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Macrofaunal Diversity and Functioning within Submarine Canyons of the Mid-Atlantic Bight, Western North Atlantic

Robertson, Craig

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Macrofaunal Diversity and Functioning within Submarine Canyons of the Mid-Atlantic Bight, Western North Atlantic

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Craig Melville Robertson

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award of Doctor of Philosophy.

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Macrofaunal Diversity and Functioning within Submarine Canyons of the Mid-Atlantic Bight, Western North Atlantic

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Thesis summary

Submarine canyon systems have been described as biodiversity hotspots that enhance benthic communities, especially when compared to nearby open slope habitats at similar depths. These complex systems act as major conduits of organic matter and sediment transport within continental shelves and promote gradients in food resources, habitat heterogeneity, sediment resuspension and sediment deposition. However, only few studies have investigated macrobenthic community metrics in relation to the multiple environmental factors that are altered by canyons. The research within this thesis was conducted as part of a 5-year multidisciplinary program funded by BOEM, USGS and NOAA, which focussed on two of the largest canyons on the shelf of the Mid-Atlantic Bight (MAB) (western North Atlantic shelf, USA), Baltimore and Norfolk canyons. The overarching aim of this study was to describe the physical characteristics of these canyons and relate these to different aspects of macrobenthic ecology.

Firstly, the main oceanographic drivers acting within the two canyons and their adjacent slopes were described. Canyons and slopes exhibited similar hydrographic features in terms of the presence of characteristic water masses, namely the shelf-slope front, Western North Atlantic Central Water (WNACW) and Western Atlantic Sub-Arctic Intermediate Water (WASIW) were observed. However, near-bottom measurements from a year of data revealed several clear differences between the two canyons. Current speed and direction in both canyons were driven by semidiurnal tides (M_2) that were strongest near the heads of both canyons and exhibited a persistent up-canyon directionality. In both canyons, benthic nepheloid layers were present that were not observed in adjacent slope transects. It is likely that differences observed, are related to a difference in canyon morphology, the orientation of the canyons to the shelf and differing interactions with internal waves.

Secondly, the benthic macrofaunal ecology of Baltimore and Norfolk canyons and respective adjacent slopes were described from replicated sediment cores that were collected along their main axes (~180-1200 m) and at comparable depths on the adjacent slopes. Cores were sorted and whole community macrofaunal (>300 μm) abundance, diversity and standing stocks were assessed. Coupling family-level community data, with sediment grain-size and biogeochemistry data yielded insight into community dynamics across depth and biogeochemical gradients. Canyon communities were significantly different from slope communities with differences in diversity, abundance patterns and community assemblages,

which were attributed to high levels of organic matter enrichment within the canyons. The two canyons hosted different communities that were indicative of environmental disturbance, with bivalves dominating mid-canyon depths in Baltimore Canyon, and deposit-feeding polychaetes in Norfolk Canyon. Abundance-biomass curve comparisons confirmed that lower canyon communities (800-1180 m) were disturbed, as well as upper slope communities (180-555m) on the adjacent slope.

Thirdly, for the first time in a canyon system, a biological traits approach was used to define functional differences between the two MAB canyons and their adjacent slope communities. A total of 49 trait modalities across 10 biological traits were used to characterise the community and showed that higher functional richness was present within upper and middle canyon communities compared to slope communities across the studied depth gradient. Lower canyon communities (800-900 m) were less functionally rich, a feature attributed to substantial biomass contribution of opportunistic and dominant taxa that benefited from organically enriched sediment in the canyons. Bioturbation potential was higher in the canyons than adjacent slope, especially within Baltimore Canyon, and was attributed to the high affinities for surface and subsurface sediment modifiers and sediment ingestion or filter-feeding bioturbators. The trait affinities within canyons showed propensity for sediment reworking to greater depths, suggesting that canyon communities may enhance nutrient fluxes and burial of accumulated organic matter. The findings confirmed that enhanced macrofaunal community ecosystem function and higher bioturbation occurred within the canyons compared to the adjacent slopes and provided new insight into the distinct functional roles found within canyon and slope macrofauna.

This study was the first to characterise the physical setting and macrofaunal communities of the Baltimore and Norfolk canyons in detail. Overall, the canyons were notably more dynamic than the adjacent slopes, acting as true disruptors to established shelf/slope patterns in biodiversity, abundance and functioning of macrofauna.

Chapter 1

Introduction to submarine canyons: One of the most dynamic of all deep-sea habitats

Robertson CM

1 Introduction

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; Vieross et al., 2009), occupies 91 % of this area (Harris, 2014). The deep ocean is the largest biome on the planet (Glover et al., 2010) and despite its enormous size, the deep-sea floor is the least explored part of the planet, with only 5 % of the area being surveyed with remote instruments and less than 0.01 % sampled and studied in any detail (Ramirez-Llodra et al., 2010). However, even with so little area studied, the deep sea is known to harbour high biodiversity and provides a wealth of economic, ecological and cultural resources (Armstrong et al., 2012; Ramirez-Llodra et al., 2011).

One of the first meaningful, and perhaps ground-breaking, scientific expeditions to research the deep sea was that of the HMS *Challenger* 1872-76. The expedition was partly a consequence of the economic value of submarine telegraph communication as new cable routes were surveyed (Corfield, 2003), but was also designed to contribute to the 19th century regarding the debate as to whether life occurred at depths below 300 m (Forbes, 1844; Anderson & Rice, 2006). The concept of the deep ocean being barren was posited as early as 1834, yet it was Edward Forbes, who popularised the idea with the publication of the "azoic hypothesis" (Forbes, 1844). Even prior to the publication of this theory, there was mounting evidence that the deep sea was not devoid of life, rather it contained a variety of organisms across a range of size classes (Anderson & Rice, 2006).

In the late 1960's, the biologists Robert Hessler and Howard Sanders refuted another long-held theory, that the deep sea was occupied only by a small number of specialised species that existed within a relatively quiescent environment (Hessler & Sanders, 1967; Sanders & Hessler, 1969). Their quantitative investigations using an epibenthic sled demonstrated high diversity, which exceeded that of equivalent shallow temperate marine habitats (Hessler & Sanders, 1967). Since this seminal work, the deep sea has emerged to be a dynamic and heterogonous environment, which varies over many spatial and temporal scales (Lins et al., 2016; Ramirez-Llodra et al., 2010; Rex & Etter, 2010), driven largely through advances in ship-based technologies and the ability to explore the deep sea through direct observation (Danovaro et al., 2014). However, the characteristics and natural variations of deep-sea communities and the underlying processes that drive such patterns remain an active area of research that is under debate (McClain & Schlacher, 2015; Rogers, 2015; Thurber et al., 2014).

2 Physical conditions in the deep sea

Five major biomes are recognised in the deep sea, the upper bathyal (300-800 m), lower baythal (800-3500 m), abyssal (3500-6500 m) and hadal (> 6500 m) (Gage and Tyler, 1991). Pressure increases by 1 atmosphere per 10 m of water depth, whilst bottom temperatures reach ~2-4 °C on the abyssal plain (Sverdrup et al., 1942; Thistle, 2003). Within bathyal regions, temperatures can vary between 4 and 10 °C, with the lowest temperatures found in the deep waters of the Antarctic and the warmest in the Mediterranean (Gage & Tyler, 1991). Unlike in coastal regions, salinity in the deep-ocean remains relatively constant below 2000 m, at around 35 on the practical salinity scale (Sverdrup et al., 1942) and varies little over time (Thistle, 2003). The majority of the deep-ocean floor has near saturation oxygen values (5-6 ml l^{-1}), with exception of oxygen minimum zones and older water masses (Gage & Tyler, 1991, Rogers, 2015). The North Pacific gyre comprises the world's largest oxygen minimum zone, which occurs between 400 and 1000 m (Rogers, 2015).

Exposed bedrock is relatively uncommon in the deep sea, with most hard substrate located on steep continental margins, seamounts and mid-ocean ridges (Gage & Tyler, 1991). Soft sediments dominate many areas of the deep sea. The upper continental margins mostly comprise terrigenous derived course sediments that are transported by turbidity currents and sediment gravity flows (Etter & Grassle, 1992; Gage & Tyler, 1991). On continental slopes, the main sediment constituents are detrital sand and silt, reducing clay and calcareous siliceous oozes (Berger, 1974; Gage & Tyler, 1991). Although sediments are inorganic, they carry with them organic matter, depending on the productivity of overlying waters and distance from coast (Gage & Tyler, 1991). Much of the deep sea is considered a food-limited environment (Rogers, 2015), and is highly dependent on fluxes of organic matter from surface waters and coastal areas (Jones et al., 2014; McClain et al., 2012).

Most regions of the deep sea are accepted to be somewhat physically quiescent, largely due to low bottom current speeds. Speeds in the bathyal zone tend to be less than 10 cm s^{-1} at 1 m above the bottom, whilst those in the abyssal zone are less than 4 cm s^{-1} (Eckman & Thistle, 1991; Thistle, 2003). These flows are accepted to be benign, in that they are too slow to erode or suspend some sediments and benthic organisms. The flow does move some material, in particular phytodetritus (flocculent material of low specific density consisting of phytoplankton cells in an organic matrix, Billett et al., 1983), which generally accumulates in depressions or on topographic features (Lampitt, 1985; Morris et al., 2016). Phytodetrital supply to the seafloor can occur as a steady supply, in the form of marine snow and in large, episodic food falls (Beaulieu, 2002; Thomsen et al., 2017).

One factor that can override general expectations of physical quiescence in the deep sea are benthic storms (Gardner & Sullivan, 1981). Such storms can mobilise and redistribute deep-sea sediments across the global ocean. They are characterised by high current regimes occurring at regular frequencies (e.g. exceeding 20 cm s^{-1} at some time over a 2-year period are estimated to cover about 8% of abyssal sea floor), typically last between 2 to 22 days, and commonly have a frequency of eight to 10 storms per year in some areas (Harris, 2014). They effect the erosion of habitat, increased sediment instability and the sweeping of surficial organic matter and microorganisms from the storm-affected area (McClain & Schlacher, 2015). Whilst fundamentally different in origin, several similarities can be drawn with turbidity flows, whereby dense, sediment-laden waters flow rapidly down a slope (Puig et al., 2014). Naturally occurring current induced sediment disturbances, such as benthic storms, nepheliod layers and turbidity flows, are a key factor structuring benthic communities (Hall, 1994).

3 Continental margins

In the deep ocean, substantial bathymetric relief generally begins on the continental margins, where large depth gradients are traversed by steep slopes and canyons incise and drain the continental shelf (Van Dover, 2000). Continental margins were generally perceived up until the 1960's as ubiquitous zones of soft sediments of little consequence to humankind, but it is now known that it is one of the most extensive habitats on earth and contains highly diverse marine communities (Etter & Grassle, 1992; Grassle & Maciolek, 1992; Levin & Dayton, 2009; Levin & Sibuet, 2012; Menot et al., 2010; Ramirez-Llodra et al., 2010; Stocks et al., 2012). Targeted studies involving seafloor mapping and direct observation of continental margin ecosystems has revealed unexpected heterogeneity, with rich, complex habitats and ecosystems linked to geomorphological, geochemical, and hydrographic features that influence patterns of diversity and abundance (Levin & Sibuet, 2012; McClain & Barry 2010).

Other seafloor features that provide bathymetric relief include seamounts, hydrothermal vents, mid-ocean ridges and hadal trenches, amongst many others (Greene et al., 1999). Seamounts share some similarities in many respects to continental margins and are understood to be ubiquitous habitats in the deep sea. Similar to continental margin features, they are also poorly understood and seldom sampled (Rogers, 2015; Yesson et al., 2011). They are mainly associated with mid-ocean ridges, island arcs convergent areas, and intraplate hot spots where chains of seamounts may be generated (e.g. Hawaii) (Kvile et al., 2014; Rogers, 2015). Early studies posited seamounts as unique habitats supporting high levels of endemic species (Richer de Forges et al., 2000) alongside higher species richness and biomass than surrounding areas (Rowden et al., 2010). More recent works have discounted the 'endemism hypothesis' (Howell et al., 2010; O'Hara 2007; McClain et al., 2009a), in favour of the 'oasis hypothesis'; where inventories of seamount species may be similar to nearby continental slopes, although community structure can be very different (McClain et al., 2009a; Rowden et al., 2010). Drivers of community differences at seamounts include environmental conditions (O'Hara et al., 2010) and the availability of hard substratum (Clark et al., 2010), which promotes extensive biogenic habitats often dominated by sessile suspension feeding taxa (Rowden et al., 2010).

4 Diversity and benthic standing stocks in the deep sea

Patterns of diversity in the deep sea are more complicated than previously thought. Sanders (1968), in an influential comparative study of marine benthic diversity, showed that bathyal diversity exceeded coastal diversity in the temperate zone and approached that of shallow-water tropical diversity. Later assessments centred on the bathymetric gradients in the north western Atlantic, one of the most extensively sampled regions of the deep sea (Blake & Grassle, 1994; Blake & Hilbig, 1994; Blake & Maciolek, 1986; Etter & Grassle, 1992). Quantitative sampling with precision box corers confirmed Sanders (1968) finding that diversity increases with depth below the continental shelf (Levin et al., 2001), and suggested that peak diversity of the whole macrofaunal assemblage occurred at around 1000-1500 m on the continental slope (Etter & Grassle 1992). However, for the majority of the deep sea, the depth of maximum diversity depends on the taxa considered, species' ranges and dispersion patterns, and the spatial scales covered by different sampling gears (Rex & Etter, 2010; Stuart et al., 2003).

In general, a unimodal diversity-depth relationship seems well-established in most regions of the deep sea (McClain et al., 2009b; McClain & Schlacher, 2015), although the drivers of these patterns may vary geographically (Flach & De Bruin, 1999; Rex et al., 1997; Stuart et al., 2003; Tittensor et al., 2011). The diversity-depth relationship coincides with a decline in standing stock, generally as a function of the decline in food availability with increasing depth (Rex & Etter, 2010). Rex (1981) suggested that depressed diversity at upper bathyal depths, where standing stocks are high, might be due to local competitive displacement driven by pulsed carbon loading from high seasonal productivity in coastal waters. In most circumstances, this is true, as heavy carbon loading associated with upwelling, topographic focusing of sinking organic material, sediment erosion and deposition results in high standing stocks and depressed diversity irrespective of depth (McClain et al., 2009b).

Given that shallow water is mostly adjacent to land, there are generally higher levels of productivity, a shorter food-particle settling period (i.e. the amount of time the particle travels before it reaches the bed), and hence larger fluxes of high quality organic material to the seabed. This led to the generalisation that the abundance of organisms in the deep sea decreases with depth and distance from a major land mass (Murray, 1895). Rowe (1983) first showed that the exponential decrease in the abundance of organisms, measured as population density or biomass, with depth to be a global phenomenon. Subsequently, it has become clear that the pattern is modulated in a predictable way by food availability at depth (McClain et al., 2009b). Biomass of megafauna (Lampitt et al., 1986), macrofauna (Rowe et al., 1982), and meiofauna (Tietjen, 1992) have also been shown to decrease with depth.

5 Sampling methods

Sampling deep-sea benthos is logistically challenging due to the extreme hydrostatic pressure at depth, the large distance from the surface to the seafloor and the distance from land. Collecting deep-sea samples is therefore both time consuming and expensive (Jamieson et al., 2013). Historically, the first attempts at sampling the deep-sea benthos were reliant on a variety of trawling nets with large mesh sizes, resulting in the majority of specimens passing through, which led to the assumption that benthic abundance and diversity was relatively low (Gage & Tyler, 1991). These early techniques were insensitive to the decrease in body size and increase in diversity with depth. The abundance of biodiversity in the deep sea first emerged after Hessler and Sanders (1967) developed the epi-benthic sled, equipped with a fine mesh capable of collecting large samples of fauna from the sediment-water interface, over wide spatial areas (Fleeger et al., 1988). In order to quantify faunal richness and abundance, the accurate measurement of the unit area sampled is essential, as well as detailed knowledge on the efficiency of the specimen collection (Narayanaswamy et al., 2016). As these parameters were difficult to quantify for towed sampling devices, they were at best qualitative and later only used for exploratory benthic surveys.

For research questions that required quantitative sampling of macrobenthic organisms, grabs and cores have long been the preferred sampling equipment (Narayanaswamy et al., 2016; O'Hara et al., 2016). The first quantitative survey devices were simple closed grab benthic samplers, which allowing for the calculation of the sample surface area and were designed for use in shallow shelf seas. In essence, these samplers were equipped with a of pair scooping bins, which once in contact with the seabed, were triggered thus capturing a quantity of sediment and closed by the upward tension of the deployment wire upon retrieval from the seabed. Up to the 1970's the main quantitative samplers were the Okean, Campbell and Petersen grabs (Spärck, 1951). A drawback in their use was the shallow and uneven sediment penetration, due to the scooping action of the grab (Narayanaswamy et al., 2016), which prompted the development of sediment coring devices, the forbearers of modern quantitative benthic sampling devices.

In the sampling of the soft sediment benthos, there have been three main devices used over the last forty years, namely the epi-benthic sled, the boxcorer and the multicorer. To assess the prevalence of the use of such equipment, a search of deep-sea macrofauna publications via the ISI Web of Science catalogue returned a total of 889 publications between 1978 and 2017 (Figure 1). The majority of macrobenthic sampling was conducted using boxcorers (347 publications) and multicorers (335 publications), although recently the multicorer has increased in popularity (28 publications in 2017 alone). More recently, there has been an increase in remotely operated vehicle (ROV) cores (44 publications; 6 in 2017), largely due to their increased availability, capability and more frequent use in recent multidisciplinary projects (Danovaro et al., 2014).

The boxcore is a marine geological sampling tool for soft sediments in oceans or lakes. The first device was developed by Hessler and Jumars (1974) in conjunction with the United States Navel Electronic Laboratory, giving rise the USNEL boxcore (Figure 2a). These became popular due to their reliability and the large sampling area (0.06-0.25 m^2). Other boxcores designed for use in deep-water are the GOMEX (Boland & Rowe, 1991) and NIOZ boxcorers (Gage & Bett, 2005). Despite their success in acquiring quantitative samples, in recent years, the use of large boxcores has been criticised (Bett et al., 1994; Blomqvist, 1991; Montagna et al., 2017). It has been suggested that such devices may underestimate the abundance and diversity of benthic macro- and meiofauna, due to creation a bow wave or downward-flush effect when sampling (Bett et al., 1994), which likely disturbed the sediment-surface in the few moments before impact, thus sweeping away any surface sediment associated fauna (Montagna et al., 2017).

Later designs incorporated modifications to minimise the bow wave effect. The first was the use of paired vent valves (Figure 2a), mainly in USNEL boxcores (Blomqvist, 1991), which were incorporated to allow the flow of water through the bucket, thus reducing the bow-wave effect. Yet, once at the surface, the vent valves are mobile and can spill sample water, leading to disturbance of upper sediment layers of the sample and the washing out of associated fauna. Sample integrity can be compromised by this washout through vent valves or poorly sealed closed buckets (Narayanaswamy, et. al., 2016). In an effort to maintain the integrity of the consistent sediment layers in a sample, the NIOZ developed a cylindrical boxcoring device, replacing the usual vent valves with a rubber lined steel seal plate (Figure 2b). The steel seal plate is closed during the engagement of the spade arm after impacting the seabed, thus allowing the retrieval of completely sealed sediment core and overlying supernatant water, which remained sealed until arrival on deck. In very simple terms, for a representative biological sample, a core must return all of the specimens present in the sediment volume sampled by the device. This completeness is not the case for USNEL-type boxcores, but through design is likely true for the NIOZ boxcore (Narayanaswamy, et. al., 2016).

To address the short comings of USNEL boxcores, multiple coring devices were developed (Narayanaswamy et al., 2016), which have gained popularity amongst benthic surveyors (Figure 2c). The main advantage of multicoring devices is the almost complete absence of the bow wave effect prior to sediment penetration, due to the hydraulically dampened contact at the seabed and a more streamlined design, which allows for collection of fauna at the sediment-water interface (Barnett et al., 1984; Bett et al., 1994). However, a major disadvantage is the limited sample size returned when compared to the boxcore. Typically, multicoring devices have an array of 12 x 10 cm diameter cores, returning 0.096 m^2 of seabed. Various studies have compared the sampling accuracy of boxcore and multicore devices with mixed results (Bett et al., 1994; Glover et al., 2008). Montagna et al. (2017)

analysed a series of studies performed over a 14-year period comparing boxcore (GOMEX) and multicore meio- and macrofauna samples from the Gulf of Mexico continental margin. The study concluded that boxcores where better at estimating overall species diversity due the large sample area compared to multicores, although they underestimated abundance relative to area sampled. When using multicorers, there was more variability between cores within deployments (i.e., pseudo-replicates) than between deployments (true replicates), thus spatial studies should consider sampling more stations with fewer true replicates.

Clearly, care should be taken when compiling data from sampling coring devices with different sampling performances. The present study employed a truly replicated sampling design consisting of three replicates in each of four depth groups (~180, 550, 900 and 1180m), along two canyon and two slope transects, divided equally between Baltimore and Norfolk study sites. Sampling was conducted using only the NIOZ boxcore, a robust and easily deployed device that is ideally suited for sampling with dynamic and topographically variable regions such as canyons.

6 Submarine canyons

Submarine canyons are the dramatic and widespread topographic features crossing continental and island margins in oceans, which connect the shelf to deep-ocean basins (Harris & Whiteway, 2011). Studies estimate that the ocean contains 5,849 submarine canyons (Figure 3a) and are of three distinct types: 1) Those that are shelf incising connected to a river, 2) shelf-incising and 3) blind canyons, those that are headless, arising only from the continental slope (Figure 3b) (Harris & Whiteway, 2011). Their evolution is generally considered to be driven by two processes; erosive turbidity flows derived from fluvial shelf and upper slope sources as in shelf incising canyons and slumping, slope failure and other mass wasting events, such as in blind canyons (Harris & Whiteway, 2011).

Several large-scale research programmes have highlighted the variety of continental shelf processes to which canyons contribute (e.g. Canals et al., 2006; Palanques et al., 2006; Weaver & Gunn, 2009, and see Puig et al., 2014 for a review). These systems are often characterised by unique and complex patterns in hydrography, geomorphology, sediment transport and sediment accumulation patterns that lead to the development of canyon-specific conditions (García et al., 2008). These result in an array of physical and ecological drivers that can influence the organisms found within canyons. For example, the displacement of deep-water species to coastal zones, topographically induced upwelling, enhanced mixing via internal tides and the focusing of tidal bores (Cacchione et al., 2002; Vetter & Dayton, 1998). In addition, enhanced organic matter flux (García et al., 2008) and deposition through entrainment of coastal detrital export, dense shelf water cascades (Ribó et al., 2011) and channelling of re-suspended particulate material leading to increased sediment deposition (De Leo et al., 2010), are now established as the major sedimentary pathways that operate within canyon systems (Figure 4). Complex interactions between steep-sloping topographic features and local hydrology create regions of intensified near-bottom flow in canyons (Gage, 1997; Lamont et al., 1995) where turbidity currents may also be active (Jorissen et al., 1994). The delivery of fresh organic matter to sustain rich benthic communities derives from the oceanographic characteristics of the area and the focusing effect of canyons (Huvenne et al., 2011). It is important to develop an understanding of these physical regimes and the resultant ecological patterns within canyon systems (Levin et al., 2001), as uniqueness of ecosystems is an important factor in conservation and management (Auster et al., 2011).

Over the last two decades, canyons have increasingly been described as important biodiversity hotspots on continental margins (e.g. Baker et al., 2012; De Leo et al., 2010; Gunton et al., 2015; Lamont et al., 1995; Paterson et al., 2011; Vetter & Dayton, 1998). Recent studies have concluded that physical environmental drivers within a canyon system are a primary factor in determining habitat variability, and as such, the ecological patterns that arise within the confines of a canyon (De Leo et al., 2014; Levin et al., 2001; McClain & Barry, 2010). Substrata heterogeneity and the concentration of organic matter are frequently cited as explaining higher faunal diversity, abundance and benthic productivity in canyons compared to surrounding areas (De Leo et al., 2010; Levin & Sibuet, 2012).

Bathymetric patterns of species' diversity have been attributed to changes in sediment characteristics (Etter & Grassle 1992), productivity, currents, oxygen, disturbance, and the interplay of biotic effects with depth and latitude (Levin et al., 2001, Carney, 2005). Commercial fishing activities have recently been shown to be an additional anthropogenic disturbance for canyons and their surrounding rims (Martín et al., 2014; Wilson et al., 2015). Canyon flanks are frequently targeted by commercial trawling fisheries, an activity that may enhance the input of resuspended particles into canyons, and eventually trigger down-canyon sediment gravity flows. The changes in sedimentary regimes are attributed to the strong increment of engine power of the fishing fleets from the seventies and the fishing gears towed along the canyon rims have been causing stronger disturbances on the bottom sediment (Martín et al., 2014).

Within the soft sediment communities, near-bottom currents have been reported as disturbance mechanisms that can modify the structure and composition of the benthic fauna (Hall, 1994). However, the critical factor may be sediment mobility, which depends not only on sedimentary characteristics (Levin et al., 1994) but also on the fauna inhabiting them (Green et al., 2002; Meysman et al., 2006) through sediment engineering and bioturbation. Individual canyons may show endemic hydrodynamic regimes which could give rise to canyon-specific benthic habitat niches, however, the understanding is how these processes regulate diversity and the influence of cascade effects within these ecosystems remains incomplete (McClain & Barry, 2010).

7 The Mid-Atlantic Bight

The Mid-Atlantic Bight (MAB) on the eastern United States continental margin, stretches from Cape Hatteras to the Nantucket Shoals. Circulation in this area is strongly influenced by two large-scale currents, 1) the northward flowing, warm but nutrient poor Gulf Stream (Liu et al., 2010) and 2) the southward flowing, cold but nutrient-rich Labrador slope current (Lohrenz & Verity, 2006). The relatively wide MAB shelf is separated from the Gulf Stream by a warm outer shelf front and slope sea (the narrow band of ocean between the Gulf Stream and the MAB shelf edge; Linder & Gawarkiewicz, 1998). Yet, the MAB is influenced by the Gulf Stream, largely through warm-core eddies that sporadically transport warm Sargasso water onto the shelf break. The meandering of the shelf-slope front and occasional interactions with warm-core rings generate the cross-shelf exchange occurring along the entire shelf edge (Hofmann et al., 2008). Although this shelf-slope front is present year-round, it has strong seasonal variability and significantly influences the MAB ecosystem (Ryan et al., 1999).

In winter, the front extends from the bottom to the surface, and the MAB is limited by light and replete in nutrients (Mouw & Yoder, 2005). Phytoplankton typically bloom in spring (dominated by micro-phytoplankton; Verity et al., 1996; Redalje et al., 2002), when the shoaling mixed layer releases the phytoplankton from light-limitation. During summer, the front is capped by a strong thermocline and the region becomes nutrient limited and is dominated by pico-phytoplankton (Redalje et al., 2002). The transition from winter light-limitation to summer nutrient-limitation also leads to a shift in phytoplankton species, from micro-plankton to nano-plankton (O'Reilly & Zetlin, 1998; Redalje et al., 2002; Dandonneau et al., 2004; Mouw & Yoder, 2005). In terms of their spatial distribution, the fraction of micro-phytoplankton generally increases onshore. Smaller phytoplankton size-classes typically dominate the outer shelf waters, whereas micro-phytoplankton are more likely found in high productivity areas such as the nearshore MAB (Redalje et al., 2002). Such shifts in productivity may have implications for the marine organisms that inhabit the continental margin of the MAB.

7.1 Mid-Atlantic Bight Canyons

The north-eastern United States has been at the forefront of offshore marine science since the late 1960's, providing valuable insights into global continental margin research. In this area, there are several large submarine canyons that intersect the slope and rise throughout the outer continental shelf (Figure 3b). These submarine canyons have been known for over a hundred years (i.e. Hudson Canyon was the first to be discovered and reported by Lindenkohl, 1885), however, detailed scientific investigation of them has only occurred from the 1970s onwards. The region is known for the high variety of seafloor features which cross broad depth range (Quattrini et al., 2015) and latitudes, providing an exemplary margin setting to further the understanding of relationships between habitat features, benthic communities and environmental conditions in the deep sea.

There are 26 major canyons between Nova Scotia and Cape Hatteras (Shepard & Dill, 1966), Baltimore and Norfolk canyons are two of the largest canyons of the MAB, lying south of the largest of all, Hudson Canyon (Obelcz et al., 2014). Previous studies have reported these two canyons to be inactive in terms of sediment transport, with profiles rich in silt and clay (Keller & Shepard, 1978). They are known to be important conduits of anthropogenic pollutants, organic carbon (Hecker et al., 1983), and sediments from shallow to deeper waters and support ecologically important ecosystems, such as cold seeps (Bourque et al., 2017) and coral habitats (Brooke & Ross, 2014; Quattrini et al., 2015) as well rich soft-sediment communities (e.g. Demopoulos et al., 2017). However, despite general interest and their high productivity, biological data from these canyons are limited and largely reside within unpublished project reports (e.g. Hecker et al., 1983). MAB canyons are the subject of potential oil and gas exploration, whilst the MAB shelf supports some intensive fishery activity, and as of 2015, have been designated as one of the U.S. outer-continental shelf

National Marine Sanctuaries, covering some 40,000 square miles. MAB canyons are therefore important ecosystems that are likely vulnerable to human activities.

7.2 Baltimore Canyon

Baltimore Canyon is positioned on the continental shelf, 125 km southeast of the entrance to Delaware Bay, cutting back 13 km inside the shelf break (Figure 5). The canyon has a typical V-shaped cross-section, cutting 17 km into the continental shelf and is 700 m deep and 8 km wide at the shelf break (Gardner, 1989a). On emerging onto the continental rise, relief decreases to 100 m and the canyon takes the form of a fan valley. No existent channel is evident from the canyon head across the shelf to Delaware Bay. The canyon axis curves southward at its head before turning eastward with increasing depth, until it is oriented due east-west at 3000 m (Hecker et al., 1983). At about 1500 m the canyon turns into a leveed system as it merges with the upper continental rise without a distinct fan formation (Gardner, 1989a). The canyon extends for a distance of 25 km between its head and 1500 m depth as it merges onto the abyssal plain. The width is 3 km near the canyon head increasing to 8 km at the shelf break. Hecker et al. (1983), collected the first detailed bottom profile for the canyon that showed a flat floor with a width of about 500 m at depths between 600 and 1000 m, although between 1000 and 1500 m, the width of the floor narrows to only 100 m.

Baltimore Canyon is thought to be largely inactive and has been reported as a site of high net deposition, characterised by high sedimentation rate and predominantly silt substratum with little exposed outcrop. Silt and sand are the predominant sediment types in Baltimore Canyon, particularly in the shallower portion of the canyon and on the canyon walls (Gardner, 1989b; Hecker et al., 1980; Pratt, 1967). Modern supply of material to the canyon is from pelagic and reworked shelf sediments (Gardner 1989a). Gardner (1989a, 1989b) observed shelf break sediment re-suspension in the Baltimore Canyon coupled with subsequent advection by currents, as detached turbid layers moving away from adjacent slopes (Pierce, 1976). Significant re-suspension occurred in the upper canyon, but there was no evidence of turbidity currents moving down the canyon axis to 1000 or 1500 m (Churchill, 1989). Fishing activity is known to occur around the rims of the canyons although it is not clear as to how much impact trawling activity has on the sediment regimes within the MAB canyons.

7.3 Norfolk Canyon

Norfolk Canyon is located 45 km south of Chesapeake Bay (Forde et al., 1981). Norfolk Canyon has a sigmoidal shape running in a west to east orientation, perpendicular to the shelf (Figure 5). The broad axial bend (9-10 km) seaward of the canyon head coincides with a change from relatively smooth downward slope in the upper reaches of the thalweg to a more rugose profile in the lower reaches of the canyon (Obelcz et al., 2014). Various degrees of steep wall habitat are found in the lower reaches of Norfolk Canyon that run parallel to the axis of the canyon and are dissected by numerous tributaries. The rim morphology and sub-bottom stratigraphy are more distinct than in other MAB canyons, with the southern rim having a highly irregular morphology, showing short escarpments and steep indentations (Obelcz et al., 2014). The northeast wall of the canyon contains several notches, possibly areas where blocks of sediment have slumped from the steep canyon walls. Terrace-like modulations on both canyon walls at 300 m depth and several smaller terraces on the northeast wall between 100 and 200 m are reported (Forde et al., 1981).

To date, very few published works on the hydrography of Norfolk Canyon exist. However, Hecker et al. (1983) noted that Norfolk Canyon is unique amongst MAB canyons in general and briefly reported unusually high current velocities and evidence of recent erosional activities in Norfolk Canyon, exceptions for most MAB canyons. The only directly measured current parameter in the canyon was by Shepard and Dill (1966), who reported periodic current velocities in excess of 30 cm s^{-1} at 30 m above bottom in 573 m water depth, and they suggested that these current speeds in the upper reaches are important mechanisms for sediment displacement in Norfolk Canyon. The canyon is situated within a similar oceanographic setting to Baltimore, with a similar distance to coast, shelf-sourced sediments and an apparent absence of fluvial influence (Obelcz et al., 2014). The canyon has been suggested to be important for the transport of fine grained sediment with high organic carbon content, and high suspended particulate concentrations have been found within (Bennett et al., 1985).

8 The Atlantic Deep-water Canyons Project

In 2010 the Bureau of Ocean Energy Management (BOEM) initiated a 5-year multi-disciplinary *Atlantic Deep-water Canyons* study, which focused on ecologically significant habitats (cold seeps, hard-bottoms and shipwrecks) in Baltimore and Norfolk canyons. The study was a collaborative effort between BOEM, the National Oceanic and Atmospheric Administration's Office of Ocean Exploration and Research (NOAA-OER), the U.S. Geological Survey (USGS) and CSA Ocean Sciences Inc. Eleven academic institutions, from the U.S. and Europe, participated in the programme. The project findings along with others advised on the newly designated 40,000 square mile Northeast Canyons and Seamounts Marine National Monument in 2015. In an area that supports intensive fisheries and is under consideration for future oil and gas exploration, this represents the first such monument in the Atlantic. Federal agencies now plan to phase out all commercial fishing activities in the Northeast Canyons Monument by 2023.

The overall objectives of the project were to explore the hard-bottom biological communities and shipwreck sites in the vicinity of the Mid-Atlantic Bight (MAB) canyons, particularly with respects to coral-dominated vulnerable marine ecosystems. The study included four research cruises between June 2011 and August 2013. A review of the historical data from MAB canyons initially focused the study area and data from the first cruise (2011) provided high resolution mulitbeam maps of Baltimore and Norfolk canyons. All subsequent cruises focused on intensive surveying and sampling of Baltimore and Norfolk canyons. Water column profiling and sampling were also conducted using conductivity-temperature-depth (CTD) profilers and Niskin bottle arrays. Benthic samples were collected from soft sediment areas using NIOZ boxcores, ROV cores and otter trawls. Four instrumented benthic landers and two moorings were deployed in the two canyons to collect oceanographic data continuously for one year. The study also included an archaeological component directed at identifying and studying shipwrecks in the area and exploration for cold-seep habitats.

Thirteen research topics related to the MAB canyons were addressed during the programme: 1) physical oceanographic processes, 2) geological studies, 3) predictive habitat modelling, 3) benthic invertebrate communities (corals and VME's), 4) benthic macrofauna communities, 5) Anomura biodiversity (molecular), 6) invertebrate reproductive ecology (corals), 7) microbiology (coral and sediment), 8) coral taxonomy and connectivity, 9) scleractinian coral biodiversity, 10) fish communities, 11) food web studies, (coral, macrofauna, megafauna, and fish), 12) paleoecology of MAB canyon corals, 13) education and outreach. For a full list of lead investigators and affiliations, see Ross et al. (2017).

9 Description of thesis

9.1 Background

It was through the ambitious *Atlantic Deep-water Canyons* project that this BOEM funded Ph.D. project was developed. The principle aim of the PhD project was to conduct an evaluation of environmental settings within Baltimore and Norfolk Canyon assessing the oceanography, sediment regimes, and organic inputs that governed macrofauna community dynamics and the associated patterns of abundance, biomass, diversity and ecosystem functioning. All data for this thesis were collected during two research cruises to Baltimore and Norfolk canyons (2012-13) by Craig Melville Robertson (CMR) and collaborators (See Chapters 2-4). The Physical Oceanographic work package was led by Bangor University (Andrew J Davies [AJD] and CMR), with colleagues from NIOZ (Gerard Duineveld [GCAD] and Furu Mienis [FM]), and UNCW (Steve Ross [SWR] and Michael Rhode [MR]). All physical oceanography data was processed and analysed by CMR with support from AJD. Geological work packages we led by NIOZ (FM and GCAD), who contributed sedimentological and biogeochemistry data for Chapters 3 and 4 of this thesis. Macrofauna studies were led by CMR with support from AJD in conjunction with colleagues from USGS (Amanda Demopoulos [AWD] and Jill Bourque [JRB]) and NIOZ (GCAD, FM and Marc Lavaleye [MSSL]). All samples were processed and analysed by CMR. Sediment macrofauna vertical distribution data were contributed by JRB and AWD for Chapter 3 of the thesis. Martin Solan (BENTHIS Project EU FP7; University of Southampton) contributed the macrofauna biological traits database used in the analysis of Chapter 4.

9.2 Aims and thesis structure

The overall aim of this thesis is to further understand the patterns and drivers of abundance, biomass, diversity, community structure and function of benthic macrofauna that are found within submarine canyons. This thesis is written in a journal style and as such the author apologises for the repetition that will be found between the various chapters, particularly with respects to site descriptions. Given the confines of the *Atlantic Deep-water Canyons* project, the thesis is geographically focussed on the Baltimore and Norfolk canyons within the Mid-Atlantic Bight. Various sampling was conducted within the canyons and also on the adjacent slope in relation to oceanographic, sedimentary and organic enrichment regimes. Each chapter seeks to resolve a number of hypotheses aimed at determining the environmental drivers that govern benthic macrofauna community structure and function.

Chapter Two investigated the physical oceanographic conditions found within Baltimore and Norfolk canyons, aiming to provide a baseline description of the setting that these canyons are found within. Three hypotheses were addressed: Firstly, the study aimed to determine if these two neighbouring canyons are influenced by similar temperature and salinity conditions. Secondly, the study addressed whether turbidity profiles were similar between canyons and adjacent slopes and finally the study asked whether bottom currents differ between the two canyons. Given the close proximity of the MAB canyons and the fact that the MAB water column has been well studied in the last three decades, this area offered an opportunity to compare the oceanography of neighbouring canyons that are in relative close proximity.

Chapter Three presents the first insights into the whole community macrofauna diversity and structure along the axes of Baltimore and Norfolk canyons, compared to the respective adjacent slopes. The benthic macrofaunal communities and the principal environmental drivers were described during a multidisciplinary study that bridged ecology, physics and geology. Three hypotheses were tested. Firstly, the study addressed whether canyon macrofaunal community assemblages differ in abundance, diversity, biomass and community composition from those found on adjacent slopes. Secondly, the study asked if canyon axis and slope macrofauna communities were structured by the same set of environmental parameters along the depth gradient. Thirdly, the study assessed if the signatures of disturbance within macrofauna communities were more prevalent within canyons than on slopes. Finally, the study reported on differences in the unimodal diversity-productivity relationship between canyons and slopes.

Chapter Four investigated benthic community ecosystem function through the novel application of biological trait analysis. Many studies have shown that highly distinct and variable benthic communities are not uncommon in outer continental margins. In submarine canyons, species patterns are driven by high levels of habitat heterogeneity, enhanced hydrodynamic drivers, the accumulation of organic matter and sediment dynamics. However, there are a paucity of deep-sea studies linking biodiversity, community ecosystem function and environmental processes. Three hypotheses were addressed. Firstly, the study addressed whether macrofaunal functional diversity differs between canyon and adjacent slope habitats.

Secondly, the study assessed if key macrofaunal community biological traits differed between canyon and adjacent slope habitats and finally, the study addressed if community bioturbation potential differed between areas of organic enriched sediment and surrounding areas.

Chapter Five, the concluding chapter of this thesis, attempts to synthesise the main findings of each experimental chapter and conceptualise a framework that explains the macrofaunal community distributions and patterns in relation to environmental gradients, productivity, disturbance and functioning, and to generate new avenues for future research.

