. Species richness and diversity indices were higher on the slope compared with inside the canyon, and the slope site had higher species evenness. Within the canyon, species diversity between branches was broadly similar. Despite depressed diversity within the canyon compared with the adjacent slope, the fact that 46 of the 99 polychaete species found in the Whittard Canyon were not present on the adjacent slope suggests that this feature may enhance the regional species pool. However, our sampling effort on the adjacent slope was insufficient to confirm this conclusion.

1. Introduction

Describing and understanding patterns of biodiversity on our planet is a fundamental aim in biology (Gaston, 2000). The deep-sea floor may harbour some of the highest levels of local (alpha) species diversity on earth (Hessler and Sanders, 1967; Sanders, 1968; Sanders and Hessler, 1969; Grassle and Maciolek, 1992). A parabolic pattern of local diversity with water depth, with peaks at intermediate (i.e. mid to lower bathyal) depths and reduced diversity at upper bathyal and abyssal depths, is evident among some macrofaunal taxa, including polychaetes, in intensively studied areas of the North Atlantic (Rex, 1981; Rex, 1983; Etter and Grassle, 1992; Levin et al., 2001; Rex and Etter, 2010; Paterson and Lambshead, 1995). However, this pattern may not be a universal phenomenon across different taxa and deep-sea regions (Stuart et al., 2003; Stuart and Rex, 2009).

Submarine canyons, major deep-sea topographic features incising the continental shelf and slope, are among the potential exceptions to this pattern. They may show either increased species richness in their deeper parts (Cunha et al., 2011) or depressed diversity due to strong dominance, as in shallow parts (100 m depth) of the La Jolla Canyon system, which is influenced by significant macrophyte detritus input (Vetter and Dayton, 1998). Faunal diversity also varies down the canyon axis and across the adjacent canyon fan (Tyler et al., 2009), as reported for foraminifera in the Whittard Canyon (Duros et al., 2011) and polychaetes in the Nazaré, Setúbal and Cascais Canyons on the Iberian Margin (Paterson et al., 2011). There is, however, no general agreement on whether alpha diversity is typically higher inside canyons (Vetter and Dayton, 1998, 1999; Vetter et al., 2010; De Leo et al., 2012) or higher on the adjacent slope outside canyons (Gage et al., 1995; Curdia et al., 2004; Garcia et al., 2007; Koho et al., 2007).

The drivers that influence marine diversity at regional and local scales are not well understood (Levin et al., 2001; Snelgrove and

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Smith, 2002). In the case of submarine canyons, a complex interplay of numerous factors is likely to regulate the diversity of biological communities (McClain and Barry, 2010). These topographic features are typically associated with high surface water productivity, high levels of physical disturbance and a considerable degree of habitat heterogeneity, all of which could influence species diversity. Canyons have also been described as benthic biomass 'hotspots' (Vetter, 1994; De Leo et al., 2010), reflecting an enhanced food supply compared with the surrounding continental slope and abyssal plain. They can act as conduits for the delivery of sediment and organic matter to the abyssal plains (Vetter and Dayton 1998). This enhanced supply of organic matter could increase diversity. Conversely, if enrichment is excessive, it may favour opportunistic species (Paterson et al., 2011) and act to depress species diversity (Stuart et al., 2003; Whittaker, 1965), as in the Nazaré Canyon (Curdia et al., 2004). Diversity may also be influenced by physical disturbance, for example, when steep topography focuses internal tides in the upper reaches of canyons (Gardner, 1989), while tidal currents, episodic slumps, turbidity flows and dense shelf water cascading may periodically transport sediments into the deeper parts (Shepard, 1951; Canals et al., 2006).

Factors such as extreme topography, diverse current regimes, varying substratum types, and detrital funnelling from the continental shelf serve to increase habitat heterogeneity within canyons (Levin et al., 2010). For example, currents may distribute organic matter and sediment in a patchy manner (McClain and Barry, 2010). Similarly, sediment granulometry can be expected to vary throughout a canyon, with potential impact on macrofaunal (Etter and Grassle, 1992) and meiofaunal (Leduc et al., 2012) diversity. Sessile megafauna add to the habitat complexity inside canyons; they include deep-water corals that are found in many canyon systems and provide refuge for diverse associated faunal communities (Mortensen and Buhl-Mortensen, 2005; Buhl-Mortensen et al., 2010; Huvenne et al., 2011). All of these factors may increase small and medium-scale environmental heterogeneity, particularly within active canyons, and thereby enhance diversity compared with the adjacent slope (Tews et al., 2004). Indeed, increased macrohabitat heterogeneity inside canyons has been linked to the high beta diversity of nematode assemblages (Vanreusel et al., 2010).

On a larger scale, it is unclear whether canyons act to enhance regional diversity across continental margins. Evidence from canyons in the Hawaiian Archipelago suggest that they lead to an increase in megafaunal (Vetter et al., 2010) and macrofaunal (De Leo et al., 2014) species turnover (beta diversity). Beta diversity links local and regional scales of diversity and has been understudied in deep ocean settings (Paterson et al., 1998; Glover et al., 2002; Ellingsen et al., 2007a). In deep-sea, soft-sediment habitats, variation in beta diversity is expected to be gradual except when interrupted by topography, hard substratum, intense bottom currents, nutrient depo-centres, abrupt shifts in water masses, or other extreme environmental circumstances (Rex and Etter, 2010). Many of these factors operate inside canyons. Thus, as in continental shelf settings (Ellingsen and Gray, 2002), it seems likely that changes in environmental variables within canyons will have a stronger effect on beta diversity than spatial distance between sites. The bathymetric and geographical ranges of species, and hence beta diversity, are influenced by the interplay between adaptive traits and environmental drivers. Adaptive traits include feeding type, metabolic and locomotory capacity, morphological specialisation, larval dispersal, adult mobility, body size and shape, and enzymatic pressure sensitivity (reviewed by Rex and Etter, 2010). Those traits typical of canyon settings will depend on the species present, which in turn will reflect the environmental conditions. Thus the interaction of species traits and environmental influences that determine the bathymetric and geographical ranges of species will be complex (Rex and Etter, 2010). Since the environmental conditions inside canyons are often very different from those on the open slope, the faunal assemblages may differ correspondingly. This would act to increase faunal turnover across the continental margin and lead to enhanced regional diversity.

Much less quantitative data on species richness is available from deep-sea soft sediments than from comparable shallow-water settings (Gray, 2002). As a result of their rugged terrain and inaccessibility, submarine canyons are particularly hard to sample. Thus, relatively little is known about the patterns and drivers of canyon diversity. This study will investigate diversity inside the Whittard Canyon system (NE Atlantic), focussing on sites at a common water depth (3500 m). A previous study, on the same samples from the Whittard Canyon, reported macrofaunal abundance and community composition at the higher taxon level (Gunton et al., 2015).

In the present study, a species-level assessment of polychaete assemblages, typically the dominant deep-sea macrofauna taxon, will be used to address the following hypotheses. (1) Species composition is not consistent between Whittard Canyon branches. (2) Species composition for the canyon site as a whole (including all three branches) is different from that of the slope site. (3) Species diversity is depressed inside the Whittard Canyon as a whole compared with the slope site. (4) Regional diversity is enhanced by the Whittard Canyon system.

2. Methods

2.1. Sample collection and processing

Sediment samples were collected using a Megacorer (Gage and Bett, 2005) at three sites inside the Whittard Canyon system (NE Atlantic) and one on the adjacent continental slope to the west of the canyon during RRS *James Cook* cruise 036 in June and July 2009 (Table 1; Fig. 1). All sites were located at ~3500 m depth. The Megacorer was fitted with eight large (100 mm internal diameter) core tubes. For one deployment at each site one of the larger core tubes was replaced with a single smaller tube (59 mm internal diameter) (Table 1). Five deployments were conducted in the Western branch, six in the Central and Eastern branches and five at the slope site. One extra deployment was made in the Central and Eastern branches to compensate for the failure to recover sufficient cores. Core slices from the same sediment layer from one deployment were pooled to make one replicate sample. The number of cores pooled per deployment ranged from 3 to 7 and the area of seabed sampled varied accordingly (Table 1). Samples were fixed with 10% borax-buffered formalin. Full details of macrofaunal sample processing are given in Gunton et al. (2015). In the present study, the top three sediment horizons (i.e. 0–1, 1–3 and 3–5 cm) were analysed *in toto*.