10 Contribution to submitted and published works

10.1 Major contributions

Chapter Two: First author of *'Distinct hydrodynamic conditions in neighbouring Mid-Atlantic Bight submarine canyons'*. This chapter will be submitted to the journal *Regional Studies in Marine Science* due to the descriptive nature of the study. CMR analysed benthic lander and mooring data and CTD data from the two canyons and adjacent slopes. AJD advised on all analyses. AJD, GCAD and FM advised on the manuscript development, with additional comments from other co-authors.

Chapter Three: First author of *'Macrofaunal community patterns within neighbouring Mid-Atlantic Bight (USA) submarine canyons: The role of depth gradients and location-specific environmental conditions'*. The manuscript will be submitted to the *Journal of Deep-sea Research Part I*. CMR identified, enumerated and weighted the macrofauna, with sample processing and sorting help from Karoliina Kiovisto and Gillian Peacock. AJD, GCAD, MSSL, AWD and JRB advised on the development and writing of the manuscript, with additional comments from other co-authors.

Chapter Four: First author of *'Submarine canyons as centres of bioturbation activity and distinct ecosystem functioning'*. This manuscript will be submitted to the *Journal of Functional Ecology*. AJD advised on all analyses and assisted with the functional diversity analyses. Dr Marija Sciberras, Profs Jan Hiddink and Michel Kaiser advised on the application of biological trait analysis. Prof. Martin Solan and Dr Marija Sciberras provided the biological trait database. AJD and GCAD advised on the manuscript development and writing, with additional comments by co-authors.

10.2 Additional contributions arising from this study

CMR contributed macrofaunal identification, analysis and development of the manuscript for:

> Bourque, J.R., Robertson, C.M., Brooke, S., Demopoulos, A.W.J., 2017. Macrofaunal communities associated with chemosynthetic habitats from the U.S. Atlantic margin: A comparison among depth and habitat types. Deep-Sea Research Part II: Topical Studies in Oceanography 137, 42–55. doi:10.1016/j.dsr2.2016.04.012

CMR contributed physical oceanographic data analysis to:

> Prouty, N.G., Mienis, F., Campbell-Swarzenski, P., Roark, E.B., Davies, A.J., Robertson, C.M., Duineveld, G., Ross, S.W., Rhode, M., Demopoulos, A.W.J., 2017. Seasonal variability in the source and composition of particulate matter in the depositional zone of Baltimore Canyon, U.S. Mid-Atlantic Bight. Deep-Sea Research Part I: Oceanographic Research Papers 127, 77–89. doi:10.1016/j.dsr.2017.08.004

CMR Contributed to several chapters of the BOEM Project Report:

> Robertson, C.M., Bourque, J.R., Demopoulos, A.W.J., 2017. Benthic Infaunal Communities of Baltimore and Norfolk Canyons, Chapter 9: Exploration and research of Mid-Atlantic deep-water hard bottom habitats and shipwrecks with emphasis on canyons and coral communities: Atlantic Deep water Canyons Study Vol. 1. CSA Ocean Sciences Inc. for U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Atlantic OCS Region, OCS Study BOEM 2017-060.

> Davies, A.J., Robertson, C.M., Mienis, F., Duineveld, G.C.A., Prouty, N.G., Roarke, B., Ross, S.W., Brooke, S.D., 2017. Physical Oceanographic Processes within Mid-Atlantic Bight Canyons, Chapter 5: Exploration and research of Mid-Atlantic deep-water hard bottom habitats and shipwrecks with emphasis on canyons and coral communities: Atlantic Deep water Canyons Study Vol. 1. CSA Ocean Sciences Inc. for U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Atlantic OCS Region, OCS Study BOEM 2017-060.

> Davies, A.J., Robertson, C.M., Rhode, M., Wolff, M., Ross, S.W., Brooke, S.D., 2017. Chapter 7: Predictive Habitat Modeling, Chapter 7: Exploration and research of

Mid-Atlantic deep-water hard bottom habitats and shipwrecks with emphasis on canyons and coral communities: Atlantic Deep water Canyons Study Vol. 1. CSA Ocean Sciences Inc. for U.S. Dept. of the Interior, Bureau of Ocean Energy Management, Atlantic OCS Region, OCS Study BOEM 2017-060.

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12 Tables and Figures

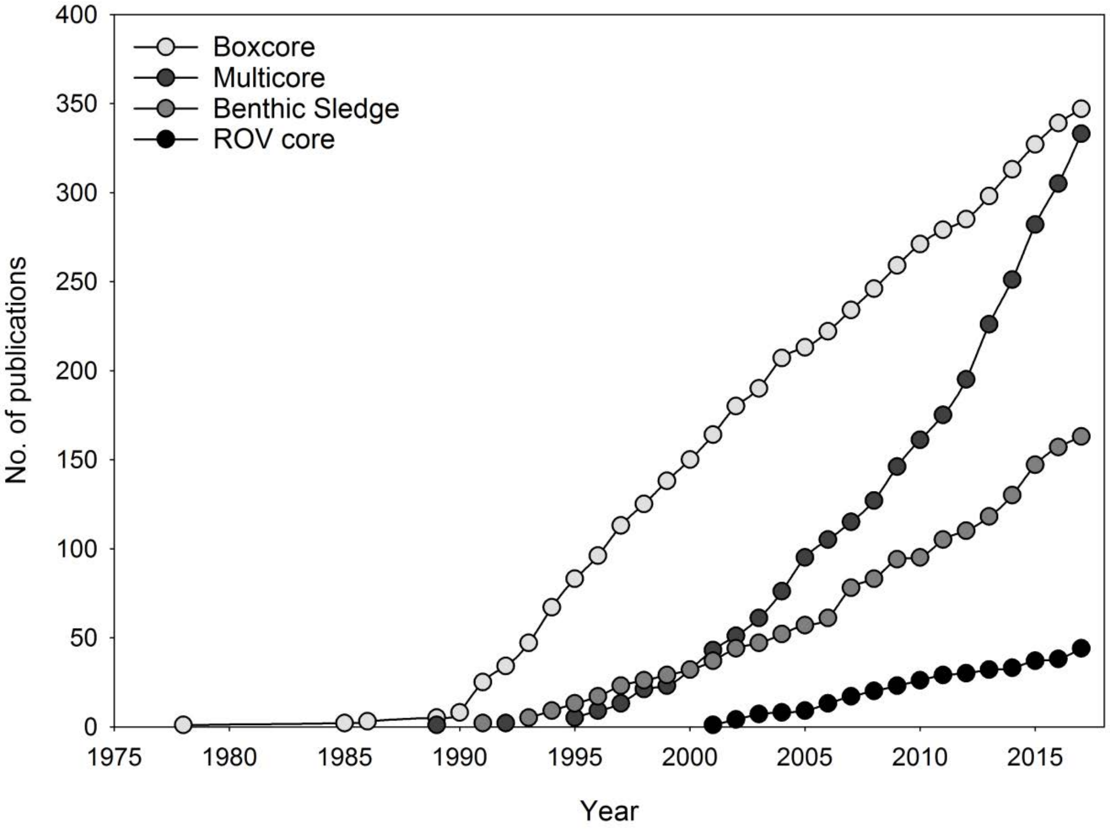

Figure 1. The number of deep-sea macrofauna publications utilising sampling the four main sampling devices between 1978 and 2017. Data were obtained from the ISI Web of Knowledge using the Science Expanded Citation Index databases and the search terms, inclusive of all names, and variations thereof, for each sampling device in the titles and keywords of all document types e.g. (“deep sea” OR “deep-sea”) AND (“macrofauna”) AND (“Boxcore” OR “Box-core” OR “Boxcorer” “Box-corer)”.

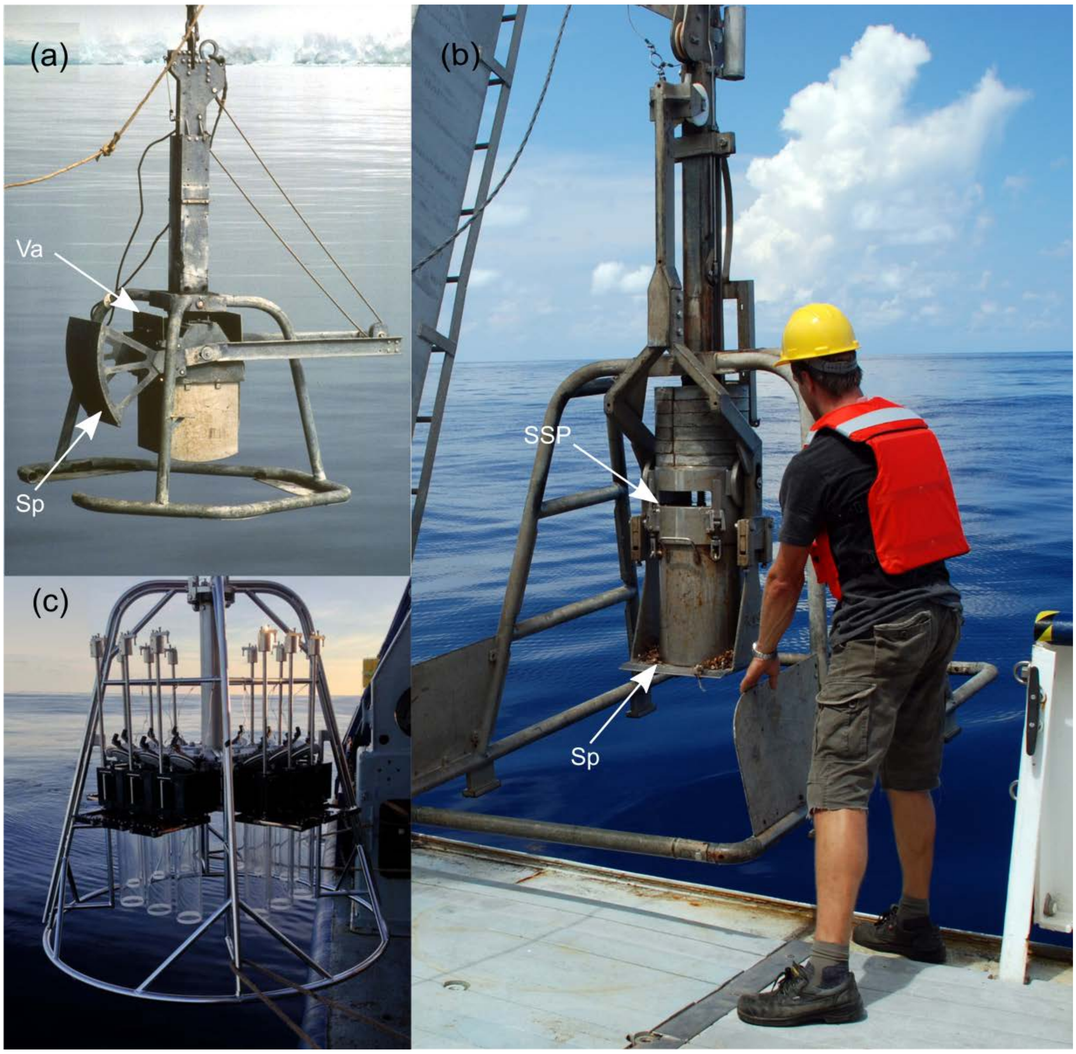

Figure 2. The three main benthic sampling devices used in soft sediment biodiversity surveys. (a) USNEL boxcore (0.25 m^2), (b) Recovery of the cylindrical NIOZ boxcore (0.07 m^2) during the May 2012 Baltimore Canyon sampling campaign on board the NOAA ship *Nancy Foster* and (c), an example of the modern multicorer. Note the steel and rubber seal plate (SSP) at the top of the NIOZ boxcore, in place of inspection ports or hatches (Va) which is common in the USNEL and other boxcore models. The NIOZ boxcore therefore minimises bow-wave effect and returns a completely sealed sample when the spade (Sp) is engaged preventing washout of the sample or loss of overlying water.

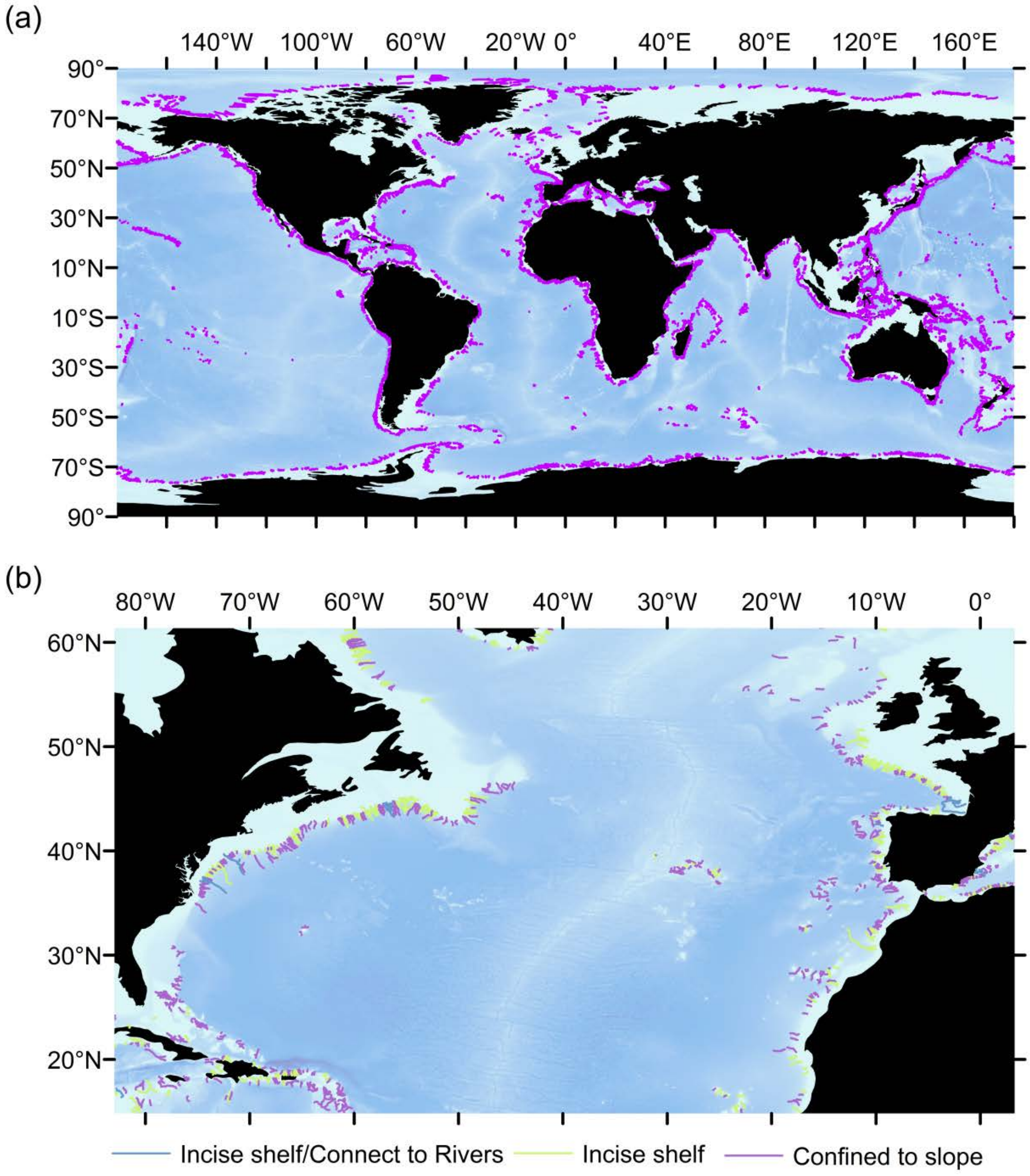

Figure 3. Locations of canyons around the world. (a) Global density of shelf incising slope confined canyons. (b) The locations of North Atlantic shelf-incising canyons, including canyons connected to riverine systems (Harris & Whiteway, 2011).

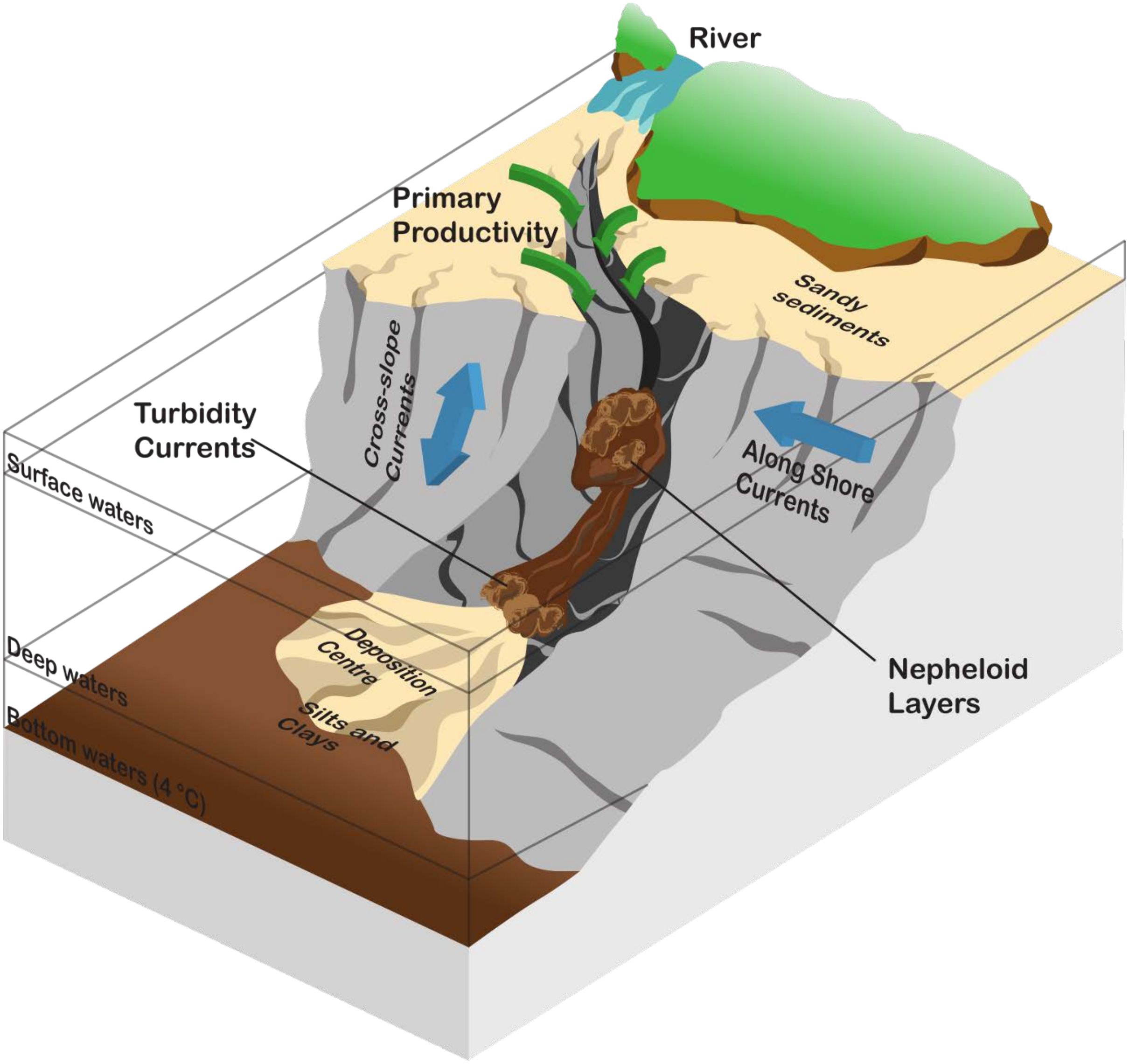

Figure 4. 3-dimensional schematic of a submarine canyon and some of the key processes hydrographic and sedimentary processes influencing these habitats.

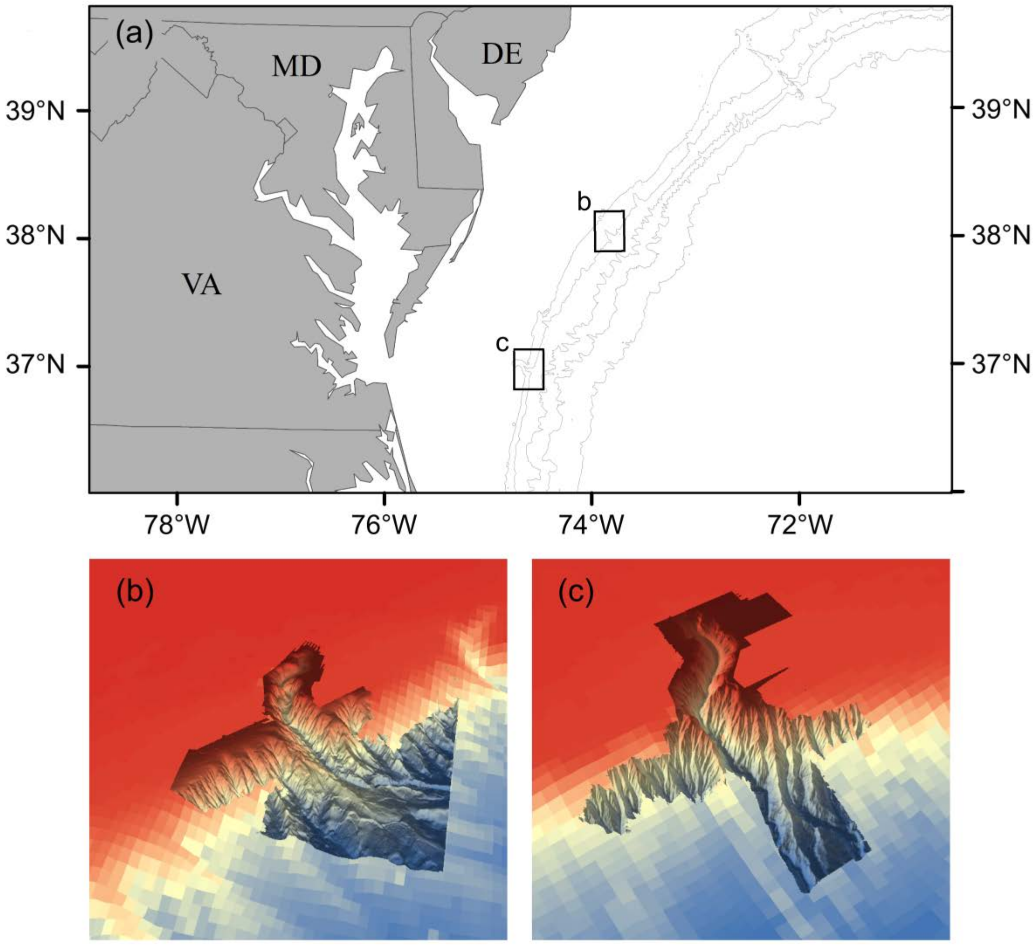

Figure 5. Location and 3D visualisations of Baltimore and Norfolk canyons within the Mid-Atlantic Bight, (a) site locations, grey contour lines indicate bathymetric intervals, (b) 3-dimensional bathymetric model derived from multibeam data of Baltimore Canyon and (c) Norfolk Canyon, both scenes have a 5x vertical exaggeration.

Chapter 2

Distinct hydrodynamic conditions in neighbouring Mid-Atlantic Bight submarine canyons

Robertson CM[1], Mienis F[2], Ross SW[3], Davies AJ[1],
Demopoulos AWJ[4], Prouty N[5], Bourque JR[4], Brooke SD[6],
Rhode M[3] and Duineveld GCA[2]

[1] Bangor University, School of Ocean Sciences, Bangor, UK. [2] NIOZ Royal Netherlands Institute for Sea Research and Utrecht University P.O. Box 59, 1790 AB Den Burg, the Netherlands. [3] UNC-Wilmington, Center for Marine Science, Wilmington, USA. [4] U.S.G.S. Wetland and Aquatic Research Centre, Gainesville, USA. [5] U.S.G.S., Pacific Coastal and Marine Science Center, 2885 Mission St., Santa Cruz, CA 95060, United States [6] Florida State University, Coastal and Marine Lab, St Teresa, USA.

Author contributions

CMR led the analysis and writing of the manuscript, to which all authors contributed. AJD provided additional analyses. CMR, AWJD, JRB, FM, GCAD, SDB, SWR and MR contributed to shipboard sampling. FM, GCAD, AWJD, NP and SWR provided lander and mooring equipment.

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1 Abstract

Submarine canyons are significant topographic features that incise continental slopes and act as major conduits for the transport of material from the shelf to the deep sea. Their pronounced and often irregular topography interacts with the local hydrography, resulting in enhanced turbulence and mixing processes that conversely influence (food) particle transport. Moreover, due to the funnelling of organic matter and their heterogeneity canyons provide a multitude of habitats for deep-sea fauna and can be considered hotspots of biodiversity and biomass. Previous studies have shown that particle transport processes in canyon systems worldwide differ and can be triggered by different mechanisms. In this study oceanographic conditions and related particle transport processes of Baltimore and Norfolk canyon, which are only separated by a distance of approximately 140 km, are compared, using a combination of water column hydrographic measurements, and year-long in situ benthic current measurements. Both canyons are influenced by similar hydrographic conditions, largely driven by the MAB shelf-slope front. Below the shelf-slope front Western North Atlantic Central Water (WNACW) and Western Atlantic Sub-Arctic Intermediate Water (WASIW) were observed. On the contrary, year-long near-bottom measurements revealed several clear differences between the two canyons. Current speed and direction in both canyons were driven by semidiurnal tides (M_2) that were strongest near the heads of both canyons and exhibited a persistent up-canyon directionality. Mean current speeds in Baltimore Canyon were 8 cm s^{-1} while Norfolk Canyon experienced greater mean speeds of 16 cm s^{-1}. In both canyons, benthic nepheloid layers were present that were not observed in adjacent slope transects. It is likely that observed disparities, are related to a difference in canyon morphology, the orientation of the canyons to the shelf and differing interactions with internal waves. Similarities between the two canyons were largely driven by the influence of shared water masses and the presence of nepheloid layers, but they were distinct with respect to their hydrodynamics. This study highlights how submarine canyons in close proximity can have differing physical oceanographic regimes.

2 Introduction

Submarine canyons are dramatic and widespread topographic features that connect ocean shelves to the deep ocean (Harris & Whiteway, 2011). They are intrinsically complex and dynamic systems that are often characterised by unique geomorphology (Obelcz et al., 2014), hydrography (Durrieu de Madron, 1994), sediment transport and accumulation (Duineveld et al., 2001; García et al., 2008) and enhanced organic matter flux (Puig et al., 2014). These characteristics interact to create habitats that can support high diversity, abundances and biomasses of deep-sea fauna (De Leo et al., 2010). Over the last several decades, it has become increasingly important to characterise the physical oceanographic and related sedimentary regimes that occur within canyon systems (Levin et al., 2001), principally driven by need to understand their biological "uniqueness", a factor of increased importance in conservation and management efforts (Auster et al., 2011). However, many canyon systems remain poorly understood in terms of their physical parameters (e.g. turbidity, sediments, current speeds, temperature), and particularly their temporal (i.e. a paucity of long-term observation) and spatial variability (i.e. most previous studies have used observations from only a single site within a canyon) of physical processes.

Within canyons, flow patterns are driven by physical processes such as regional currents, barotropic and baroclinic tides, and internal waves, (Hunkins, 1988; Keller & Shepard, 1978; Rona et al., 2015). Canyon geomorphology can strongly interact with these physical processes, leading to endemic hydrodynamic regimes that influence transport of particulate and dissolved matter (Puig et al., 2014). These dynamics give rise to canyon-specific benthic assemblages, for example, varied structure-forming species (Huvenne et al., 2011; Quattrini et al., 2015), soft sediment communities (Cunha et al., 2011; Duineveld et al., 2001; Vetter & Dayton, 1998) and fish populations (Quattrini et al., 2015; Ross et al., 2015). Therefore, detailed information on the hydrodynamics and hydrography is a necessity for predicting the distribution of vulnerable species and ecosystems within canyons, as in many other deep-sea habitats (e.g. Morris et al., 2016).

The Mid-Atlantic Bight (MAB) extends over 500 km of the U.S. continental shelf from the Nantucket Shoals to Cape Hatteras. It is a dynamic region, characterised by strong climatic cycles, high surface productivity and some of the highest benthic standing stocks in the North Atlantic, but has also been impacted by a number of human activities (Rex & Etter, 2010). It is host to 13 major canyons, the largest being Hudson, followed by Wilmington, Baltimore, Norfolk and Washington canyons. The canyons are variable in size, shape, and geomorphological complexity, and most contain exposed hard substrata colonised by species that may be classified as “vulnerable marine ecosystems” (Brooke et al., 2017; Quattrini et al., 2015). The interaction between topography of the MAB slope with near-bottom currents (Csanady et al., 1988), internal tides and tidal bores (Cacchione et al., 2002; Gardner, 1989a; 1989b), are known to be important factors influencing the occurrence of turbid nepheloid layers and particle transport within the MAB canyons.

Given the close proximity of the MAB canyons and the fact that the MAB water column has been well studied in the last three decades, this area offers an opportunity to compare the oceanography of neighbouring canyons that are in relative close proximity. The question whether MAB canyons that incise the same continental slope at close proximity are similar, is relevant in the light of economic activity (e.g. oil/gas) progressing into deeper water including areas that were previously under protection (Duke Scipol, 2017). Insight into uniqueness of nearby MAB canyons (‘seen one, you’ve seen all?’) in terms of oceanography and particle distribution will support environmental management of MAB canyons through the ability to more accurately predict local distribution of species and ecosystems.

In this study, the local oceanographic characteristics of the Baltimore and Norfolk canyons and their adjacent slopes were described from hydrographic surveys (CTD profiles), which included across-shore transects both within the canyons and over the adjacent slopes as well as long-term (one year) deployments of benthic landers and moorings within both the canyons. The study aimed to determine if these two neighbouring canyons are influenced by similar hydrography and hydrodynamics, and addressed the following hypotheses: (i) the temperature and salinity conditions within the canyons and adjacent slopes are similar, (ii) nepheloid layer distribution within the canyons are similar due to the shelf-scale influence of internal waves, and (iii) canyon bottom currents differ between Baltimore and Norfolk canyons due to individual canyon morphology.

3 Materials and methods

3.1 Site description and survey location

Water movement within the MAB is generally slow and driven by complex and usually seasonal interaction between major current circulation patterns (Csanady & Hamilton, 1988), position of shelf-slope fronts (Garvine et al., 1988; Houghton et al., 1986; Voorhis et al., 1976), entrainment of shelf waters by Gulf Stream eddies and meanders (Churchill et al., 1989; Lillibridge et al., 1990), seasonal water column stratification, and upwelling events (Csanady & Hamilton, 1988; Houghton et al., 1982). Most characteristic of MAB hydrography is the presence of the shelf-slope front (Ribó et al., 2011), formed through changes in water mass density and temperature characteristics (Huthnance, 1995). As surface water temperatures increase in the spring along the southern offshore edges of Nova Scotia, Georges Bank and the MAB, a seasonal pycnocline develops, which isolates a relatively cold water mass, namely the cold pool, below the seasonal thermocline (Bigelow, 1933; Houghton et al., 1982; Townsend et al., 2006). The exchange between local fronts, oceanic water masses and the continental slope occurs mainly at the shelf break (Church et al., 1984), where the sediment transport along the continental slope is enhanced, particularly at shelf breaks adjacent to shelf-incising canyon systems (García et al., 2010). As a result, canyons act to increase carbon export from shelf seas to the deeper continental rise (García et al., 2008; Linder & Gawarkiewicz, 1998).

Baltimore and Norfolk are shelf-sourced canyons, which begin at the shelf break around 100 m water depth, and continue to a depth of approximately 1900 m, with axes lengths of 25 km. Baltimore Canyon lies 125 km southeast of the entrance to Delaware Bay (Figure 1a), and its cross-thalweg width is 3.0 km at the head and 8 km at the terminus (Figure 1b). Norfolk Canyon is located 140 km southwest (alongshore) of Baltimore Canyon (Figure 1a) and is 2.5 km wide at its head, reaching 6 km wide at its terminus (Figure 1c). Both canyons have sigmoidal bends in the upper reaches, and differing canyon head orientation, although the canyons are orthogonal to the open shelf at their mouths. The head of Baltimore Canyon sits at 45° to the shelf break (NW-SE), whereas Norfolk Canyon head is 90° relative to the shelf break (W-E) (Obelcz et al., 2014). Baltimore Canyon has a higher degree of sinuosity (1.19) with a lower critical slope (seabed) gradient (2.1°) than Norfolk (1.07 and 2.7°, respectively) (Obelcz et al., 2014).

3.2 Hydrographic surveys and processing

Using ship-board CTD systems, water column profiles were collected during the 2011, 2012 (NOAA Ship *Nancy Foster*) and 2013 (NOAA Ship *Ronald H. Brown*) surveys between depths of 104 and 1384 m (Table 1a & 1b). The hydrographic profiles conducted in 2011 and 2012 utilised a SeaBird 911+ CTD array mounted within a rosette of 12 five-litre Niskin bottles. In addition to conductivity (Siemens m^{-1}), temperature (°C) and depth (m), the array also measured turbidity (Seapoint, formazin turbidity units), fluorescence (relative units) and dissolved oxygen (ml L^{-1}). Hydrographic transects conducted in 2013 utilised a SeaBird 09+ CTD array with a rosette of 12 ten-litre Niskin bottles. In addition, the CTD array also measured turbidity (Seapoint, formazin turbidity units), dissolved oxygen (ml L^{-1}), depth (m), conductivity (Siemens m^{-1}), temperature (°C), pH, and fluorescence (relative units). All CTD arrays were subject to laboratory calibrations of the CTD pressure, temperature, conductivity, fluorescence, and oxygen sensors (Hooper & Baringer, 2012, 2013). When sampling, for both single point profiles and transects, the CTD array was lowered from the surface to as close to the seafloor as feasible (usually 10 m above bottom).

In total, 15 complete CTD transects were collected and used in the temperature-salinity analysis of MAB waters. Of these, 7 transects (2012 and 2013) were sufficiently synoptic (i.e. within one tidal cycle) and therefore suitable for geostrophic flow calculations and cross-shelf analyses. In Baltimore and Norfolk canyons, two main across-isobath transects were collected: one along the axis of the canyon and one on the adjacent slope (Figure 1, Table 1a). In addition, across-canyon transects (Figure 1b & Table 1a) were used to investigate changes in the water column across the width of the canyons; three across-canyon transects were collected for Baltimore Canyon and only one for Norfolk Canyon due to logistical constraints.

Downcast CTD data were resampled to a 1 m bin size using the SeaBird data processing software and checked to remove erroneous values. Visualisation of the water column characteristics for each transect was conducted using the Surfer 8 contouring package (Golden Software, LLC). The Inverse Distance to Power interpolation method (Bello-Pineda & Hernández-Stefanoni, 2007) was used to create grid-based contour maps of the water column along the transect length based on distance, depth and water parameters of interest. Six parameters were used: temperature, salinity, fluorescence, turbidity, density (sigma theta, σ_θ) and oxygen, to assess water column patterns. Transect bottom profiles were created from bathymetric data for each canyon in ArcGIS 10.4 (ESRI) and were inserted as a post-map layer to visualise seabed topography for each contour map. Temperature-Salinity (T-S) diagrams were drawn in the statistical program R using the "*oce*: Analysis of Oceanographic data" package (Kelley et al., 2017) to characterise the water masses present within the sampled areas.

An estimate of the geostrophic transport of canyon water masses was determined by application of the geostrophic flow equation, also referred to as the thermal wind relation (Simpson & Sharples, 2012). The calculation is a simplification of the equations governing the horizontal component of velocity and can be used to calculate the horizontal velocity under geostrophic approximation and has been used in previous canyon studies (Rona et al., 2015). The geostrophic equation gives the following formula for the estimated velocity of canyon water masses across water column profiles, where g is gravity (9.81m s^{-2}), ρ is the reference density (1027 kg m^{-3}), f is the Coriolis force parameter for a latitude of 37° N (8.75 x 10^{-5}) for Norfolk Canyon and 38° N (8.95 x 10^{-5}) for Baltimore Canyon, $\Delta\rho$ is the difference in density between two water profiles (for each 1 m bin) and Δx is the distance between stations in the transect (across-canyon SW to NE):

$$\frac{du}{dz} = \frac{g}{\rho f} \cdot \frac{\Delta\rho}{\Delta x}$$

In applying the geostrophic flow equation, a reference level was set at which the velocity is known (or assumed to be zero). In all calculations in this study velocities were zero referenced at the seabed. Differences in water density, for all profiles in each transect from the surface to the seafloor, were calculated at 1 m depth intervals, to determine the horizontal velocity over the entire water column, assuming constant geostrophic flow.

3.3 Benthic landers and moorings

Four benthic landers and two moorings were deployed in mid-August and early September 2012 (Figures 1b & 1c, Supplementary Figure 1) for the duration of a year to monitor near-bed physical properties through time. Instruments were placed shallow (~600 m), mid (~1000 m) and deep (~1300 m) sites with the depths consistent between the two canyons. The duration of the deployment was approximately one full year (August 2012 to August 2013), although the Baltimore landers were recovered after 8 months for servicing (2 days in May 2013) and redeployed in roughly the same depths. In Baltimore Canyon, the benthic landers were equipped with Aanderaa RCM loggers, which logged temperature, salinity, turbidity, dissolved oxygen, and current speed and direction. All RCM probes were mounted 1.5 m above the seafloor with the exception of the current meter, which was attached 2 m above the seafloor (Table 2). All instrumentation was subject to pre-cruise laboratory calibration by Aanderaa (Xylem. Inc, U.S.A).

In Norfolk Canyon, the benthic landers consisted of two designs. First, the shallow ALBEX lander (Duineveld et al., 2004) logged currents using a Nortek Aquadopp current meter mounted about 1.5 m above the seafloor, and temperature, salinity, pressure measured by a Sea-Bird MicroCAT CTD. Turbidity and fluorescence were measured using a Wetlabs sensor mounted at 1.5 m above the seafloor. This lander (Figure 1c and Table 2), failed to return and was assumed lost. The deep BOBO lander (Table 2; Van Weering 2000), was equipped with an upward looking 1200 kHz RDI ADCP programmed with a bin distance of 0.5 m over 39 bins mounted at 2 m above bottom. In addition, a Sea-Bird 16+ CTD monitoring temperature and salinity was mounted at 1.5 m above the seafloor. Turbidity and fluorescence were measured using a Wetlabs sensor at 1.5 m above the seafloor with a second turbidity sensor (Seapoint), also positioned at 1.5 m. All lander sensors logged at a 15-minute interval.

In August 2012, within each canyon, a mooring was placed at the approximate mid-point between the two landers (Figure 1b & 1c; Table 2). Both moorings had the same instrument configuration, whereby temperature and salinity were measured using a SeaBird MicroCAT 37 mounted at 9 m above the seafloor (5-minute interval). An upwards-looking 300 kHz ADCP was mounted at 10 m above the seafloor with a bin distance of 2 m over 54 bins to measure water column current speed and direction at 15-minute intervals.

Upon recovery of landers and moorings, time-series data from the moorings were down-sampled to match the time interval of the other lander systems (5 to 15 minutes). Only the initial deployment data for Baltimore Canyon landers (August 2012-May 2013) were used to calculate tidal parameters, power spectra and mean conditions as these analyses required a continuous time series from a single location. Data analysis was conducted within the statistical program R (R Core Team 2015), using the package "*oce*: Analysis of Oceanographic Data" (Kelley et al., 2017) and power spectra calculated using the *spectrum* function within the core R package (Chan & Ripley, 2012). Tidal analysis was conducted in the Matlab package t_tide (Pawlowicz et al., 2002), using a power spectra analysis to partition the variance of the time-series data as a function of frequency. Power is defined as energy (cm^2 s^{-1}), per unit time (counts per day). Up-down canyon current flow was calculated by rotating uv velocity components from current meters and ADCPs using the following equation, where c (constant of 90°) and θ (bearing of canyon axis in the region of the lander deployment to determine up/down motion) are in radians, where negative values indicate an up-canyon flow and positive values a down canyon flow:

$$Canyon\,flow = \; v(\sin(c-\theta)) + u(\cos\,(c-\theta)$$

4 Results

4.1 Water masses

Five major water masses were identified through T-S analysis, all characteristic of the MAB region (Table 3). From surface to bottom, these water masses were: (1) shelf surface water, (2) cold pool water trapped beneath warmer shelf waters, (3) warm shelf break water forming the shelf-slope, (4) Western North Atlantic Central Water (WNACW) and (5) West Atlantic Subarctic Intermediate Water (WASIW). Slope water in the MAB region is usually warmer (< 17 °C) and more saline (< 35) than shelf water, due to the proximity of the Gulf Stream (Rasmussen et al., 2005). The region where these two water masses meet is termed the shelf-slope front, which is formed by T-S and density differences between the cold pool water and warm shelf-break water. All hydrographic profiles portrayed an inverted "v" shape (Figure 2) that persisted throughout the different sampling periods (June 2011, Sept 2012, and May 2013), as being characteristic of the MAB shelf-slope front (Figure 2). In this study, the shelf-slope front was bound within a density range of σ_θ 25-26.3 kg m^{-3} for cold and relatively fresh pool waters and warm more saline shelf-break water with a density range of σ_θ 26.4-26.9 kg m^{-3}.

Sampling over multiple years revealed a degree of temporal variability in the position of MAB water masses (Figure 2), most notably with respect to the shelf-slope front T-S signatures. Within the Baltimore Canyon area, the front was characterised by a temperature of 12-14.5 °C and salinities of 33.4-36 in June 2011, differing from August 2012, when the range was wider, ranging from 8-15 °C and salinities of 32.9-36 (Figures 2a & 2c). This variability in the temperature range was related to the presence of a larger volume of cold pool water (5-12 °C, salinity of 32.5-34.8) in 2012. For Norfolk study sites, the shelf-slope front was characterised by temperatures ranging between 8.5-15 °C and salinities of 33-36 in June 2011, and was cooler (7.7-14.5 °C) and more saline (33.6-36) in May 2013 (Figures 2b & 2d). In addition, a trace of inner shelf water in May 2013 (Figure 2b; 12 °C and salinity of 33) was found in the slope waters adjacent to Norfolk Canyon. Both canyons and adjacent slopes exhibited the prominence of the shelf-slope front as well as the presence of WNACW and WASIW up the length of the canyon axes, although the latter deep water masses were more pronounced in Baltimore Canyon (Figures 2a & 3a).

4.2 Water mass distribution

In Baltimore Canyon, a clear transition in the water column structure was present along the length of the axis transects (Figure 3a) that differed from the adjacent slope (Figure 3c). Shelf surface water, forming a thermocline was present at ~100 m (25 °C, salinity < 34.7) and was more defined along the canyon axis. Towards the head of the canyon the presence of the shelf-slope front was a dominant feature (Figure 3a), and was present along the entire axis of the canyon, developing into an increasingly stratified band of saline water with a relatively narrow temperature range (12-15 °C) at approximately 100-200 m water depth during August 2012 (Figure 3a blue dashed lines, Figure 4a and 4b). Warm slope water, occurring as an intrusion layer above the front, was not observed until the outer most stations (16.3-18.5 km), and cold pool water was located on the outer shelf, inshore of the shelf break between 40-80 m water depth. Below the front, WNACW (< 500 m, temperature 4-5 °C, salinity ~35) and WASIW (> 500m, 3-9 °C, salinity 34-35.1) were observed (Table 3, Figures 3a and 4a). Cross-section transects showed similar patterns to the canyon axis transect and confirmed that the front was in contact with the seafloor, at the shelf edges of the canyon (Supplementary Figure 2).

In Norfolk Canyon, the distribution of water masses was recorded at a different time of year compared to Baltimore Canyon. Several differences were observed: 1) the shelf-slope front was more prominent than in Baltimore Canyon and was attached to the seafloor in the upper canyon reaches (0-1.7 km). 2) The front consisted of a much larger proportion of cold pool water with a temperature ranging from 7.5-13 °C. WNACW did not reach the head of the canyon but was met by the shelf-slope front at 3.7 km along the transect (Figure 4b). Very little surface shelf water signature was evident for the majority of Norfolk Canyon except, in far offshore profiles (19-22 km, Figure 3b). Below the front, WNACW was first observed at the 3.7 km station, extending close at to the seafloor. The Norfolk Canyon axis also contained Labrador Sea Water (LSW, temperatures ~8.5 °C and salinity of 34.3; the small cluster of points between the shelf-slope front and WNACW; Drinkwater et al., 1999) between the 5.9 and 13.8 km stations (Figure 3b).

Along both canyons, oscillations in the density isopycnals of ~80 m occurred (Figures 4a & 4b, σ_θ 26.5-27.5 kg m^{-3}). Density contours also showed a tilted σ_θ 27 kg m^{-3} isopycnal across Baltimore Canyon, between 100 m depth on the western side and 250 m depth on the eastern side, suggesting an unequal distribution of cold pool water and a thickening of the warm slope water layer on the south-eastern side of the upper Baltimore Canyon (Supplementary Figure 2).

4.3 Other water column characteristics

Turbidity measurements along the axis of Baltimore Canyon revealed a large benthic nepheloid layer reaching intermediate water depths that was not observed on the adjacent slope (Figure 4a). This layer extended from the head of the canyon at 200 m to around 900 m and was recorded in both 2011 and 2012, suggesting a persistent feature. In both canyon and slope transects, a low oxygen (minimum 3.1 ml L^{-1}) zone between 100 and 300 m was found, below which levels increased to 5.5 ml L^{-1} (Supplementary Figure 3 & 4). Fluorescence in all transects was high in surface waters, with no detectable amounts below the shelf surface water at around 50 m (Supplementary Figures 3 & 4).

A nepheloid layer that appeared as a series of smaller discreet nepheloid layers at the bed were observed in Norfolk Canyon (e.g. 200 m and 300 m), with the largest turbidity clouds being present between 400 -1100 m depths (Figure 4b). These clouds were absent from the adjacent slope (Figure 4b). Fluorescence was low below 200 m, with no detectable patterns in deeper waters (Supplementary Figures 5 & 6). Oxygen concentrations also decreased from the surface to around 3.1 ml L^{-1} at 300 m and then increased in deeper waters to a high of 5.5 ml L^{-1} (Supplementary Figures 5 & 7).

4.4 Canyon geostrophic flow

Surface waters (< 200 m) in the upper and middle reaches of Baltimore Canyon demonstrated down-canyon current flow accompanied by small pockets of up-canyon flow in the upper canyon surface waters (< 50 m, 0.5 m s^{-1}) on either side (NW and SE) of the canyon axis (Table 4 & Supplementary Figure 7). Mid canyon showed estimated mean down-canyon velocities of 0.42 m s^{-1}, slowing in the lower canyon to 0.07 m s^{-1}. The lower canyon demonstrated a bottom water mass moving up-canyon (mean 0.04 m s^{-1}), and an increase in the size of the pockets of up-canyon flowing water either side of the canyon axis, estimated at ~0.3 m s^{-1} (Supplementary Figure 7). These lower transect up-canyon flowing waters were identified as WASIW, which intersected with the down-canyon WNACW water mass along the σ_θ 27.5 kg m^{-3} isopycnal (~450-500 m). In Norfolk Canyon, a large layer of up-canyon flowing bottom water was estimated extending from 400 to 1100 m (Supplementary Figure 7). This water mass can be identified as WASIW, and compared to the Baltimore lower canyon transect, the up-canyon flow velocity in the deeper reaches of Norfolk was four times that of Baltimore. Overall, all transects showed similar down-canyon flow at shallow and intermediate water depths, corresponding to the presence of WNACW (Supplementary Figure 7).

4.5 Lander and mooring observations

In Baltimore Canyon, at the shallow station (603 m water depth), current direction was predominantly topographically steered along the canyon axis (Figure 5a & 5b), with variability in all recorded parameters (Table 2b). Intense and periodic sediment resuspension/transport events at this location were indicated by pronounced peaks in turbidity (Figure 5d), which positively corresponded with increases in temperature (Spearman's Rank Correlation on 24-hour moving average data, $r = 0.48$, $p < 0.001$). Warmer waters were also positively correlated with higher current speeds (Spearman's Rank Correlation on 24-hour moving average data, $r = 0.49$, $p < 0.001$), but no clear relationship with current direction was observed. In the mid-canyon, waters were cooler and denser, with lower mean and maximum current speeds (Table 2b). This site demonstrated a moderate positive correlation between current speed and temperature (Spearman's Rank Correlation on 24-hour moving average data for the first deployment, $r = 0.43$, $p < 0.001$). In the deeper region of Baltimore Canyon (1364 m water depth) water flowed in a predominantly northerly direction (approximately 15°, Figure 5i & 5j), was again cooler, denser and had lower mean and maximum current speeds (Table 2b). At this site, peaks in turbidity were positively correlated with current speed (Spearman's Rank Correlation on 24-hour moving average data for the first deployment, $r = 0.62$, $p < 0.001$), and there was a positive relationship between current speed and temperature (Spearman's Rank Correlation on 24-hour moving average data for the first deployment, $r = 0.75$, $p < 0.001$). There were no significant correlations between temperature and current direction, or turbidity and direction. The T-S and density signatures recorded by the landers and mooring confirmed the two most predominant water masses observed in the canyon hydrographic transects, namely WNACW and WASIW within the benthic boundary layer.

The near-bottom flow direction (corrected to reflect the flow along the canyon axis), demonstrated that all stations in Baltimore Canyon had a net flow direction that was generally up-canyon (Figure 5d, 5h & 5l). This was most pronounced at the deepest station, where cumulative water flux moved approximately 400 km up canyon over the entire time series (approximately 5 cm s^{-1}; Figure 5l, bottom panel). In the mid-canyon, the flux was approximately 220 km up-canyon over the entire time series (approximately 2.75 cm s^{-1}; Figure 5h, bottom panel). Whilst at the shallow station, the pattern included periods of tidally modulated flow with the cumulative flux distance eventually reached 71 km of up-canyon travel (approximately 0.89 cm s^{-1}; Figure 5d, bottom panel). There was clear evidence of a strong tidal influence within Baltimore Canyon that extended throughout in most major variables, including current speed components and temperature. In particular, the semi-diurnal lunar tidal constituent M_2 was particularly pronounced in current speed data at all stations (Figure 5c, 5g & 5k). In the shallow station, the M_2 amplitude from the harmonic tidal analysis was greatest at 9.155 cm s^{-1}, with the next strongest constituent being the S_2 (the semi-diurnal solar tidal constituent) with an amplitude of 3.974 cm s^{-1}. The same relative pattern was detected in the mid canyon with decreased amplitude for M_2 of 4.43 cm s^{-1} and 1.87 cm s^{-1} for S_2. Finally, at the deepest station, the amplitude of the M_2 constituent was 1.43 cm s^{-1} and 0.49 cm s^{-1} for S_2. Temperature (not shown) demonstrated a similar pattern in the shallow and mid-canyon, with a strong M_2 tidal modulated pattern. However, this signal was absent in the deep canyon, reflecting a less variable temperature regime at depth.

In Norfolk Canyon, the shallow lander (630 m) was lost, and therefore no data were available for this area of the canyon. Water flow at the mid canyon (917 m water depth), was predominantly in a 300° and 130° direction (Figure 6), and relative to Baltimore Canyon, had much higher current speeds (Table 2b). Warmer waters were weakly positively correlated with higher current speeds (Spearman's Rank Correlation on 24-hour moving average data, $r = 0.3$, $p < 0.001$). In the deeper region of Norfolk Canyon, current flow was orientated along a 240° and 90° direction (Figure 6a & 6b). Temperatures and current speeds were lower than at the mid canyon (Table 2b). Turbidity was weakly positively correlated with current speed (Spearman's Rank Correlation on 24-hour moving average data for the first deployment, $r = 0.37$, $p < 0.001$), and was intermediately positively correlated with fluorescence (Spearman's Rank Correlation on 24-hour moving average data for the first deployment, $r = 0.57$, $p < 0.001$). Temperature was also positively correlated with current speed (Spearman's Rank Correlation on 24-hour moving average data for the first deployment, $r = 0.38$, $p < 0.001$). T-S signatures confirmed, as in Baltimore Canyon, the presence of the two most predominant water masses, namely WNACW and WASIW.

At both stations in Norfolk Canyon cumulative up-canyon flow was observed (Figure 6d & 6h, bottom panel). This was more pronounced at the mid-canyon station, where the cumulative water flux moved approximately 380 km up canyon over the entire time series (approximately 4.75 cm s^{-1}; Figure 6d). At the deep-canyon station the residual flow was also characterised by up-canyon movement, however, a singular, large episodic event in March with sustained down-canyon flow dominated the time series (Figure 6h). There was also clear evidence of a strong tidal influence within Norfolk Canyon. The semi-diurnal M_2 constituent was pronounced in current speed at both stations (Figure 6c & 6g). At the mid-canyon station, the M_2 amplitude from the harmonic tidal analysis was greatest at 15.23 cm s^{-1}, with the next strongest constituent being the S_2 with an amplitude of 3.04 cm s^{-1}, the M_4 constituent was also observed with an amplitude of 1.94 cm s^{-1}. The deep station also exhibited strong amplitude in the M_2 tide of 4.71 cm s^{-1}, and lower S_2 at 0.84 cm s^{-1}. These tidal signals were stronger than those observed in Baltimore Canyon at similar depths.

5 Discussion

In this study, CTD transects, long temporal (8 months Baltimore; 12 months Norfolk) and high frequency (5-15 minute) near-bottom measurements supported many observations from previous canyon studies, which noted the presence of water masses interacting with topography, frontal structures, nepheloid layers and tidally-driven bottom currents in governing the environmental conditions within canyons (Palanques et al., 2006; de Stigter et al., 2007; Wilson et al., 2015). Baltimore and Norfolk canyons shared similar water column structures with their adjacent slopes, leading to similar conditions in temperature and salinity. However, differences in other environmental conditions arose from the interaction between local hydrodynamics, topographically steered tidal currents, and flushing of the upper canyons, possibly driven by the focusing of internal tides and canyon orientation differences. Current speeds and directions showed both canyons had a dominant net up-canyon flow of bottom water, which is a common feature in canyons worldwide (e.g. Amaro et al., 2015; De Stigter et al., 2007).

5.1 Water mass distribution

This study recorded shelf-slope frontal signatures in both canyons over the shelf break (~100 m), which are typical of the MAB (Cacchione et al., 2002; Churchill & Gawarkiewicz, 2014; Rasmussen et al., 2005). The front was present in all transects in this study and was previously noted as an important feature of the MAB region (Linder & Gawarkiewicz, 1998; Rasmussen et al., 2005). The amount of cold pool water contributing to the shelf-slope front differed between the two canyons, which was attributed to the season (i.e. the different timings of sampling within the two canyons). Baltimore Canyon had a strongly stratified water column, typical of summer (August), whereas Norfolk Canyon, demonstrated a weakly stratified water column in May. Generally, the front was less defined with increasing distance offshore, where the foot of the shelf-slope front isolated the cold pool from denser offshore slope water. The position of the front is known to be highly variable over space and time (Houghton et al., 1994), due to seasonal changes in water temperature, salinity, interaction with Gulf Stream and slope water eddies and onshore wind events. It entrains coastal waters on the shelf with potential implications for enhanced phytoplankton production and likely export onto the shelf and slope (Malone et al., 1983; Mouw & Yoder, 2005).

This study identified two deeper offshore water masses, namely WNACW and WASIW (Emery, 2001) that were present along the entire length of both canyon axes, which is consistent with observations from Rona et al. (2015) and Rasmussen et al. (2005). WNACW and WASIW were confined below the σ_θ 27 kg m^{-3} and σ_θ 27.5 kg m^{-3} isopycnals, respectively. Geostrophic flow calculations from Baltimore Canyon provided evidence of down-canyon flowing WNACW in the upper water column (surface to ~450 m) and up-canyon flowing WASIW bottom water (>450 m). This water mass convergence zone may be attributed to the entrainment of the prevailing south-westerly shelf boundary current flowing into the upper reaches of Baltimore Canyon (Hunkins, 1988; Gardner 1989a, 1989b).

5.2 Canyon flushing and tidal currents

Compared to Baltimore Canyon, few published studies on the hydrodynamics of Norfolk Canyon exist. High current speeds and evidence of recent erosional activities in Norfolk Canyon were reported by Hecker et al., (1983) as being exceptional when compared with other MAB canyons. Shepard & Dill (1966), reported periodic current speeds in Norfolk Canyon in excess of 30 cm s^{-1} at 30 m above the seafloor at 573 m water depth and suggested that upper canyon current speeds are important mechanisms for sediment displacement within the canyon. In this study, similar correlations between high current speeds and increased turbidity were observed in both Baltimore and Norfolk Canyons, likely indicating repeated sediment resuspension events. Over the sampling period in this study, Norfolk Canyon (16 cm s^{-1}) had twice the total mean current speed of Baltimore Canyon (8 cm s^{-1}), despite the similar size and close proximity of the two canyons. Canyons further north have similar or even higher mean bottom current speeds of 16 cm s^{-1}, 19 cm s^{-1} and 21 cm s^{-1} in Lydonia (Hunkins, 1988), Oceanographer, and Hudson canyons (observations from ~600 m), respectively (Hecker et al., 1980).

Spectral analyses confirmed that semi-diurnal M_2 internal tidal currents were energetic and dominated the current patterns in the near-bottom time series, especially in the upper and middle canyon reaches. Internal tides are a proven mechanism leading to enhanced currents and sediment transport within many canyon systems (Canals et al., 2006; de Stigter et al., 2011; Hall et al., 2014; Martín et al., 2011; Xu & Noble, 2009). Internal wave energy in combination with the critically sloping canyon thalweg, can lead to the breaking of internal waves (Wunsch & Webb, 1979; Hotchkiss & Wunsch, 1982; van Haren., 2005; van Haren et al., 2014). Although the current study did not directly measure the internal wave field, there was some evidence that suggests the presence of internal wave propagation within both canyons. Canyon axis and slope hydrographic transects show oscillations in the deep isopycnals (σ_θ 27-27.5 kg m^{-3}; ~200-600 m) within both canyons, which were less prevalent on the adjacent slopes. These waves had peak to peak amplitudes of ~80 m for Norfolk Canyon and ~120 m for Baltimore Canyon at wavelengths beyond the scale of our measurements (i.e. > 20 km), which are similar to Hudson Canyon (Rona et al., 2015). Here, internal waves were detected at scales of 5-20 km with an amplitude of 50 m. The authors noted that across the canyon, an uneven current flow developed, favouring the eastern side of Hudson Canyon, consistent with their geomorphological finding and rotational Coriolis effects (Allen & Durrieu de Madron, 2009). Equally, the present study showed tilted isopycnals (σ_θ 27-27.5 kg m^{-3}; Supplementary Figure 3a & 3b), revealing an uneven flow on the eastern side of Baltimore, suggestive of a dynamic upper canyon region where topographic steering, internal waves and rotational effects are evident (Gardner, 1989a; Hall & Carter, 2011; Noble & Butman, 1989).

5.3 Turbidity and nepheloid layer distribution

Both canyons were highly turbid when compared to the adjacent slope and demonstrated the presence of substantial nepheloid layers. Similar turbid layers have been found within other canyons on both sides of the Atlantic Ocean (Martín et al., 2011; Wilson et al., 2015; Wunsch & Webb, 1979). Such turbidity is common within canyon systems and may be related to the occurrence, under certain circumstances of; 1) water mass convergence zones (Gardner, 1989a; Hecker et al., 1983), 2) tidal bores (Gardner, 1989a; Huthnance, 1995), and 3) episodic benthic storm events (Gardner et al., 2017), 3) the canyon flushing by focusing of internal wave energy (Hall et al., 2017; Hall & Carter, 2011) and 4) fishing activities (Puig et al., 2001; Wilson et al., 2015). In Baltimore Canyon the nepheloid layer had a conspicuous seaward-entrained finger-like projection, identical to that described during previous surveys (Gardner 1989a). Previous studies on the dynamics of nepheloid layers (Durrieu de Madron, 1994; Durrieu de Madron et al., 1990) showed that these features follow density surfaces between water masses, which in Baltimore Canyon is the boundary between WNACW and WASIW. The opposing flow direction between these two water masses intensifies the suspended sediment and limits its distribution within the canyon (Durrieu de Madron et al., 1990). Nepheloid distributions within Norfolk Canyon were observed as smaller discreet intermediate nepheloid layers, between 400 and 1100 m water depth, perhaps representative of separate tidally-driven resuspension events, the lack of a water mass convergence or seasonal differences.

The presence of distinct turbidity layers has been reported to drive differences in the benthic assemblages found within canyons (Cunha et al., 2011; Liao et al., 2017; Vetter & Dayton, 1998). The observed nepheloid layers in the present study originate below 400 m water depth and this may have consequences for the colonisation of sessile fauna such as corals (Huvenne et al., 2011) and associated food-web ecology and trophic diversity (Demopoulos et al., 2017). Ample evidence exists that high sediment loads have detrimental effects on stony corals, causing suffocation in extreme cases (Brooke et al., 2009; Rogers, 1990). In both canyons, the distribution of octocoral species living on the canyon walls (*Paragorgia arborea, Paramuricea placomus*) were strongly positively correlated with turbidity levels of the canyon nepheloid layers, while hard coral species (*Lophelia pertusa, Desmophyllum dianthus*) preferred lower turbidity levels (Brooke et al., 2017), suggesting that turbidity may influence coral community structure. Turbidity also affects canyon soft sediment environments, where deposition of particulate organic matter enriches canyon thalweg areas, thus impacting benthic soft-sediment communities, (Paterson et al., 2011; Vetter & Dayton, 1998), standing stocks (De Leo et al., 2010) and sediment biogeochemistry (Kiriakoulakis et al., 2011; Prouty et al., 2017).

5.4 Summary

Canyons are characterised by complex topography and oceanography, forming a link between the shelf boundary and the deep-sea regions (Hotchkiss & Wunsch, 1982). Due to the interaction between topography and regional hydrography canyon systems are highly dynamic in terms of physical processes through both time and space (Canals et al., 2006; Levin & Sibuet, 2012; Puig et al., 2014). This study characterised the hydrodynamics and hydrography of Baltimore and Norfolk canyons and assessed the overarching oceanographic conditions. Generally, this study shows both canyons differ in terms of modelled tidally-driven water movement, near bottom current speeds and nepheloid layer distributions. It appears that neighbouring canyons, whilst sharing similar general larger scale hydrography (i.e. the same water masses) can differ in environmentally important aspects with consequences for distributions of species and ecosystems.

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9 Tables and Figures

Table 1. CTD transects utilised for water-column profiling in Baltimore and Norfolk canyons. (a) CTD casts used to generate transect analyses. (b) Individual CTD station casts used for water mass identification in Baltimore and Norfolk canyons. Data from both (a) and (b) were used to characterise water masses near Baltimore and Norfolk canyons.

(a)

Transect	**Date**	**Station**	**Distance (Km)**	**No. of casts**	**Depth range (m)**
Baltimore Canyon					
i Canyon Axis	21/08/12	NF12 036-044	18.5	9	251 - 1032
ii Slope	28/08/12	NF12 096-105	27.9	10	105 - 1068
iii Upper Transverse	19/08/12	NF12 013-018	8.1	6	104 - 586
iv Middle Transverse	20/08/12	NF12 022-027	8.8	6	123 - 854
v Lower Transverse	24/08/12	NF12 057-061	7.4	5	914 - 1257
Norfolk Canyon					
i Canyon Axis	03/05/13	RB13 003-012	22	10	237 - 1312
ii Slope	13/05/13	RB13 061-068	11.1	8	277 - 1078
iii Lower Traverse	18/08/12	NF12 001, 003-004	2.6	3	1067 - 1384

(b)

Canyon	**Transect**	**Date**	**Station**	**Coordinates**		**Depth (m)**
Baltimore	Canyon Axis	09/06/11	NF 2011-010	-73.7949	38.0903	1005
		09/06/11	NF 2011-011	-73.8258	38.1117	873
		09/06/11	NF 2011-012	-73.8503	38.1324	710
		09/06/11	NF 2011-013	-73.8454	38.1564	625
		09/06/11	NF 2011-014	-73.8665	38.1815	495
		09/06/11	NF 2011-015	-73.8464	38.2062	348
		09/06/11	NF 2011-016	-73.8353	38.2439	163
Norfolk	Canyon Axis	13/06/11	NF 2011-024	-74.5837	37.0421	1001
		13/06/11	NF 2011-025	-74.6178	37.0393	751
		13/06/11	NF 2011-026	-74.6423	37.0609	528
		13/06/11	NF 2011-027	-74.6686	37.0798	492
		13/06/11	NF 2011-028	-74.6984	37.0887	295
		13/06/11	NF 2011-029	-74.7311	37.0934	268
		13/06/11	NF 2011-030	-74.7613	37.1029	106

Table 2. Landers and moorings within Baltimore and Norfolk canyons; (a) deployment positions and depths and (b) recorded environmental parameters. * Recovered for servicing in May 2013. † Lost due to technical failure or burial. - No data due to lack of appropriate sensor.

(a)

Canyon	**Position**	**Depth**	**Coordinates**	
Baltimore	Shallow *	603 m	-73.8492	38.1504
	Mid	1082 m	-73.7826	38.0776
	Deep*	1318 m	- 73.7359	37.0424
Norfolk	Shallow†	630 m	-74.6519	37.0646
	Mid	917 m	-74.6193	37.0388
	Deep	1364 m	-74.5337	37.0646

(b)

	Baltimore			**Norfolk**	
Variable	**Shallow**	**Mid**	**Deep**	**Mid**	**Deep**
Temperature (°C)					
Min	4.5	4.0	3.8	3.96	3.7
Max	8.6	5.1	4.7	6.1	5.2
Mean	5.4 (0.47)	4.5 (0.17)	4.2 (0.2)	4.9 (0.3)	4.19 (0.15)
Oxygen (ml L^{-1})					
Min	4.65	-	6.8	-	-
Max	7.4	-	7.4	-	-
Mean	6.6 (0.3)	-	7.1 (0.1)	-	-
Density (σ_θ, kg m^{-3})					
Min	26.03	27.55	26.07	27.18	27.47
Max	27.63	27.9	28.09	27.9	27.8
Mean	27.4 (0.1)	27.7 (0.02)	27.99 (0.03)	27.58 (0.08)	27.71 (0.04)
Current speed (cm s^{-1})					
Min	0.1	0	0.03	0.1	0
Max	66.2	42.3	29.2	81.7	94
Mean	14.6 (9.03)	9.26 (5.6)	6.6 (3.3)	17.6 (11.3)	8.0 (5.6)

Table 3. Temperature and salinity signatures for the major water masses and water mass constituents within the Baltimore and Norfolk canyons. WNACW = Western North Atlantic Central Water, WASIW = Western Atlantic Subarctic Intermediate Water and NADW = North Atlantic Deep Water. pss = Practical salinity scale. Depths are cited as per Emery & Meincke (1986).

Oceanic Source		**MAB component**	**Diagnostic Signature**		
Water Mass	**Depth (m)**	**Water Mass**	**Temp (°C)**	**Sal (pss)**	**Reference**
Shelf water	< 200	Shelf surface water	11-25	30-34.75	Church et al., (1984), Csanady & Hamilton (1988)
WNACW	< 500		2-18	34.9-36	Csanady & Hamilton (1988)
	< 500		7-20	35-36.7	Emery & Meincke (1986), Drinkwater et al., (1999)
		Shelf-slope front	5-15	34.8-35.2	Horne (1978)
		Warm slope water	> 8-15	> 34.8-35.6	Csanady & Hamilton (1988), Drinkwater et al., (1999)
			5-11	32.5-34.8	Church et al., (1984), Csanady & Hamilton (1988)
		Cold pool water			
Gulf Stream		Gulf Stream shallow	> 23	> 35	Csanady & Hamilton (1988), Rasmussen et al., (2005)
		Gulf Stream deep	9-19.4	> 35-36.3	Csanady & Hamilton (1988), Churchill & Cornillon (1991), Rasmussen et al., (2005)
WASIW	> 500 - 1500		3-9	34-35.1	Emery & Meincke (1986)
NADW	1500 - bottom		1.5-4	34.8-35	Emery & Meincke (1986)

Table 4. The net up or down canyon current velocities for Baltimore Canyon (upper, mid and lower) and Norfolk Canyon (lower), estimated by geostrophic flow equation which takes into account the whole water column. Arrows indicate up (↑) and down (↓) canyon flow velocities, both is the overall mean velocity (i.e. from all casts in the transect. Negative values indicate down-canyon flow, positive, up-canyon flow).

Canyon	**Transect**	**Depth (m)**	**Direction**	**Net mean Flow (m/s^{-1})**
Baltimore	i Upper	107-390	Both	- 0.268
			↑	0.157
			↓	- 0.296
	ii Mid	153-495	Both	- 0.396
			↑	0.054
			↓	- 0.419
	iii Lower	733 - 1047	Both	- 0.022
			↑	0.042
			↓	- 0.076
Norfolk	iii Lower	1154 - 1195	Both	- 0.022
			↑	0.888
			↓	- 0.744

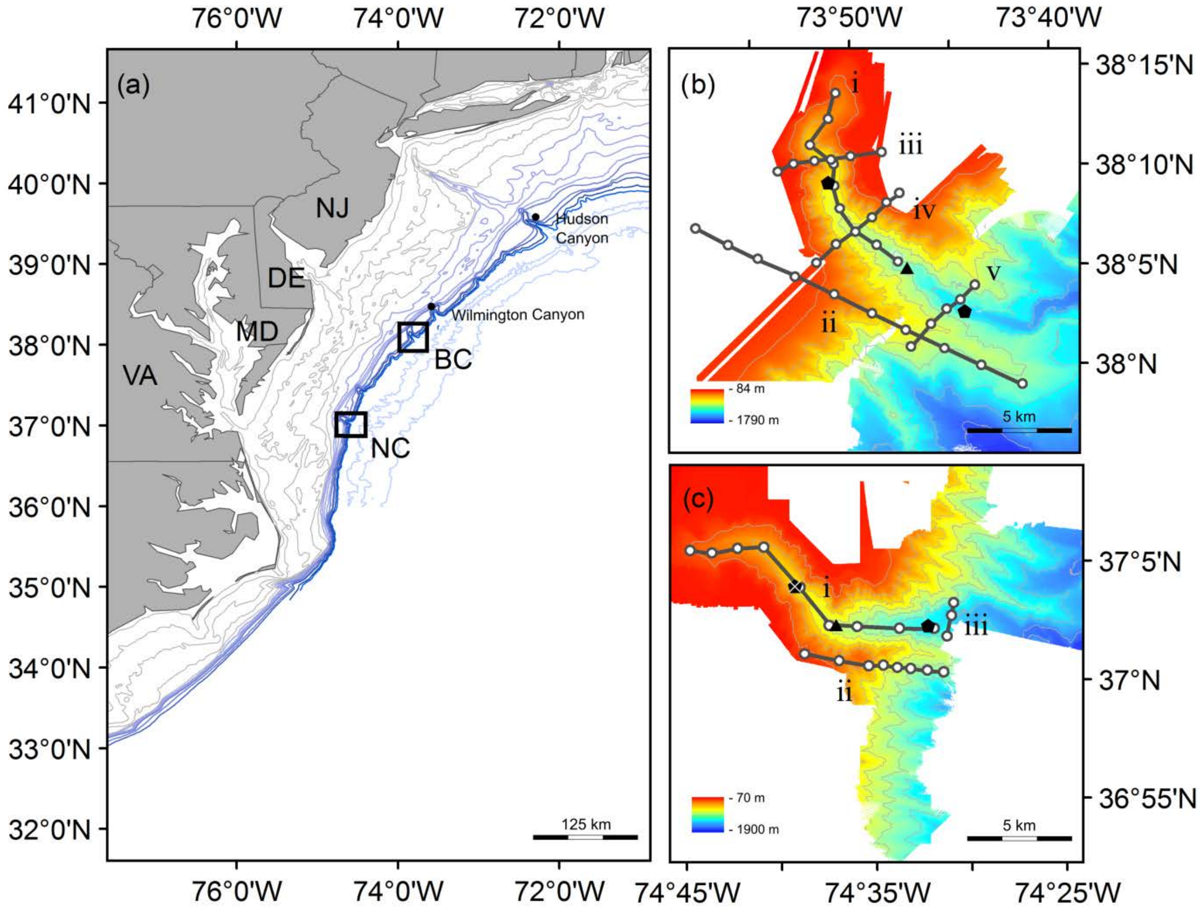


Figure 1. The Mid-Atlantic Bight off the Eastern United States. (a) Overview of the MAB shelf showing numerous incising canyons, location of Baltimore Canyon (BC) and Norfolk Canyon (NC) are shown as inset frames and neighbouring states; Virginia (VA), Maryland (MD), Delaware (DE) and New Jersey (NJ). Dark blue contours represent the shelf break at ~100 m. Sub-figures (b) and (c) show the sampling design carried out during the research cruises in 2011, 2012 and 2013. (b) In Baltimore, (i) canyon CTD transect, (ii) slope CTD transect, (iii) upper canyon traverse CTD transect, (iv) mid canyon traverse CTD transect, (v) lower canyon traverse CTD transect, ⬟ shallow benthic lander, ▲ mid-canyon mooring and (viii) deep benthic lander. (c) In Norfolk, (i) canyon CTD transect, (ii) slope CTD transect, (iii) lower canyon traverse CTD transect, ⊗ shallow benthic lander (lost), ▲ mid-canyon mooring and ⬟ deep benthic lander. Bathymetry on figures b and c is shown as the inset colour scale bar.

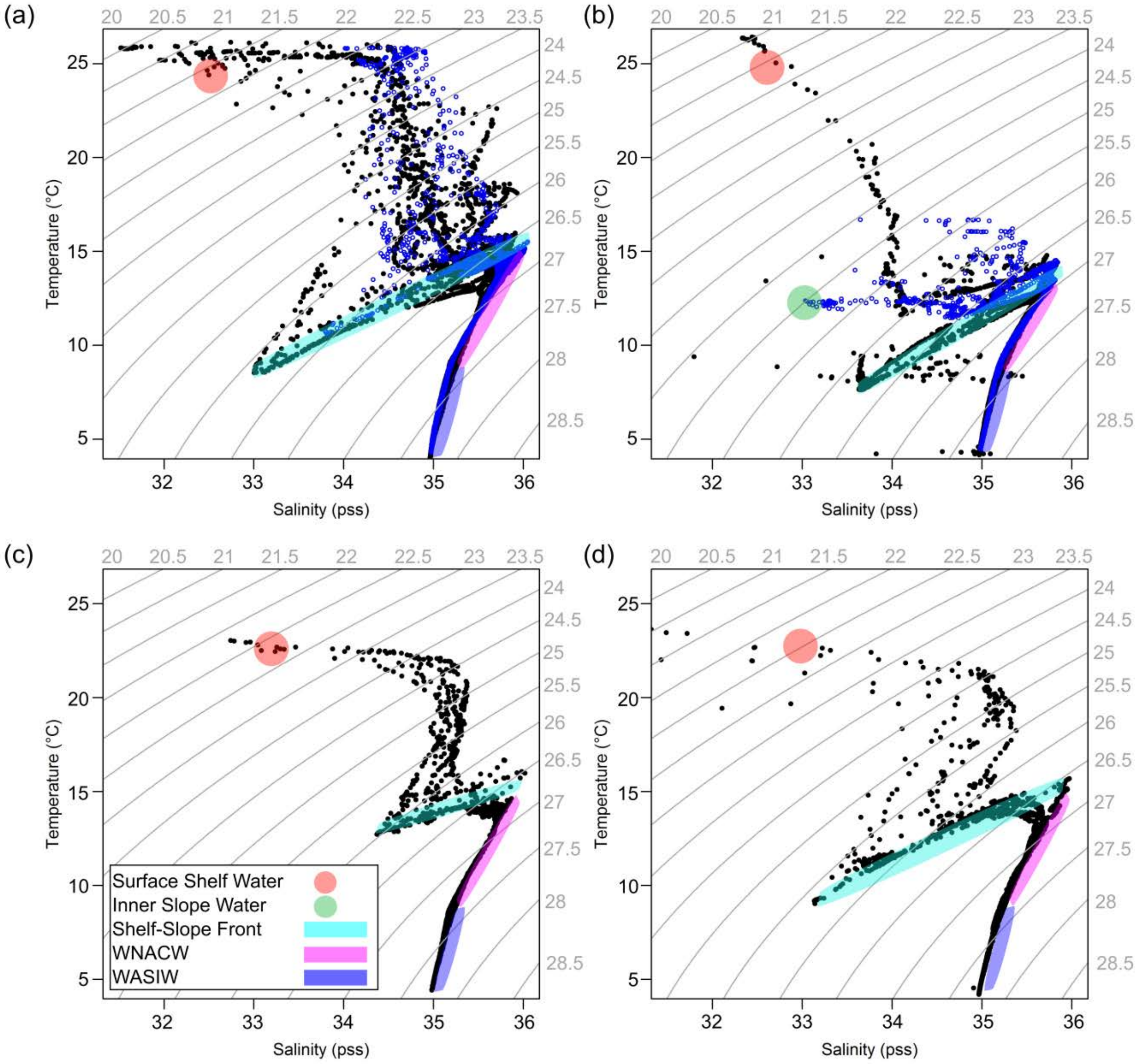


Figure 2. Temperature-Salinity diagrams indicating major water masses observed in the MAB study area, from CTD surveys conducted for; (a) all Baltimore Canyon (black) and adjacent slope (blue) profiles from August to September 2012, (b) all Norfolk Canyon (black) and adjacent slope (blue) profiles from April to May 2013, (c) all Baltimore Canyon profiles from June 2011 and (d) all Norfolk Canyon profiles from June 2011. Water masses are labelled, WNACW = Western North Atlantic Central Water, and WASIW = Western Atlantic Sub-Arctic Intermediate water. Grey contours indicate density (σ_θ kg m^{-3}).

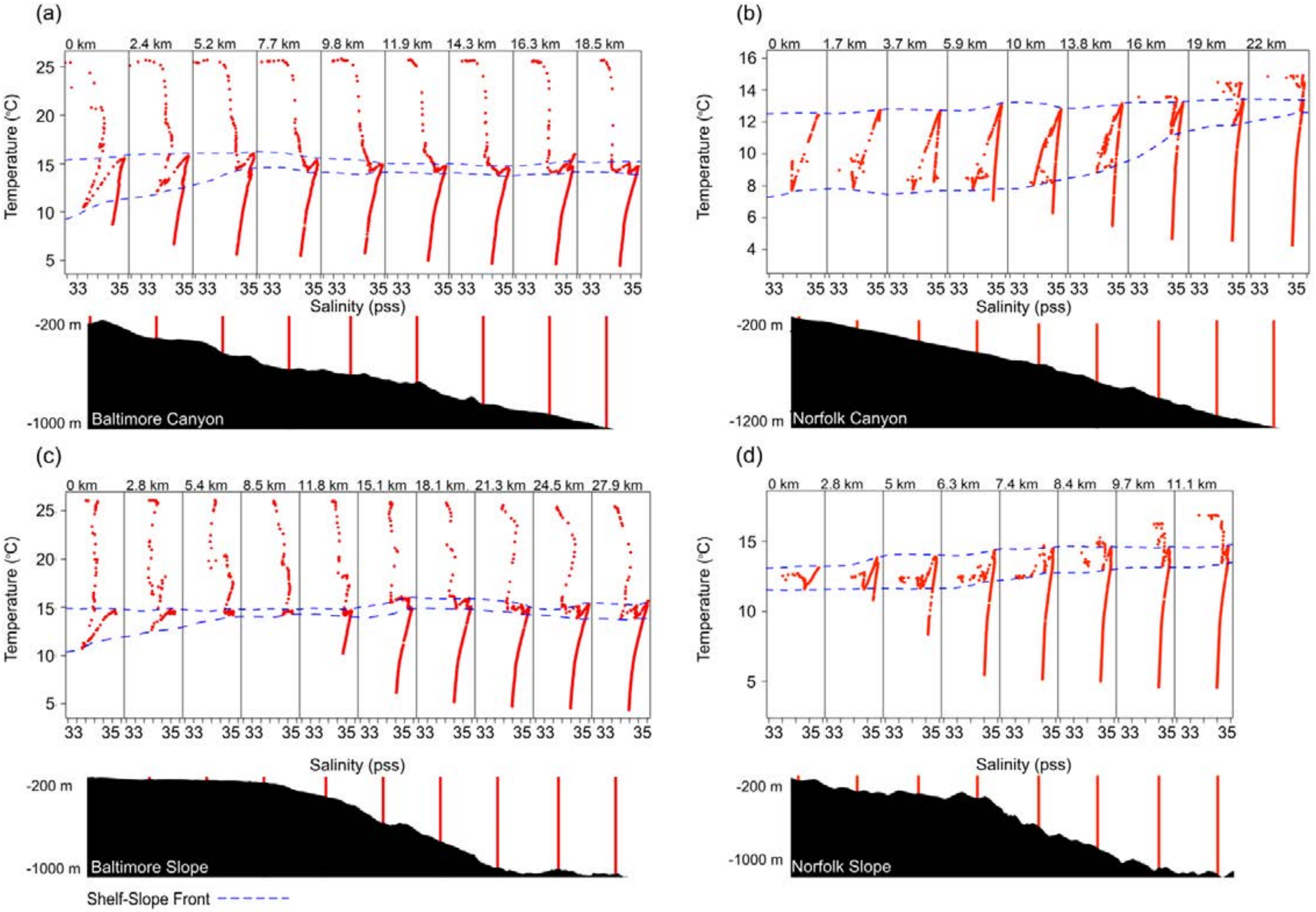


Figure 3. Temperature-Salinity diagrams from hydrographic CTD transects in August 2012, for (a) Baltimore Canyon and (b) Norfolk Canyon axes, (c) Baltimore adjacent slope and (d) Norfolk adjacent slope. The corresponding location for each profile is shown as red vertical lines on the topographic profile below each plot. Blue dashed lines indicate the estimated position of the shelf-slope front.