2.2. Faunal analyses

In the laboratory, polychaetes were transferred from the formalin onto a 300 μm mesh sieve, rinsed with fresh water and sorted in 70% ethanol. A Leica MZ9.5 stereomicroscope and a DM5000 compound microscope were used to identify polychaete specimens to species level. Polychaetes were assigned a Latin binomial name where possible using published identification keys. Where specimens could not be assigned to a described species they were recorded as an informal morphospecies in a genus (e.g. *Prionospio* sp. A) or family (e.g. Spionidae sp. A). Fragmented specimens were only counted if they included a head. The full

Table 1
Sites and diversity summary.

Deploy.	Lat. (N)	Long. (W)	Depth (m)	Cores recovered	Area (m^{-2})	Density (ind. m^{-2})	Total species	J'	H' (log2)	$1-\lambda'$	Rank 1 dom. (%)	Chao 1
SI016	47° 56.79′	10° 46.85′	3511	8	0.063	939	21	0.876	3.848	0.902	22.6	38.81
SI017	47° 56.78′	10° 46.85′	3512	7	0.055	982	23	0.923	4.175	0.932	13.7	35.91
SI018	47° 56.81′	10° 46.91′	3514	6	0.047	1358	28	0.885	4.253	0.927	15.9	64.80
SI019[a]	47° 56.74′	10° 46.94′	3505	8	0.063	1337	30	0.857	4.207	0.920	18.5	50.10
SI020	47° 56.78′	10° 46.85′	3514	7	0.055	1364	25	0.870	4.039	0.910	23.0	32.68
Ave. SI							**25.4**	**0.882**	**4.104**	**0.918**	**18.7**	**44.46**
W002[a]	48° 09.18′	10° 33.70′	3670	8	0.063	1226	22	0.800	3.567	0.870	26.7	34.18
W003	48° 09.17′	10° 33.70′	3661	7	0.055	1328	22	0.818	3.646	0.875	27.9	39.03
W011	48° 09.22′	10° 32.36′	3582	6	0.047	1422	24	0.861	3.949	0.905	20.3	37.58
W026	48° 09.18′	10° 33.73′	3670	5	0.039	1223	19	0.891	3.784	0.904	19.1	24.87
W043	48° 09.15′	10° 33.76′	3657	6	0.047	1443	23	0.792	3.582	0.848	34.4	47.59
Ave. W							**22.0**	**0.832**	**3.706**	**0.880**	**25.8**	**36.65**
C063[a]	48° 16.89′	10° 18.74′	3375	6	0.047	1995	25	0.748	3.474	0.799	42.7	29.67
C064	48° 16.97′	10° 18.65′	3382	8	0.063	2388	34	0.762	3.877	0.850	35.6	33.71
C065	48° 17.04′	10° 18.89′	3373	7	0.055	2165	36	0.810	4.187	0.887	29.8	42.41
C067	48° 16.98′	10° 18.72′	3376	7	0.055	1528	27	0.791	3.761	0.854	34.2	39.35
C066	48° 16.83′	10° 18.72′	3381	3	0.063	2308	37	0.798	4.155	0.891	27.1	33.28
C068	48° 17.01′	10° 18.83′	3375	5								
Ave. C							**31.8**	**0.782**	**3.891**	**0.856**	**33.9**	**35.68**
E093[a]	48° 15.89′	10° 09.56′	3424	8	0.063	1942	35	0.723	3.709	0.797	43.6	42.06
E094	48° 15.78′	10° 09.57′	3429	7	0.055	2583	33	0.762	3.842	0.845	36.2	35.91
E095	48° 15.78′	10° 09.58′	3429	4	0.063	3184	43	0.712	3.866	0.821	40.1	40.22
E096	48° 15.76′	10° 09.60′	3424	4								
E097	48° 15.89′	10° 09.54′	3425	5	0.039	4304	29	0.662	3.214	0.764	45.2	28.93
E098	48° 15.76′	10° 09.60′	3432	4	0.031	4330	32	0.730	3.652	0.843	33.6	39.78
Ave. E							**34.4**	**0.718**	**3.656**	**0.814**	**39.7**	**37.38**

[a] Deployment where sample for sediment grain-size analysis was collected. Ave.=mean of five deployments. J', Pielou's evenness; H' (log2), Shannon index; $1-\lambda'$, Simpson index; Chao 1 values rarefied to 47 individuals.

species list, including abundance counts, is given as supplementary data (Table S1).

2.3. Data analysis

2.3.1. Diversity measures

Simple polychaete species dominance was calculated as the Berger–Parker index (i.e. Rank 1 Dominance; Magurran, 2004). K-dominance plots (Lambshead et al., 1983) were drawn in SigmaPlot V12.5. The software package PRIMER V6 (Clarke and Gorley, 2006) was used to calculate conventional diversity indices from the polychaete count data: Shannon index (Pielou, 1966), Simpson's index (Simpson, 1949) and Pielou's evenness (Pielou, 1975). Rarefied polychaete species richness ($E[S_{47}]$) was estimated based on values derived from individual-based rarefaction curves (Gotelli and Colwell, 2001, 2011). The rarefaction curves based on polychaete count data were constructed using the EstimateS software package (Colwell, 2009). This approach was also applied to comparative polychaete species-level data available from canyons on the Iberian Margin (Paterson et al., 2011). Finally, species richness was estimated using values of Chao 1 from the EstimateS output.

In order to assess beta diversity across the canyon system, Whittaker's measure $\beta_W=\gamma\ /\ \bar{\alpha}$ (Whittaker, 1960, 1972) was calculated, where γ is the diversity of the complete system (i.e. all relevant sites combined), and $\bar{\alpha}$ is average sample diversity, where each sample is of a standard size (i.e. by rarefaction). Beta diversity was calculated using the number equivalents (Hill numbers) of species richness $^0D=S$, Shannon index $^1D=\exp(-\Sigma_{pi}\ \log_{pi})$ and Simpson index $^2D=1/\ \Sigma_{pi}{}^2$ (See Chao et al., 2012, 2014a; Jost, 2007), derived from the output of EstimateS, after individual samples had been rarefied to 47 individuals and pooled samples (the γ value) rarefied to 235 individuals (i.e. 5 replicate samples of 47 individuals). We adopted this approach following the rationale of Chao et al. (2014b), where the use of Hill number diversity values simplifies the calculation of reasonable beta diversity values. Similarly, we assess ^0D, ^1D and ^2D to examine the potential variation in richness, heterogeneity, and dominance aspects of beta diversity, according to the general framework proposed by Chao et al. (2014b).

2.3.2. Composition assessment

Polychaete species density data were transformed to square root, and the Bray–Curtis similarity calculated between samples. The resultant similarity matrix was visualised using non-metric multidimensional scaling plots (nMDS plots), and further assessed using the Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER) methods given in PRIMER V6.