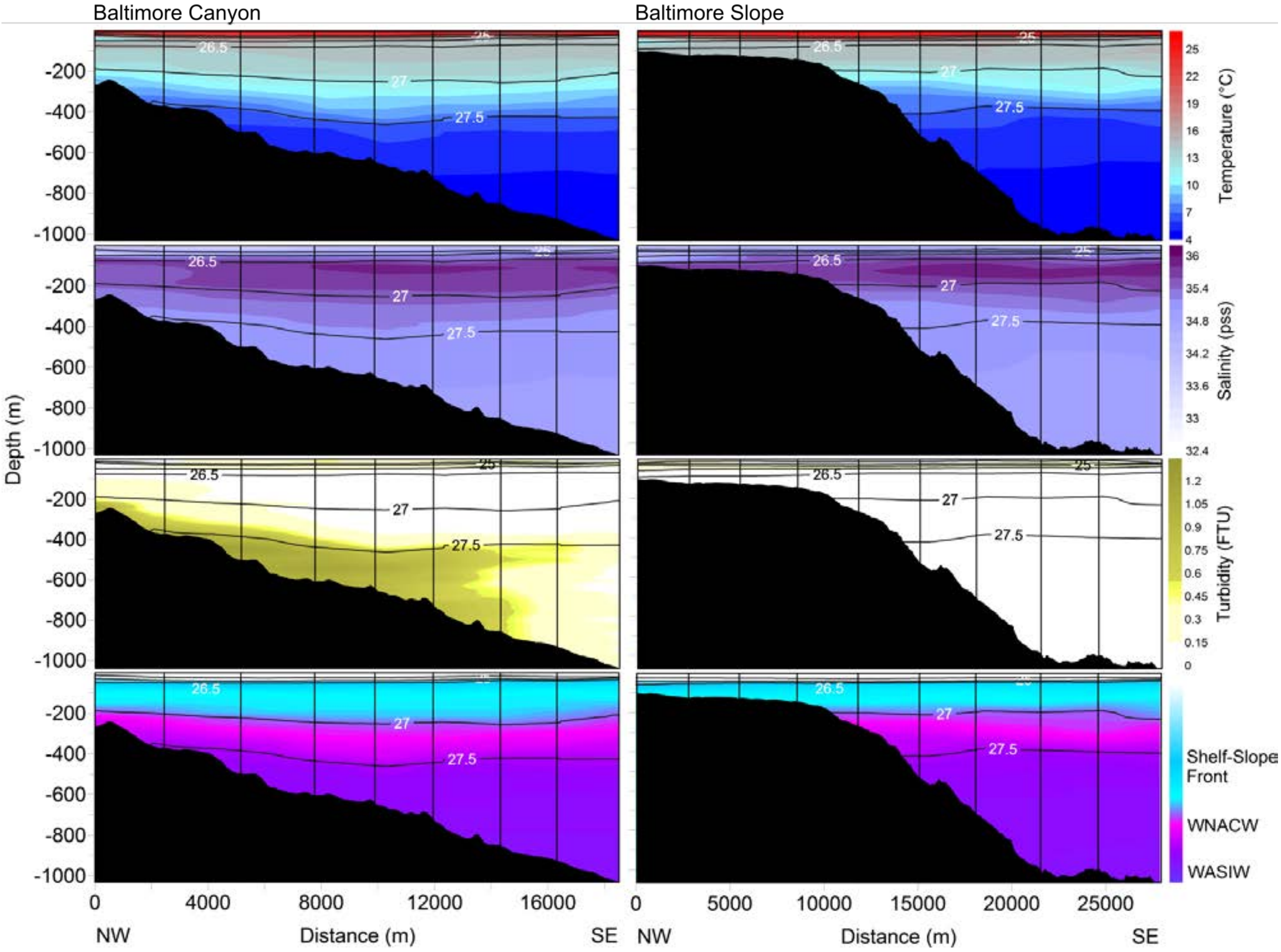


Figure 4a. Temperature, salinity, turbidity and corresponding water mass profiles derived from CTD hydrographic survey along Baltimore Canyon axis and respective adjacent slope. Potential density (σ_θ kg m^{-3}) contours are overlain. WNACW = Western North Atlantic Central Water and WASIW = Western Sub-Arctic Intermediate Water. Dark vertical lines indicate the position of CTD casts, including the margins. (No. of casts: Baltimore Canyon = 9 and slope = 10).

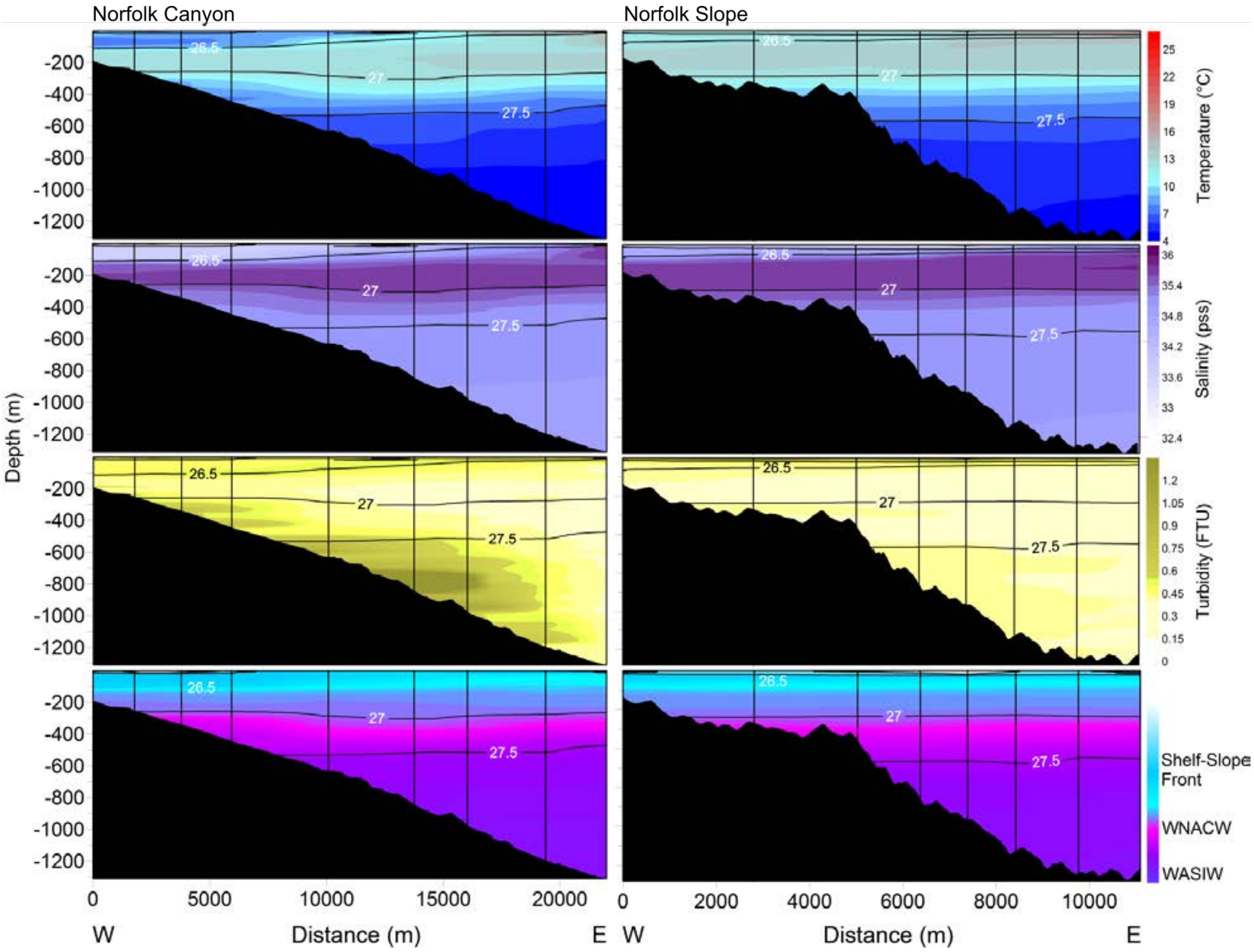


Figure 4b. Temperature, salinity, turbidity and water mass profiles derived from CTD hydrographic survey along Norfolk Canyon axis and respective adjacent slope. Potential density (σ_θ kg m^{-3}) contours are overlain. WNACW = Western North Atlantic Central Water and WASIW = Western Sub-Arctic Intermediate Water. Dark vertical lines indicate the position of CTD casts, including the margins. (No. of casts: Norfolk Canyon = 9 and slope = 8).

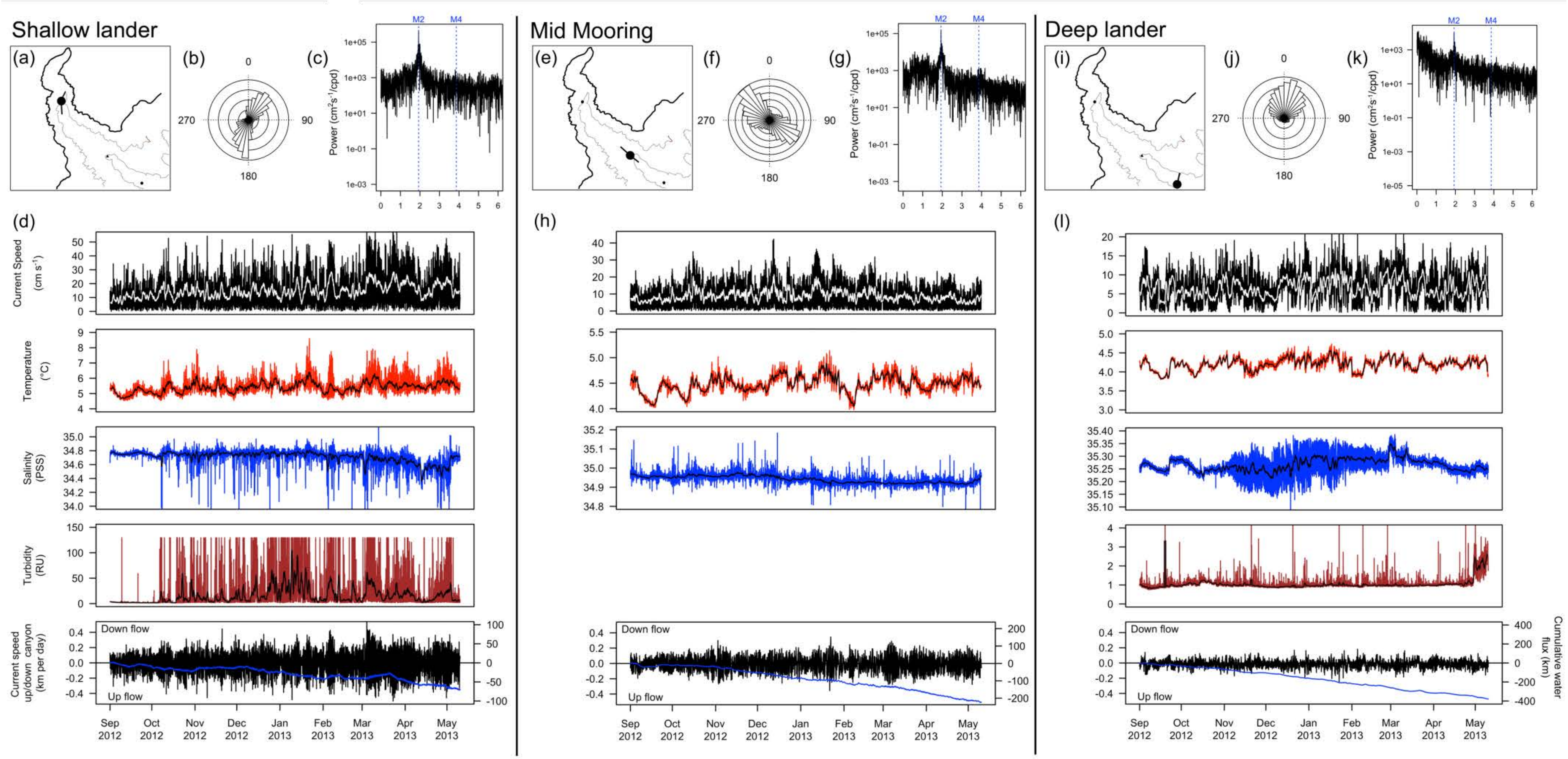


Figure 5. Time-series of environmental conditions along the Baltimore Canyon axis (Prouty et al., 2017). Upper panels show, location of lander/mooring (a, e & i), current direction radial histogram (b, f & j) and tidal signal (c, g & k). Lower panels show time-series plots for current speed, temperature, salinity, turbidity and cumulative water flux (blue line) along the canyon axis at each station (d, h & l).

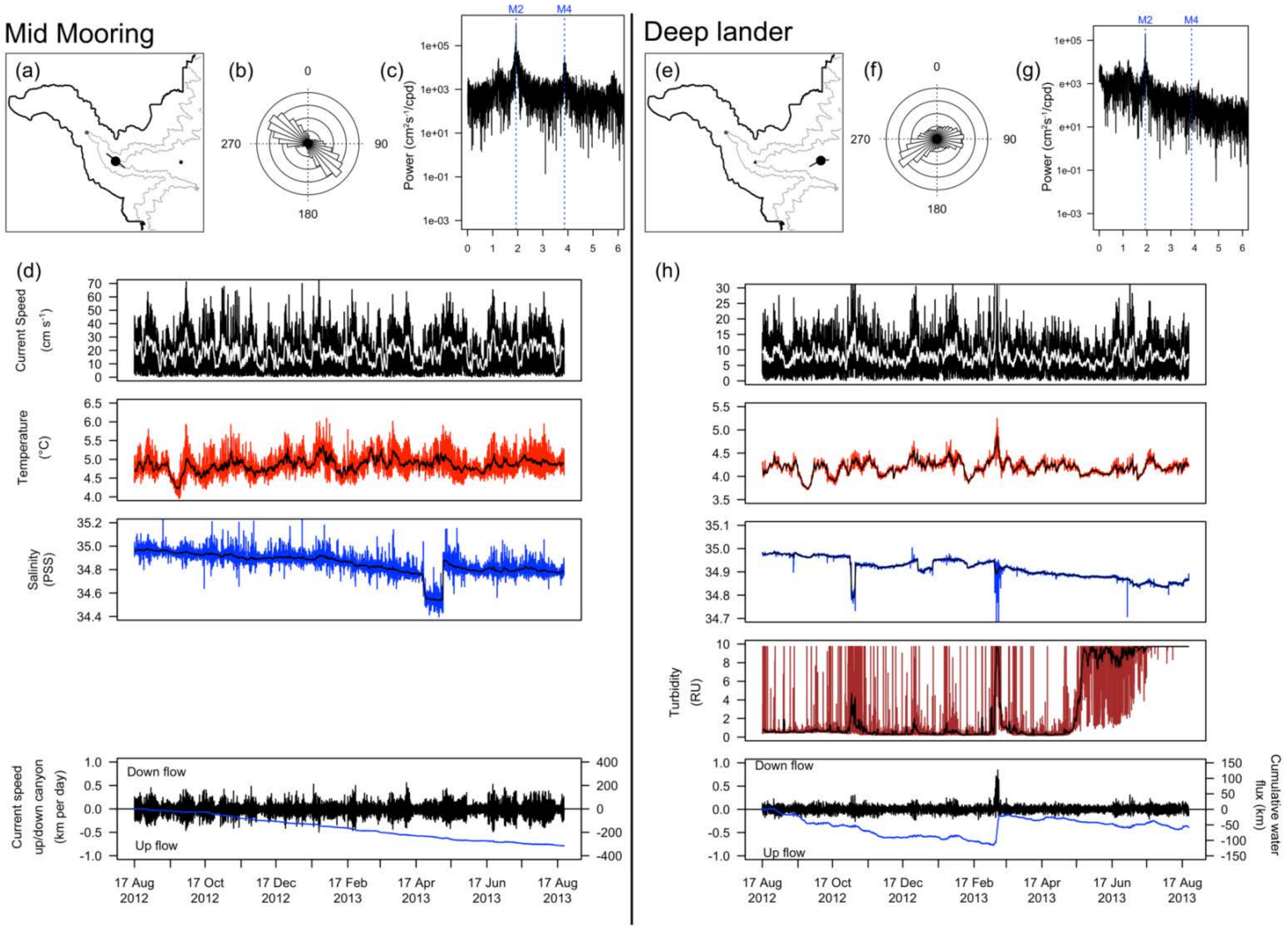
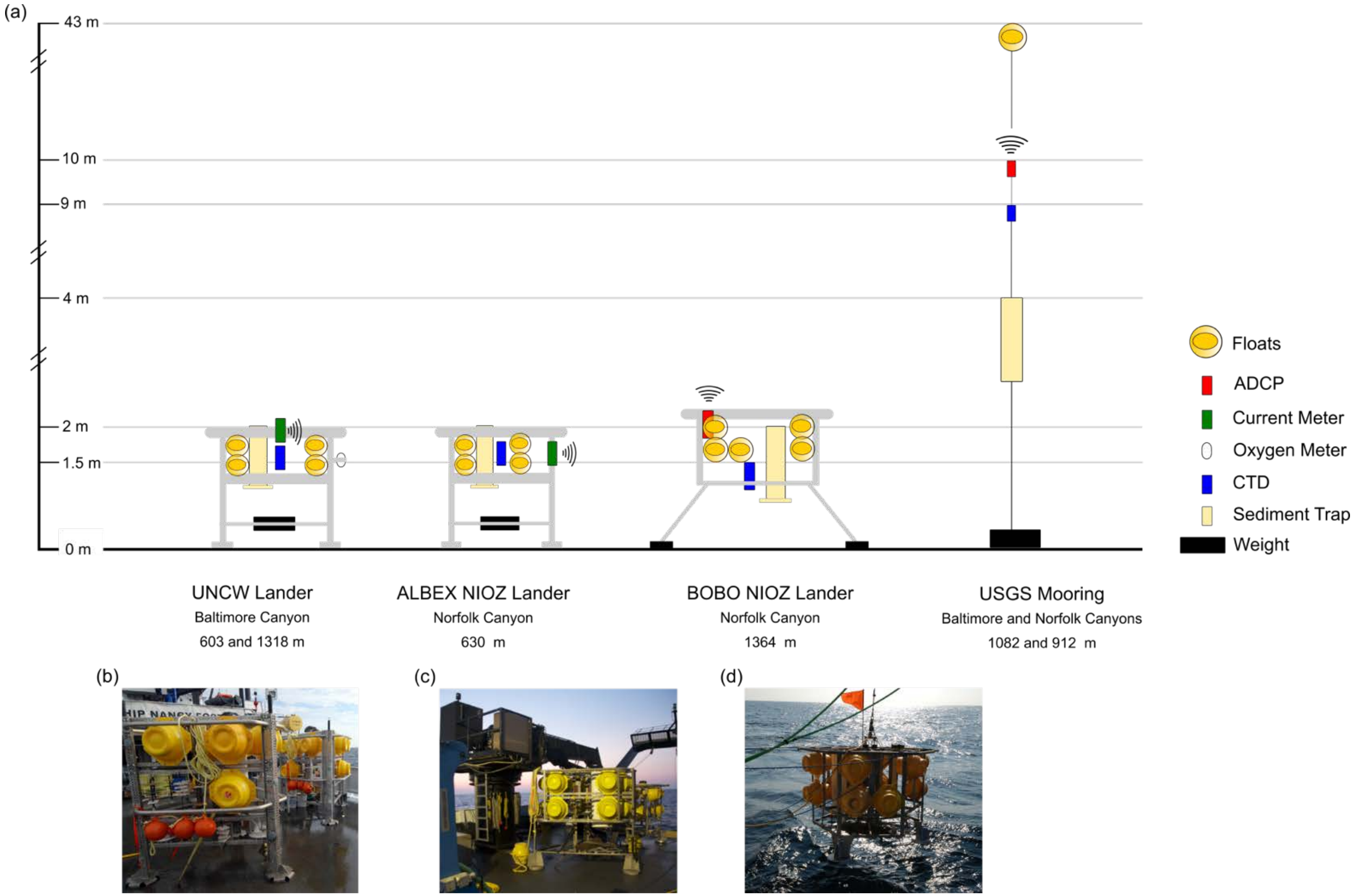
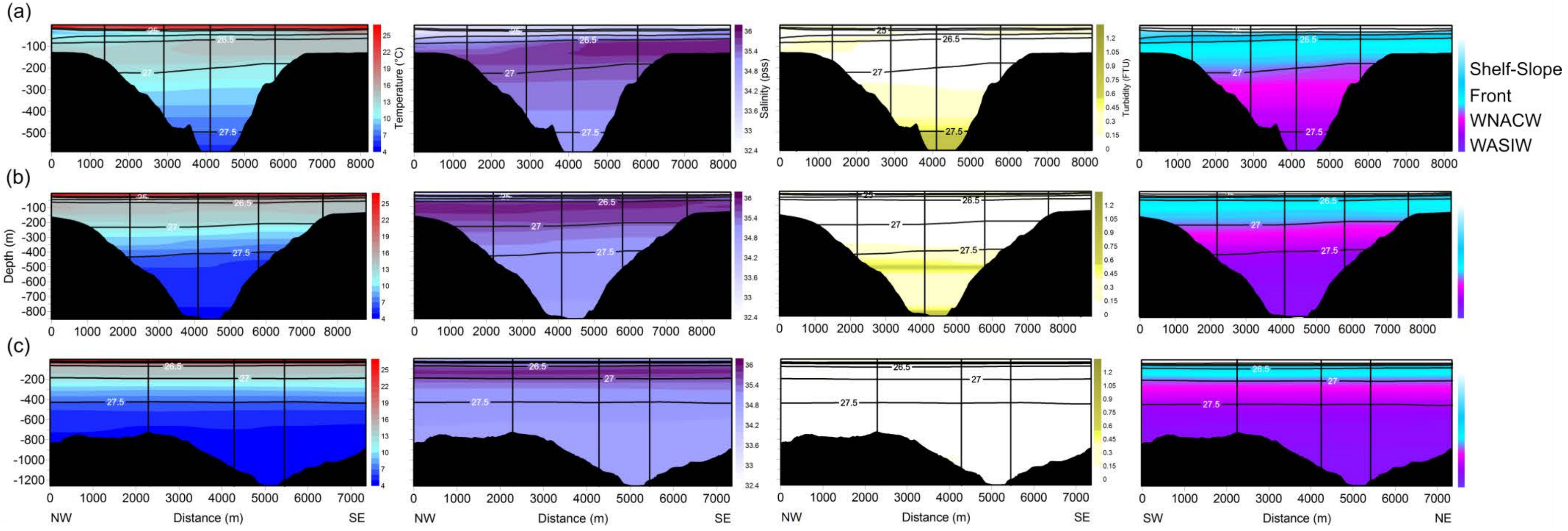


Figure 6. Time-series of environmental conditions along the Norfolk Canyon axis. Upper panels show location of lander/mooring (a & e), current direction radial histogram (b & f) and tidal signal (c & g). Lower panels show time-series plots for current speed, temperature, salinity, turbidity and cumulative water flux (blue line) along the canyon axis at each station (d & h).

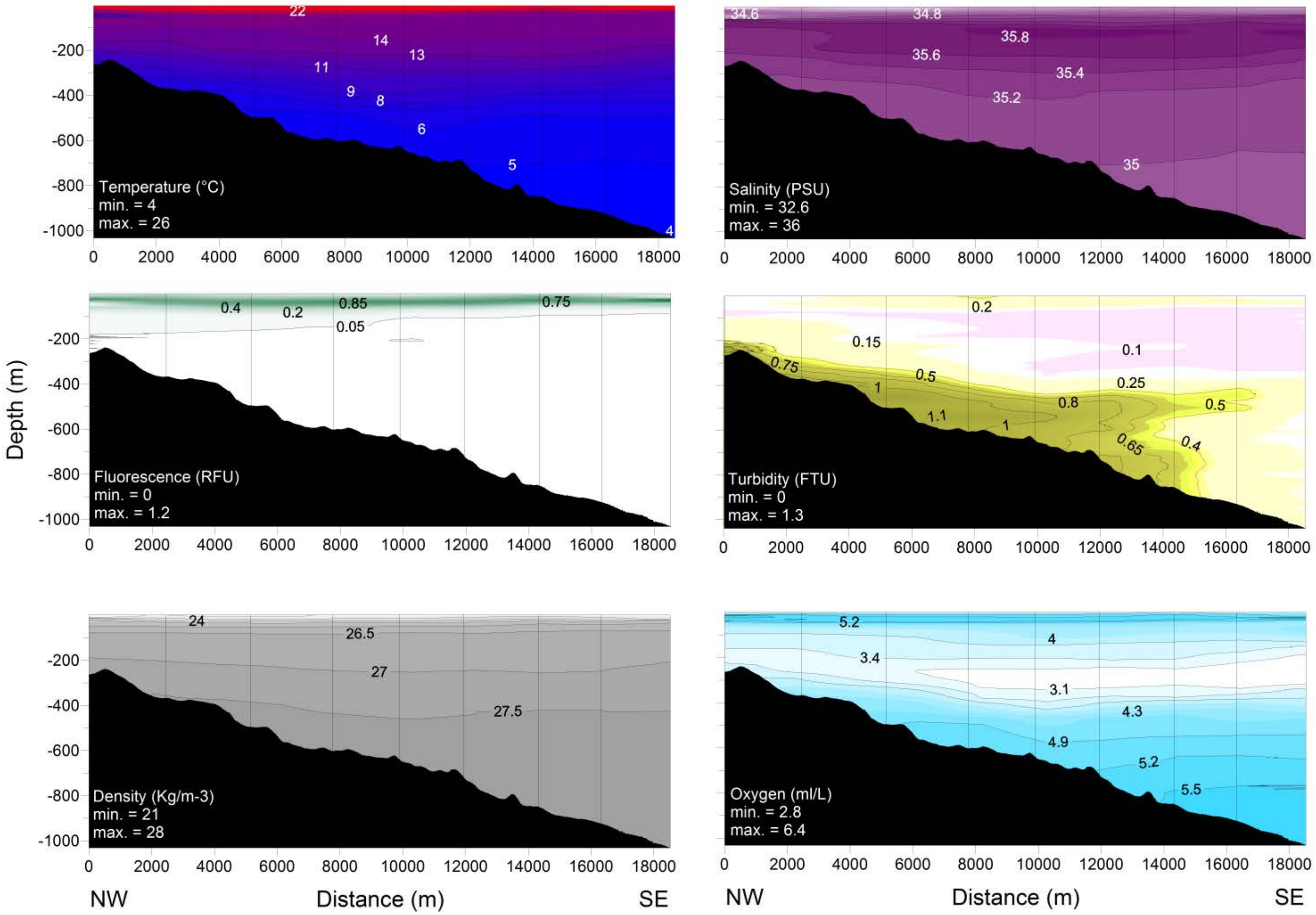
10 Supplementary Materials



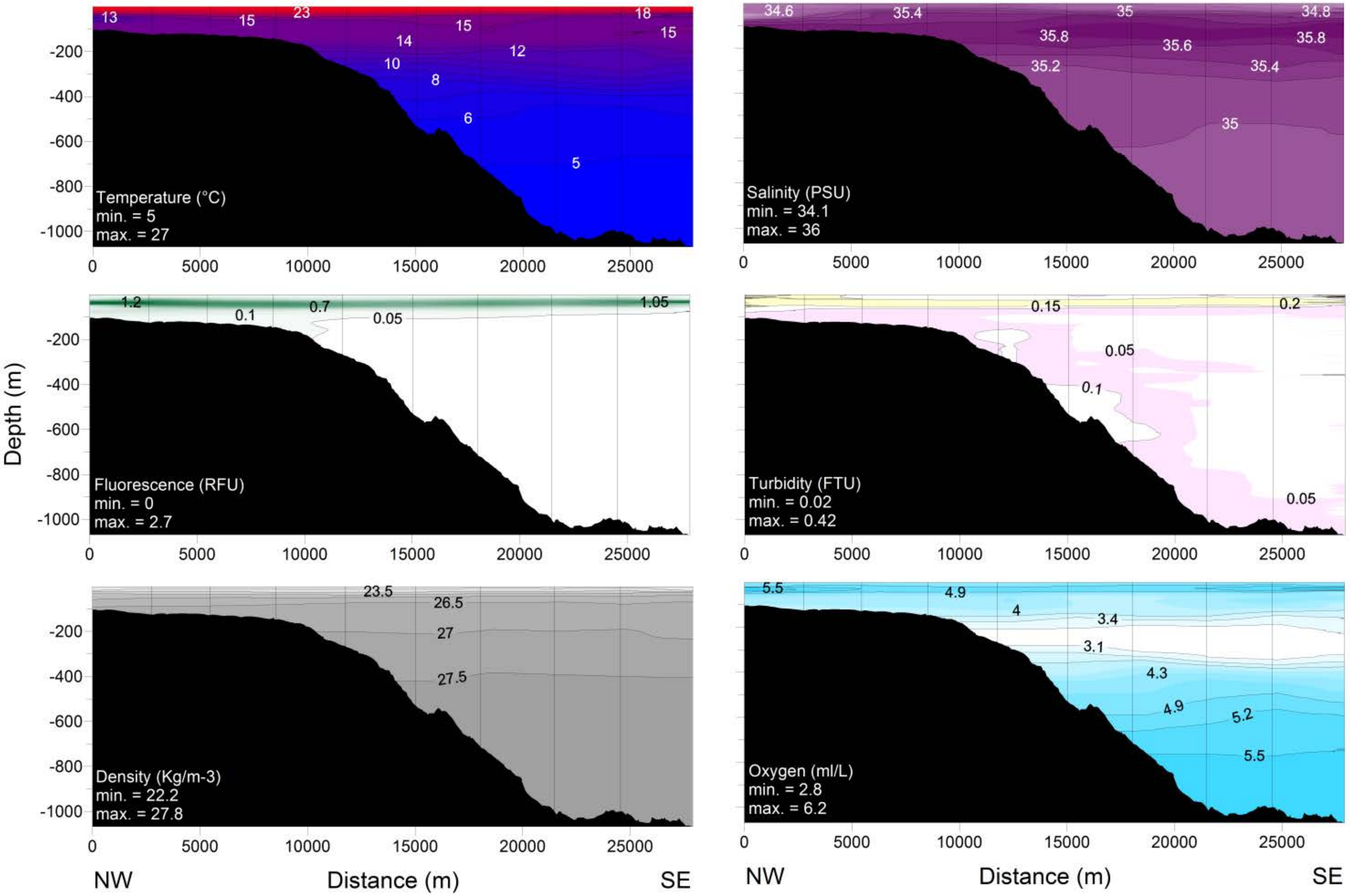
Supplementary Figure 1. (a) Schematic diagram showing the benthic landers and moorings and the positions of associated environmental monitoring instrumentation used in Baltimore and Norfolk Canyon. (b) UNCW landers (c) NIOZ ALBEX and (d) NIOZ BOBO landers.



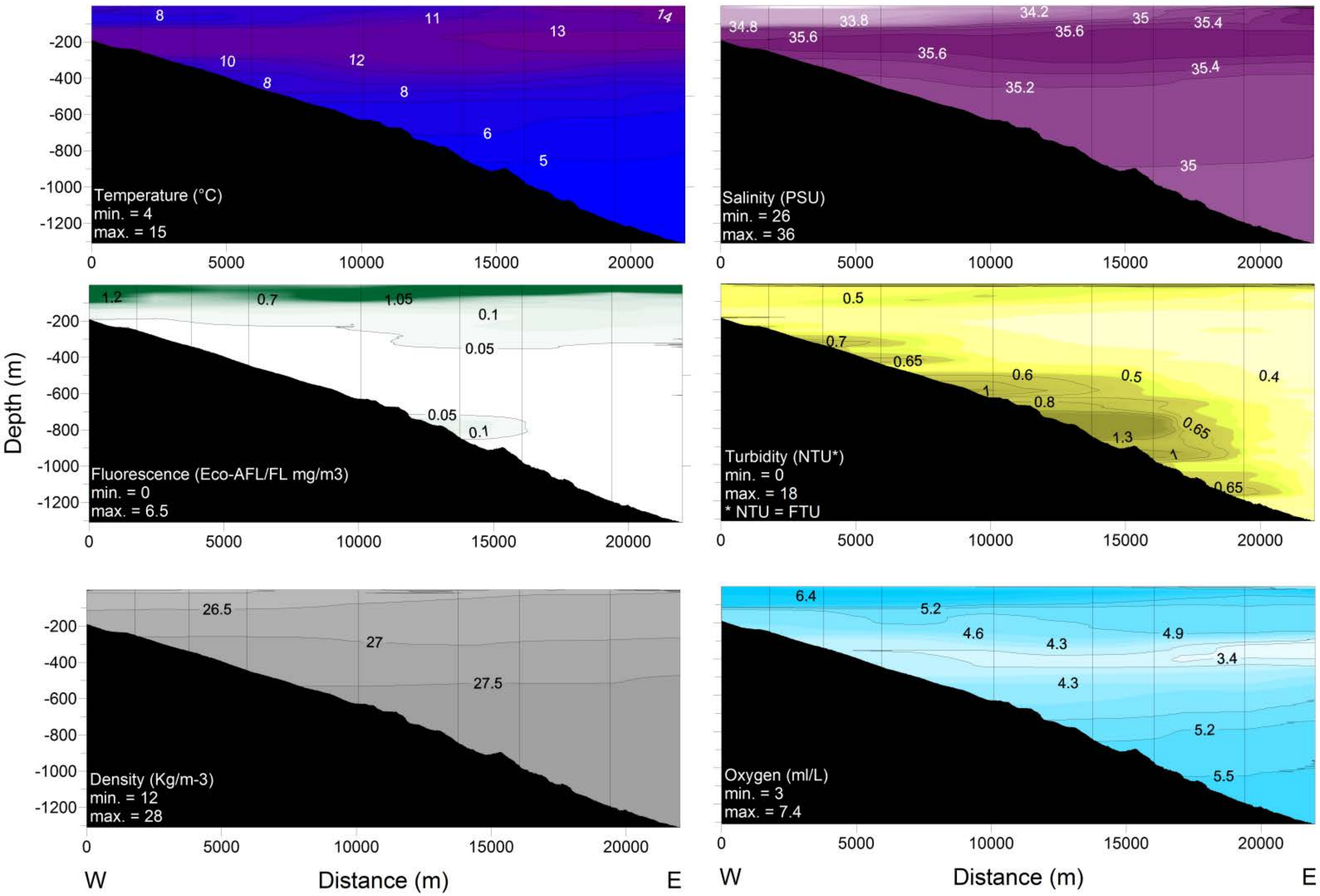
Supplementary Figure 2. Temperature (°C), salinity (pss), turbidity (FTU) and water mass profiles for across-canyon hydrographic CTD transects in Baltimore Canyon during May 2013. (a) upper canyon, (b) middle canyon and (c) lower canyon. Potential density (σ_θ kg m^{-3}) anomaly contours are overlaid. Dark vertical lines indicate the position of CTD casts, including the extreme margins. WNACW = Western North Atlantic Central Water and WASIW = Western Sub-Arctic Intermediate Water. (No. of casts: upper canyon = 6, middle canyon = 6 and lower canyon = 5).



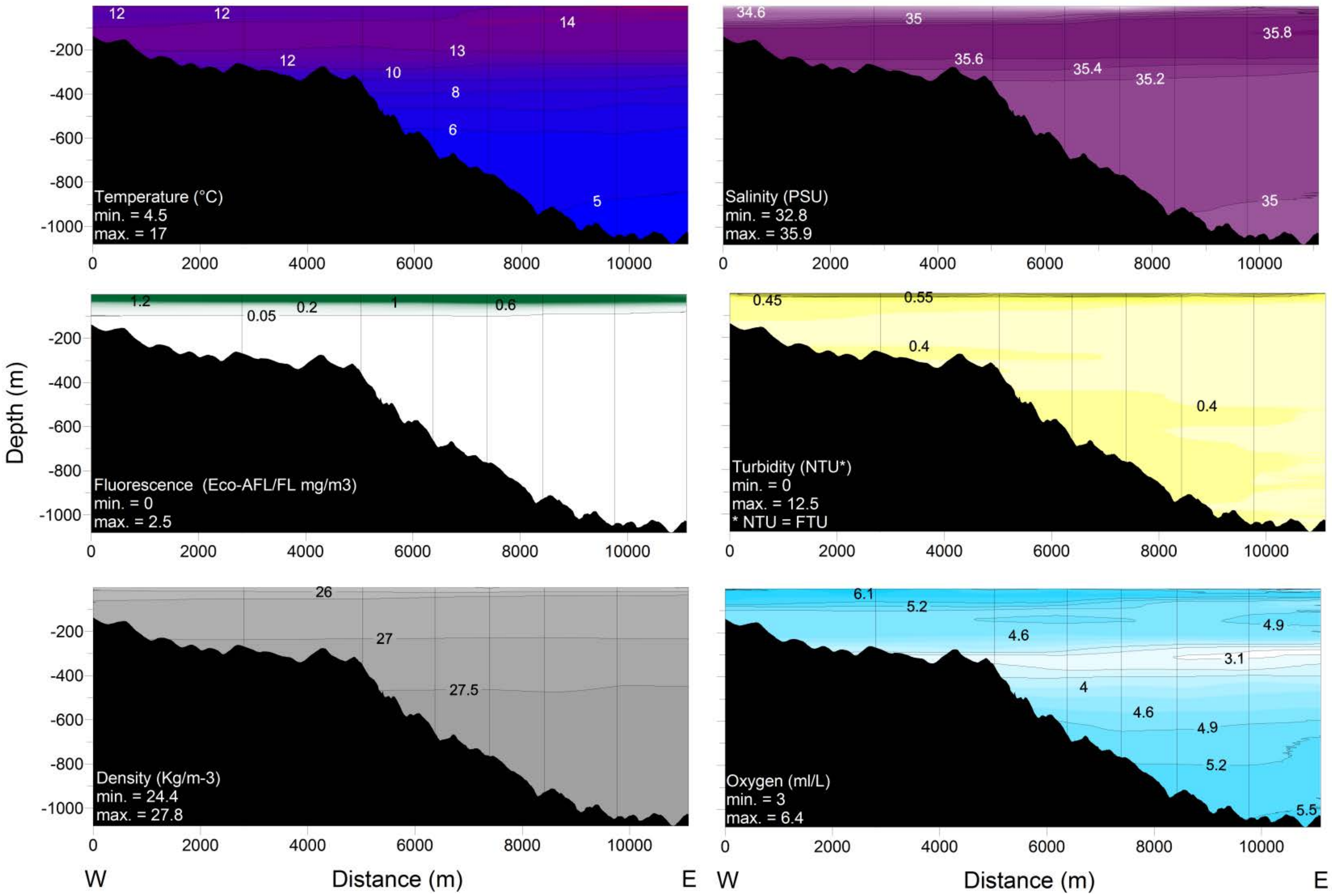
Supplementary Figure 3. Temperature (°C), salinity (psu), fluorescence (RFU), turbidity (FTU), density (σ_θ kg m^{-3}) dissolved oxygen (ml L^{-1}) contour profiles for Baltimore Canyon. Dark vertical lines represent CTD casts (n = 9).



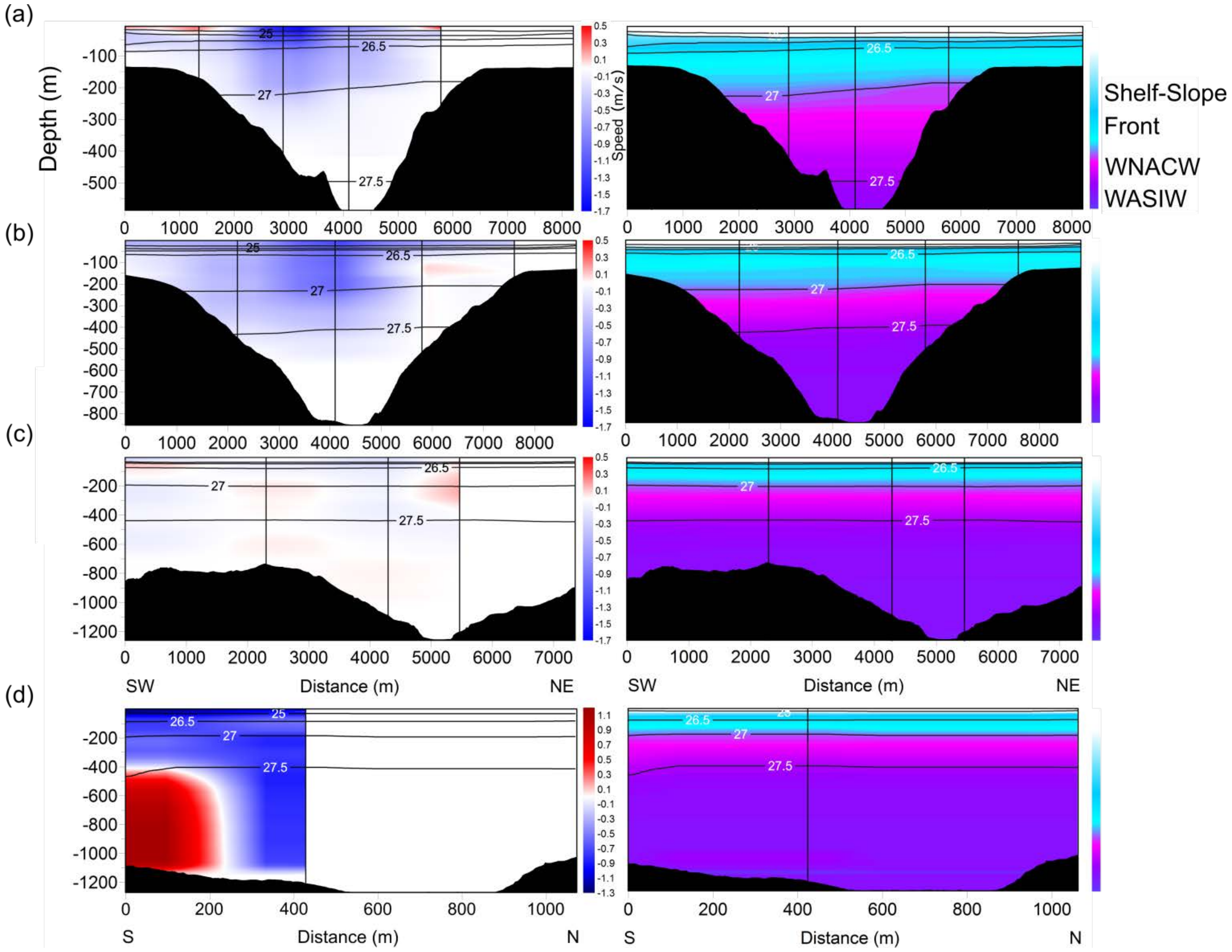
Supplementary Figure 4. Temperature (°C), salinity (psu), fluorescence (RFU), turbidity (FTU), density (σ_θ kg m^{-3}) dissolved oxygen (ml L^{-1}) contour profiles for Baltimore slope. Dark vertical lines represent CTD casts (n = 10).



Supplementary Figure 5. Temperature (°C), salinity (psu), fluorescence (FL mg/m^{-3}), turbidity (NTU), density (σ_θ kg m^{-3}) dissolved oxygen (ml L^{-1}) contour profiles for Norfolk Canyon. Dark vertical lines represent CTD casts (n = 9), inclusive of the extreme margins. * NTU = FTU.



Supplementary Figure 6. Temperature (°C), salinity (psu), fluorescence (FL mg/m^{-3}), turbidity (NTU), density (σ_θ kg m^{-3}) dissolved oxygen (ml L^{-1}) contour profiles for Norfolk slope. Dark vertical lines represent CTD casts (n = 8), inclusive of the extreme margins. * NTU = FTU.



Supplementary Figure 7. Calculated geostrophic velocities (left column) and water mass profiles (right column) for (a) upper, (b) middle and (c) lower Baltimore Canyon cross section CTD transects, and (d) for lower Norfolk Canyon. Positive flow (red) is up canyon, out of the page, and negative flow (blue) is down canyon, out of the page. Potential density (σ_θ kg m^{-3}) anomaly contours are overlaid. WNACW = Western North Atlantic Central Water and WASIW = Western Sub-Arctic Intermediate Water. Dark horizontal lines show the position of CTD casts along transects, including extreme margins in the plot. (No. of casts: Baltimore, upper canyon = 6, middle canyon = 6, lower canyon = 5 and Norfolk lower canyon = 3).

Chapter 3

Macrofaunal community patterns within neighbouring Mid-Atlantic Bight (USA) submarine canyons: The role of depth gradients and location-specific environmental conditions

Robertson CM[1], Demopoulos AWJ[2], Bourque JR[2], Mienis F[3],
Duineveld GCA[3], Lavaleye MSS[3], Koivisto RK[1], Brooke SD[4], Ross SW[5],
Rhode M[5] and Davies AJ[1]

[1] Bangor University, School of Ocean Sciences, Bangor, UK. [2] U.S.G.S. Wetland and Aquatic Research Centre, Gainesville, USA. [3] NIOZ Royal Netherlands Institute for Sea Research and Utrecht University P.O. Box 59, 1790 AB Den Burg, the Netherlands. [4] Florida State University, Coastal and Marine Lab, St Teresa, USA. [5] UNC-Wilmington, Center for Marine Science, Wilmington, USA.

Author contributions

CMR led the design of experiments and writing of the manuscript, to which all authors contributed. CMR, AWJD, JRB, FM, GCAD, MSS, SDB, SWR and MR contributed to shipboard sampling. AWJD and JRB contributed taxa sediment vertical distributions. CMR and RKK processed boxcore samples for macrofauna. CMR conducted taxa identifications. MSS and JRB provided taxonomic advice on various taxa. FM processed biogeochemical data from boxcore samples. CMR conducted all statistical analyses.

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1 Abstract

Submarine canyons are morphologically complex systems, acting as major conduits of organic matter along continental shelves, promoting gradients in food resources, habitat heterogeneity, and areas of sediment resuspension and deposition. This study focusses on the Baltimore and Norfolk canyons, in the western North Atlantic, and investigates how biogeochemical drivers shape the differences between canyon and slope macrofaunal communities. Replicated sediment cores were collected along the main axes (~180-1200 m) of Baltimore and Norfolk canyons and at comparable depths on the adjacent slopes. Cores were sorted and whole community macrofaunal (>300 µm) abundance, diversity and standing stocks were assessed. Coupling family-level community data, with sediment grain-size and biogeochemistry data yielded insight into community dynamics across depth and biogeochemical gradients. Canyon communities were significantly different from slope communities with differences in diversity and, abundance patterns and community assemblages, which were attributed to high levels of organic matter enrichment within canyons. The two canyons hosted different communities that were indicative of environmental disturbance, with bivalves dominating mid-canyon depths in Baltimore Canyon, and deposit-feeding polychaetes in Norfolk Canyon. There was a significant departure from the expected western North Atlantic unimodal diversity-depth curve in both canyons driven by depressed diversity (species richness as well as evenness) between 800-900 m canyon depths. Abundance-biomass curve comparisons confirmed lower canyon communities (800-1180 m) were disturbed as well as upper slope communities (180-555m) on the adjacent slope. In contrast to other studies on canyons, this study did not confirm that macrofauna biomass or average body size was greater in the canyon. Bathymetric zonation, sediment dynamics, organic enrichment, and disturbance events were clear factors that structured the benthic community in both Baltimore and Norfolk canyons. This study has provided further evidence that canyons host distinct ecosystems compared to adjacent areas, enhancing our understanding of how communities can be structured by gradients in the deep ocean.

2 Introduction

Submarine canyon systems have often been described as biodiversity hotspots in the deep ocean (Levin & Sibuet 2012). In the deep sea, many organisms are limited by the availability of surface-derived or advected organic material (Billett et al., 1983; Rex et al., 2006; Rowe et al., 1982; Smith et al., 2008), with densities generally declining with increasing depth and distance from the shore (Houston & Haedrich, 1984; Rex et al., 2006; Rowe et al., 1982). Diversity, in contrast, generally increases from shallower waters, peaks at mid-slope depths (approximately 2000-3000 m) before declining with greater depth (Etter & Grassle, 1992; Rex, 1981; Rex & Etter, 2010). In the western Atlantic, diversity is known to increase from the continental shelf (200 m) to the upper-mid bathyal depths (~1500-2500 m). Quantitative (Etter & Grassle, 1992) studies indicate that diversity-depth patterns in the deep sea are unimodal with a peak at intermediate depths and depressed diversity at upper bathyal and abyssal depths. However, the pattern does not appear to be universal (Rex et al., 1997; Stuart et al., 2003). Where differing patterns occur in other basins, they have been attributed to varied environmental conditions (Cosson-Sarradin et al., 1998). Diversity patterns can be disrupted by several factors that act across different spatial and temporal scales (Levin et al., 2001), with the most significant being habitat heterogeneity (e.g. Levin et al., 2010 and references therein), productivity and its potential biological interactions (Rex 1976; 1981). Variation in species diversity is associated with large-scale variation in sediment grain-size diversity, nutrient input, and productivity as well as oxygen availability, hydrologic conditions, and catastrophic events (Levin et al., 2001).

Canyons are a major source of heterogeneity along continental margins (e.g. Puig et al., 2014), and disrupt expected bathymetric patterns in species' diversity, abundance and benthic productivity, largely through the provision of substrate heterogeneity (Levin et al., 2010), alteration to sediment characteristics (Etter & Grassle, 1992), and elevated organic matter provision (Amaro et al., 2015; De Leo et al., 2010; Martín et al., 2011). Canyons connect the relatively shallow shelf to deep-ocean basins and act as conduits for the rapid transport of sediments and organic matter (Harris & Whiteway, 2011). It is the accumulation of organic material within canyons that appears to substantially enhance organismal abundance and biomass within canyons when compared to adjacent areas (e.g. De Leo et al., 2010; Vetter & Dayton 1998). However, due to their complex and often abrupt topography, canyons also give rise to very unique physical environments (Puig et al., 2014), even within neighbouring canyons that have similar hydrographies such as shared water masses and tidally-driven bottom currents (see Chapter 2). As such, this can lead to canyons maintaining locally distinct faunas in terms of biomass, abundance and diversity (e.g. Cunha et al., 2011; De Leo et al., 2014; Gunton et al., 2015; Ramirez-Llodra et al., 2010a), as well as high levels of variability at different locations within individual canyons (Cunha et al., 2011; Cúrdia et al., 2004; Gage, 1997; Gunton et al., 2015; Rowe & Menzel, 1971).

The Mid-Atlantic Bight (MAB) on the east coast of the U.S. is known for its high organic inputs, derived from the interplay of continental shelf topography with circulation patterns of the South Atlantic Bight, the influence of the Gulf Stream near Cape Hatteras and enhanced surface productivity export to the neighbouring shelf and slope (Csanady & Hamilton, 1988; DeMaster et al., 1994; Rex & Etter, 2010; Schaff et al., 1992; Yoder, 1985). As a result, this region is known to contain some of the highest macrofaunal abundances and biomasses in the deep ocean (Blake & Grassle, 1994; Blake & Hilbig, 1994; Grassle & Maciolek, 1992). However, macrofauna data from submarine canyons in this region is somewhat lacking. The MAB contains 13 major canyons, each with variable shape, size and complexity (Obelcz et al., 2014). Two of the most studied are Baltimore and Norfolk Canyons and were chosen for the present study due to their close proximity to each other and higher occurrence of vulnerable marine ecosystems (VME), namely cold-water coral habitats (Hecker et al., 1980; 1983; Quattrini et al., 2015).

Baltimore and Norfolk Canyons are considered two of the largest shelf-incising canyons in the MAB region (Farre et al., 1983). These two neighbouring canyons are similar in size, length and complexity and are situated 137 km apart, making an excellent area for compelling comparative studies. Baltimore Canyon lies 125 km south-east of Delaware Bay and Norfolk Canyon is situated 115 km east of Chesapeake Bay. Both canyons have considerable steep-sided wall habitat (Obelcz et al., 2014), colonised by cold-water corals (Brooke et al., 2017) and communities of anemones and sea-pens (Hecker et al., 1983). Although high canyon megafauna abundances were reported, no significant differences between slope and canyon assemblages were found (Hecker et al., 1983; Quattrini et al., 2015). Physical observations from the two canyons imply that there are significant differences in current speeds and turbidity layers, whilst containing similar water masses (see Chapter 2). It is likely that these differences will reflect within macrofaunal communities due to differing levels of disturbance within varying locations. For example, Baltimore Canyon contains a temporally persistent turbidity layer that extends from 200-600 m and sometimes down to 800 m, largely driven by tidal currents focused by the canyon axis in winter, early spring and sometimes during other periods of the year (Gardner, 1989). Norfolk Canyon, whilst less studied, demonstrated smaller clouds of suspended sediments that were present at multiple areas of the canyon. The adjacent slopes of the two canyons appear to be largely free of these sediment clouds, although some detached turbid layers have been observed moving away from the adjacent mid-slopes near Baltimore Canyon (Gardner, 1989).

Disturbance and facilitation are predicted to be of particular importance in mediating environmental effects on diversity in the deep sea (Ramirez-Llodra et al., 2010b). Over recent decades, the community structure of benthic macro-invertebrates has been used as a tool for monitoring ecosystem health (Borja & Muxika, 2005; Munari & Mistri, 2008) and for establishing biodiversity hotspots such as canyons (e.g. De Leo et al., 2010). Benthic macro-invertebrates respond rapidly to both anthropogenic and natural disturbance (Pearson & Rosenberg, 1978), making this component of the fauna an ideal model system to better understand how communities respond to change (Jörgensen et al., 2005; Rice, 2000). One easily interpreted method for detecting change in benthic communities is the comparative assessment of k-dominance curves (Clarke et al., 2006; Magurran & McGill, 2011; Rice, 2000). Community rank abundance distributions extract universal features (e.g. the species abundance or biomass) of community structure, which are not explicitly a function of the specific taxa present but may be related to levels of environmental disturbance or biological stress across gradients (Warwick et al., 2008). The method has been applied in the detection of community shifts due to environmental disturbance and stressors, particularly organic enrichment or pollution (Warwick, 1986; Warwick et al., 1990; Warwick & Clarke, 1994; 1998), but more recently in assessing fishery impacts (Yemane et al., 2005) and detecting disturbance in deep-sea habitats (Cunha et al., 2013; Ramirez-Llodra et al., 2010a).

The present study presents the first insight into whole community macrofauna diversity and structure along the axes of Baltimore and Norfolk canyons, compared to the respective adjacent slopes. The benthic macrofaunal communities and the principal environmental drivers were described during a multidisciplinary study that bridged ecology, physics and geology. Four hypotheses were tested: i) Canyon macrofaunal community assemblages differ in abundance, diversity, biomass and community composition from those found on adjacent slopes. ii) Canyon axis and slope macrofauna communities are structured by the same set and relative ranking of environmental parameters across the Baltimore and Norfolk areas. iii) Specific signatures of disturbance to macrofauna communities are more prevalent within canyons than on slopes. iv) Slope communities exhibit the expected unimodal relationship in diversity with depth expected for deep-sea environments, but canyons will not due to depth-specific disturbance.

3 Materials and methods

3.1 Study location

Baltimore and Norfolk canyons are situated approximately 125 km off the coasts of Delaware and Virginia, on the eastern coast of the United States and are two of the four largest submarine canyons on the Mid-Atlantic Bight (Figure 1a). Baltimore Canyon has a sinuous thalweg of approximately 25 km in length, which is orientated in a NE-SW direction to the shelf break. The upper canyon has a width of 3 km (~ 100 m) increasing to 8 km in the lower canyon reaches, at 1500 m water depth (Figure 1b). Norfolk Canyon lies 137 km south of Baltimore Canyon, oriented in W-E direction orthogonal to the shelf (Figure 1c). The two canyons are similar in size and width although Norfolk is less sinuous in the upper reaches. The canyon is 2.5 km wide in the upper canyon widening to 6 km in the lower reaches at 1500 m water depth. The geology of both canyons has been reviewed by Obelcz et al. (2014).

3.2 Sampling design

Samples of sediment for macrofauna analysis were collected at Baltimore Canyon, (NOAA ship *Nancy Foster*) in August 2012 (Table 1), followed by sampling in Norfolk Canyon collected in May 2013 (NOAA Ship *Ronald H. Brown*). The sampling campaign followed a replicated design along two transects from the shelf break (~200 m) to the continental rise (~1200 m); one tracing the thalweg of the canyon and the other in similar depths along the adjacent slope (Figure 1b and c). Four sampling depths were chosen along each transect. Replicate boxcores were taken using a 30 cm Ø (0.07 m^2) NIOZ boxcorer, equipped with a trip valve to prevent flushing of the sample during ascent. Three replicates per site (12 from each canyon, 12 from each adjacent slope) were used for macrofauna community analysis (Table 1). During the Norfolk campaign, sedimentological and biogeochemical variables were determined from a sub-core taken from one of the 3 fauna replicates due to time constraints, whereas a fourth replicate boxcore was used for sedimentological and biogeochemical characterisation during the Baltimore campaign.

3.3 Sample processing

Recovered boxcores were initially quality controlled aboard ship by assessing the level of disturbance on the sediment surface to ensure the intact vertical distribution of sediment layers. All boxcore samples were photographed (Supplementary Material [SM] Figures 1-4) for reference and used to verify surface area calculations. Samples that showed signs of leakage, over penetration or sediment slumping were discarded. Boxcores allocated to macrofaunal analysis were processed by the following methods. 1) A polycarbonate push-core (6.35 cm Ø) was inserted into the top 15 cm sediment depth to assess the vertical depth distribution of macrofauna. These sub-cores were sectioned into 0-2, 2-5, and 5-10 cm layers by extrusion and preserved in a 10 % buffered formalin solution. 2) An additional push core (6.35cm Ø) was removed for isotopic analyses and although not presented here (see Demopoulos et al., 2017), the surface of the core was subtracted from total surface area and macrofauna density calculations in the present study. 3) Overlying water from the boxcore was drained over a 300 µm mesh and added to the sample during washing. 4) The top 15 cm of sediment within the boxcore was removed for whole macrofauna community analysis. The sample was resuspended in filtered (0.2 µm) surface seawater in a 20 L bucket, washed over a sieve of 300 µm mesh size, using a gentle shower hose to avoid damage of macrofauna. Samples were preserved and stored in 10 % buffered formalin solution.

The boxcore allocated for sedimentological analysis was processed as follows: 1) Full length boxcore sub-cores for sediment grain-size analysis were collected by insertion of a PVC liner (20 cm Ø) to the base of the core, capped and stored at ambient temperature. 2) Smaller acrylic sub-cores (6 cm Ø) were taken for biogeochemical analyses (i.e. organic carbon, nitrogen, stable isotopes and chlorophyll *a*), and were collected by inserting into the boxcore, sliced into 1 cm sections and stored at -20 °C.

3.4 Laboratory analysis

Macrofauna samples were stained with Rose Bengal prior to rinsing over a 300 µm sieve using freshwater under a fume hood. Macrofauna was sorted from the sediment, enumerated using stereo- microscopy and identified to family level (not possible for all taxa), aided by compound-microscopy where required. Overall 91 taxonomic resources were used in the whole community identifications (See SM Table 1). In certain cases, particularly for some genera of Polychaeta, additional histological stains (Methylene-blue and Methyl green) were used to aid identification. Following sorting, specimens were stored in 70 % Industrial Methylated Spirits. Family level wet weights were determined by the blotting excess preservative fluids and weighing using a Satorius Secura analytical balance accurate to 0.0001 g. Tube-dwelling genera were removed from their tubes prior to weighing, although in the case of very small or fragile species (e.g. Oweniidae) this was not always practical or possible. For analysis, biomass and individual weight data were standardised to preserved wet weight (g Wwt m^{-2}) and individual preserved wet weight (g ind.$^{-1}$ m^{-2}) per unit area per taxa.

All samples for sedimentological and biogeochemical analysis were freeze dried and weighed. Grain-size measurements (0-10 cm) were undertaken (bulk fraction) using a Beckman Coulter LS 12 320 particle size analyser, that used laser diffraction and optical diffraction to determine the particle size (range from 0-2000 µm). Biogeochemistry sediment slices from the cores were analysed for stable carbon and nitrogen isotopes, percent organic carbon and nitrogen, and ^{210}Pb in the top 5 cm, and for phytopigments in the surface slice (0-1 cm) using High-Performance Liquid Chromatography and Mass Spectrometry (for a detailed description of the methods, see Ross et al., 2017). Intact chlorophyll *a* concentration derived from the phytopigment analysis were taken as a proxy for fresh phytodetrital biomass.

3.5 Data analysis

Univariate and multivariate statistics were performed using PRIMER (PRIMER_E Ltd) statistical software version 6.0 with the PERMANOVA+ add-on (Anderson et al., 2008; Clarke & Gorley, 2006).

3.5.1 Abundance and biodiversity metrics

Macrofauna diversity was examined using species richness (at the family level), Shannon-Wiener diversity index ($H'log_e$), Pielou's evenness (J') and ES(n) rarefaction analysis based on untransformed abundance data using the DIVERSE routine (Clarke & Gorley, 2006). Data was square-root transformed and used to generate Bray-Curtis similarity resemblance matrices. Differences in mean species richness, macrofaunal density (ind. m^{-2}), biomass (g Wwt m^{-2}), individual weight (g ind.$^{-1}$ m^{-2}) and evenness (Pielou's J') were assessed using a three-way crossed univariate and distance-based PERMANOVA (PERmutational Multivariate ANalysis Of Variance; McArdle & Anderson, 2001), and pairwise comparisons. The 3-factor model used the following *a priori* defined factors habitat (Canyon vs Slope, *ha*), site (Baltimore vs Norfolk, *si*), and depth levels 1-4 (1: 180-190 m, 2: 550-555m, 3: 800-900 m, 4: 1110-1180 m). Because PERMANOVA is sensitive to differences in multivariate dispersion among groups, the PERMDISP routine was used to test for homogeneity of dispersion when significant factor effects were found (Anderson et al., 2008). Where univariate variables failed homogeneity of variance tests, (PERMDISP $p < 0.05$), a weighted dispersion transformation (Clarke et al., 2006) was performed, followed if necessary, by removal of extreme outliers (after nMDS visual inspection). Even after transformation, diversity (Shannon-Wiener diversity index *H'*) did not meet the assumptions of PERMANOVA, and was omitted from analysis. To obtain homogeneity of dispersions (PERMDISP), after weighted dispersion transformation, an outlier within species richness and evenness data was also removed from analysis (Norfolk 800 m; RB-13-060).

3.5.2 Community assemblages

Macrofauna community structure was assessed by examining the overall proportion (% density m^2) of higher level taxa i.e. Polychaeta, Oligochaeta, Crustacea, Mollusca, and Other taxa. Other taxa included Anthozoa, Hydrozoa, Sipuncula, Priapulida, Nemertea, Halacaridae, Platyhelminthes, Holothuroidea, Ophiuroidea, Enteropneusta and Xenophyophoroidea. Differences in community assemblages were assessed by PERMANOVA, as a function of three *a priori* factors (crossed and fixed levels; as described in section 2.5.1) with PERMDISP tests, using square-root transformed data (density m^2) and Bray-Curtis similarities. Pairwise comparisons followed where appropriate. A Similarity of Percentages analysis (SIMPER) was used to identify the taxa most responsible (≤ 30 % total) for discriminating between and within canyon and slope communities across the depth gradient.

3.5.3 Environmental drivers

Prior to analysis of biogeochemical and grain-size parameters, data were assessed for collinearity using Draftsman plot and Spearman's rank correlation matrices (Primer 6; Clarke & Gorley, 2006). Highly correlated environmental parameters ($R^2 > 0.95$) where removed and where necessary, data were transformed ($\log x$+0.1) and normalised (Anderson et al., 2008). The influence of environmental drivers on canyon and slope macrofaunal communities was then assessed via DISTLM (DISTance-based Linear Model) multiple regression analyses. DISTLM performs nominal tests of each variable's explanatory power on the community assemblage, building a multivariate statistical model for all possible combinations of predictor variables (See SM Table 2 for a summary of environmental variables used in the explanatory model). Models were run selecting Akaike's Information Criterion (AICc) and the *BEST* model procedure. DISTLM results were visualised in multivariate space using

Principal Component Ordination (PCO) plots, which displayed the significant linear regressions for the environmental variables as eigenvectors.

3.5.4 Community disturbance

To investigate the degree of macrofaunal community disturbance, abundance (ind. m^{-2}) and biomass (g Wwt m^{-2}) data, averaged for each depth along canyon and adjacent slope transects were used to generate abundance-biomass comparison (ABC) curves, where ranked species *k*-dominance curves of abundance and biomass are plotted against the percentage cumulative dominance. ABC curves were developed as a method for assessing the status of disturbed populations, without the need for reference to temporal or spatial series of control samples (Lambshead et al., 1983; Warwick, 1986). The ABC procedure generates an associated *W*-statistic as a measure of differentiation between two *k*-dominance curves ranging from -1, severely degraded and 1, pristine habitats (Clarke, 1990). The shape of curve and *W* can be interpreted as an indication of benthic community disturbance when comparing similar communities, based on the degree of community shift to higher species dominance with increasing levels of environmental disturbance (Pearson & Rosenberg 1978; Ramirez-Llodra et al., 2010a). The associated ABC Warwick statistics (*W*) were calculated and compared via the same three-way crossed PERMANOVA tests (*habitat* x *site* x *depth*). The *W*-statistic as a measure of macrofaunal community disturbance was also included in the environmental DISTLM model.

4 Results

4.1 Sedimentological and biogeochemical variability

Sediment grain-size was negatively correlated with depth (sand, $R^2 = -0.82$, $p = 0.014$; silt & clay $R^2 = 0.81$, $p = 0.014$) in all transects (Figure 2a and 2b). Grain-size patterns did differ slightly between canyons and adjacent slopes, with Baltimore Canyon exhibiting a sharp increase in the proportions of sand at mid-canyon depths (550 m), in contrast, Norfolk Canyon contained a greater proportion of clay and silt at that depth (Figure 2a-b, SM Table 2). Organic carbon and nitrogen were positively correlated with the proportion of silt and clay ($R^2 = 0.81$, $p = 0.015$, $R^2 = 0.77$, $p = 0.025$ respectively). Both canyons were generally more enriched in carbon, nitrogen and chlorophyll *a* than their adjacent slopes across the depth gradient (Figure 2c-e). Norfolk Canyon and slope were the most enriched compared to Baltimore Canyon and slope. In both canyons, chlorophyll *a* peaked at mid canyon depths (550-555 m; Figure 2c), and slopes generally contained less chlorophyll *a*. In contrast, percent carbon and percent nitrogen increased along the depth gradient, with the highest values found at deeper canyon depths (> 800 m, Figure 2d-e). There was increased $\delta^{13}C$ depletion at intermediate water depths (550-555m) across all canyons and slopes, with the upper reaches of Baltimore Canyon having the lowest. Baltimore Canyon (550 m) and the adjacent slope (1180 m) had the highest $\delta^{15}N$ values, but Norfolk Canyon and slope was generally enriched in $\delta^{15}N$ throughout (SM Table 2).

4.2 Biodiversity

From 2.81 m^2 of seabed sediment surface area analysed to a depth of 15 cm, a total of 40,208 individuals were extracted, representing 162 taxa across both canyon and slope areas (for full list of taxa see SM Table 3). The canyons yielded a greater number of individuals (23,776) and taxa (142) than adjacent slopes (16,442 individuals from 138 taxa). Polychaetes were the most diverse taxonomic group (51 taxa), followed by bivalves (28), and amphipods (20). Of the total number of taxa recorded, 25 were found exclusively in the canyon and 23 were found exclusively in slope habitats. The majority of canyon-only taxa were bivalves, whereas slope-only taxa were mostly comprised of peracarid crustaceans, gastropod molluscs and isopods. Both study sites and habitats exhibited differences in the occurrence of rare taxa (singleton taxa, represented by a single individual; doubleton taxa, represented by two individuals). Between the two study areas, Baltimore (canyon and slope combined) had higher percentages of singleton and doubleton taxa (11 % and 8.5 %, respectively) (compared to Norfolk (7.9 % and 7.9 % respectively). Canyons (Baltimore and Norfolk combined) exhibited higher occurrences of singleton taxa (15.2 %) and doubleton taxa (7.9 %) compared to slopes (7.9 % and 7.3 % respectively). For a summary of various diversity metrics at each station, see SM Table 4.

4.2.1 Species richness

Species richness generally decreased along the depth gradient, with significant differences identified across sites, habitats and depths (Figure 3a; Table 2 *ha* x *si* x *de* term). The three-way interaction (see pairwise tests in SM Table 5) indicated a complex pattern of differences. For example, species richness at Baltimore Canyon was significantly lower than the adjacent slope only at 900 m, in contrast, no significant differences were detected between the Norfolk Canyon or slope. Baltimore Canyon had the most distinct depth gradient, with all depths being significantly different from each other with the exception of 550 and 900 m. The two slope habitats expressed some depth-specific differences. Baltimore slope followed the canyon negative trend in richness with depth, although not significantly at intermediate depth communities (550 and 900 m), ending with lowest community richness values at the deepest slope habitats. The Norfolk slope followed the same pattern as Baltimore slope, although only the shallowest slope habitats were richer than 555 m habitats.

4.2.2 Rarefaction curves

Family-level rarefaction curves (SM Figure 5) showed that estimated slope diversity appeared to exceed canyon diversity (indicated by the steeper initial curve compared to canyon habitats). Of the two curves for canyons and slopes (SM Figure 5c), the slope did not reach an asymptote, suggesting further sampling may be required to fully assess the diversity on the slope. The rarefaction curves also indicated within canyons, that shallow depths (180-190 m) contributed the most to diversity followed by 900 m depth. The 550 m depth had the steepest curve, suggesting diversity was the least assessed at this depth, despite relatively high diversity and evenness (Figure 3b and 3c). On the slope habitats 180 m and 900 m depths were the greatest contributors to diversity, although 1180 m had the steepest rising curve (SM Figure 5c).

4.2.3 Diversity and evenness

Baltimore Canyon and slope appeared to be more diverse (*H'*) than Norfolk (Figure 3b, SM Table 4). The general pattern suggested, particularly in Baltimore, that shallower sites (180 and 550 m) were more diverse in canyons than on slopes. In contrast, Norfolk slopes were more diverse in the deeper sites than the canyon; a pattern shared at the 900 m Baltimore Canyon station (Figure 3b, SM Table 4). Statistical analysis was not possible on diversity data due to failing to meet the assumptions of the PERMANOVA test. Species evenness was found to significantly differ between habitat, sites and depths (Figure 3c, Table 2 *ha* x *si* x *de* term), but there were no significant differences between the two canyons or the adjacent slopes (see pairwise tests in SM Table 5). Baltimore Canyon had significantly greater evenness than the adjacent slope at 180 m, but was lower at 900 m. Norfolk Canyon, in contrast, showed no significant differences when compared with the adjacent slope. Only one pair of depths demonstrated a significantly different evenness in Norfolk Canyon (190 and 800 m), where diversity was highest at 800 m. Baltimore Canyon, however, was more variable, with 900 m being significantly different to all other depths, with greatest evenness in the deepest site, and lowest at the shallow and intermediate depths (SM Table 5).

4.3 Standing stock

4.3.1 Density

Norfolk Canyon and slopes had the greatest mean densities of macrofauna (SM Table 4, 18,758 ± 4,437 and 17,515 ± 2,400 ind. m^{-2} respectively), compared to Baltimore Canyon and slope (SM Table 4, 13,399 ± 792 and 7,126 ± 1,242 ind. m^{-2} respectively). Densities significantly decreased on slopes with the highest at the shallow stations (180-190 m; Table 2, SM Table 5 *ha x de* term), canyons in contrast had a bimodal pattern, with the 180-190 m depths having similar densities to the 800-900 m station, both of which were higher than the other depths in the study (Figure 3d). When compared with slopes, canyons significantly decreased in density at 550-555 m, with a significant increase at 800-900 m (Figure 3d, SM Table 5 *ha x de* term). Lower macrofauna densities were generally found both at lower canyons and slopes (1110-1180 m), with no significant difference between the two habitats. Norfolk Canyon had significantly higher densities at 550 m compared to Baltimore Canyon at the same depth (SM Table 5 *si* x *de* term).

4.3.2 Biomass

Following density, Norfolk Canyon and slopes had a mean macrofaunal biomass of 19.2 ± 9.1 and 38.7 ± 23.7 g Wwt m^{-2} respectively (SM Table 4), whereas Baltimore Canyon and slope were lower 16.2 ± 4.7 and 11.5 ± 5.3 g Wwt m^{-2} respectively (SM Table 4), but there were no significant differences between canyons, slopes or the Norfolk and Baltimore areas (Table 2). Biomass did significantly decrease with depth (Table 2 and SM Table 5). Two peaks that contrasted against a generally decreasing biomass with depth were attributed to the presence of single large-bodied individuals of Sipunculidae (*Sipunculus norvegicus;* Peanut worm, 3.5 g) and Edwardsiidae (*Edwardsia spp.* Burrowing anemone, 10.0 g) which increased biomass on the slopes of Baltimore (1180 m) and Norfolk (800 m) (Figure 3e, SM Figure 6).

4.3.3 Individual weight

Mean individual weight (g ind.$^{-1}$ m^{-2}) revealed significant differences with depth (Table 2, Figure 3f), but not between sites (Norfolk or Baltimore areas) or habitats (canyons or slopes). Significantly larger bodied macrofauna were found at 550-555m compared to 800-900m (SM Table 5) in canyons. Slope habitats in general, were inhabited by larger-sized macrofauna individuals across the whole depth range, with the smallest-bodied macrofauna occurring in the Baltimore Canyon and slope communities at 900 m.

4.4 Community composition

Across the Baltimore study areas, the majority of macrofauna were Polychaeta (46 %) followed by Mollusca (31 %) and Crustacea (12 %). The Norfolk site had higher proportions of Polychaeta (67 %) followed by Mollusca (16 %) and Crustacea (6 %). The most notable change in community composition was in Baltimore Canyon (900 m) were large proportions of Mollusca (74 %), namely bivalves (Yoldiellinae and Thyasiridae) which contributed greatly to differences between canyon and slope habitats. Baltimore Canyon communities showed higher proportions of Mollusca (36 %) across depth groups compared to the slope (27 %). Additionally, Baltimore slope habitats showed higher proportions of Crustacea and Oligochaeta (17 % and 8 %). Examining the proportions of phyla biomass in canyon communities (SM Figure 6) revealed that upper canyon communities were dominated, in both canyons by Mollusca (specifically Lucinidae, *Lucinoma foliosa*) and Other phyla (Actiniaria sp., specifically Edwardsiidae and Ophiuroidea, namely Amphiuridae sp.) despite Polychaeta and Mollusca being most numerous (SM Figure 6). While polychaete abundance decreased with depth in both canyons, polychaete biomass remained constant in Baltimore Canyon. In Norfolk Canyon, polychaete biomass varied with depth, increasing at 800 m. On the adjacent slopes, polychaete biomass decreased with depth, although slope habitats showed largest biomass contributions from Other Phyla in both instances, driven by the singular occurrences of large-bodied Sipunculidae on the Baltimore slope at 1180 m and Edwardsiidae sp. on the Norfolk slope at 800 m.

The vertical distribution of macrofauna (maximum 10 cm sediment depth) revealed that more than 50 % of macrofauna was located in the uppermost 2 cm in both canyons and slopes (SM Figure 7). Generally, both canyons and slopes exhibited similar vertical distribution patterns, however, the most distinct change was evident in Baltimore Canyon 900 m sediment where 85% of the macrofauna found was located in the upper 0-2 cm of the sediment.

4.5 Community structure

Multivariate PERMANOVA analysis revealed that communities differed significantly between habitats, study sites and across the depth gradient (Table 3 *ha* x *si* x *de* term). Baltimore Canyon communities differed significantly from Norfolk Canyon at each depth (SM Table 6 *ha* x *si* x *de* term). In contrast, the slopes differed only in the upper communities at 180-190 m and 550-555 m, whilst lower slope community structure was similar (Figure 4). Canyon communities were separated from slope assemblages along differing trajectories (Figure 4, indicated by solid and dashed lines), which was most distinct in the Norfolk study site. Baltimore Canyon communities were divided into two groups (Figure 4a), indicating strongly dissimilar community assemblages between the upper (180 m and 550 m) and lower (900 m and 1180 m) canyon. The upper canyon communities (180 m) and mid-canyon (550 m) were the most distinct, whilst lower canyon communities (990-1180 m) was more similar to lower slope communities.

Community similarity across the depth gradient, (between replicates), was higher in Baltimore Canyon than in Norfolk Canyon, ranging from 81-68 % and 59-48 % respectively. The larger similarities within canyon habitats suggest lower habitat heterogeneity and community patchiness in the canyons in contrast to slope habitats, which, in general exhibited lower community similarities across the depth gradient (Table 4). In Baltimore, two bivalve Families were found to dominate the change in macrofauna community structure between canyon and slope communities, namely Thyasiridae, and Yoldiellinae, both of which, were found in high abundances (7,322 ± 333 and 3,132 ± 157 ind. m^{-2} respectively) at Baltimore Canyon 900 m (SM Figure 6a). Similarly, Yoldiellinae ranked as third most important taxon separating Norfolk Canyon and slope communities, preceded firstly by Capitellidae and Cirratulidae. Examinations of the taxa contributing to community differences suggest some depth derived zonation pattern exists in canyon and slope community structure. This was most clear in Baltimore Canyon, where taxa driving the macrofauna assemblage turn-over with increasing depth (180-1180 m), were the bivalves Families Lucinidae, Yoldiellinae and Thyasiridae, and the polychaete family Spionidae. In Norfolk Canyon, the 800 m assemblages were distinguished from the other canyon communities by two taxa occurring in high mean abundances, namely the polychaete family Captellidae (12,812 ± 5,188 ind. m^{-2}) and the bivalve Yoldiellinae (2,329 ± 662 ind. m^{-2}), meaning that the two canyons can be differentiated from lower slope assemblages by these four highly dominant taxa. The canyons communities were 59 % dissimilar to slope communities (Table 4b) and the most important discriminating taxa were Dentalidae, Capitellidae, Ophiuroidea and Nephtyidae, all of which occurred more abundantly in canyons. Slope communities were less dissimilar (52 %) and distinguished by a high contribution from the polychaete taxa Cirratulidae, followed by Oligocheata and Lumbrineridae.

4.6 Environmental drivers of community structure

DISTLM analysis revealed sediment organic enrichment, grain-size, disturbance and depth all had significant effects on the observed community patterns across both sites and habitats (Tables 5a and 6a). Depth was the most explanatory variable (17.9 and 20.8 %) followed by the proportion of sand (17.7 % and 20.0 %). In the Baltimore site, $\delta^{15}N$ alone explained 17.2 % of the community pattern followed by the percentages of carbon (11.8 %) and chlorophyll *a* (11.3 %). For the Norfolk study site, stronger relationships where evident, with percent carbon explaining 18.2 % of variation, followed by percent nitrogen (18 %) and chlorophyll *a* (14.4 %). At both sites, community disturbance (*W*-Statistic) explained 11.7 % and 10.4 % of variation in Baltimore and Norfolk respectively. The most explanatory multivariate linear regression was for the Baltimore site, which explained 78 % of variation (Table 5b). In contrast, the most explanatory model for Norfolk, explained 45 % of variation. Both sites showed strong relationships between macrofauna community structure and depth, sediment grain-size and sediment organic enrichment (Figure 4).

4.7 Community disturbance

Community disturbance analyses (assessed by ABC curves and the *W*-Statistic) revealed considerable species dominance within macrofauna assemblages, which was consistent across both study sites (Figure 5). Disturbance was detected in the deeper reaches of the canyons (800-1180 m), as well as in uppermost and mid-slope communities (180-555m) (Figure 5, highlighted by orange and red circles). PERMANOVA results on the community disturbance measure (*W*-Statistic) confirmed significant disturbance between canyons and slopes and depth (Table 2). Pairwise tests revealed increased disturbance occurred within the canyons between mid-canyon (550-555m) and lower canyon depths (1110-1180 m), while for slope habitats community disturbance was significantly higher in the upper shelf break and decreased with depth (SM Table 5 *ha x de* term).