A canonical correspondence analysis (CCA) on untransformed polychaete density was performed to examine the potential relationships between assemblages and environmental variables. The CCA was performed using R statistical software (RCoreTeam, 2014) with the Vegan: Community Ecology package (Oksanen et al., 2013). Details of environmental variables used and their measurement, are given in Gunton et al. (2015). Briefly – a post-processed bathymetry map of the Whittard Canyon was downloaded from the INFROMAR website (www.gsiseabed.ie). Using the software ArcMap 10 (ESRI) and the Benthic Terrain Modeler ArcGIS Desktop Extension alpha version (Wright et al., 2005), the following environmental descriptors were derived from the bathymetry map; 'Slope', bathymetric position index (BPI) and vector ruggedness measure (VRM). Sediment particle-size was obtained from the smaller cores collected at each site (see Section 2.1). Subsamples from the 0–0.5, 1–1.5, 2–3 and 4–5 cm sediment layers from each core were analysed using a Malvern Mastersizer

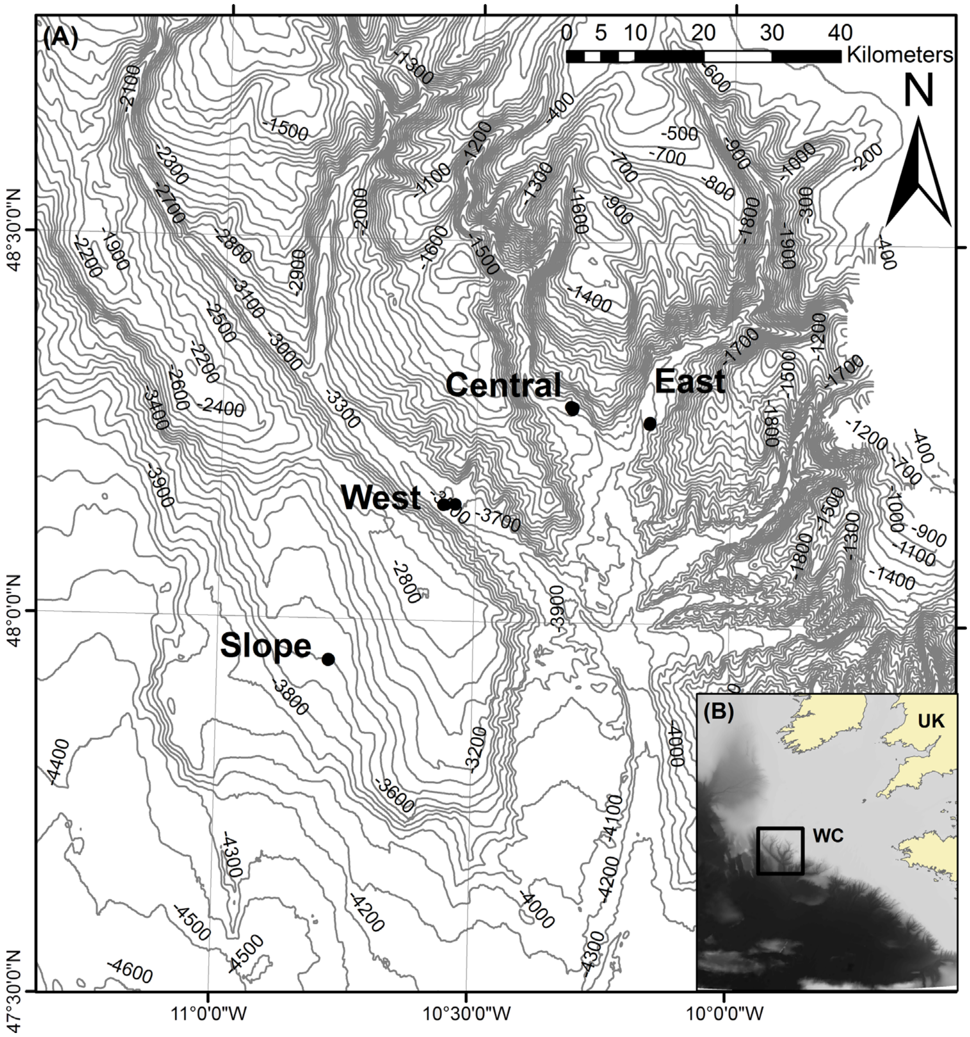

Fig. 1. (A) Bathymetric chart of Whittard Canyon, based on data provided by the Geological Survey of Ireland (www.gsiseabed.ie). The four study sites are indicated: Western Branch, Central Branch and Eastern Branch of the canyon and one site on the adjacent slope. (B) Location map of Whittard Canyon (WC) in NE Atlantic, based on GEBCO data (www.gebco.net).

2000 laser diffraction particle size analyser (Abbireddy and Clayton, 2009).

3. Results

3.1. The polychaete assemblages

In total, 2225 polychaetes were examined; 1959 (88%) of these were assigned to species, the remainder being considered as indeterminate. Across all sites, we recognised 110 species, of which 35 were described, and 75 could not be assigned to a known species and were possibly new to science. The Eastern branch yielded the highest number of species (68), followed by the Central branch (65), slope (64) and Western branch (53) sites. Overall, 46 species were found only in the canyon branches, and 11 were found only at the slope site. Among the 10 top-ranked species at each site (Table 2) (21 species in total), 3 were found only on the slope, 11 only in the canyon and 7 in both settings. Between site

Table 2
Top ten most abundant species at each site. Relative abundance shown in brackets.

Slope	Western branch	Central branch	Eastern branch
Aurospio sp. B (14.3%)	*Paramphinome jeffreysii* (21.2%)	*Paramphinome jeffreysii* (33.6%)	*Paramphinome jeffreysii* (39.6%)
Paramphinome jeffreysii (12.9%)	*Aurospio* sp. B (11.2%)	*Aurospio* sp. B (8.3%)	Opheliidae sp. A[a] (11.0%)
Anguillosyllis capensis (9.3%)	*Ancistrosyllis* sp. A[a] (10.2%)	*Ophelina abranchiata* (4.9%)	*Prionospio* sp. I (5.5%)
Prionospio sp. I (7.1%)	*Levinsenia gracilis* (6.5%)	*Levinsenia gracilis* (3.8%)	*Aurospio* sp. B (5.5%)
Aurospio dibranchiata (6.3%)	*Prionospio* sp. I (6.0%)	*Chaetozone* sp. F (3.4%)	*Leitoscoloplos* sp. B[a] (2.2%)
Flabelligella cf. biscayensis (5.4%)	*Leanira hystricis* (3.9%)	*Ophelina cylindricaudata* (3.3%)	*Ophelina abranchiata* (2.1%)
Ampharetidae sp. A (4.7%)	*Ophelina abranchiata* (3.8%)	Polychaeta larva sp. A[a] (3.0%)	*Glycera capitata* (2.0%)
Glycera capitata (3.4%)	*Chaetozone* sp. F (3.1%)	*Aurospio dibranchiata* (2.8%)	*Aricidea simplex* (1.8%)
Chaetozone sp. F (3.4%)	*Chaetozone* sp. C (1.8%)	*Chaetozone* sp. A[a] (2.5%)	*Prionospio* sp. B (1.7%)
Levinsenia gracilis (2.8%)	*Chaetozone* sp. A[a] (1.7%)	*Leitoscoloplos* sp. B[a](2.5%)	*Ophelina cylindricaudata* (1.4%)

[a] Species observed only in the canyon.

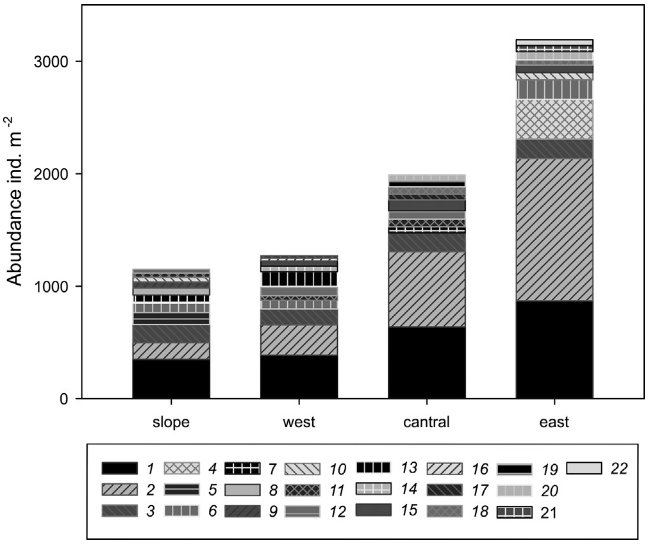

Fig. 2. Composition of the most abundant polychaete species at each of the four study sites. 1, Others; 2, *Paramphinome jeffreysii*; 3, *Aurospio* sp. B; 4, Opheliidae sp. A; 5, *Anguillosyllis capensis*; 6, *Prionospio* sp. I; 7, *Aurospio dibranchiata* 8, *Flabelligella* cf. *biscayensis*; 9, Ampharetidae Genus A; 10, *Glycera capitata*; 11, *Chaetozone* sp. F; 12, *Levinsenia gracilis*; 13, *Ancistrosyllis* sp. A;14, *Leanira hystricis*; 15, *Ophelina abranchiata*; 16, *Chaetozone* sp. C; 17, *Chaetozone* sp. A; 18, *Ophelina cylindricaudata*; 19, Polychaet larva sp. A; 20, *Leitoscoloplos* sp. B; 21, *Aricidea simplex*; 22, *Prionospio* sp. B.