5 Discussion

There are several benthic studies that have examined the macrofaunal abundance and diversity along the U.S. East Coast continental margin and rise (Blake & Grassle, 1994; Blake & Hilbig, 1994; Hilbig & Blake, 1991; Maciolek et al., 1987). This study represents the first canyon-specific macrofaunal study in the MAB and is one of few studies that compare two neighbouring canyon systems with their respective adjacent slopes (Cunha et al., 2011; De Leo et al., 2014; Paterson et al., 2011; Vetter & Dayton, 1998). There were differences between the two canyon and slope assemblages, which were structured by strong depth, sediment grain-size and organic enrichment gradients.

5.1 Diversity and productivity in canyons and on slopes

This study found that the long-established patterns of species richness, diversity and evenness with depth held only in slope habitats, and not within the two studied canyons. Global diversity-depth (i.e. species richness) relationships are unimodal, reflecting the well-known macroecological relationship between diversity and productivity across large scales (Figure 6; Kadmon & Benjamini, 2006; Leduc et al., 2012; McClain et al., 2009b; McClain & Schlacher, 2015). Their most typical feature is that diversity is low in shallower waters, high in the narrow bathyal zone (~2000 m) and decreases towards the abyss (Etter & Grassle, 1992; Levin et al., 2001; Rex et al., 1997; Sanders, 1968). Slope habitats agreed with the descending limb of the diversity-productivity curve (Etter & Grassle, 1992), demonstrating decreasing macrofaunal densities and increasing diversity across productivity and depth gradients (Figure 6).

There was a significant departure from the diversity-depth unimodal curve in the two canyons which can be attributed to depressed diversity, richness and evenness at 800-900 m depth. These decreases corresponded with shifts in sediment composition to fine silts and clays and increased sediment organic enrichment, resulting in a concave up as opposed to the usual concave down unimodal curve for the canyons (Figure 6a). This study represents only a small-scale example given the limited range of depths sampled but detected substantial shifts in diversity patterns due to localised canyon disturbance. Theoretically, a higher incidence of disturbance shifts the peak of the diversity-depth curve towards higher levels of productivity (Kondoh, 2001; Worm et al., 2002). In this case, supressed species richness at 800-900 m shifted the diversity minimum of the diversity-depth curve to the right, as organic enrichment increased in the canyons (Figure 6a). Although there is widespread acceptance of the diversity-depth model in deep-sea ecology, the underlying driving mechanisms remain uncertain (Rex & Etter, 2010). Depressed species richness and evenness under circumstances of unusually high organic carbon flux to the seafloor and elevated benthic standing stocks appears to be a general phenomenon in deep-sea communities (Rex & Etter, 2010). Recent studies have shown that productivity, specifically POC flux, is the principle energy source promoting high diversity in deep-sea habitats (Woolley et al., 2016). The depth at which maximum diversity occurs may depend on the taxa considered, species' ranges and dispersion patterns, and the spatial scales covered by different sampling gears (Stuart et al., 2003).

5.2 Macrofauna density in canyons and on slopes

The pattern of standing stock with depth in the western North Atlantic is well-established, whereby biomass and abundance show an exponential decline from the shelf-break to abyssal depths (Figure 6b, Rex and Etter, 2010). Whilst few canyon-specific studies exist for the western North Atlantic, earlier continental margin studies provide a general context for comparisons with the present study (Blake et al., 1986; 1987; Blake & Grassle, 1994; Blake & Hilbig, 1994; Maciolek et al., 1987). Most studies have reported considerable variation in macrofaunal densities on the shelf, especially between shelf break depths and the continental slope (500-1200 m). Slope densities in the present study were within the range previously reported for the continental margin off the northeast USA (Blake et al., 1986; 1987; Blake & Grassle, 1994; Blake & Hilbig, 1994; Houston & Haedrich, 1984; Maciolek et al., 1987). In contrast, canyon densities were higher than estimates for the more northerly MAB, Hudson Canyon (1,880-9,280 ind. m^{-2}, Rowe et al., 1982) and were more than ten times higher than reports for eastern North Atlantic canyons on the Portuguese margin (474-583 ind. m^{-2}, Cunha et al., 2011, who analysed the > 500 µm fraction, whereas this study analysed the > 300 µm fraction) at comparable depths.

Slope macrofauna density decreased steadily with depth, a typical global pattern for upper continental slopes (Figure 6b) (Levin and Gooday, 2003; Rex and Etter, 2010). However, canyon densities were depressed at 550-555 m followed by a sharp rise at 800-900 m (Figure 3), forming a distinct bimodal density distribution along the canyon axis (Figure 6b). These peaks in macrofaunal density likely represent bathymetric preferences of different species. For example, in Baltimore canyon, the high density zones were dominated by the bivalves

Lucinidae and Periplomatidae at the canyon heads and the bivalves Yoldiellinae and Thyasiridae in the secondary peak (800-900 m), reflecting depth range preferences for these Families. The bimodal density distribution in canyon macrofauna has not been recorded previously in the MAB. Rowe et al. (1982) reported that highest macrofaunal densities for Hudson Canyon were limited to only in upper canyon depths (< 570 m). In the study south of New England, Hecker (1990) demonstrated a bimodal distribution in megafauna, specifically burrowing cerianthid anemones, with a sparse population at ~1200 m and an abundant population at ~1900 m.

5.3 Biomass and body size in Canyons and on slopes

Whilst canyons have been shown to maintain enhanced biomass compared to the slope habitats, e.g. for canyon mega-benthic invertebrates (De Leo et al., 2010), macrofauna communities (Cunha et al., 2011; Escobar Briones et al., 2008; Vetter & Dayton, 1998) and meiofauna (Ingels et al., 2009; Ramalho et al., 2014), in the present study biomass in the canyons did not differ significantly from the adjacent slope. Biomass estimates were within the range of previously reported estimates from the western North Atlantic continental margin (1.2-12.2 g Wwt m^{-2}, Rowe et al., 1974) and Hudson Canyon (10.4- 46.2 g Wwt m^{-2}, Rowe et al., 1982), although biomass from upper canyon depths (180-190 m) were lower (30.28 g Wwt m^{-2}) than reported for similar depths in Hudson Canyon (46.2 g Wwt m^{-2}, Rowe et al., 1982). In this study, canyon areas that were organically enriched contained macrofauna that had smaller body sizes than slope habitats, likely reflecting communities dominated by small opportunistic species (Pearson & Rosenberg, 1978). Body size overall, decreased with depth, in agreement with current views (Rex et al., 2006; Wei et al., 2010).

5.4 Macrofauna communities

Shifts in community composition (beta diversity) were evident across the depth gradient, reflecting the bathymetric preferences and niche partitioning of macrofaunal communities (Carney, 2005); e.g. Lucinidae (*Lucinoma foliosa*) in the upper canyons and slopes were restricted to upper shelf depths, while Thyasiridae and Yoldiellinae prefer deeper slope habitats (< 200 m and >500 m respectively, Oliver et al., 2016). Both sites were numerically dominated by polychaeta, followed by bivalves and crustaceans, with the exception of the bimodal peak in Baltimore Canyon, which saw an increase in bivalves. Key community members driving differences between the canyons and slopes were two dominant sub-surface detritivore bivalve families, Thyasiridae and Yoldiellinae. Thyasirid bivalves are burrowing species that favour organic-rich silts and clays (Duperron et al., 2013), and are known to contain chemoautotrophic endosymbionts (Dando, 1991; Dando et al., 1994). Yoldiellinae are also often associated with organically-enriched fine-grained sediments (Grassle and Morse-Porteous, 1987; Quiroga et al., 2012; Reed et al., 2014). In addition, two deposit-feeding opportunistic polychaete families distinguished canyon communities (particularly in Norfolk Canyon) from other slope habitats, namely Capitellidae and Cirratulidae. Both are well established indicators of disturbance and organic input (Pearson & Rosenberg, 1978), and likely indicate different levels of disturbance between the two canyon systems.

Overall, the enriched canyon habitats showed higher proportions of the community residing in the upper two centimetres of the sediment, while slope habitats showed the majority of the community resided in the upper 5 cm. Deeper penetration of macrofauna is likely a consequence of larger grain-sizes and therefore higher porosity, allowing a deepening of the community due to greater oxygenation. Interestingly, the 190 m depth within Norfolk Canyon had a higher proportion within 2-5 cm, possibly due to the fact that this site had increased sediment porosity (highest proportions of sand), coupled with high concentrations of chlorophyll *a* of all the shallower stations. The 900 m depth in Baltimore Canyon recorded the highest proportion of macrofauna in the 0-2 cm layer, due to the large densities of partially chemosynthetic bivalve Thyasiridae and sub-surface deposit-feeding Yoldiellinae.

5.5 Environmental drivers of community patterns

There were clear differences in the conditions at the two canyon and slopes, suggesting the presence of canyon-specific environmental drivers. The sediment grain-sizes across canyons and slopes generally decreased with increasing depth, as expected in continental margin deep sea habitats (Gardner et al., 1996; Karl, 2006; Valentine et al., 1980). However, at depths of 550 m in Baltimore Canyon and 800 m in Norfolk Canyon, there were higher proportions of sand, indicative of higher current speeds and sediment winnowing (Bouma, 1965; Vetter & Dayton, 1998; see Chapter 2). Such variation in the distribution of sediments is known to influence organic content and may enable resource partitioning promoting higher faunal diversity (Levin et al., 2001).

Organic matter availability decreases with increasing distance from coastal regions, and recently it has been suggested that patterns in deep-sea species can be predicted by estimates of organic carbon flux to the seafloor (Woolley et al., 2016). In areas where organic carbon is enhanced through biotic and abiotic factors, elevated standing stocks are common. Submarine canyons have become prime examples of this, as topography, bottom currents (Gardner, 1989; Palanques et al., 2006a), upwelling (Allen & Hickey, 2010) and deposition of particulate organic matter (de Stigter et al., 2011; Martín et al., 2006) are important mechanisms that concentrate food in canyons (Cunha et al., 2011; Cúrdia et al., 2004; de Stigter et al., 2007; Kiriakoulakis et al., 2011; Vetter & Dayton, 1998). This study found enrichment to be variable along the canyon depth gradient, was higher within canyons than adjacent slopes and that Norfolk Canyon was most enriched, by almost two-fold, when compared to Baltimore. Whilst such differences may be a direct consequence of the differing timing of sampling (August for Baltimore sampling and May for Norfolk), they demonstrate the spatially and temporally variable nature of these systems even amongst neighbouring canyons and that the high surface productivity of the MAB region can lead to the deposition of significant food supplies (Schaff et al., 1992; DeMaster et al., 1994; Rex & Etter 2010).

One objective of the present study was to determine if community disturbance was more prevalent in canyon habitats than slope habitats, and how may this affect the community composition. Combining abundance and biomass data allowed for holistic community assessments of species dominance and standing stock (Warwick, 1986; Clarke, 1990), and confirmed that community disturbance occurred in deeper canyon habitats. These communities were dominated by burrowing bivalve species Yoldiellinae and Thyasiridae as well as high abundances of Capitellidae, Cossuridae and Gymnonereidinae. The organically-enriched sediments found in the lower canyons benefited communities dominated by small-bodied opportunistic species and suppressed diversity and community evenness, a classic benthic response to enrichment processes (Diaz & Rosenberg, 1995; Gray et al., 2002; Pearson & Rosenberg, 1978).

Low community disturbance was detected in the shallower parts of the two canyons (180-555 m), with enhanced species richness, community evenness and suppressed densities recorded. Paterson et al. (2011) noted similar occurrences in polychaete assemblages from Portuguese canyons operating under the Dynamic Equilibrium Model (Huston, 1979; Kadmon & Benjamini, 2006), which predicts that when the effects of productivity and disturbance are in balance, diversity was highest, and may offer an explanation for high diversity and low densities at 550-555 m communities in canyons. In contrast to canyon habitats, the adjacent slopes displayed opposing patterns, whereby upper slopes contained communities that were more disturbed than those deeper. Given the low organic enrichment compared to canyon habitats, suggests that disturbance at upper slope is likely due to different stressors. A speculative explanation for higher disturbance at shallow slope sites may be associated with impacts from fishing pressure, or the interaction of the shelf with hydrography such as the shelf-break front (see Chapter 2). Similar patterns in macrobenthos have been related to trawling activities (Palanques et al., 2006b; Tuck et al., 1998; Wilson et al., 2015; Yemane et al., 2005).

6 Conclusions

The findings of this study support long-held hypotheses about canyons, including their importance as hotspots of biodiversity and support the role that sedimentary processes play in forming ecological patterns within the confines of canyon systems (Levin et al., 2001). The results support the initial hypothesis that MAB canyons support distinct macrofaunal communities, including abundance, diversity and community composition when compared to adjacent slopes. However, biomass and average body size were not conclusively shown to be enhanced in the canyons at all depths. Sediment grain-sizes and organic matter data confirmed the secondary hypothesis that canyon macrofauna communities are structured by strong environmental gradients related to depth, sediment type, and organic enrichment and disturbance regimes but the relative ranking of drivers varied between the canyons. This suggests that canyon sediment dynamics, biogeochemical gradients and oceanographic regimes act in synergy to create canyon-specific conditions that structure the observed macrofaunal patterns. Differing disturbance patterns were observed between canyons and slopes, supporting the third hypothesis, whereby slopes were more disturbed in shallower areas, and canyons in deeper areas. Expected patterns of species richness, diversity and evenness with depth held only in slope habitats, and not within the two studied canyons, supporting the fourth hypothesis. The results of this study are congruent with previously published studies on macrofauna within submarine canyons worldwide and highlight the important role of canyon habitats in contributing to regional diversity (Buhl-Mortensen et al., 2010; Galéron et al., 2009) and organic matter cycling (Ingels et al., 2011; Kiriakoulakis et al., 2011) on continental margins.

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9 Tables and Figures

Table 1. Locations of sampling stations (decimal degrees) for samples collected in (a) Baltimore Canyon, (b) Baltimore Slope, (c) Norfolk Canyon and (d) Norfolk Slope. * = Boxcore reserved for geological / biogeochemical assessment in Baltimore. In Norfolk, a subcore was taken for these variables out of the macrofauna boxcore due to logistical constraints.

(a)

Baltimore Canyon

Date	Station	Depth (m)	Latitude	Longitude
19/08/12	NF-2012-019	189	38.243217	-73.8436
19/08/12	NF-2012-020*	189	38.243183	-73.84353
20/08/12	NF-2012-028	191	38.242817	-73.84352
20/08/12	NF-2012-029	191	38.242833	-73.84352
20/08/12	NF-2012-030	563	38.1661	-73.85018
21/08/12	NF-2012-032	563	38.166183	-73.85018
21/08/12	NF-2012-034	565	38.166217	-73.85007
21/08/12	NF-2012-035*	567	38.166267	-73.84998
22/08/12	NF-2012-046*	844	38.11722	-73.83532
22/08/12	NF-2012-045	840	38.11722	-73.8358
22/08/12	NF-2012-047	848	38.1174	-73.8348
23/08/12	NF-2012-049	844	38.11752	-73.83453
23/08/12	NF-2012-053*	1120	38.0709	-73.7783
23/08/12	NF-2012-055	1179	38.0724	-73.7732
23/08/12	NF-2012-056	1179	38.0724	-73.7732
24/08/12	NF-2012-062	1180	38.0721	-73.77337

(b)

Baltimore Slope

Date	Station	Depth (m)	Latitude	Longitude
24/08/12	NF-2012-064	168	38.06258	-73.86562
24/08/12	NF-2012-065*	170	38.06258	-73.86558
25/08/12	NF-2012-066	170	38.06258	-73.86562
25/08/12	NF-2012-067	168	38.06258	-73.86562
25/08/12	NF-2012-070*	515	38.04352	-73.80347
25/08/12	NF-2012-072	514	38.04352	-73.80344
25/08/12	NF-2012-076	510	38.04352	-73.80344
26/08/12	NF-2012-088	502	38.0436	-73.8032
26/08/12	NF-2012-082	990	38.01388	-73.7535
26/08/12	NF-2012-084*	990	38.013883	-73.7534
26/08/12	NF-2012-085	991	38.0139	-73.7534
26/08/12	NF-2012-087	991	38.0139	-73.7534
27/08/12	NF-2012-090	1185	37.9774	-73.6694
27/08/12	NF-2012-091*	1185	37.997383	-73.66938
27/08/12	NF-2012-092	1187	37.97742	-73.6694
27/08/12	NF-2012-093	1186	37.97742	-73.6694

Table 1 cont…

(c)

Norfolk Canyon

Date	Station	Depth (m)	Latitude	Longitude
11/05/13	RB-2013-046*	195	37.09475	-74.74658
11/05/13	RB-2013-047	195	37.09478	-74.74657
11/05/13	RB-2013-048	195	37.09478	-74.74657
11/05/13	RB-2013-043*	559	37.07597	-74.66063
11/05/13	RB-2013-044	557	37.07597	-74.66058
11/05/13	RB-2013-045	558	37.07595	-74.66058
10/05/13	RB-2013-040*	805	37.04273	-74.62917
10/05/13	RB-2013-041	803	37.04275	-74.6292
10/05/13	RB-2013-042	804	37.0428	-74.62925
10/05/13	RB-2013-038*	1110	37.03863	-74.57986
10/05/13	RB-2013-039	1110	37.03868	-74.57995
15/05/13	RB-2013-077*	1108	37.03875	-74.57964

(d)

Norfolk Slope

Date	Station	Depth (m)	Latitude	Longitude
11/05/13	RB-2013-049*	187	37.02307	-74.64577
11/05/13	RB-2013-050	187	37.02445	-74.64729
11/05/13	RB-20 13-051	187	37.02415	-74.64594
12/05/13	RB-2013-054*	549	37.0158	-74.5782
12/05/13	RB-2013-055	549	37.0158	-74.57815
12/05/13	RB-2013-056	548	37.0158	-74.57817
13/05/13	RB-2013-059	790	37.00903	-74.56478
12/05/13	RB-2013-060	790	37.00905	-74.56472
14/05/13	RB-2013-069*	804	37.00902	-74.56496
14/05/13	RB-2013-071*	1118	37.00577	-74.53373
15/05/13	RB-2013-073	1105	37.00577	-74.5337
15/05/13	RB-2013-075	1103	37.00588	-74.53365

Table 2. Univariate PERMANOVA 3-factor models analysing patterns in observed species richness (Taxa), evenness (Peilou's *J'*), macrofauna density, biomass, individual weight, and community disturbance (W-statistic) within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), † = square–root or * = weighted dispersion transformed.

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Species richness (Taxa) *						
Habitat (*ha*)	1	24.426	24.426	0.31857	0.6075	9924
Site (*si*)	1	126.89	126.89	1.655	0.2021	9935
Depth (*de*)	3	1405.7	468.56	6.1112	**0.0023**	9954
ha x *si*	1	10.027	10.027	0.13077	0.7860	9934
ha x *de*	3	145.04	48.347	0.63057	0.6129	9945
si x *de*	3	121.37	40.456	0.52765	0.6861	9956
ha x *si* x *de*	3	1277.4	425.8	5.5535	**0.0024**	9948
Residual	32	2376.8	76.672			
Total	47	5418.5				
Evenness (*J'*) *						
Habitat (*ha*)	1	0.08977	0.08977	0.04073	0.8484	9890
Site (*si*)	1	4.7935	4.7935	2.1747	0.1468	9877
Depth (*de*)	3	7.5676	2.5225	1.1444	0.3541	9956
ha x *si*	1	1.9594	1.9594	0.88893	0.3533	9890
ha x *de*	3	23.789	7.9297	3.5976	**0.0226**	9952
si x *de*	3	5.4328	1.8109	0.82158	0.4935	9955
ha x *si* x *de*	3	28.618	9.5394	4.3278	**0.0098**	9957
Residual	31	68.33	2.2042			
Total	46	145.32	0.08977			
Macrofauna density (ind. m^{-2}) †						
Habitat (*ha*)	1	700.9	700.9	4.7774	**0.0228**	9934
Site (*si*)	1	1,393.5	1,393.5	9.498	**0.0017**	9937
Depth (*de*)	3	6,432.1	2,144	14.614	**0.0001**	9944
ha x *si*	1	311.88	311.88	2.1258	0.1351	9946
ha x *de*	3	3,190.6	1,063.5	7.2493	**0.0002**	9950
si x *de*	3	1,216.4	405.48	2.7638	**0.0321**	9942
ha x *si* x *de*	3	456.8	152.27	1.0379	0.3935	9953
Residual	32	4,694.8	146.71			
Total	47	18,397				
Biomass (g Wwt m^{-2}) †						
Habitat (*ha*)	1	467.29	467.29	0.86238	0.3834	9941
Site (*si*)	1	343.08	343.08	0.63314	0.4857	9944
Depth (*de*)	3	6,473.7	2,157.9	3.9823	**0.0077**	9954
ha x *si*	1	517.94	517.94	0.95584	0.3521	9945
ha x *de*	3	1571	523.68	0.96644	0.4348	9934
si x *de*	3	838.64	279.55	0.5159	0.7642	9947
ha x *si* x *de*	3	824.6	274.87	0.50726	0.7617	9951
Residual	32	17,340	541.87			
Total	47	28,376				

Table 2 cont…

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Individual weight (g ind.$^{-1}$ m^{-2}) †						
Habitat (ha)	1	351.23	351.23	0.59318	0.5148	9939
Site (*si*)	1	152.45	152.45	0.25746	0.7382	9937
Depth (*de*)	3	6130.9	2043.6	3.4514	**0.0118**	9963
ha x *si*	1	107.11	107.11	0.1809	0.8198	9950
ha x *de*	3	3355.6	1118.5	1.889	0.1149	9963
si x *de*	3	2374.7	791.56	1.3368	0.2663	9945
ha x *si* x *de*	3	1377.3	459.09	0.77533	0.5680	9944
Res	32	18948	592.12			
Total	47	32797				
Community disturbance (*W*-Statistic) †						
Habitat (*ha*)	1	3.1142	3.1142	0.98962	0.3271	9895
Site (*si*)	1	24.5	24.5	7.7855	**0.0101**	9910
Depth (*de*)	3	98.096	32.699	10.391	**0.0001**	9965
ha x *si*	1	0.01182	0.01182	0.00376	0.9787	9913
ha x *de*	3	121.12	40.375	12.83	**0.0002**	9958
si x *de*	3	16.695	5.5651	1.7685	0.1734	9948
ha x *si* x *de*	3	4.1157	1.3719	0.43596	0.7336	9959
Res	32	100.7	3.1469			
Total	47	368.36				

Table 3. Multivariate PERMANOVA 3-factor model analysing patterns in observed macrofauna community structure (square–root transformed) within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), after transformation all factors met the assumptions of the permutations of dispersions test (PERMDISP $p > 0.05$).

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Habitat (*ha*)	1	5,325.9	5,325.9	9.0651	**0.0001**	9916
Site (*si*)	1	5,601	5,601	9.5333	**0.0001**	9920
Depth (*de*)	3	18,971	6,323.7	10.763	**0.0001**	9910
ha x *si*	1	3,807.3	3,807.3	6.4804	**0.0001**	9910
ha x *de*	3	8,148.9	2,716.3	4.6234	**0.0001**	9870
si x *de*	3	6,187	2,062.3	3.5102	**0.0001**	9859
ha x *si* x *de*	3	8,438.7	2,812.9	4.7878	**0.0001**	9864
Residual	32	18,801	587.52			
Total	47	75,280				

Table 4. Similarity Percentage (SIMPER) analysis for macrofauna assemblages at canyon and adjacent slope habitats, showing Families (Total ≥ 30 %) contributing the most to (a) average similarity differences within canyon and slope depth groups, and (b) average dissimilarity between canyon and slope habitat.

(a)

Baltimore Canyon (75.0 %)							
180 m (81.6 %)		**550 m (66.6 %)**		**900 m (81.4 %)**		**1180 m (68.9 %)**	
Lucinidae	8.0	Spionidae	9.5	Yoldiellinae	18.9	Thyasiridae	6.0
Cossuridae	7.6	Cirratulidae	7.8	Thyasiridae	12.3	Capitellidae	5.6
Dorvilleidae	5.1	Oligochaeta	6.9			Gymnonereidinae	5.4
Oweniidae	5.0	Polycirrinae	6.0			Nemertea	5.2
Paraonidae	4.3					Aplacophora	5.1
						Cossuridae	4.7
Baltimore Slope (65.6 %)							
180 m (69.0 %)		**550 m (58.8 %)**		**900 m (67.4 %)**		**1180 m (67.1 %)**	
Paraonidae	14.2	Thyasiridae	11.2	Oligocheata	7.6	Macrostylidae	8.0
Oligochaeta	7.5	Paraonidae	11.9	Macrostylidae	5.9	Aplacophora	6.9
Cirratulidae	6.4	Nuculidae	8.1	Paraonidae	5.6	Paraonidae	6.8
Onuphidae	4.8			Aplacophora	5.1	Oligocheata	6.1
				Maldanidae	4.9	Tanaidomorpha	5.8
				Tanaidomorpha	4.5		
Norfolk Canyon (63.3 %)							
190 m (58.7 %)		**555 m (68.2 %)**		**800 m (58.1 %)**		**1110 m (68.4 %)**	
Cossuridae	12.8	Oligocheata	9.4	Capitellidae	20.2	Yoldiellinae	10.1
Paraonidae	8.7	Dentalidae	8.6	Yoldiellinae	10.1	Dentalidae	8.8
Ophiuroidea	6.7	Capitellidae	7.0			Cossuridae	8.1
Oligocheata	5.4	Maldanidae	6.7				
Norfolk Slope (65.5 %)							
190 m (78.0 %)		**555 m (73.9 %)**		**800 m (48.6 %)**		**1110 m (61.6 %)**	
Paraonidae	11.9	Cirratulidae	18.7	Thyasiridae	13.8	Thyasiridae	8.2
Oligocheata	6.6	Paraonidae	9.9	Paraonidae	13.0	Gymnonereidinae	6.3
Ampharetidae	6.5	Lumbrineridae	6.9	Phoxocephalidae	12.2	Cirratulidae	5.4
Cirratulidae	5.7					Maldanidae	5.0
						Lumbrineridae	5.0
						Paraonidae	5.0

Table 4 Cont…

(b)

Baltimore (56.7 %) Canyon vs Slope		**Norfolk (53.7 %) Canyon vs Slope**		**Canyons (59 %) Baltimore vs Norfolk**		**Slopes (52 %) Baltimore vs Norfolk**	
Thyasiridae	5.5	Capitellidae	7.6	Dentalidae	6.5	Cirratulidae	15.5
Yoldiellinae	4.9	Cirratulidae	5.7	Capitellidae	5.6	Oligochaeta	5.1
Cossuridae	4.4	Yoldiellinae	4.0	Ophiuroidea	4.8	Lumbrineridae	4.1
Paraonidae	2.7	Cossuridae	3.5	Nephtyidae	3.8	Spionidae	3.3
Dentalidae	2.6	Paraonidae	3.0	Oligochaeta	3.7	Paraonidae	3.2
Nuculidae	2.5	Dentalidae	2.8	Cossuridae	3.6		
Phoxocephalidae	2.4	Ophiuroidea	2.7	Maldanidae	3.5		
Oligochaeta	2.3	Nephtyidae	2.6				
Pelecypoda	2.1						
Maldanidae	1.9						

Table 5. Distance-based linear modelling (DISTLM) on species abundance data at Baltimore Canyon and adjacent slope showing (a) the proportion of macrofaunal assemblage pattern explained by each explanatory variable and (b) the most explanatory models using the *BEST* selection procedure.

(a)

Variable	**SS (trace)**	**Pseudo-*F***	**P (perm)**	**Prop. (%)**
Depth	6,365.4	4.7891	0.001	17.9
% Sand	6,318.8	4.7465	0.001	17.7
δ^{15}N	6,132.3	4.5772	0.001	17.2
% Carbon	4,201.1	2.9429	0.003	11.8
Chl *a*	4,012.6	2.7941	0.003	11.3
W	4,158.8	2.9094	0.001	11.7
δ^{13}C	3,856.7	2.6724	0.003	10.8
% Nitrogen	3,328.7	2.2688	0.017	9.3

(b)

AICc	R^2	**RSS**	**Selections**
164.2	0.78291	7,729.9	Chl *a*, % C, % N, δ^{13}C, δ^{15}N, Sand, Depth
167.25	0.70141	10,632	Chl *a*, % N, δ^{13}C, δ^{15}N, Sand, Depth
167.25	0.70135	10,634	Chl *a*, % N, δ^{13}C, δ^{15}N, Depth
167.32	0.70051	10,664	Chl *a*, % N, δ^{15}N, Sand, Depth
167.77	0.63860	12,868	Chl *a*, % C, % N, δ^{13}C, Depth
167.97	0.69228	10,957	W, Chl *a*, % C, δ^{15}N, Sand, Depth
168.15	0.79438	7,321.3	W, Chl *a*, % C, % N, δ^{13}C, δ^{15}N, Sand, Depth
168.19	0.63212	13,099	Chl *a*, % N, δ^{13}C, Sand, Depth
	Total SS (trace):	35,607	

Table 6. Distance-based linear modelling (DISTLM) on species abundances at Norfolk Canyon and adjacent slope showing (a) the proportion of macrofaunal assemblage pattern explained by each explanatory variable and (b) the most explanatory models using the *BEST* selection procedure.

(a)

Variable	**SS (trace)**	**Pseudo-*F***	**P (perm)**	**Prop. (%)**
Depth	7,077.7	5.768	0.0001	20.8
% Sand	6,804.8	5.4901	0.0001	20.0
% Carbon	6,196.9	4.8906	0.0001	18.2
% Nitrogen	6,135.1	4.8312	0.0001	18.0
Chl *a*	4,909.1	3.7032	0.0005	14.4
$\delta^{13}C$	4,012.9	2.9369	0.0045	11.8
$\delta^{15}N$	3,777.4	2.7431	0.0076	11.1
W	3,533.4	2.5454	0.0136	10.4

(b)

AICc	***R*²**	**RSS**	**Selections**
170.09	0.44692	18,845	% N, $\delta^{13}C$, Sand
170.15	0.4454	18,897	% C, $\delta^{15}N$, Sand
170.17	0.44491	18,913	% N, $\delta^{15}N$, Sand
170.24	0.58135	14,265	Chl *a*, % C, % N, $\delta^{13}C$, Sand
170.28	0.51268	16,604	Chl *a*, % C % N, $\delta^{13}C$
170.31	0.44171	19,022	% C, $\delta^{13}C$, Sand
170.45	0.50923	16,722	% N, $\delta^{13}C$, $\delta^{15}N$, Sand
170.56	0.43588	19,221	Chl *a*, Sand, Depth
170.66	0.43356	19,300	% N, Sand, Depth
170.68	0.36029	21,797	% N, Sand
	Total SS (trace):	34,073	

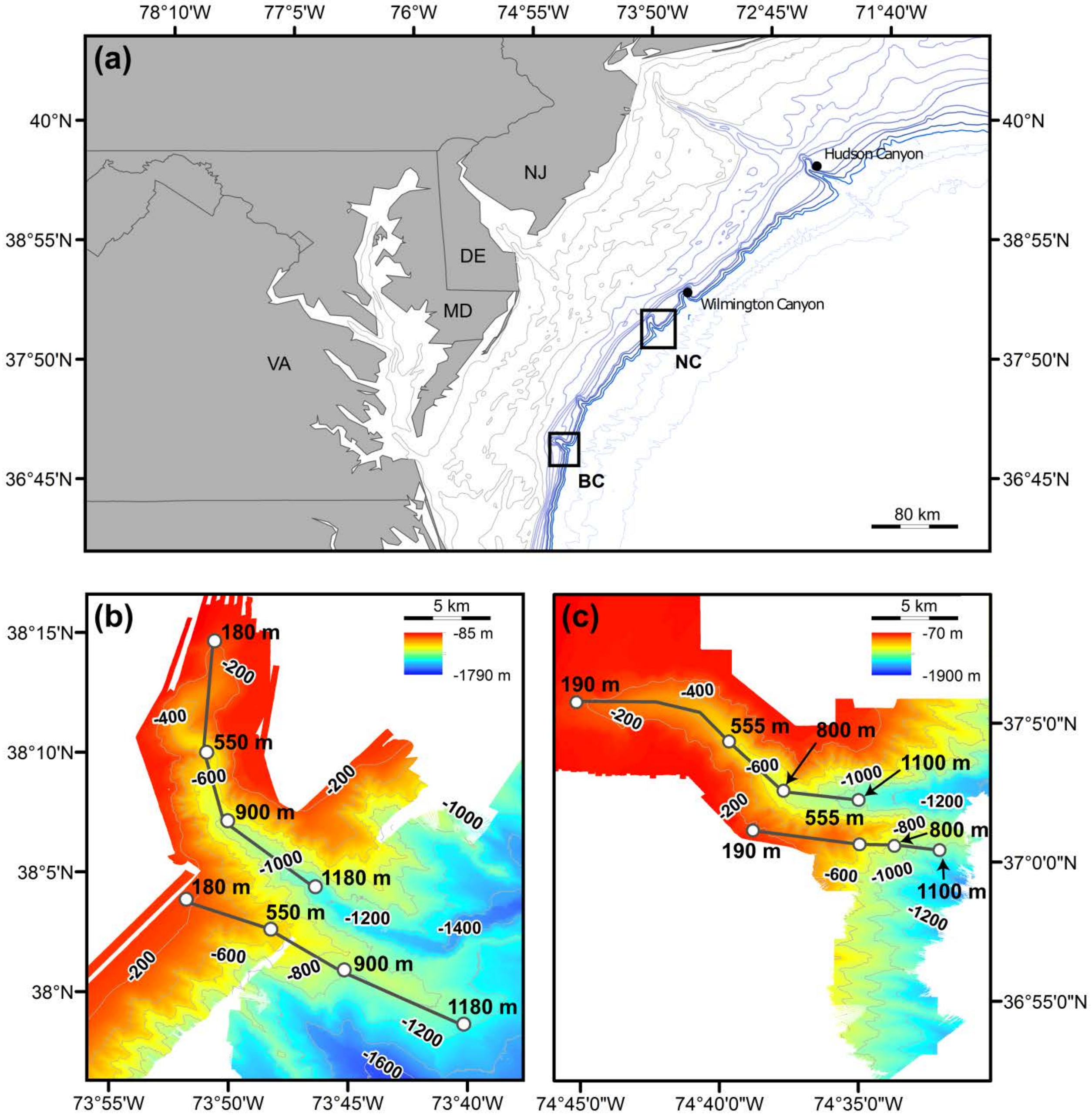

Figure 1. Maps of study locations: (a) Study area in the Mid Atlantic Bight, North West Atlantic showing location of the two canyons, (b) Baltimore Canyon macrofauna boxcores (white circles) collected along canyon and adjacent slope transects in 2012 across comparable depths and (c) Norfolk Canyon and adjacent slopes sampled in 2013. Bathymetry on all figures is shown as the inset colour scale bar.

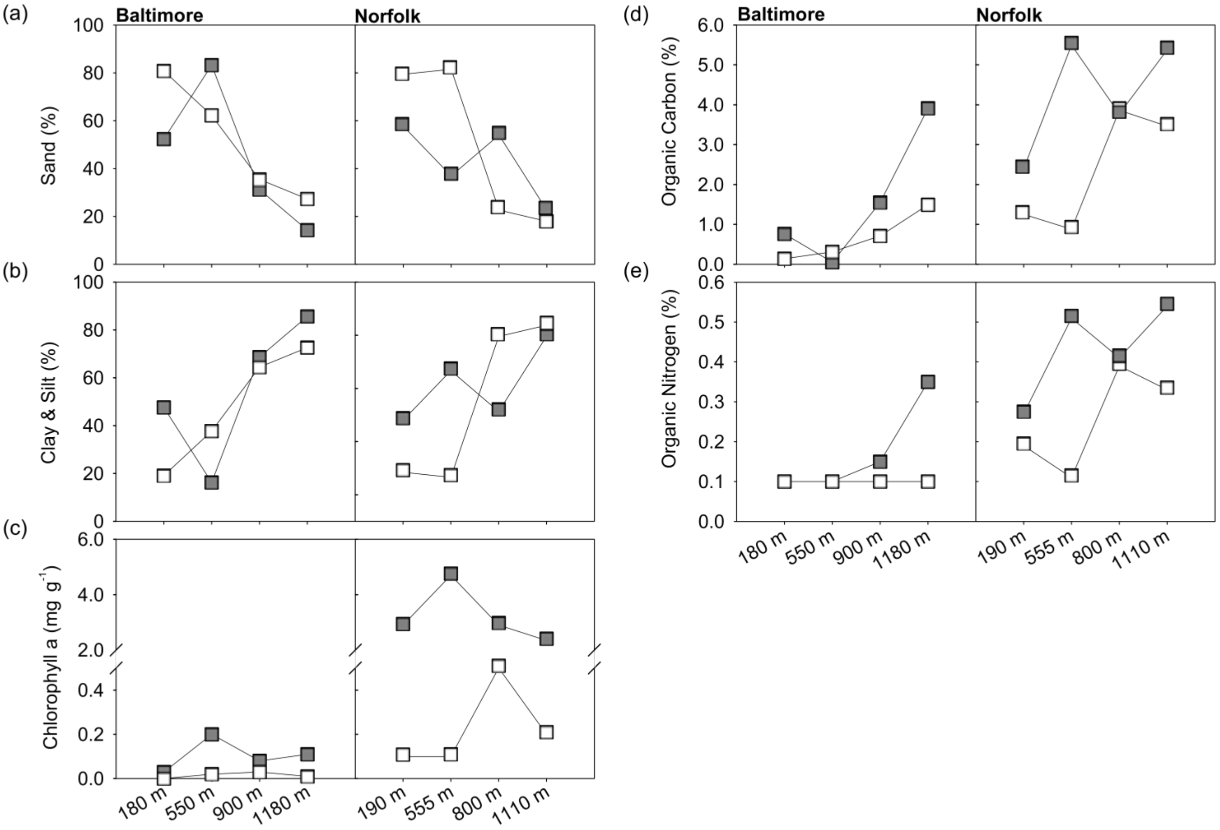

Figure 2. Sediment parameters for Baltimore and Norfolk canyons (grey squares) and adjacent slopes (white squares) across the depth gradient. (a) Percent sand, (b) percent silt and clay, (c) surface chlorophyll *a*, (d) percent organic carbon and (e) percent organic nitrogen.

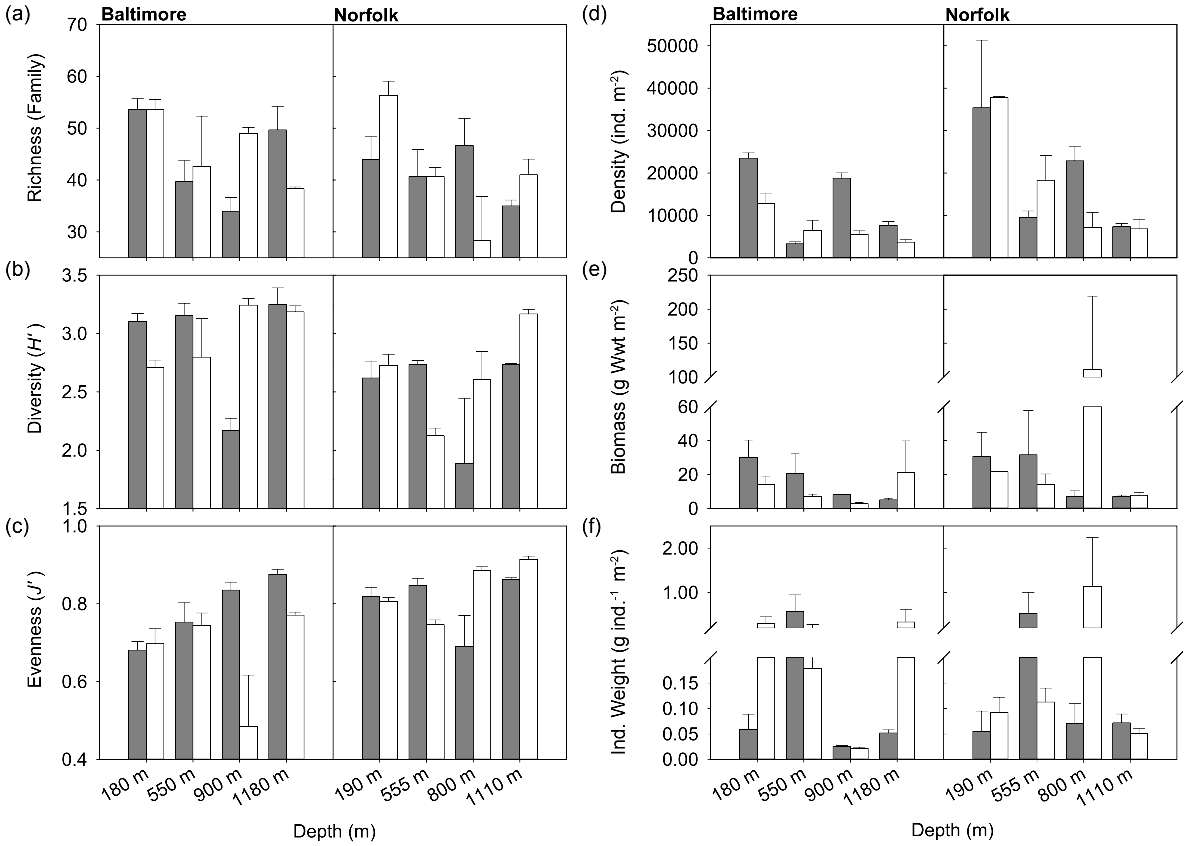

Figure 3. Biodiversity measures (mean ± 1 SE.) for Baltimore and Norfolk canyons (grey bars) and adjacent slope (white bars), across the depth gradient. (a) species richness (Taxa), (b) diversity (Shannon-Wiener *H'*) and (c) evenness (Pielou's *J'*), (d) Macrofauna density, (e) total biomass, (f) individual weight.

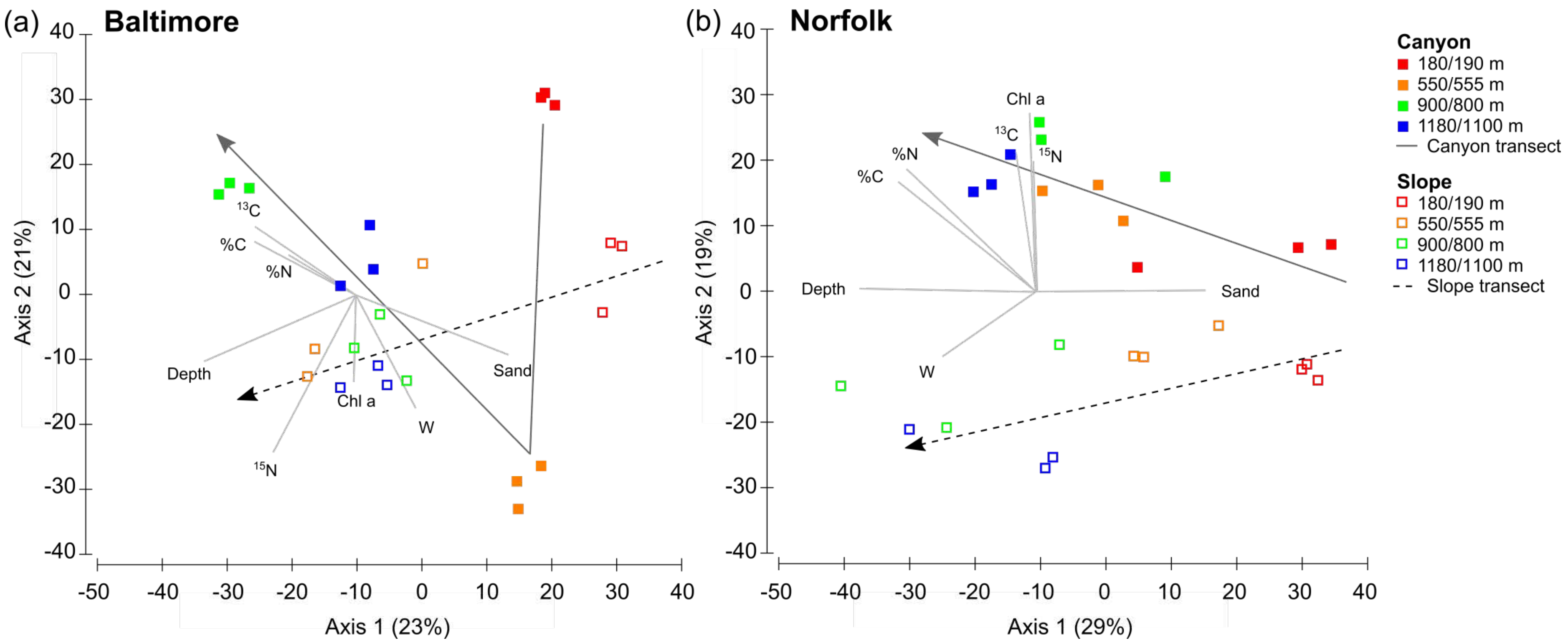

Figure 4. Principal Component Ordination for benthic community assemblages, including environmental eigenvectors (blue lines), based on square-root transformed abundance data at (a) Baltimore Canyon and adjacent slope, and (b) Norfolk Canyon and adjacent slope. Environmental parameters included sediment grain-size, surface sediment chlorophyll *a*, percent organic carbon, percent total nitrogen, δ^{13}C, δ^{15}N, *W*-Statistic and depth.

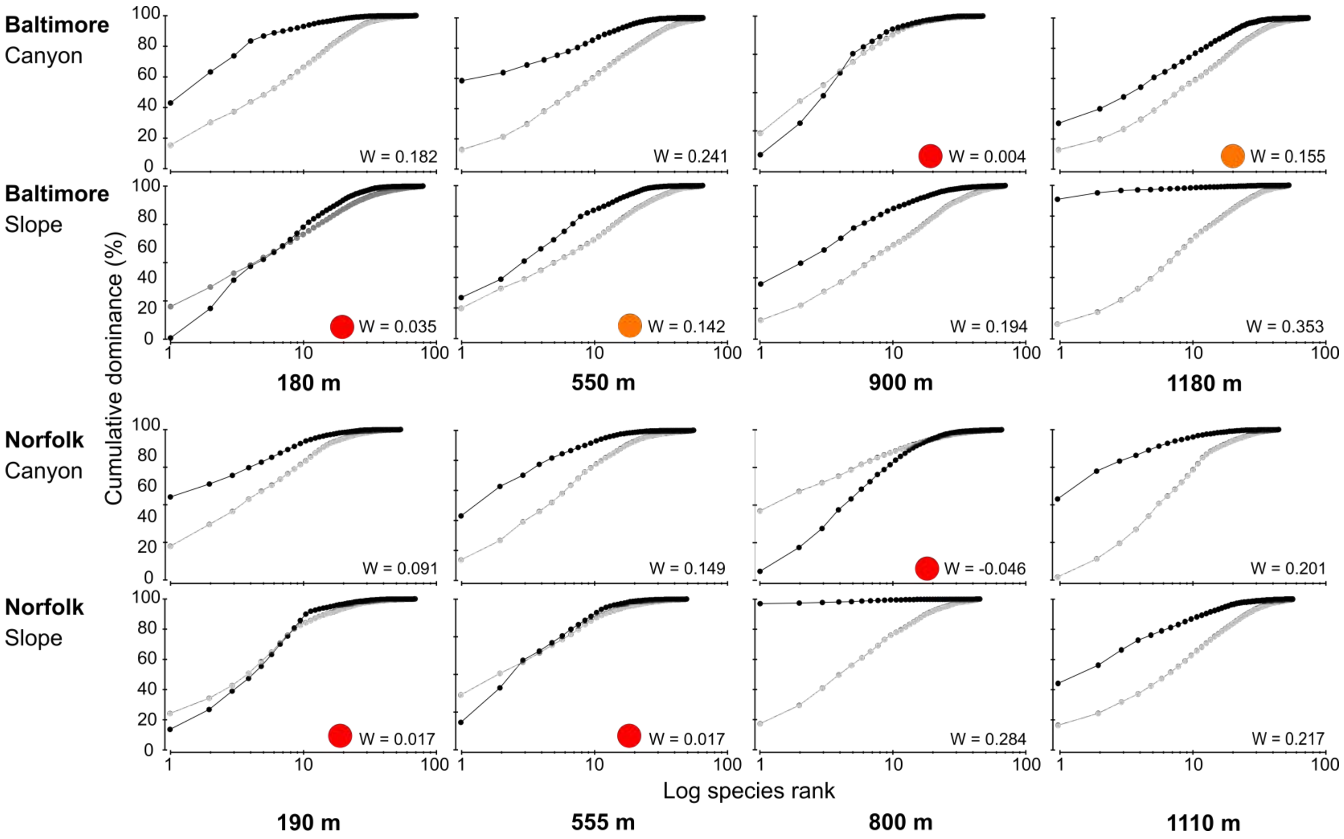

Figure 5. Abundance (Grey) biomass (Black) comparison (ABC) curves based on mean macrofaunal density (ind. m^2) and biomass (g Wwt m^2) data for Baltimore and Norfolk canyons and adjacent slopes across the depth gradient. Moderately disturbed (orange circles) and severely disturbed (red circles) community structure are highlighted. *W* is the associated Warwick statistic, a measure of distance between the two dominance curves (-1 = very disturbed, 1 = undisturbed).

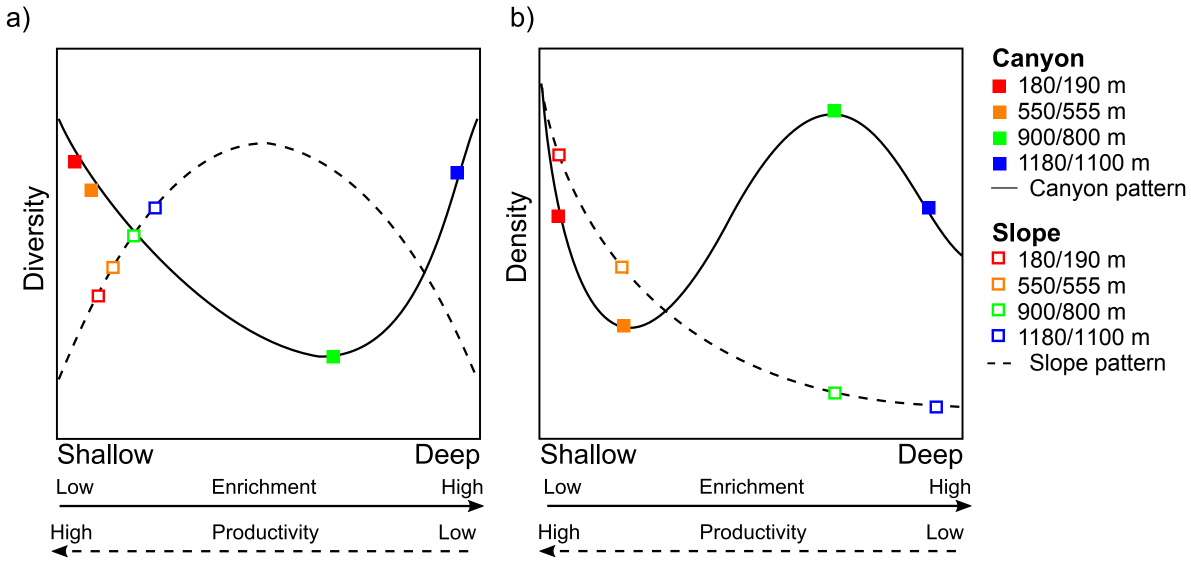

Figure 6. The diversity-depth conceptual model adapted from Rex and Etter (2010), (a) shows macrofaunal species diversity and (b) density against productivity and enrichment. The dashed lines on both plots refer to the expected pattern (Rex and Etter 2010), which in this study, the adjacent slopes followed (canyon and slope are conceptually drawn as opposed to statistically fitted). The solid line reflects the divergent pattern that was observed in the Baltimore and Norfolk canyons.

10 Supplementary Materials

SM Table 1. List of taxonomic sources used to aid macrofaunal identification in this study. ID numbers refer to specific taxa listed in SM Table 3.

ID	Reference
1.	Cornelius, P. F. S. *North-west European athecate hydroids and their medusae. Part:2. Synopses of the British Fauna Vol. 50 (2)* (The Linnean Society of London and the Estuarine and Brackish-water Sciences Association, 1995).
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deep water polychaete from the Northwestern Atlantic (Polychaeta: Hesionidae). *Scientia Marina* **70,** 157–165 (2006).

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SM Table 2. Sediment pigment concentrations, carbon and nitrogen isotopic values and grain-size percentages from Baltimore and Norfolk canyons and their adjacent slope habitats. * indicates environmental variable not used in distance-based linear modelling.

Location	**Chl *a* (mg g^{-1})**	**C (%)**	**N (%)**	**$\delta^{13}C$**	**$\delta^{15}N$**	**Sand (%)**	**Clay+Silt (%) ***
Baltimore Canyon							
180m	0.03	0.76	0.1	-23.7	4.4	52.37	47.64
550m	0.2	0.05	0.1	-24.6	5.5	83.27	16.27
900m	0.08	1.55	0.15	-22.1	5.2	31.3	68.69
1180m	0.11	3.91	0.35	-22.1	5.2	14.33	85.68
Baltimore Slope							
180m	< 0.001	0.14	0.1	-22.2	4.8	80.84	19.17
550m	0.02	0.31	0.1	-21.9	4.8	62.28	37.74
900m	0.03	0.71	0.1	-22.2	5.2	35.5	64.49
1180m	0.01	1.49	0.1	-23.4	5.5	27.35	72.66
Norfolk Canyon							
190m	2.9	2.4	0.27	-21.7	5.86	57.73	42.27
555m	4.7	5.5	0.51	-21.6	5.72	36.95	63.05
800m	2.9	3.77	0.41	-21.6	5.85	54.09	45.91
1110m	2.35	5.38	0.54	-21.7	5.55	22.62	77.38
Norfolk Slope							
190m	0.1	1.25	0.19	-21.8	5.36	79.45	20.55
555m	0.1	0.88	0.11	-22.2	4.86	81.53	18.47
800m	0.5	3.86	0.39	-21.8	5.37	22.68	77.32
1110m	0.2	3.46	0.33	-21.9	5.45	18.01	81.99

SM Table 3. List of taxa (Families where possible) in the study of Baltimore and Norfolk canyons and adjacent slopes macrofauna communities. Indet., indeterminate; spp., species (plural); cf., confer. Resource number refers to references in SM Table 1; *BPJ*, best professional judgement

Taxa	**Resource**
Acteonoidea	76
Actiniaria	2
Ammotheidae *Paranymphon spinosum*	51
Ampeliscidae	52,54,58,57,
Ampharetidae	8,44,45,46
Amphilochidae	52
Amphinomidae	9,17
Amphipoda indet.	*BPJ*
Anthuridae *Cyathura carinata / Ptilanthura / Leptanthura*	60,61
Aoridae	54
Apistobranchidae	26
Aplacophora	72,73
Astartidae	79,83
Asteroidea	*BPJ*
Astropectinidae *Astropecten* spp.	90
Buccinidae	75,77
Capitellidae	8,9
Caprellidae	*BPJ*
Cardiidae *Parvicardium pinnulatum*	74,79
Carditidae	74,79
Cerianthidae *Cerianthus* spp.	2
Chaetopteridae *Spiochaetopterus costarum*	8
Cirolanidae *Natatolana* spp. near *honu*	62
Cirratulidae	8,9,34,35,26,
Columbellidae	75
Corophiidae *Jassa* spp.	54
Cossuridae *Cossura longocirrata*	26
Ctenodrillidae *Ctenodrilus serratus*	27
Cumacea	69,70,71
Cuspidariidae	83
Cylichnidae *Cylichna* cf. *verrillii*	76
Dentaliidae	74
Desmosomatidae	64,66
Dorvilleidae	8,9,17
Dulichiidae *Dulichia* spp. cf.	54
Echinoidea	*BPJ*
Echiura spp.	*BPJ*
Edwardsiidae *Edwardsia* spp.	2
Emarginulinae	74
Eulimidae *Eulima* spp.	74,75
Eumalacostraca	*BPJ*
Eunicidae	8, 26

Euphausiacea	*BPJ*
Eurycopeinae	64
Fabriciidae *Pseudofabricia aberens*	8,47
Fauvelliopsidae *Laubieriopsis brevis*	30
Fissurellidae	74
Flabelligeridae	36,38
Gastropoda indet.	*BPJ*
Glyceridae	8,10,11
Gnathiidae *Gnathia* female	*BPJ*
Goniadidae	8,11
Gymnonereidinae *Ceratocephale loveni*	8
Halicharidae	*BPJ*
Haploniscidae *Haploniscus* spp. cf.	64,65
Hemichordata Enteropneusta	*BPJ*
Hesionidae	9,12
Heterobranchia spp. cf.	*BPJ*
Heterospionidae indet.	27
Holothuroidea	*BPJ*
Ilyarachnidae	63
Isaeidae	54
Ischnomesidae	63,64
Ischyroceridae	54
Kelliellidae	84
Lacydoniidae *Paralacydonia paradoxa*	8
Lasaeidae	79,83
Leptochitonidae *Leptochiton* spp.	*BPJ*
Liljeborgidae	52
Limidae *Limatula*	74,83
Limopsidae *Limopsis sulcata*	74,79,83
Lucinidae *Lucinoma foliosa*	74,79,83
Lumbrineridae	18,19,20,21
Lysianassidae	54
Macrostylidae sp.1 *Macrostylis* / Nannoniscidae cf.	64
Majidae *Hyas* spp.	*BPJ*
Maldanidae	8,9,27,39
Malgelonidae *Magelona* spp.	8,9,33
Malletiidae cf.	74
Melinninae *Melinna* spp.	8,44
Melitidae	54
Montocutidae *Montacuta / Tindaria / Neilonella* spp. cf.	74
Munnidae	63
Mysidae	*BPJ*
Mytilidae	74,78
Naticidae *Natica* spp.	75
Nebaliidae *Nebalia abyssicola*	*BPJ*
Neilonellidae *Neilonella* spp.	74,79, 81
Nemertea	*BPJ*
Nephtyidae	8,9,15
Nereididae	22,23

Nerillidae *Paranerilla* spp.	41
Noetiidae *Striarca / Bathyarca* spp.	74,79
Notophyllinae	8,9
Nuculanidae	78,81
Nuculidae	79,80
Nymphonidae *Boreonymphon* spp.	51
Octocorallia	*BPJ*
Oediceratidae spp.	54
Oenonidae	18,19,20,21
Oligochaeta	49,50
Onuphidae	8,9,16,17
Opheliidae	8,9,40
Ophiactidae *Ophiopholis aculeata*	90
Ophiuroidea	90
Opistobranchia	76
Orbiniidae	8,9,24
Oweniidae	8,9
Paguroidea spp.	*BPJ*
Pandoridae *Pandora gouldiana / inflata*	78,79,83
Paramunnidae *Pleurogonium* sp 2	63
Paraonidae	8,9,24,25
Pardaliscidae	*BPJ*
Pelecypoda indet.	*BPJ*
Pennatulacea	2
Periplomatidae *Periploma* spp.	83
Photidae	54
Phoxocephalidae	54,55,56,57
Phyllodocidae	8,9
Phyllophoridae *Thyone*	89,90
Pilargidae	8,9,13
Pleustidae *Stenopleustes* spp.	*BPJ*
Poecilochaetidae	9
Polycirrinae	9,44,45
Polynoidae	6,7
Portunidae *Liocarcinus* cf.	*BPJ*
Propeamussidae	74,79,83
Pyramidellidae	75
Questa cf.	27
Retusidae *Retusa obtusa*	76
Rissoidae	74,77
Sabellidae	8,47
Scalibregmatidae	43,44
Scalpellidae	*BPJ*
Semelidae *Abra longicallus*	74,79,83
Serpulidae	8,27
Siboglinidae	48
Sigalionidae	8
Sipuncula	4,5
Solemyidae *Solemya velum*	74,79
Sphaerodoridae	9

Spionidae	8,9,26,28,29,31,32
Stenothoidae	54
Sternaspidae *Sternaspis scutata*	8,9
Syllidae	8,14
Synaptidae	90
Synopiidae *Syrrhoe crenulata*	54
Tanaidomorpha	67,68
Tellinidae	74,79,83
Terebellidae indet.	8,9,44
Thyasiridae	74,85,86,87
Trichobranchinae	9,44
Trochidae *Margarites / Solariella* spp.	74,75
Trochochaetidae	8,9
Tunicata indet.	*BPJ*
Unciolidae *Unciola laticornis / irrorata*	52,54
Ungulinidae *Diplodonta*	74,79
Veneridae *Arctica* / *Pitar* type cf.	79,83
Vesicomyidae indet.	*BPJ*
Xenophyophore cf.	*BPJ*
Yoldiellinae	82,79
Zoanthidea	2

SM Table 4. Summary of macrofaunal abundance and diversity metrics from boxcore samples collected in Baltimore and Norfolk canyons and adjacent slopes. *H'* = Shannon-Wiener diversity; *J'* = Pielou's evenness; *W*-Statistic calculated from pooled replicate ABC curves. Values in parentheses represent one standard error.

Location	**n**	**Area (m^2)**	**Density (ind. m^{-2})**	**Species Richness (Taxa)**	**Biomass (g Wwt^{-2})**	***H'***	***J'***	***W*-Stat**
Baltimore Canyon								
180 m	3	0.061	23,594 ± 1,035	53.7 ± 1.7	30.70 ± 8.56	3.11 ± 0.05	0.78 ± 0.01	0.182
550 m	3	0.061	3,301 ± 411	39.7 ± 3.3	20.82 ± 9.36	3.15 ± 0.09	0.87 ± 0.00	0.241
900 m	3	0.061	18,812 ± 982	34.0 ± 2.2	8.19 ± 0.10	2.17 ± 0.09	0.62 ± 0.02	0.004
1180 m	3	0.059	7,879 ± 738	49.7 ± 3.7	5.10 ± 0.61	3.25 ± 0.12	0.83 ± 0.01	0.155
Mean			**13,399 ± 792**	**44.3 ± 2.7**	**16.22 ± 4.66**	**2.92 ± 0.09**	**0.77 ± 0.01**	**0.15**
Baltimore Slope								
180 m	3	0.061	12,699 ± 2,038	53.7 ± 1.5	14.29 ±3.97	2.71 ± 0.05	0.68 ± 0.02	0.035
550 m	3	0.061	6,538 ± 1,818	42.7 ± 7.9	7.54 ± 1.24	2.80 ± 0.27	0.75 ± 0.04	0.142
900 m	3	0.061	5,546 ± 660	49.0 ± 0.9	2.94 ± 0.59	3.24 ± 0.047	0.84 ± 0.02	0.194
1180 m	3	0.061	3,721 ± 454	38.3 ± 0.3	21.23 ± 15.24	3.19 ± 0.04	0.88 ± 0.01	0.353
Mean			**7,126 ± 1,243**	**45.9 ± 2.7**	**11.50 ± 5.26**	**2.98 ± 0.1**	**0.79 ± 0.02**	**0.18**
Norfolk Canyon								
190 m	3	0.062	35,338 ± 13,021	44.0 ± 3.6	30.71 ± 11.61	2.62 ± 0.12	0.70 ± 0.03	0.091
555 m	3	0.062	9,521 ± 1,299	40.7 ± 4.3	31.66 ± 21.31	2.73 ± 0.03	0.75 ± 0.03	0.149
800 m	3	0.062	22,803 ± 2,808	46.7 ± 4.3	7.27 ± 2.62	1.89 ± 0.45	0.49 ± 0.11	0.046
1110 m	3	0.061	7,321 ± 620	35.0 ± 0.9	7.16 ± 0.70	2.73 ± 0.01	0.77 ± 0.01	0.201
Mean			**18,758 ± 4,437**	**41.6 ± 3.3**	**19.20 ± 9.06**	**2.49 ± 0.15**	**0.67 ± 0.04**	**0.12**
Norfolk Slope								
190 m	3	0.062	37,752 ± 199	56.3 ± 2.2	21.80 ± 0.22	2.73 ± 0.07	0.68 ± 0.01	0.017
555 m	3	0.054	18,322 ± 4,726	40.7 ± 1.4	14.19 ± 5.05	2.12 ± 0.05	0.58 ± 0.02	0.017
800 m	3	0.043	7,125 ± 2,903	28.3 ± 7.0	110.99 ± 88.38	2.61 ± 0.20	0.81 ± 0.01	0.284
1110 m	3	0.041	6,860 ± 1,773	41.0 ± 2.5	7.90 ± 1.23	3.17 ± 0.03	0.86 ± 0.01	0.217
Mean			**17,515 ± 2,400**	**41.6 ± 3.3**	**38.72 ± 23.72**	**2.66 ± 0.09**	**0.73 ± 0.01**	**0.13**

SM Table 5. Univariate PERMANOVA pairwise comparisons for significant terms (see Table 2), for species richness (Taxa), evenness (Peilou's *J'*), macrofauna density, biomass, mean weight and community disturbance (*W*-Statistic) within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), for explanation of the codes used see methods. † = square–root or * = weighted dispersion transformed.

Factors	**Comparison**	**df**	***t*-statistic**	***P*(perm)**	***P* (MC)**	**Unique Perms**
Species richness (Taxa) *						
ha x *si* x *de*	C x S Baltimore (1)	4	0.1171		0.9157	5
	C x S Baltimore (2)	4	0.2588		0.8345	7
	C x S Baltimore (3)	4	4.3588		**0.0098**	10
	C x S Baltimore (4)	4	2.7081		0.0556	10
	C x S Norfolk (1)	4	2.5187		0.0605	7
	C x S Norfolk (2)	4	0.1480		0.9135	10
	C x S Norfolk (3)	3	1.2037		0.3137	10
	C x S Norfolk (4)	4	1.7576		0.1510	10
	BC x NC (1)	4	2.1814		0.0881	10
	BC x NC (2)	4	0.2163		0.8587	10
	BC x NC (3)	4	2.1863		0.0874	10
	BC x NC (4)	4	3.3750		**0.0284**	10
	BS x NS (1)	4	0.9058		0.4179	7
	BS x NS (2)	4	0.2763		0.8337	10
	BS x NS (3)	3	1.5881		0.2128	10
	BS x NS (4)	4	0.7425		0.5031	7
	BC (1 x 2)	4	2.9863		**0.0354**	10
	BC (1 x 3)	4	5.2770		**0.0050**	10
	BC (1 x 4)	4	0.8324		0.4470	10
	BC (2 x 3)	4	0.9431		0.4110	10
	BC (2 x 4)	4	1.7676		0.1499	10
	BC (3 x 4)	4	3.0436		**0.0357**	10
	BS (1 x 2)	4	1.3714		0.2452	7
	BS (1 x 3)	4	2.0885		0.1055	7
	BS (1 x 4)	4	9.5080		**0.0008**	7
	BS (2 x 3)	4	0.9673		0.3891	10
	BS (2 x 4)	4	0.3668		0.7468	10
	BS (3 x 4)	4	7.2893		**0.0022**	10

SM Table 5 cont..

Factors	Comparison	df	*t*-statistic	*P*(perm)	*P* (MC)	Unique Perms
Species richness (Taxa) *						
ha x *si* x *de*	NC (1 x 2)	4	0.5090		0.6415	7
	NC (1 x 3)	4	0.4679		0.6687	7
	NC (1 x 4)	4	2.0916		0.0975	7
	NC (2 x 3)	4	0.8611		0.4450	10
	NC (2 x 4)	4	1.0155		0.3676	10
	NC (3 x 4)	4	2.2883		0.0787	7
	NS (1 x 2)	4	5.2223		**0.0062**	10
	NS (1 x 3)	3	2.0333		0.1259	10
	NS (1 x 4)	4	3.8008		**0.0195**	10
	NS (2 x 3)	3	0.8771		0.4421	10
	NS (2 x 4)	4	0.1652		0.8878	7
	NS (3 x 4)	3	0.8787		0.4498	10
Evenness (*J'*) *						
ha x *de*	C x S (1)	8	2.5257	**0.0313**		8814
	C x S (2)	8	0.6351	0.5493		8843
	C x S (3)	7	2.1077	**0.0806**		8887
	C x S (4)	8	0.1281	0.8793		8751
	Canyon (1 x 2)	8	0.4293	0.7222		8882
	Canyon (1 x 3)	8	2.6323	**0.0256**		8835
	Canyon (1 x 4)	8	0.7721	0.4838		8875
	Canyon (2 x 3)	8	2.6949	**0.0259**		8830
	Canyon (2 x 4)	8	0.5099	0.6385		8838
	Canyon (3 x 4)	8	2.2510	0.0565		8827
	Slope (1 x 2)	8	0.8206	0.4532		8864
	Slope (1 x 3)	7	2.0752	0.0783		8904
	Slope (1 x 4)	8	2.2943	0.0575		8820
	Slope (2 x 3)	7	0.3642	0.7305		8850
	Slope (2 x 4)	8	0.4326	0.7097		8694
	Slope (3 x 4)	7	0.0443	0.9655		8845
ha x si x de	C x S Baltimore (1)	4	4.3542		**0.0118**	10
	C x S Baltimore (2)	4	0.7470		0.4921	10
	C x S Baltimore (3)	4	4.0812		**0.0143**	10
	C x S Baltimore (4)	4	1.3771		0.2420	10
	C x S Norfolk (1)	4	1.5985		0.1903	10
	C x S Norfolk (2)	4	0.1324		0.9015	10
	C x S Norfolk (3)	3	0.5473		0.6189	10
	C x S Norfolk (4)	4	1.1265		0.3262	10

SM Table 5 cont..

Factors	**Comparison**	**df**	***t*-statistic**	***P*(perm)**	***P* (MC)**	**Unique Perms**
Evenness (*J'*) *						
ha x si x de	BC x NC (1)	4	0.0434		0.9750	10
	BC x NC (2)	4	0.4839		0.6580	10
	BC x NC (3)	4	2.6342		0.0601	10
	BC x NC (4)	4	0.4013		0.7166	10
	BS x NS (1)	4	1.0350		0.3695	10
	BS x NS (2)	4	0.9323		0.4014	10
	BS x NS (3)	3	1.8572		0.1540	10
	BS x NS (4)	4	2.0946		0.0981	10
	BC (1 x 2)	4	0.8395		0.4492	10
	BC (1 x 3)	4	4.0253		**0.0148**	10
	BC (1 x 4)	4	1.0965		0.3244	10
	BC (2 x 3)	4	3.3333		**0.0282**	10
	BC (2 x 4)	4	0.08697		0.9336	10
	BC (3 x 4)	4	3.5587		**0.0251**	10
	BS (1 x 2)	4	0.26531		0.8040	10
	BS (1v 3)	4	3.4058		**0.0292**	10
	BS (1 x 4)	4	0.10327		0.9228	10
	BS (2 x 3)	4	1.1738		0.3045	10
	BS (2 x 4)	4	0.28931		0.7936	10
	BS (3 x 4)	4	2.3142		0.0815	10
	NC (1 x 2)	4	0.09752		0.9316	10
	NC (1 x 3)	4	0.30558		0.7751	10
	NC (1 x 4)	4	0.51066		0.6455	10
	NC (2 x 3)	4	0.32529		0.7593	10
	NC (2 x 4)	4	0.68885		0.5253	10
	NC (3 x 4)	4	0.17268		0.8717	10
	NS (1 x 2)	4	2.0575		0.1087	10
	NS (1x 3)	3	0.70287		0.5316	10
	NS (1 x 4)	4	2.6918		0.0573	10
	NS (2 x 3)	3	1.1146		0.3517	10
	NS (2 x 4)	4	0.40506		0.7127	10
	NS (3 x 4)	3	1.6795		0.1926	10
Macrofauna density (m^2)						
ha x *de*	C x S (1)	8	0.36991	0.7501		8865
	C x S (2)	8	2.2552	**0.0403**		8922
	C x S (3)	8	4.0895	**0.0043**		8862
	C x S (4)	8	2.0503	0.062		8797

SM Table 5 cont..

Factors	**Comparison**	**df**	***t*-statistic**	***P*(perm)**	***P* (MC)**	**Unique Perms**
Macrofauna density (m^2)						
ha x *de*	Canyon (1 x 2)	8	4.0070	**0.0091**		8866
	Canyon (1 x 3)	8	0.6884	0.5514		8897
	Canyon (1 x 4)	8	3.4247	**0.0136**		8908
	Canyon (2 x 3)	8	9.1434	**0.0022**		8813
	Canyon (2 x 4)	8	2.4304	**0.0349**		8910
	Canyon (3 x 4)	8	8.8415	**0.0017**		8816
	Slope (1 x 2)	8	2.9080	**0.0250**		8915
	Slope (1 x 3)	8	3.9423	**0.0050**		8912
	Slope (1 x 4)	8	5.5642	**0.0019**		8844
	Slope (2 x 3)	8	1.5382	0.1379		8853
	Slope (2 x 4)	8	2.2717	**0.0415**		8901
	Slope (3 x 4)	8	0.3789	0.7554		8886
si x *de*	Baltimore (1 x 2)	8	6.0765	**0.0029**		8880
	Baltimore (1 x 3)	8	3.5415	**0.0101**		8879
	Baltimore (1 x 4)	8	7.2623	**0.0023**		8854
	Baltimore (2 x 3)	8	4.1293	**0.0065**		8884
	Baltimore (2 x 4)	8	1.0069	0.3466		8866
	Baltimore (3 x 4)	8	4.8858	**0.0026**		8907
	Norfolk (1 x 2)	8	2.4656	**0.0411**		8862
	Norfolk (1 x 3)	8	2.0540	0.0565		8911
	Norfolk (1 x 4)	8	3.7092	**0.0088**		8869
	Norfolk (2 x 3)	8	0.6657	0.6609		8955
	Norfolk (2 x 4)	8	2.2062	**0.0405**		8930
	Norfolk (3 x 4)	8	1.4510	0.1748		8885
	1 (Baltimore x Norfolk)	8	1.7906	0.1041		8875
	2 (Baltimore x Norfolk)	8	4.1076	**0.0063**		8899
	3 (Baltimore x Norfolk)	8	0.5915	0.6716		8971
	4 (Baltimore x Norfolk)	8	0.9015	0.3920		8870
Biomass (g Wwt m^2)						
de	1 x 2	16	1.7564	0.0873		9939
	1 x 3	16	3.2063	**0.0020**		9945
	1 x 4	16	3.3799	**0.0027**		9945
	2 x 3	16	1.3409	0.1774		9932
	2 x 4	16	1.1173	0.2753		9938
	3 x 4	16	0.6064	0.6934		9957
Mean weight (g ind.$^{-1}$ m^2)						
de	1 x 2	16	1.5492	0.1143		9951
	1 x 3	16	1.7056	0.0683		9943
	1 x 4	16	0.5218	0.7439		9943
	2 x 3	16	2.7711	**0.0057**		9939
	2 x 4	16	1.9113	0.0543		9944
	3 x 4	16	1.4468	0.1389		9945

SM Table 5 cont..

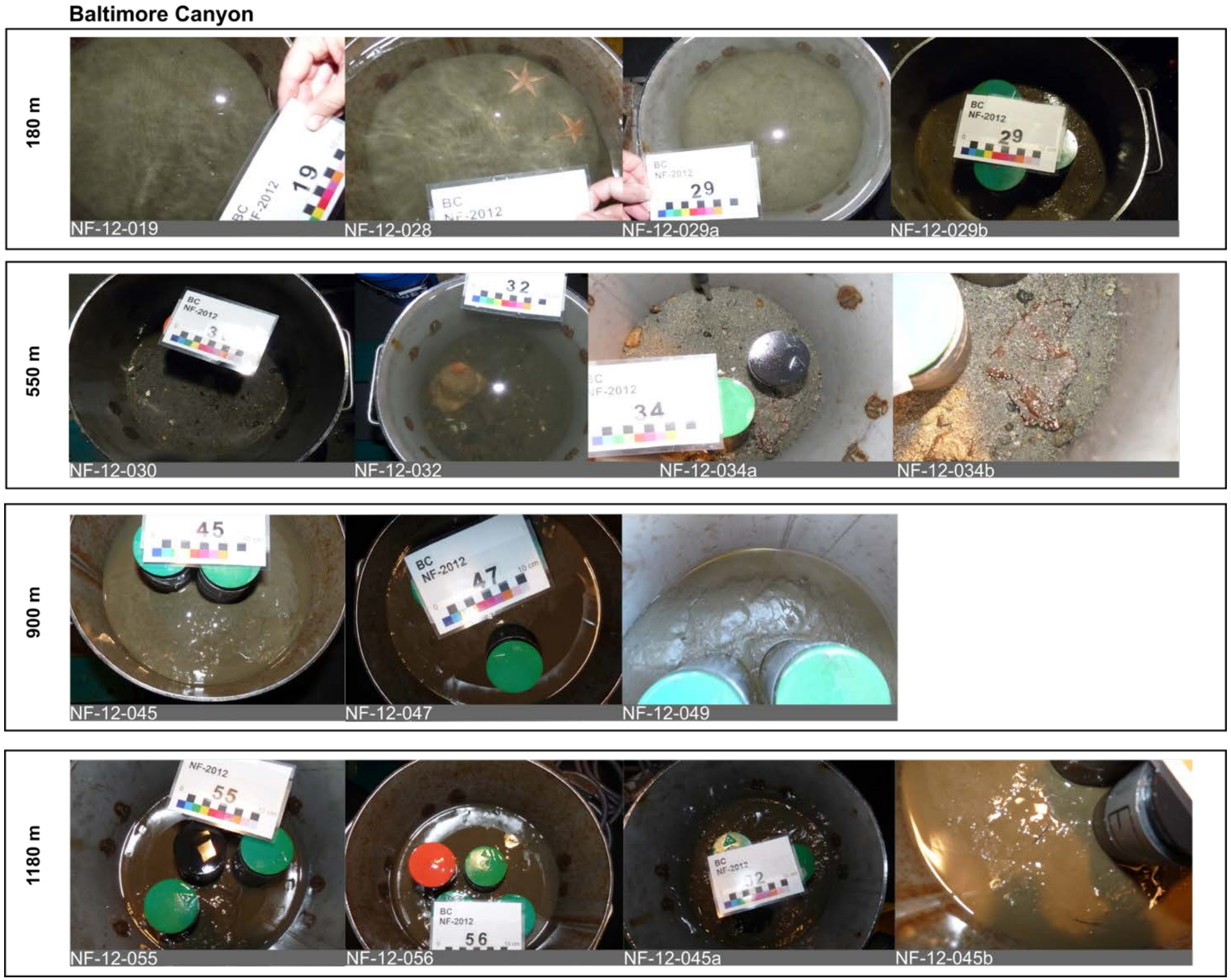
Factors	**Comparison**	**df**	***t*-statistic**	***P*(perm)**	***P* (MC)**	**Unique Perms**
Community disturbance (*W*-Statistic)						
ha x de	C x S (1)	8	2.0483	0.0535		8814
	C x S (2)	8	2.5049	0.0396		8830
	C x S (3)	8	4.387	**0.0031**		8869
	C x S (4)	8	2.6143	**0.0363**		8847
	Canyon (1 x 2)	8	0.54189	0.5929		8874
	Canyon (1 x 3)	8	3.103	**0.0076**		8839
	Canyon (1 x 4)	8	0.9347	0.3785		8795
	Canyon (2 x 3)	8	3.8797	**0.0053**		8842
	Canyon (2 x 4)	8	0.31822	0.7621		8790
	Canyon (3 x 4)	8	5.175	**0.0021**		8834
	Slope (1 x 2)	8	0.58374	0.5808		8821
	Slope (1 x 3)	8	3.7301	**0.0094**		8803
	Slope (1 x 4)	8	8.8331	**0.0019**		8753
	Slope (2 x 3)	8	3.0422	**0.0175**		8832
	Slope (2 x 4)	8	7.0872	**0.0017**		8847
	Slope (3 x 4)	8	2.4071	**0.0446**		8799

SM Table 6. Multivariate PERMANOVA pairwise comparisons for significant terms (see Table 2) for macrofauna community structure. Bold text indicates significant differences ($p < 0.05$), for explanation of the codes used see methods.