variation in species composition is illustrated in Fig. 2. By far the most abundant species was the amphinomid *Paramphinome jeffreysii* with a total of 2326 ind. m^{-2}, followed by *Aurospio* sp. B (646 ind. m^{-2}), Opheliidae sp. A (393 ind. m^{-2}, represented by juvenile individuals), *Prionospio* sp. I (380 ind. m^{-2}) and *Ophelina abranchiata* (277 ind. m^{-2}). *Paramphinome jeffreysii* increased in relative abundance from 21% in the Western branch to 34% and 40% in the Central and Eastern branches, respectively (Table 2). It was less common at the slope site, where the most abundant species was *Aurospio* sp. B (Table 2). In contrast to *P. jeffreysii, Aurospio* sp. B decreased in relative abundance from west to east (slope 14%, Eastern branch 6%).

There were notable differences in species composition with depth in the sediment profile. The percentage abundance of *Paramphinome jeffreysii* increased into the sediment across all of the sites (Fig. 3). At the Eastern branch, where it was most abundant, *P. jeffreysii* constituted 50% of the polychaete species in the 1–3 and 3–5 cm sediment layers. Juvenile opheliids (Opheliidae sp. A) were particularly abundant ($\sim$20%) in the 0–1 cm layer of the Eastern branch.

3.2. Species diversity

Rank 1 dominance differed between sites (Table 1). The Eastern branch had the highest rank 1 dominance (39.7%) and the slope the lowest (18.7%). The *k*-dominance plot (Fig. 4) revealed a similar trend in dominance, highest at the Eastern branch site and lowest at the slope site, with the Western and Central branches having intermediate values.

Simple alpha diversity measures indicated that diversity varied between sites. The average Simpson index ($1-\lambda'$) was highest at the slope site (0.918), intermediate in the Western and Central branches (0.880 and 0.856 respectively) and lowest in the Eastern branch (0.814) (Table 1). The average Shannon index (H' ($\log_2$)) was likewise highest at the slope site (4.104) and lowest in the Eastern branch (3.656). Species evenness decreased from west to east across the sites. The average evenness index (J') was highest on the slope and lowest in the canyon branches (Table 1).

Rarefied polychaete species richness was highest on the slope and all three canyon sites had a similar species richness (Fig. 5a), consistent with hypothesis 3. This pattern was also supported by the Chao 1 indices (Table 1). None of the rarefaction curves reached an asymptote, suggesting that the local diversity was undersampled even when the results were pooled. The higher richness at the slope site was evident from the individual-based (Fig. 5a) rarefaction curves, although confidence intervals overlapped, indicating that the differences were not statistically significant. When all sites were rarefied to 47 individuals, the slope site had the highest species richness (21 species). All three canyon sites had similar predicted numbers of species with $E[S_{47}]$ values decreasing only very slightly (from 20 to 18) from centre to east (Table 4). When all sites were combined (Fig. 5c, Table 4), the expected number of species was lower than at the slope site alone.

3.3. Beta diversity

There is little if any variation in beta diversity within or among the sites studied, whether assessed as Hill number 0, 1 or 2 (Table 4). However, rarefied average α diversity and rarefied γ diversity are all highest at the slope site. Similarly, rarefied average α diversity, and rarefied γ diversity are increased from canyon-level to regional-level measures. The degree of increase appears to be related to the Hill number, least in richness, and greatest in inverse Simpson (i.e. evenness). Taken together, these results suggest both increased richness and reduced dominance at the slope site relative to the canyon sites.

3.4. Multivariate analyses

A non-metric multidimensional scaling ordination of polychaete species data (Fig. 6) revealed appreciable differences in community composition between all four study sites, thereby supporting hypotheses 1 and 2. The Eastern and Central branch sites were most similar to each other. Western branch samples formed a looser grouping, which was nevertheless distinct from those at the other canyon sites. The slope samples grouped together and were distinct from the canyon sites. Global ANOSIM indicated significant variation ($p < 0.001$), with all pair-wise site comparisons significant at $p < 0.01$, except slope and Western branch, which was significant at $p < 0.02$. SIMPER analysis (Table 3) indicated that the abundance of *P. jeffreysii* was responsible for most of the observed similarity within sites. *Aurospio* sp. B abundance was second or third most important at all sites. Between-site dissimilarity was mostly driven by the abundance of *P. jeffreysii, Opheliidae* sp. A (juveniles) and *Ancistrosyllis* sp. A.

Canonical correspondence analysis (Fig. 7) showed the potential interactions between environmental factors and the distribution of polychaete species. Axis 1 was positively correlated with water depth and negatively correlated with macrofaunal density (a potential proxy of organic matter supply, Gunton et al., 2015). Axis 2 was correlated with sediment characteristics, including grain size and slope angle. Species such as *Leanira hystricis, Ancistrosyllis* sp. A, *Sternaspis* sp. A and *Chaetozone* sp. C were characteristic of the deeper and lower macrofaunal density sites in the Western branch (Supplementary Fig. S1). Opheliidae sp. B, *Anguillosyllis capensis* and Scalibregmatidae sp. B were characteristic of the coarser-grained sediment with a higher clay percentage on the slope. Opheliidae sp. A (juveniles), *Paramphinome jeffreysii* and *Leitoscoloplos* sp. B were characteristic of the Eastern and Central branches, which shared similar environmental characteristics.

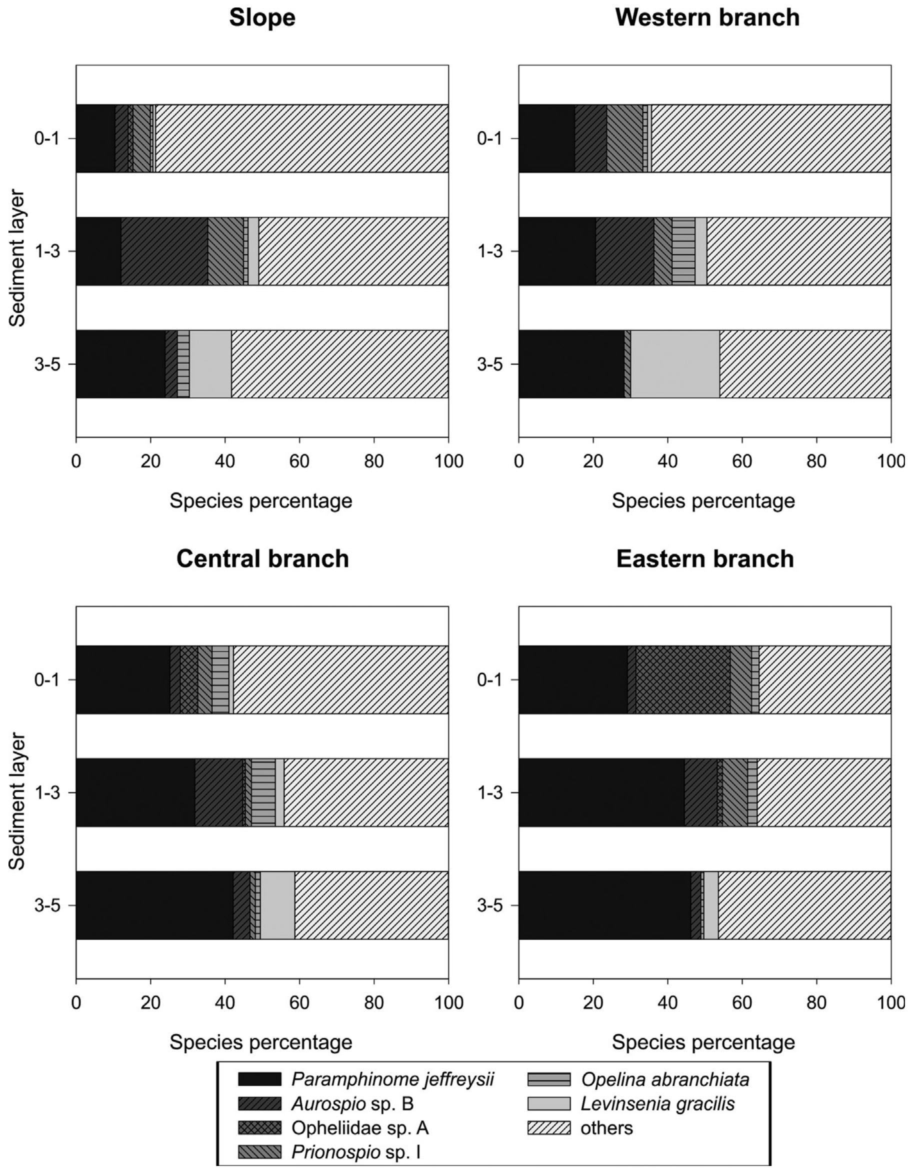

Fig. 3. Vertical distribution of polychaetes in sediments layers (0–1, 1–3 and 3–5 cm) at each site represented as percentage abundance.

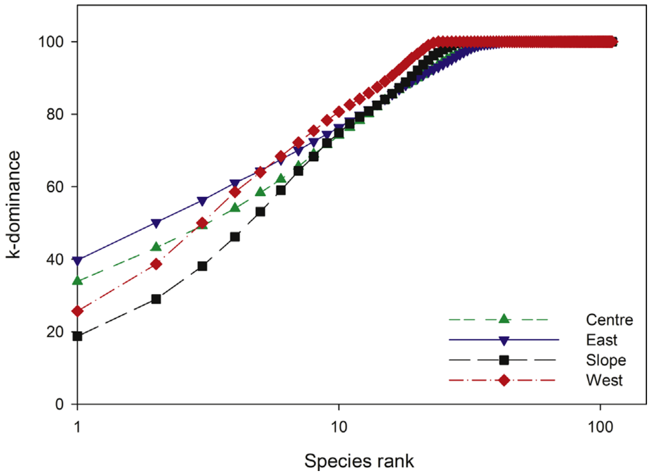

Fig. 4. k-Dominance plot for Whittard Canyon and slope sites, using pooled data from five samples at each of the four sites.

4. Discussion

4.1. Polychaete assemblages

The species composition of the polychaete assemblages differed between branches of the Whittard Canyon, in agreement with hypothesis 1. This is consistent with previous family-level studies of polychaetes in the same canyon system (Hunter et al., 2013; Gunton et al., 2015). Multidimensional scaling and CCA revealed that the Eastern and Central branch species assemblages were closely related (Figs. 6 and 7). Again, this pattern was also observed at the family level and may reflect a combination of similar environmental conditions and geographical proximity (Gunton et al., 2015). The Western branch samples yielded a more distinct assemblage, characterised by *Ancistrosyllis* sp. A (a member of the family Pilargidae), which made up 10% of the polychaete species in the Western branch but was not present in other canyon branches. There is very little information regarding the ecology of the Pilargidae (Fauchald and Jumars, 1979), making it difficult to

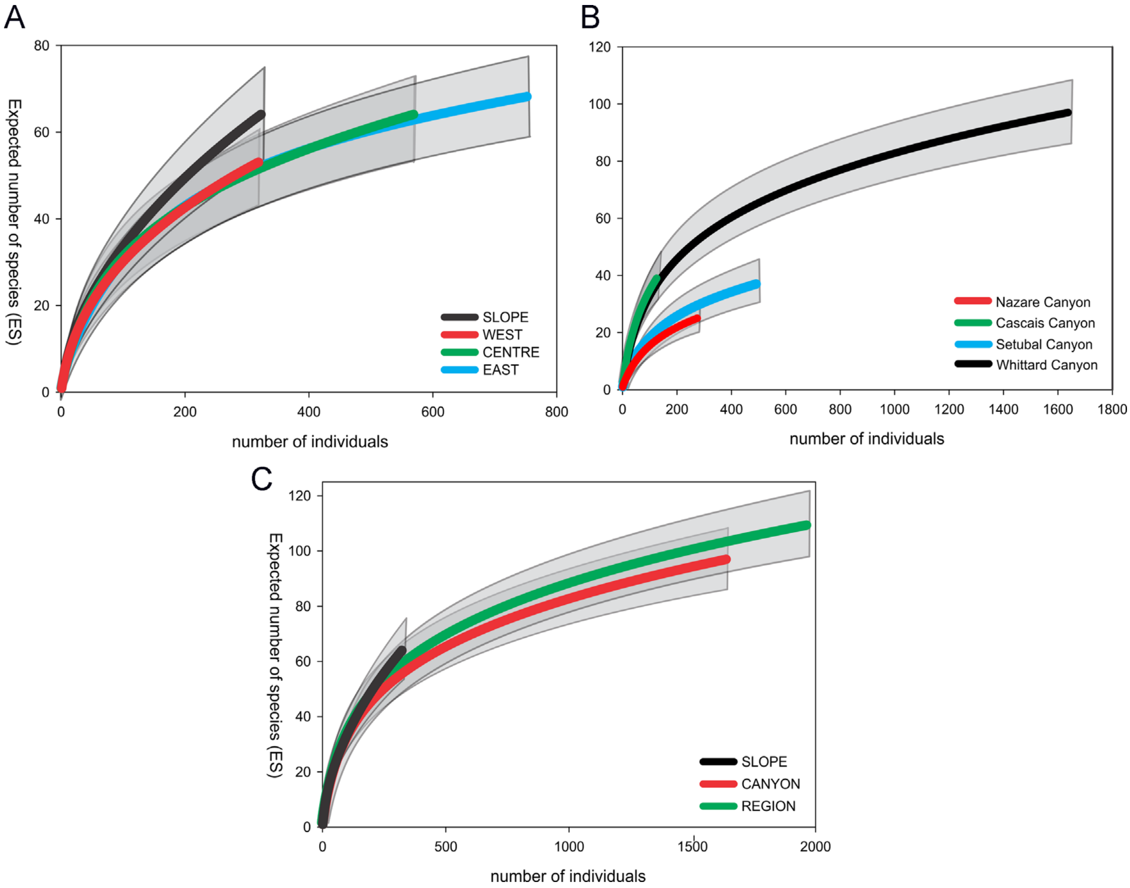

Fig. 5. Polychaete diversity estimated using rarefaction, 95% confidence intervals shown as grey shading. (A) Slope site, Western, Central and Eastern branches. (B) Combined Whittard Canyon branches (Western, Central and Eastern branches) and Iberian Margin canyons (Nazaré, Setúbal and Cascais Canyons) at 3400 m. (C) Combined Whittard Canyon branches, slope site and Whittard Canyon region (Slope site, Western, Central and Eastern branches).

speculate why this species was abundant in the Western branch.

In addition to these intra-canyon patterns, polychaete assemblage composition differed between the canyon branches, as a whole, and the adjacent open slope. This is consistent with hypothesis 2. It also agrees with the findings of De Leo et al. (2014) who recorded a difference in macrofaunal assemblage composition, particularly among polychaetes, between canyon and slope sites in the region of the main Hawaiian Islands. Our CCA results suggest that these species-level differences might be linked to the different sediment characteristics (e.g. coarser-grained sediments on the slope than in the canyon) and increased organic matter input into the canyon branches (Fig. 7). Duros et al. (2011) attributed differences in the benthic foraminiferal species composition between the branches and the slope, at depths comparable to those of the present study, to the preferential deposition of organic detritus in canyon branches.

Paramphinome jeffreysii was the top-ranked species at all sites except the slope site (Table 2). It represented, on average, 31.5% of the total assemblage composition inside the canyon compared with 14.3% on the slope. A SIMPER analysis suggests it was also responsible for much of the similarity between stations inside the canyon and between the canyon and the slope (Table 3). The relative abundance of *P. jeffreysii* increased from west to east, reaching almost 40% of the assemblage in the Eastern branch. It was also more common in the deeper sediment layers (1–3, 3–5 cm) than in the upper 1 cm horizon (Fig. 3). The abundance of this small, omnivorous polychaete (Fauchald and Jumars, 1979) throughout the canyon may indicate an opportunistic response to organic-matter enrichment inside the canyon. Significant increases in the abundance of the same species in the North Sea have been linked to an increase in food availability (Kroncke et al., 2011). High abundances of *P. jeffreysii* were also associated with organically-enriched sediments near fish farms along the Norwegian coastline (Bannister et al., 2014) and a trough (100 m depth) off the Swedish west coast (Rosenberg, 1995).

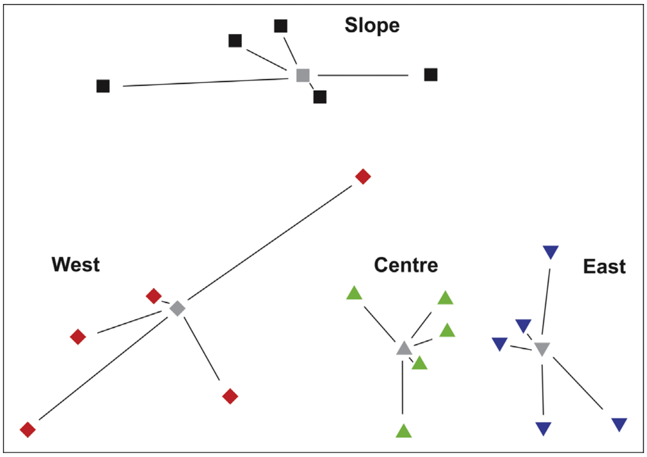

Fig. 6. nMDS ordination plot of polychaete species composition at four study sites (grey symbols represent centroids).

Juvenile polychaetes in the family Opheliidae (Opheliidae sp. A) were common in the 0–1 cm layer of samples from the Eastern branch (Fig. 3), where they accounted for 11% of the assemblage and were ranked second after *P. jeffreysii* (Table 2). This too may

Table 3
SIMPER analysis displaying the percentage contribution of the most important species responsible for within site similarity and between site dissimilarity. W – Western branch, C – Central branch, E – Eastern branch, Sl – Slope site.

Similarity between samples within sites (%) **Sl-average 51.9**	**W-average 49.0**	**C-average 61.0**	**E-average 56.1**
Paramphinome jeffreysii-6.7 *Aurospio* sp. B-6.7 *Anguillosyllis capensis*-5.8 *Aurospio dibranchiata*-4.6 *Flabelligella cf. biscayensis*-4.4	*Paramphinome jeffreysii*-9.2 *Aurospio* sp. B-6.8 *Ancistrosyllis* sp. A-4.1 *Chaetozone* sp. F-3.9 *Prionospio* sp. I-3.1	*Paramphinome jeffreysii*-11.4 *Aurospio* sp. B-4.9 *Levinsenia gracilis*-3.5 *Ophelina cylindricaudata*-3.5 *Chaetozone* sp. F-3.0	*Paramphinome jeffreysii*-12.0 Opheliidae sp. A-4.4 *Aurospio* sp. B-4.1 *Prionospio* sp. I-3.7 *Leitoscoloplos* sp. B-2.9
Dissimilarity between sites (%) **C&E-average 45.2** Opheliidae sp. A-2.6 *Paramphinome jeffreysii*-2.0 *Prionospio* sp. I-1.4 **Sl&E-average 61.8** *Paramphinome jefreysii*-5.5 Opheliidae sp. A-3.6 *Leitoscoloplos* sp. B-2.0	**C&Sl-average 57.5** *Paramphinome jefreysii*-3.8 *Anguillosyllos capensis*-2.8 *Ophelina cylindricaudata*-2.0 **E&W-average 61.7** *Paramphinome jefreysii*-4.6 Opheliidae sp. A-4.1 *Ancistrosyllis* sp. A-2.5	**C&W-average 55.4** *Paramphinome jeffreysii*-2.7 *Ancistrosyllis* sp. A-2.5 *Ophelina cylindricaudata*-2.2	**Sl&W-average 57.5** *Ancistrosyllis* sp. A-3.3 *Anguillosyllis capensis*-2.4 Ampharetidae new genus sp. A-2.1

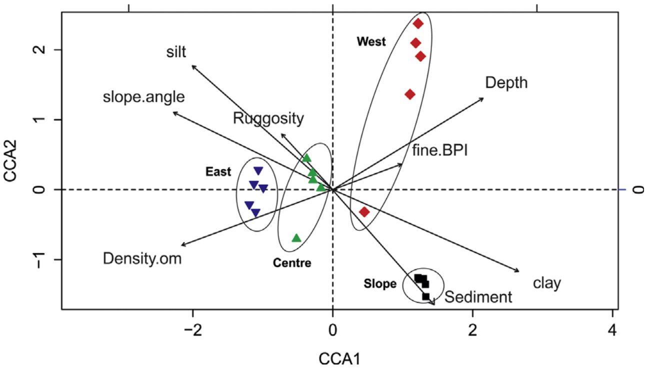

Fig. 7. Canonical correspondence analysis of polychaete species composition at four study sites. Depth=water depth; fine BPI=fine-scale bathymetry position index; clay=percentage clay; Density.om=macrofaunal density as a proxy for organic matter input; slope.angle=slope angle; silt=silt percentage; Sediment=sediment grain size.

Table 4
Assessment of beta diversity via rarefaction with Hill numbers (^{0}D, richness; ^{1}D, exponential Shannon; ^{2}D, inverse Simpson), α rarefied to 47 individuals, and γ rarefied to 235 individuals. $\beta = \text{beta diversity} = \gamma / \bar{\alpha}$. Canyon = all canyon sites. Region = all canyon sites + slope site.

Site	^{0}D			^{1}D			^{2}D		
	$\bar{\alpha}$	β	γ	$\bar{\alpha}$	β	γ	$\bar{\alpha}$	β	γ
West	18.5	2.5	46.1	12.2	1.7	20.2	8.4	1.4	11.5
Centre	19.9	2.3	45.7	11.8	1.5	18.1	7.0	1.1	7.6
East	18.4	2.5	45.9	8.8	1.5	14.5	5.4	1.0	5.6
Slope	21.2	2.6	54.0	15.7	1.6	24.8	11.9	1.3	15.0
Canyon	18.9	2.6	49.0	11.3	1.7	18.7	6.9	1.1	7.5
Region	19.5	2.7	51.8	12.4	1.7	21.1	8.2	1.1	8.7

indicate a recent input of organic matter onto the sediment surface. During a time-series study at a deeper site (~4850 m), located 464 km to the west of our study area on the Porcupine Abyssal Plain (PAP), morphologically very similar juvenile opheliids were found in high densities in the upper 2-cm layer of multicore samples (Vanreusel et al., 2001). Over the two year study period, a stable population of juvenile Opheliidae displayed a slow increase in the body size (Vanreusel et al., 2001). These opheliids were interpreted as opportunists that had recently been recruited following the deposition of a pulsed input of phytodetritus. A separate contribution to the same time-series study (Soto et al., 2010) also recorded a large increase in the abundance of opheliid juveniles at PAP. Again, this was interpreted as a recruitment event linked to phytodetritus deposition. Studies of shallow-water opheliids suggest that they have an opportunistic life history (Hermans, 1978). Experiments on the continental shelf off North Carolina showed opheliid and capitellid abundance increasing by 2–90 times in enriched sediment trays compared with unenriched trays (Renaud et al., 1999). Population densities of the opheliid *Armandia brevis* from waters off San Juan Island, Washington, fluctuate markedly throughout the year as a result of reproductive events (Woodin, 1974). The opheliids are likely to be opportunists waiting for optimal conditions before converting their energy resources into reproductive effort (Vanreusel et al., 2001). Our observations in the Whittard Canyon suggest that this species enhances the overall reproductive effort compared with the adjacent slope. Indeed, Vetter et al. (2010) suggest that canyons may act as sources for benthic invertebrates in which dense aggregates of individuals reproduce inside the canyons and send their larvae out onto the adjacent continental slope.

It is interesting to note the large depth range (3500–4850 m) of Opheliidae sp. A, which spans both the lower bathyal and abyssal zones in the NE Atlantic. It has been suggested that depth zonation amongst macrofauna is closely related to their dispersal abilities during their early development (Grassle et al., 1979). Assuming they all represent the same species, larvae of the opheliid recognised in the present study may be well adapted to dispersal, allowing them to span a large depth range. All juvenile opheliids in the study of Vanreusel et al. (2001) were presumed to belong to the same species. This species could not be determined as none of the individuals displayed full adult characteristics and all adult opheliids found at the PAP site in previous studies were new to science and not formally identified. The most abundant identified opheliid in our material was *Ophelina abranchiata*. It is not clear whether the juveniles represent this species or a complex of several species. Further work using genetic methods may elucidate this problem.

4.2. Polychaete diversity

4.2.1. Alpha diversity

Polychaete species diversity was similar in the Western, Central and Eastern branches of the Whittard Canyon, with the Western branch samples yielding slightly higher values of H' than the other two branches (Table 1). Total species numbers (species richness) were highest in the Eastern branch, followed by the Central, and Western branches, consistent with the higher abundances in the Eastern branch. All alpha diversity measures examined (Pielou's evenness J', Shannon index $H'(\log_2)$, Simpson's index $1-\lambda'$, Berger–Parker index (R1D) and the Chao1 asymptotic richness measure) indicated higher diversity (lower dominance) in the slope samples; the canyon samples had both reduced richness and increased dominance relative to the slope samples, consistent with hypothesis 3. Depressed species diversity inside canyons has been noted for macrobenthos in the Nazaré Canyon (Curdia et al., 2004), Scripps and La Jolla Canyons (Vetter and Dayton, 1998) and for polychaetes in the Portuguese canyons (Paterson et al., 2011). A number of ecological studies have suggested a unimodal relationship between diversity and productivity (Rosenzweig, 1995). In oligotrophic settings, diversity increases with increasing food availability to reach maximal values at intermediate levels of productivity. Where levels of food availability are excessive, diversity may be depressed (Levin et al., 2001). In the case of the La Jolla Canyon system, depressed diversity in shallow parts of the canyon was linked to dominance by opportunistic species associated with deposits of kelp and surfgrass detritus (Vetter and Dayton, 1998). In coastal marine systems, increased organic enrichment resulting from pollution can lead to higher infaunal standing stocks, as well as oxygen depletion and dominance by a few hypoxia-tolerant species (Pearson and Rosenberg, 1978). This has also been observed in upper bathyal oxygen minimum zones where dense, high-dominance, low-diversity benthic assemblages are associated with natural organic enrichment (Levin et al., 1994; Levin, 2003; Gooday et al., 2010). However, there is no evidence for organic enrichment from macrophyte detritus, or oxygen depletion, at our canyon study sites.

High levels of physical disturbance inside the canyon may also depress polychaete diversity in accordance with the Intermediate Disturbance Hypothesis (Connell, 1978, Huston, 1979), which predicts maximal levels of local species diversity when disturbance is neither too rare nor too frequent. At the High Energy Benthic Boundary Layer Experiment (HEBBLE) site in the NE Atlantic, disturbance generated by episodic strong currents (‘benthic storms’) was linked to high species dominance by polychaetes (58-64% ampharetids), bivalves, isopods and tanaids (Thistle et al., 1985). Most of the polychaetes were small and all were sexually immature, suggesting larval recolonisation of defaunated patches created by physical disturbance. Disturbance in the form of high-energy currents was considered important in the structuring of polychaete diversity on the Hebridean Slope in the Rockall Trough (Paterson and Lambshead, 1995). It has been suggested that community disturbance resulting from strong currents, high sedimentation rates and re-suspension may explain the depressed diversity and increased dominance among macrofauna and meiofaunal taxa in the Nazaré (Gage et al., 1995; Curdia et al., 2004; Koho et al., 2007; Ingels et al., 2009) and Setúbal (Gage et al., 1995) canyons. Paterson et al. (2011) attributed the dominance of a *Prionospio* species in the Nazaré Canyon to an opportunistic response to a disturbance event. The disturbance could have been caused by the periodic deposition of organically-enriched sediment, but a spring-tide-mediated turbidite event or increased bioturbation by larger macro/megafauna were also thought possible (Paterson et al., 2011). The lower diversity of sessile and sedentary megafauna in Hawaiian canyons was attributed to periodic disturbances, such as sediment slumps and turbidity currents, although mobile megafauna (e.g. fish and crustaceans) that were able to avoid or tolerate these disturbance events better than less mobile taxa exhibited enhanced diversity inside the canyons (Vetter et al., 2010). The depression in diversity observed at 700 m within the La Jolla Canyon system was also linked to disturbance from strong currents (Vetter and Dayton, 1998).

Polychaete diversity in the Whittard Canyon system is relatively high compared with that in the Nazaré and Setúbal canyons on the Iberian Margin, but similar to levels in the Cascais Canyon (Fig. 5b). Paterson et al. (2011) analysed polychaete diversity in these canyons, in each case at depths of 1000, 3400, and 4300 m. They attributed differences in polychaete rarefied species richness between them to different environmental characteristics. The Nazaré Canyon is active with periodic disturbances and relatively high current speeds (de Stigter et al., 2007; Garcia et al., 2007). Reduced diversity in the middle part of the Setúbal Canyon was attributed to lower productivity. The higher diversity in the Cascais Canyon suggested that it is a more quiescent canyon, where disturbance and productivity effects are balanced (Paterson et al., 2011). If correct, these inferences suggest that the Whittard Canyon is less active than the Nazaré and more similar to the Cascais Canyon, at least around 3400 m in the middle section.

4.2.2. *Beta diversity*

Levels of beta diversity on the ocean floor are poorly understood and appear to vary between taxa (Ellingsen et al., 2007a). Paterson et al. (1998) reported a difference in the species composition of polychaete assemblages at sites on NE Atlantic and equatorial Pacific abyssal plains separated by 500–1000 km. They suggested that faunal turnover occurred across scales of 1000+km on abyssal plains. Similarly, Glover et al. (2001) reported differences in polychaete species assemblages at four sites in the NE Atlantic (Porcupine, Tagus and Cape Verde Abyssal Plains) that were separated by distances of up to 3300 km. However, our data suggest there is a change in polychaete species composition across the 60 km spanned by our four study sites. It seems likely, therefore, that rates of beta diversity are considerably higher on continental margins dissected by canyons than they are on abyssal plains, which are topographically much less complex and offer fewer barriers to dispersal than the ocean margins.

Another way to assess the change in species composition across the study sites is provided by Whittaker's beta diversity (β_W). According to this metric, there was no clear variation in beta diversity, although we should note that the sample size limitations (minimum number of specimens per sample) may have restricted our ability to detect a change. Our beta diversity assessment (Table 4) nevertheless makes clear the enhanced α and γ diversity levels of the slope site compared with the canyon sites. This meant that all aspects of diversity (^{0}D, ^{1}D, ^{2}D) were reduced when canyon data were added to the slope data.

There was surprisingly little difference in the composition of species assemblages between the slope and the Western canyon branch (Fig. 8). Our canyon samples are all from soft-bottom areas that are not too dissimilar in terms of sediment characteristics from the open slope. However, the Whittard Canyon as a whole encompasses a wide range of different habitats. The head of the canyon is characterised by turbidity currents and oxygen-limited, possibly sulphidic conditions (Ingels et al., 2011). Vertical cliffs (Huvenne et al., 2011) and cold-water corals (Morris et al., 2013; Huvenne et al., 2011; Robert et al., 2014) are present in the upper to mid reaches, flat areas of soft sediment in the thalweg (Robert et al., 2014) and deeper parts of the canyon. Analyses of polychaete assemblages from these different areas inside the canyon would almost certainly increase species-level differences in the assemblages both between canyon and slope and within the canyon and thereby enhance species turnover. McClain and Barry (2010) observed that the highest rate of faunal turnover in the Monterey Canyon off the central Californian coast, USA, was closest to the canyon wall. These authors concluded that the canyon walls enhanced the input of organic debris, which significantly altered the

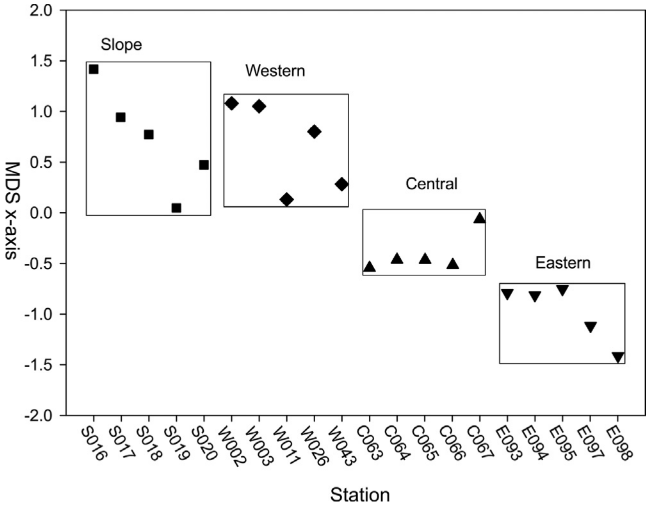

Fig. 8. Plot of nMDS ordination *x*-value against sampling identity for polychaete species composition at four study sites.

benthic assemblages. In the Whittard Channel (a continuation of the canyon system) at 4000–4400 m depth, Amaro et al. (2015) concluded that organic matter enrichment mainly resulted from the concentration within the Channel of phytodetritus deposits derived from surface production during the spring bloom, which occurs in this region from April to May (Joint et al., 2001). Our canyon samples were all collected in June/July, either from within or next to the canyon thalweg. Polychaete assemblage composition, including the high abundance of opportunistic juvenile opheliids and *P. jeffreysii*, may have been influenced in a similar way by the concentration in this depression of detrital material originating from the spring bloom.

4.2.3. *Regional species diversity*

Continental margins are characterised by high species diversity (Hessler and Sanders, 1967), related in part to the considerable habitat heterogeneity that characterises these regions of the deep sea (Levin and Dayton, 2009; Levin et al., 2010). By virtue of their extreme topography, complex current regimes, and tendency to concentrate organic matter and sediment, submarine canyons make a substantial contribution to this heterogeneity (Vetter and Dayton, 1999; McClain and Barry, 2010). Canyons in the Hawaiian Archipelago were thought to enhance the regional diversity of megafauna with high mobility, with 41 species being only found inside the canyon and not on the slope (Vetter et al., 2010). As noted above, diversity was reduced in the present study when canyon and slope data were combined. Nevertheless, 46 polychaete species were only recorded from the canyon branches, which tends to support hypothesis 4, that canyons increase regional diversity in soft-sediments by harboring species different from those found on the adjacent slope. However, our sampling effort was not equal at the canyon and slope sites (i.e. 15 and 5 samples, respectively) and therefore we do not have enough evidence to conclude that the Whittard Canyon enhances the diversity of benthic polychaetes at regional scales.

4.3. *Polychaete biogeography*

The 25 species that were found at all four study sites accounted for 72.3% of polychaete specimens. They include the two most abundant species (*Paramphinome jeffreysii* and *Aurospio* sp. B), which made up 39.4% of the total number of identified polychaetes in our samples. On the other hand, the 43 species that occurred at a single site accounted for only 2.9% of all specimens. This pattern is consistent with the observations of Glover et al. (2001), who recognised a core group of polychaete species that were widely distributed at their four NE Atlantic abyssal plain sites. These species represented about 70% of the fauna at the Madeira Abyssal Plain but around 50% or less at three other sites. However, a large majority (81%) of the species they recognised were unique to one of their sites. They attributed the large number of unique species to a vast regional species pool and inadequate sampling effort. Wide spatial distributions of the most abundant species and the apparent compressed range of the least common species were also noted in the case of polychaetes from the Southern Ocean (Ellingsen et al., 2007b). Indeed, this pattern is suggested for many groups of species, habitat types and spatial scales (Brown, 1984).

Some species found in the Whittard Canyon apparently have cosmopolitan distributions on a global scale. For example, there are records of *Aurospio dibranchiata*, which was found at all four of our sites, from the Atlantic, Pacific and Southern Oceans (Smith et al., 2006). With fewer barriers to dispersal in the deep sea, compared with shallow-water habitats, wide dispersal of species might be expected (Grassle and Morse-Porteous, 1987). However, barriers do exist and these are probably more common on continental margins than abyssal plains (McClain and Mincks Hardy, 2010). Despite these restrictions to dispersal, some species do appear to have cosmopolitan distributions in the deep sea, particularly at abyssal depths (Wilson and Hessler, 1987; McClain and Mincks Hardy, 2010; Gooday and Jorissen, 2012). In the case of certain foraminiferal species, this is supported by molecular evidence (Pawlowski et al., 2007; Lecroq et al., 2009). Conversely, some species identified morphologically as 'cosmopolitan' have proved to comprise a complex of cryptic species with smaller ranges when investigated with molecular methods (e.g.,Vrijenhoek et al., 1994; France and Kocher, 1996; Quattro et al., 2001).

Paterson et al. (2011) suggest that canyons may harbour endemic polychaete species. Forty-six polychaete species were found inside the Whittard Canyon branches but not on the adjacent slope. Of these 46 species, 34 could not be assigned a binomial Latin name. Out of the twelve species that could be given a Latin name, one was originally described from the Northeast Atlantic (*Exogone (Parexogone) campoyi*), two from the Northwest Atlantic (*Aglaophamus minusculus*, *Aricidea (Strelzovia) quadrilobata*), three from the Arctic Ocean (*Laonice blakei*, *Micronephthys minuta*, *Pseudoscalibregma parvum*), two from the Norwegian coast (*Ampharete finmarchica, Amphicteis gunneri*), two from the Californian coast (*Cenogenus fusca* and *Levinsenia oculata*), one from the Southern Ocean (*Augeneria tentaculata*) and one from off the Japanese islands (*Anobothrus patersoni*). None of these species is confined to the broader area around the canyon, although *E. (P.) campoyi* has been recorded only from the Bay of Biscay, the western Mediterranean, and the Aegean Sea. Interestingly, this species was first described from the Capbreton Canyon in the Bay of Biscay (San Martin et al. 1996), suggesting it may be common in canyons.

It is estimated that up to 90% of deep-sea species have not been formally described (Smith et al., 2006) and consequently species distributions are very poorly understood (Glover et al., 2001; McClain and Mincks Hardy, 2010). This applies as much to polychaetes as it does to other deep-sea taxa (Paterson et al., 2011). The prevalence of undescribed species in our samples makes it difficult to determine whether any are endemic to the Whittard Canyon. Two species found in the Whittard Canyon, *Aurospio* sp. B and *Prionospio* sp. I, were also recorded in the Iberian canyons and are currently being described (Paterson et al. submitted). These new species appear to be closely associated with canyons. *Prionospio* sp. I has only been found in canyons (L. Neal unpublished observations). *Aurospio* sp. B has been recorded in a non-canyon environment on the Porcupine Abyssal Plain, but only in very low densities (G. Paterson unpublished observations). Both may be (Foix, Lacaze-Duthiers and Planier canyons) and are thought to be endemic to either one or multiple Mediterranean canyons (Gili et al., 2000; Bouillon et al., 2000). The life cycles of these endemic hydromedusea are closely linked to factors specific to the canyon environment, such as topography, sedimentation and hydrographic conditions. Similarly, Paterson et al. (2011) suggested that some polychaete species are adapted to the disturbed conditions typical of some canyons rather than being restricted to one particular canyon. Further research on the taxonomy of deep-sea canyon polychaetes, using both morphological and genetic approaches, is required in order to understand endemism in canyons and species connectivity between different canyons.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.bios.2014.05.063.

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