Factors	Comparison	df	*t*-statistic	*P*(perm)	*P*(MC)	Unique Perms
ha x *si*	C (B x N)	16	3.1918	**0.0001**		9940
	S (B x N)	16	2.4979	**0.0001**		9942
	B (C x S)	16	2.7187	**0.0002**		9930
	N (C x S)	16	2.8343	**0.0001**		9932
ha x *de*	C x S (1)	8	2.4196	**0.0022**		8903
	C x S (2)	8	2.5119	**0.0018**		8922
	C x S (3)	8	2.2568	**0.0020**		8917
	C x S (4)	8	2.4272	**0.0019**		8899
	Canyon (1 x 2)	8	3.1291	**0.0037**		8895
	Canyon (1 x 3)	8	3.1364	**0.0023**		8868
	Canyon (1 x 4)	8	3.2798	**0.0019**		8914
	Canyon (2 x 3)	8	2.9736	**0.0023**		8895
	Canyon (2 x 4)	8	2.7776	**0.0019**		8831
	Canyon (3 x 4)	8	2.0301	**0.0038**		8882
	Slope (1 x 2)	8	3.2959	**0.0028**		8894
	Slope (1 x 3)	8	3.078	**0.0027**		8914
	Slope (1 x 4)	8	3.701	**0.0017**		8851
	Slope (2 x 3)	8	1.9733	**0.0044**		8959
	Slope (2 x 4)	8	2.7197	**0.0019**		8855
	Slope (3 x 4)	8	1.0177	0.3801		8886
si x de	B (1 x 2)	8	3.4400	**0.0022**		8874
	B (1 x 3)	8	4.2517	**0.0021**		8881
	B (1 x 4)	8	3.6832	**0.0033**		8895
	B (2 x 3)	8	2.9436	**0.0034**		8900
	B (2 x 4)	8	2.5982	**0.0021**		8894
	B (3 x 4)	8	2.0266	**0.0022**		8879
	N (1 x 2)	8	2.619	**0.0068**		8889
	N (1 x 3)	8	2.5487	**0.0032**		8853
	N (1 x 4)	8	3.1853	**0.0018**		8910
	N (2 x 3)	8	1.8167	**0.0058**		8908
	N (2 x 4)	8	2.3395	**0.0015**		8916
	N (3 x 4)	8	0.9803	0.4751		8915
	1 (B x N)	8	2.5876	**0.0021**		8954
	2 (B x N)	8	2.5898	**0.0022**		8891
	3 (B x N)	8	2.0291	**0.0020**		8914
	4 (B x N)	8	1.7551	**0.0053**		8856

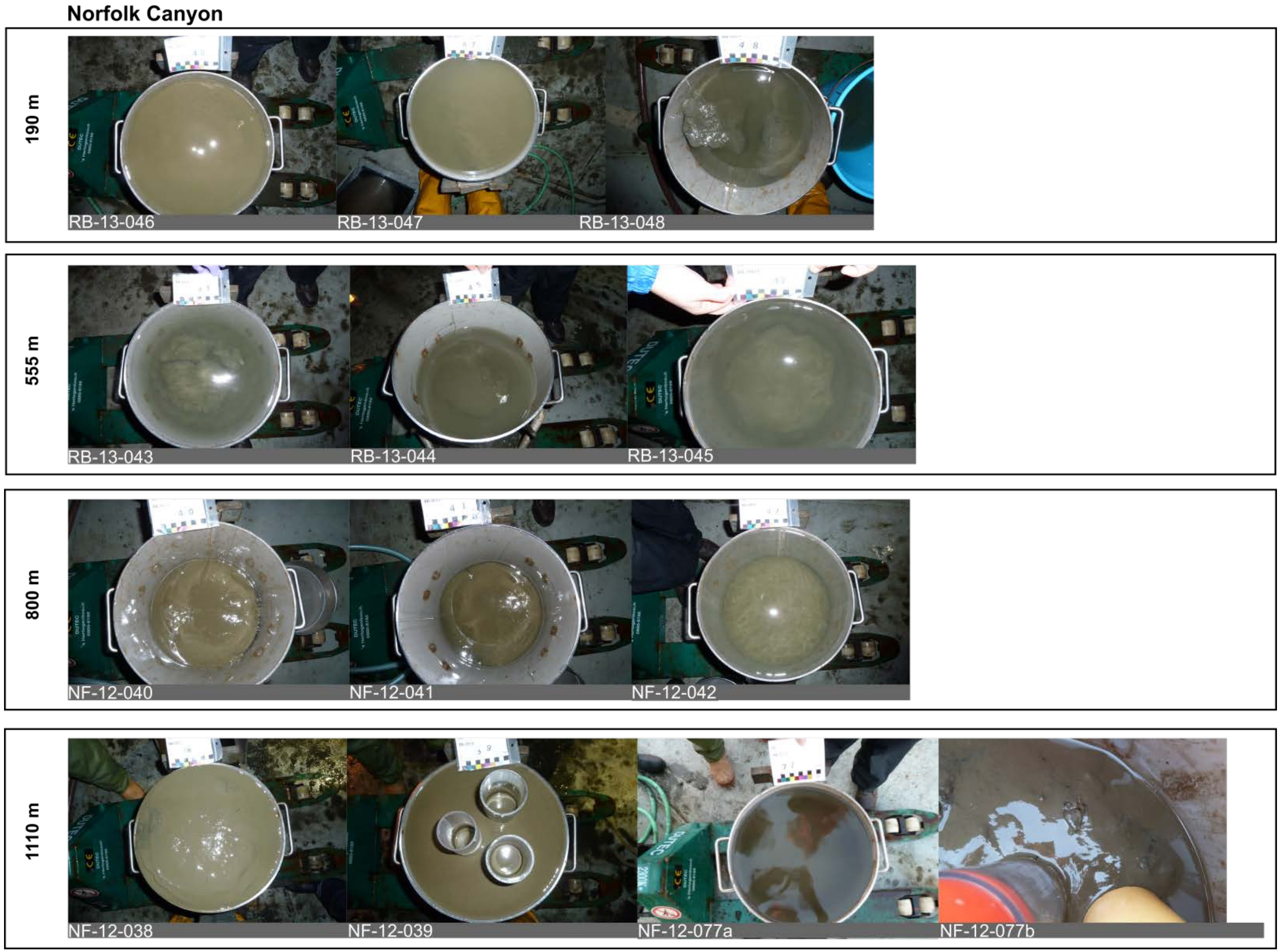
SM Table 6 cont…

ha x *si* x *de*	BC x NC (1)	4	2.3738	**0.0219**	10
	BC x NC (2)	4	2.7621	**0.0096**	10
	BC x NC (3)	4	2.5910	**0.0144**	10
	BC x NC (4)	4	2.5302	**0.0128**	10
	BS x NS (1)	4	2.5711	**0.0118**	10
	BS x NS (2)	4	2.1525	**0.0311**	10
	BS x NS (3)	4	1.7240	0.0697	10
	BS x NS (4)	4	1.7532	0.0592	10
	BC x BS (1)	4	2.9257	**0.0070**	10
	BC x BS (2)	4	2.3788	**0.0176**	10
	BC x BS (3)	4	3.2387	**0.0061**	10
	BC x BS (4)	4	2.4549	**0.0146**	10
	NC x NS (1)	4	1.9826	**0.0410**	10
	NC x NS (2)	4	2.4745	**0.0174**	10
	NC x NS (3)	4	1.7381	**0.0652**	10
	NC x NS (4)	4	2.4008	**0.0153**	10
	BC (1 x 2)	4	4.1243	**0.0021**	10
	BC (1x 3)	4	5.3960	**0.0014**	10
	BC (1 x 4)	4	3.6142	**0.0030**	10
	BC (2 x 3)	4	4.2403	**0.0030**	10
	BC (2 x 4)	4	2.9598	**0.0070**	10
	BC (3 x 4)	4	3.1067	**0.0067**	10
	BS (1 x 2)	4	2.5978	**0.0168**	10
	BS (1x 3)	4	2.5715	**0.0128**	10
	BS (1 x 4)	4	2.7820	**0.0089**	10
	BS (2 x 3)	4	2.0525	**0.0311**	10
	BS (2 x 4)	4	2.2042	**0.0231**	10
	BS (3 x 4)	4	1.3176	0.1918	10
	NC (1 x 2)	4	2.0310	**0.0413**	10
	NC (1x 3)	4	1.7341	0.0763	10
	NC (1 x 4)	4	2.2508	**0.0308**	10
	NC (2 x 3)	4	1.5233	0.1024	10
	NC (2 x 4)	4	2.0139	**0.0321**	10
	NC (3 x 4)	4	1.4585	0.1278	10
	NS (1 x 2)	4	2.9590	**0.0081**	10
	NS (1x 3)	4	2.5425	**0.0200**	10
	NS (1 x 4)	4	3.0003	**0.0070**	10
	NS (2 x 3)	4	1.9033	0.0561	10
	NS (2 x 4)	4	2.3961	**0.0171**	10
	NS (3 x 4)	4	1.0917	0.3378	10

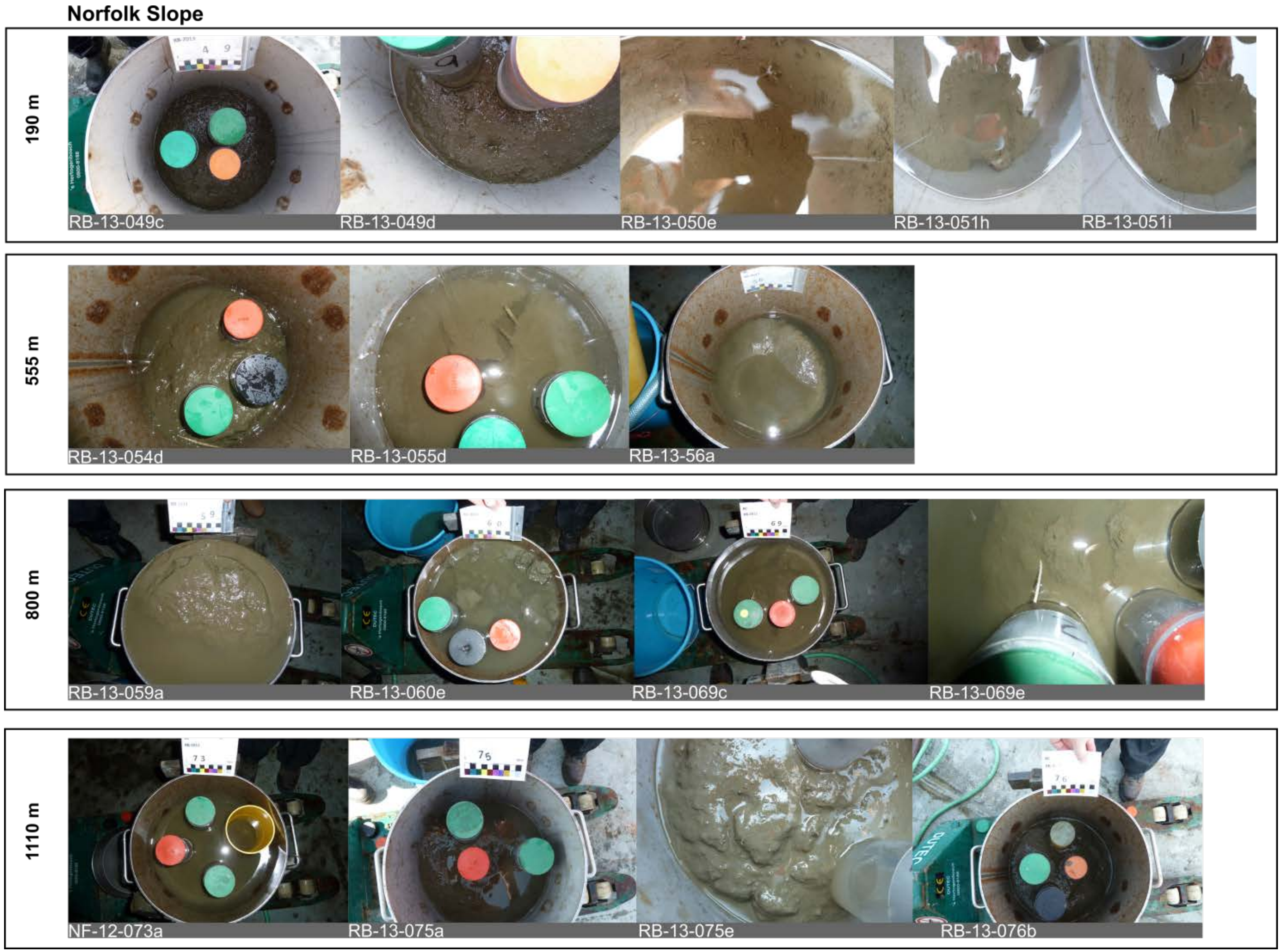


SM Figure 1. Boxcore photographs from samples taken in Baltimore Canyon during August 2012.

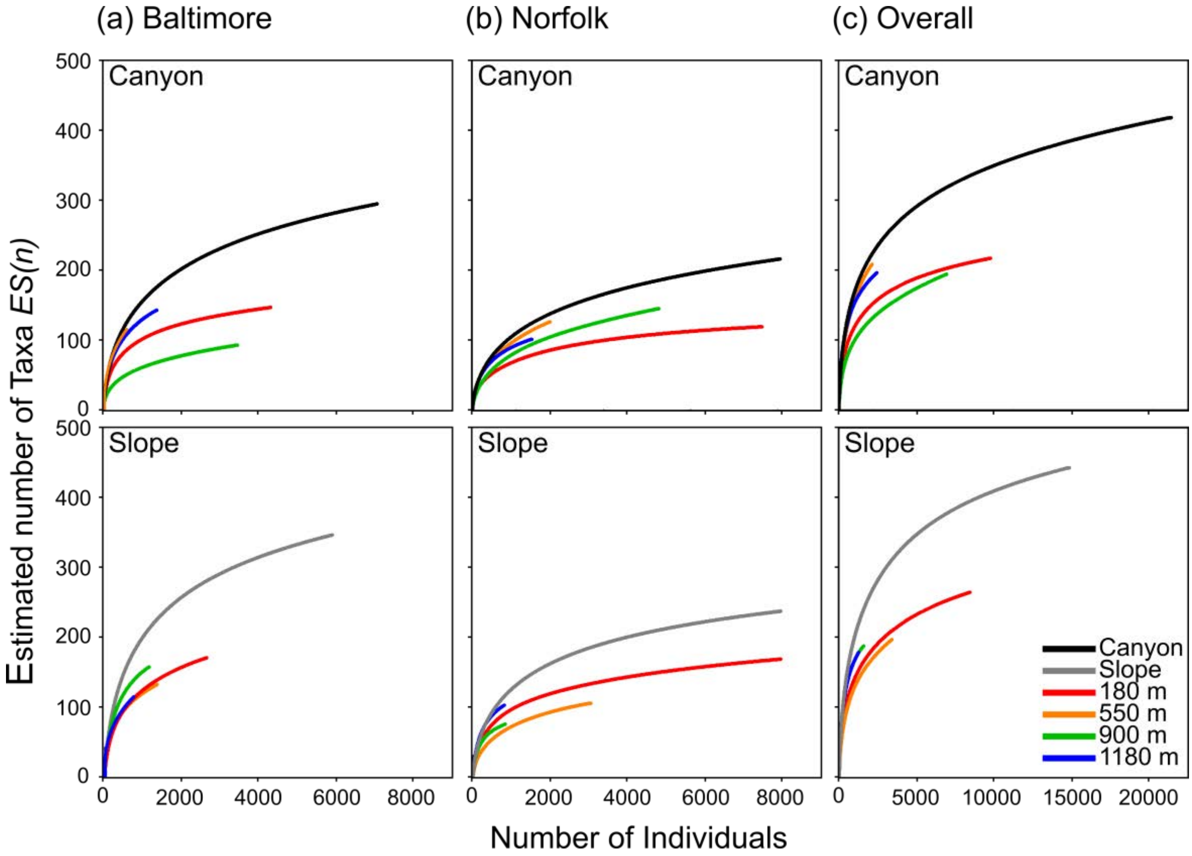
SM Figure 2. Boxcore photographs from samples taken in Baltimore adjacent slope during August 2012.



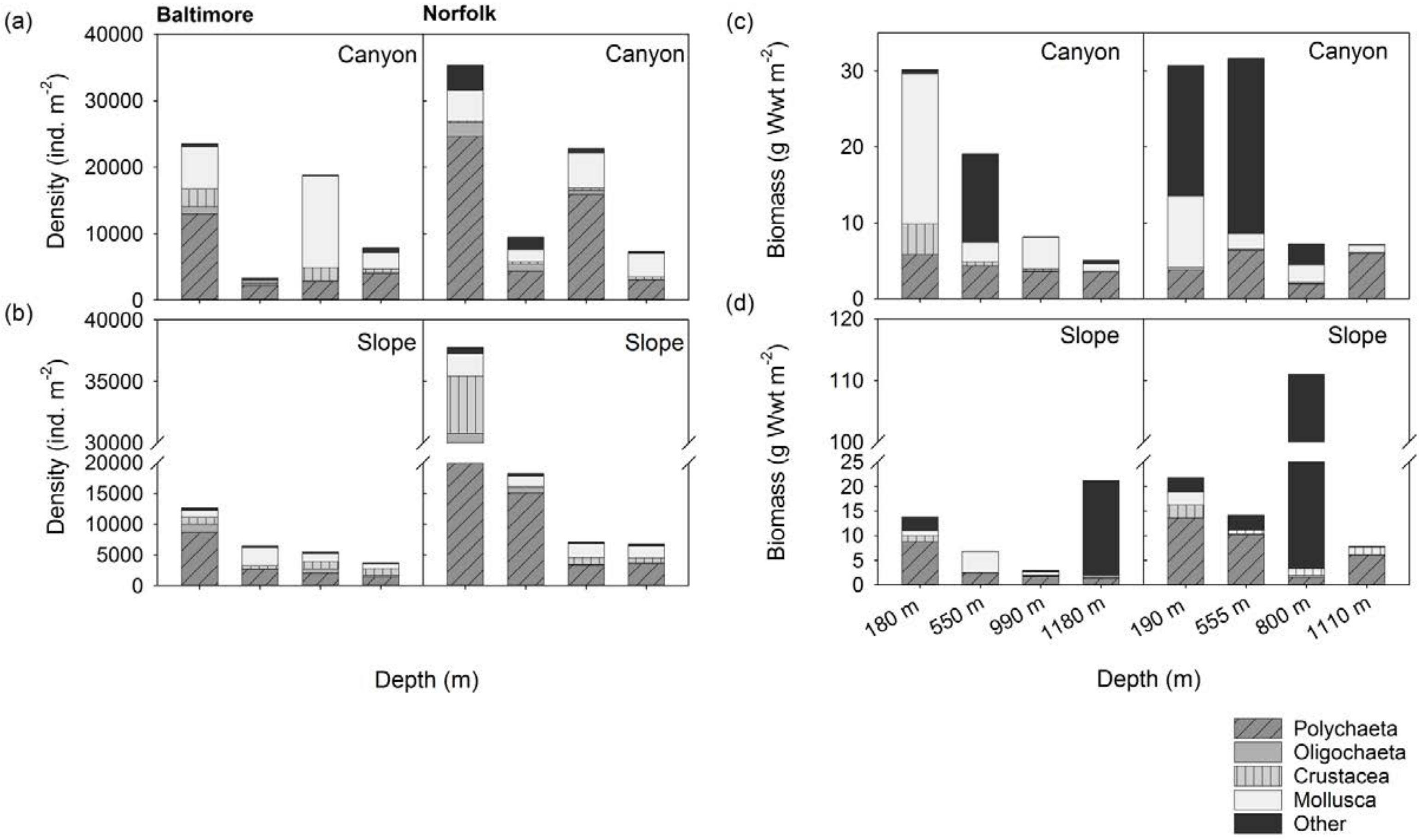
SM Figure 3. Boxcore photographs from samples taken in Norfolk Canyon during May 2013.



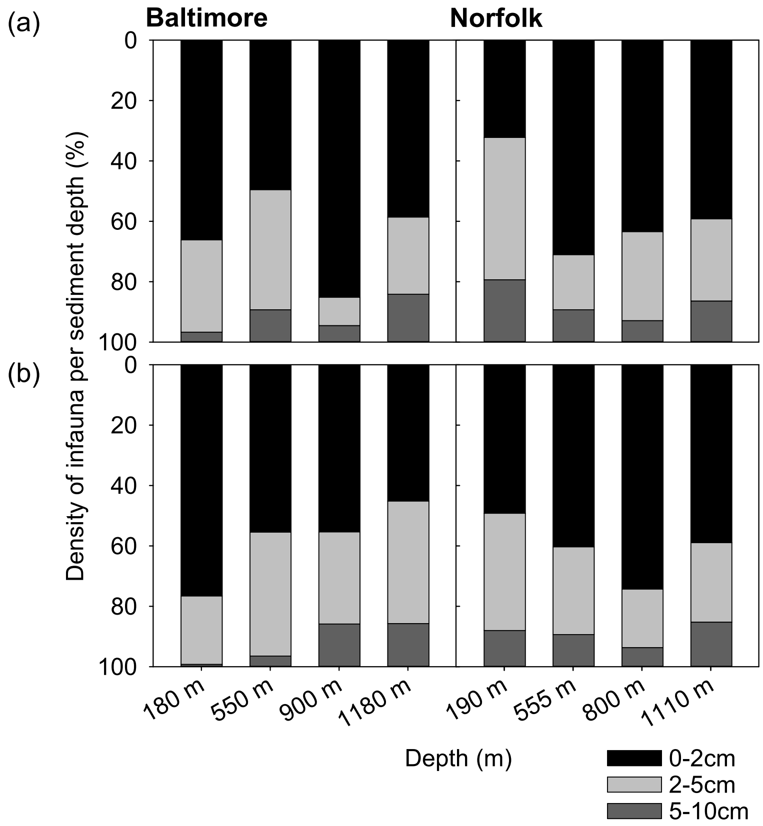
SM Figure 4. Boxcore photographs from samples taken in Norfolk adjacent slope during May 2013.



SM Figure 5. Rarefaction curves based on the estimated number of taxa for macrofaunal communities, a) Baltimore Canyon and adjacent slope habitats. b) Norfolk Canyon and adjacent slope habitats and c) data from both canyons and slopes.



SM Figure 6. The mean proportion (%) of higher macrofauna taxa (phyla) based on abundance (ind. m^{-2}) data in Baltimore and Norfolk canyons (a) and slopes (b). The mean proportion (%) of higher taxa (phyla) based on biomass (g Wwt^{-2}) data in canyons (c) and slopes (d).



SM Figure 7. Vertical distribution of macrofauna (ind. m^{-2}) within 0-2 cm, 2-5 cm and 5-10 cm sediment layers from the Baltimore and Norfolk canyons (a) and slopes (b).

Chapter 4

Submarine canyons as centres of bioturbation activity and distinct ecosystem functioning

Robertson CM[1], Demopoulos AWJ[2], Bourque JR[2], Mienis F[3],

Duineveld GCA[3], Lavaleye MSS[3], Koivisto RK[1], Brooke SD[4], Ross SW[5],

Rhode M[5] and Davies AJ[1]

[1] Bangor University, School of Ocean Sciences, Bangor, UK. [2] U.S.G.S. Wetland and Aquatic Research Centre, Gainesville, USA. [3] NIOZ Royal Netherlands Institute for Sea Research and Utrecht University P.O. Box 59, 1790 AB Den Burg, the Netherlands. [4] Florida State University, Coastal and Marine Lab, St Teresa, USA. [5] UNC-Wilmington, Center for Marine Science, Wilmington, USA.

Author contributions

CMR led the design of experiments and writing of the manuscript, to which all authors contributed. CMR, AWJD, JRB, FM, GCAD, MSS, SDB, SWR and MR contributed to shipboard sampling. CMR and RKK processed boxcore samples for infauna. MSS provided taxonomic expertise. FM processed biogeochemical data from boxcore samples. CMR conducted all statistical analyses.

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1 Abstract

The deep-sea benthos occupies more than three quarters of the planet's surface, yet our knowledge of how benthic communities contribute to ecosystem processes is still in infancy. Submarine canyons are known as conduits of organic matter and sediments from shelf to abyssal plains and are often associated with distinct macrobenthic communities, enhanced diversity and standing stocks compared to neighbouring slope environments. However, whole community canyon system studies assessing how these communities function and contribute to important deep-sea sedimentary ecosystem processes are lacking. To investigate how environmental conditions within canyons can alter ecosystem function, this study examined the functional differences between two canyons and adjacent slopes macrofaunal communities in the Mid-Atlantic Bight region in the western north Atlantic. A total of 49 trait modalities across 10 biological traits were used and showed that higher functional richness was present within upper and middle canyon communities compared to slope communities across the studied depth gradient. Lower canyon communities (800-900 m) were less functionally rich, a feature attributed to substantial biomass contribution of opportunistic and dominant taxa that benefited from organically-enriched sediment in the canyons. Bioturbation potential was higher in the canyons than adjacent slope, especially within Baltimore Canyon, and was attributed to the high affinities for surface and subsurface sediment modifiers and sediment ingestion or filter-feeding bioturbators. The trait affinities within canyons showed propensity for sediment reworking to greater depths, suggesting that canyon communities may enhance nutrient fluxes and burial of accumulated organic matter. The findings confirm that enhanced macrofaunal community ecosystem function and higher bioturbation occurred within the canyons compared to the adjacent slopes and provides new insight into the distinct functional roles found within canyon and slope macrofauna.

2 Introduction

Many studies in deep-sea benthic ecology have focused on describing the variation in species composition, abundance and biomass, and in some cases have related how such patterns are shaped by environmental factors (e.g. Levin & Dayton, 2009; Woolley et al., 2016). While these descriptive accounts are invaluable for describing communities, monitoring change or for assessing seabed status, insight into the functional properties of benthic assemblages is needed to establish the scale and resilience of services provided by deep-sea ecosystems (Leduc et al., 2013; Mengerink et al., 2014; Thurber et al., 2014). However, the functional characteristics of deep-sea macrofaunal assemblages remains largely undescribed, unsurprising perhaps, given that these communities are often poorly studied and many are undescribed.

Early studies on polychaete feeding guilds (Dauer, 1984; Fauchald & Jumars, 1979) were among the first to utilise biological characters as variables in community functional analysis. Several approaches have since been proposed for assessing the functioning of benthic assemblages, including trophic group analysis (Desrosiers et al., 2000; Roth & Wilson, 1998), functional group analysis (Padilla & Allen, 2000), integrative indices such as the index of biotic integrity (Borja et al., 2000) and estimates of functional diversity, evenness and redundancy (Mason et al., 2005). However, in deep-sea ecosystems, contemporary functional analyses have seldom been applied (Danovaro et al., 2008; Levin et al., 2017). Two recently proposed approaches for enhancing our understanding of the ecological functioning of marine benthic communities are indices describing functional diversity (Botta-Dukát, 2005; Laliberté & Legendre, 2010; Mason et al., 2005; Petchey & Gaston, 2002; Villéger et al., 2008) and biological traits analysis (BTA), (Bolam & Eggleton, 2014; Bremner et al., 2006a, 2006b; Solan et al., 2009).

Following Mason et al. (2005), functional diversity (FD) can be defined as a measure of the distribution of species, and their abundances or biomass, in the functional space of a given community (Petchey & Gaston, 2002). FD uses indices that quantify how species differ from each other according to their defined functional traits (Laliberté & Legendre, 2010; (Villéger et al., 2008). Several proposed components that describe the different facets of functional diversity are, 1) functional richness (FRic), the amount of niche space filled by species in a community, that is how much of a resource gradient could be exploited by the community and is often positively correlated with the number of species (Schleuter et al., 2010). 2)

Functional evenness (FEve), the evenness of abundance or biomass distribution in niche space, i.e. the degree to which the functions of different taxa overlap along a resource gradient, with high evenness indicating a regular distribution and low indicating clustered. 3) Functional divergence (FDiv), the degree to which abundance distribution in niche space maximises divergence in functional traits within the community, i.e. are the traits within the community clustered at certain locations along a resource gradient (Mason et al., 2005).

BTA defines the traits of a particular species by assigning available information such as life history, morphological and behavioural characteristics, which can indicate aspects of the functional role of the species within an assemblage (Bolam & Eggleton, 2014; Bremner, 2008; Bremner et al., 2006a; Lavorel & Garnier, 2002). Traits can be grouped into two broad categories (Hooper et al., 2005). 1) Functional effect traits, those that affect ecosystem properties and processes (e.g. body-size and behavioural traits), and 2) functional response traits, those that maintain species' responses to changes in the environment (Lavorel & Garnier, 2002; Hooper et al., 2005). For example, a well-known effect trait of soft sediment macrofaunal communities is the propensity for sediment bioturbation (Biles et al., 2002; Meysman et al., 2003, 2006). Bioturbation is the biogenic modification of sediments through particle re-working (Queirós et al., 2013), e.g. burrow ventilation, sediment ingestion, surficial mixing or upward and downward conveying, and therefore is a key effect trait, mediating important geochemical processes in marine systems (Volkenborn et al., 2007). Traits that redistribute sediments and organic material are fundamentally linked to nutrient and oxygen exchange at the sediment-water interface (Dauwe et al., 1998) and sedimentary biogeochemical processes (Díaz & Rosenberg, 1995; Widdicombe et al., 2000).

One recently suggested metric that, allows for the investigation of effect traits, specifically sediment reworking, is bioturbation potential, BP_c (Queirós et al., 2013). BP_c is an index that describes the potential contribution of benthic macrofauna to sediment turnover using biological traits, that determine sediment bioturbation (Solan et al., 2004b). The traits selected were sediment mobility; the propensity to move through sediment (Mi), and sediment reworking or mode of sediment turnover (Ri). These are two traits that are known to regulate biological sediment mixing and represent key components of bioturbation activity (Solan et al., 2004a, 2004b). BP_c is not a direct measure of the process of bioturbation, rather, BP_c provides an estimate of the potential of a community to contribute to bioturbation and offers a means to estimate the extent to which benthic communities are likely to affect important ecosystem properties that underpin ecosystem functioning (Queirós et al., 2013).

While approaches such as BTA, FD and BP_c have the potential to offer new insight into the relationship between communities and ecosystem processes. They are hindered by an incomplete understanding of the functional ecology of many species. In particular, the relationship between some traits and community function is often poorly defined, which greatly limits the ability to identify the causative effects of benthic processes (Bolam et al., 2015; Bolam & Eggleton, 2014). At present there is no accepted methodology for selecting traits reflecting important community functionality (Bolam & Eggleton, 2014; Marchini et al., 2008), although most studies use traits that account for taxon life history, morphological and behavioural characteristics (Bolam & Eggleton, 2014), and assign trait affinities using fuzzy approaches (Bremner et al., 2006b, Chevernet et al., 1994).

Many studies have shown that highly distinct and variable benthic communities are not uncommon in outer continental margins. In submarine canyons, species patterns are driven by high levels of habitat heterogeneity (McClain & Barry, 2010), enhanced hydrodynamic drivers (Romano et al., 2013; Sánchez et al., 2014), the accumulation of organic matter (Amaro et al., 2015) and sediment dynamics (Puig et al., 2014). However, there is a paucity of deep-sea studies linking biodiversity, community ecosystem function and environmental processes. This study utilised FD indices, BTA and BP_c to assess the functional ecology of macrofaunal communities within a well-studied canyon and slope system. Three hypotheses were tested; 1) macrofaunal functional diversity, evenness and divergence differ between canyon and adjacent slope habitats, 2) the key macrofaunal community biological traits differ between canyon and adjacent slope habitats, largely driven by traits that influence activities such as bioturbation; and 3) community bioturbation potential will increase in areas that are enriched in organic input.

3 Materials and Methods

3.1 Study site and sample collection

Baltimore and Norfolk submarine canyons are located on the western North Atlantic continental margin, approximately 125 km from the states of Delaware and Virginia in the U.S.A. They are two of the four largest submarine canyons on the Mid-Atlantic Bight (Obelcz et al., 2014), an area known for high organic inputs and dynamic oceanographic patterns (Csanady et al., 1988; DeMaster et al., 1994; Rex & Etter, 2010; Schaff et al., 1992; Yoder, 1985). The two canyons are relatively well-studied in terms of megafauna and epifauna (Hecker et al., 1983) and hydrodynamics (Gardner, 1989a, 1989b), especially when compared to other MAB canyons. These two canyons have distinct sedimentary and current regimes which support several deep-sea coral species on steep-sided canyon walls (Brooke et al., 2017; Ross et al., 2017). However, studies of the MAB canyon soft sediment macrofauna are lacking. The two canyons share the same water masses, leading to similar depth-temperature and depth-salinity gradients, but experience different hydrodynamic conditions due to differences in canyon morphology (See Chapter 2). Mean current speeds in Baltimore are approximately half that at comparable depths in Norfolk Canyon, both have benthic nepheloid layers and are more enriched in carbon and nitrogen than adjacent slopes (See Chapters 2 and 3). Norfolk slopes and canyon habitats are more enriched than at Baltimore, which in both canyons represented a factor in causing considerable community disturbance (See Chapter 3). Therefore, Baltimore and Norfolk canyons and slopes provide an ideal setting for investigating the relationship between benthic community functioning along disturbance, enrichment and depth gradients.

Sample collection utilised two NOAA vessels; the *Nancy Foster* in August 2012 and *Ron H. Brown* May 2013. In total, 48 box cores (NIOZ designed enclosed box-corer, 0.07 m^2 surface area) were collected along canyon and adjacent slope habitats for biological community and sedimentary analyses at approximately 180 m, 550 m, 900 m and 1200 m (Table 1). See Chapter 3 for a full description of the sampling design and sample processing. In brief, samples were rinsed to remove formaldehyde preservative (4 %, buffered seawater) and separated from the sediment using a 300 μm sieve. Specimens were identified and enumerated under stereo and compound microscopy, to family taxonomic level or as near to as possible and stored in 70 % industrial methylated spirit. Wet weight to the nearest 0.0001 g was determined after blotting away excess alcohol, providing taxa-level biomass standardized to per unit area (represented as g Wwt m^{-2}).

3.2 Biological Trait Analysis

Macrofaunal community functioning was characterised using a suite of 10 biological traits, sub-divided into 49 trait modalities (Table 2), adapted from the approaches used by Bolam et al. (2014) and Bremner (2006b). Traits were selected either for their importance for the structure and functioning of the benthic system or for their sensitivity to changes in environmental variables. Almost all taxa were matched with traits in the database, however, in the absence of published information on taxa life histories, as is common for many deep-sea macrobenthic taxa, information was adapted from closely-related species at the nearest taxonomic level (Bolam & Eggleton, 2014; Chevenet et al., 1994; Rijnsdorp et al., 2016). These mostly included deep-sea specialist isopods, polychaetes and various bivalve families (SM Table 1). An additional chemoautotroph modality was added to the feeding guilds trait to account for chemosynthetic strategies of the Lucinidae, Thyasiridae and Solemyidae bivalve families and the Siboglinidae polychaete family.

Each trait comprised a series of qualitative or quantitative modalities, which account for the multi-faceted behaviours and functioning of macrofaunal assemblages. To assign these, a ‘fuzzy’ logic weighting method was used (Chevenet et al., 1994), whereby a scoring from 0–3; zero for no affinity of taxa to a trait modality to 3 (high affinity). This allowed for a functional characterisation of individual taxa. Codes were converted to proportions of trait modalities per taxa and multiplied by the taxa biomass per taxa per unit area per station (at family level or as near possible), thus incorporating the standing stock of each macrofaunal taxa into the trait analysis. The biomass data were $log(x+1)$ transformed prior to analysis to prevent dominant taxa masking responses of lower biomass taxa (Warwick & Clarke, 1994). Biomass data were used, as opposed to macrofauna abundance because biomass is thought to have greater influence on community ecosystem function than abundance alone (Bolam & Eggleton, 2014; Bremner, 2008).

3.3 Bioturbation Potential

Bioturbation potential (BP_c) is an index describing the potential contribution of benthic macrofauna to sediment turnover using specific biological traits that determine sediment bioturbation (Solan et al., 2004a). The traits selected were sediment mobility, which is the propensity to move through sediment (*Mi*), and sediment reworking or mode of sediment turnover (*Ri*). These are two traits known to regulate biological sediment mixing and represent key components of bioturbation (Solan et al., 2004a, 2004b). BP_c is thus not a direct measure of the process of bioturbation. Rather, BP_c provides an estimate of the potential of a community to bioturbate, and as such the extent to which benthic communities are likely to affect important ecosystem properties that underpin ecosystem functioning (Queirós et al., 2013). Standardised scores for all taxa were obtained from Queirós et al (2013), with each taxon scored on categorical scales reflecting increasing mobility from 1 (fixed tube-dwellers) to 4, (free-living, via a burrow system) and increasing sediment reworking; 1 (limited to sediment-water interface) to 5 (regenerators, actively excavating sediment at depth to surface). The index utilised individual taxa density (A_i, ind. m^{-2}) and biomass (B_i, g Wwt m^{-2}) in a sample, for each individual taxa (BP_i), where the sum of all taxa represent whole community bioturbation potential (BP_c):

$$BP_C = \sum_{i=1}^{n} \sqrt{\frac{B_i}{A_i}} \times A_i \times M_i \times R_i$$

3.4 Data analysis

Univariate and multivariate statistics were performed using PRIMER (PRIMER_E Ltd) statistical software version 6.0 with the PERMANOVA+add-on (Anderson et al., 2008; Clarke & Gorley, 2006). Because PERMANOVA is sensitive to differences in multivariate dispersion among groups, the PERMDISP routine was used to test for homogeneity of dispersion when significant factor effects were found (Anderson et al., 2008).

3.4.1. Functional Diversity

Multidimensional functional diversity (FD) indices were calculated from trait modality scores for each taxon and weighted by taxon biomass. Functional richness (FRic and Rao’s Q), functional evenness (FEve) and functional divergence (FDiv) (Villéger et al., 2008) were calculated using the ‘FD’ package (Laliberté & Legendre, 2010), in the open-source R software. Differences in functional diversity indices across site, habitat and depths were assessed using univariate PERMANOVA, and pairwise comparisons. The 3-factor model used the following *a priori* defined factors habitat (Canyon vs Slope, *ha*), site (Baltimore vs Norfolk, *si*), and depth levels 1-4 (1: 180-190 m, 2: 550-555m, 3: 800-900 m, 4: 1110-1180 m). FD indices were normalised prior to the generation of Euclidean distance resemblance matrices. Where FD indices failed homogeneity of variance tests (PERMDISP $p < 0.05$), a *log*(x+1) transformation was applied. Even after transformation, functional divergence (FDiv) did not meet the assumptions of PERMANOVA and was omitted from analysis.

3.4.2 Biological Traits

Biomass-weighted community biological traits were visualised by hierarchical cluster analysis using Euclidean distance resemblance measures, with an integrated heat map ordered based on Whittaker's index of association among pairs of modalities, across habitats and site along the depth gradient. Trait modality variables were constrained by average linkage hierarchical clustering of Pearson's correlations and displayed as a cluster dendrogram to define groups of functional trait modalities. High values indicate high to medium levels of trait affinity for a particular trait modality operating in the sampled community, whereas low values indicate low or zero affinity levels. Differences in individual biomass-weighted biological traits were assessed by multivariate PERMANOVA, as a function of three *a priori* factors (crossed and fixed levels; as described in section 3.5.1), with PERMDISP tests, using log(x+1) transformed data (biomass m^2) and Bray-Curtis similarities, followed by pairwise comparisons where appropriate. Even after transformation, morphology and mobility traits did not meet the assumptions of PERMANOVA and were omitted from analysis. A Similarity of Percentages analysis (SIMPER) was used to identify the biological traits most responsible for characterising canyon and slope communities and for discriminating between habitats and depths.

3.4.3 Bioturbation Potential

Differences in community bioturbation potential (BP_c) was assessed using a three-way crossed multivariate PERMANOVA and pairwise comparisons (crossed and fixed levels; as described in 3.4.1). Community BP_c data were square-root transformed and used to generate Bray-Curtis similarity resemblance matrices. Where univariate variables failed homogeneity of variance tests, (PERMDISP $p < 0.05$), a weighted dispersion transformation (Clarke et al., 2006) was performed, followed if necessary, by removal of extreme outliers (after nMDS visual inspection).

3.4.4 Functional assemblages across environmental gradients

To investigate the relationship between community functioning, BP_c and environmental variables, Principle Co-ordinate Ordination (PCO, based on Euclidean distance) and distance-based linear models (DISTLM) were used. The environmental parameters included percent carbon and nitrogen, chlorophyll *a*, $\delta^{13}C$, $\delta^{15}N$, percent sand, sediment biological mixing depth, (Z_{mix}), sediment accumulation rate (ω) and depth (Table 3, Chapter 3 SM Table 2). Prior to analysis of environmental parameters, data were assessed for collinearity using Draftsman plots and Spearman's rank correlation matrices (Clarke & Gorley, 2006). Highly-correlated environmental parameters ($R^2 > 0.95$) where removed and where necessary, data were transformed using $log(x+0.1)$ and normalised (Anderson et al., 2008). The influence of environmental drivers on canyon and slope community functional trait assemblages was then assessed via DISTLM. This analysis performs nominal tests of each variable's explanatory power on the community assemblage, building a multivariate statistical model for all possible combinations of predictor variables. Models were run selecting Akaike's Information Criterion (AICc) and the *BEST* model procedure. DISTLM results were overlaid onto biological traits ordination plots (PCO) as environmental variable Eigenvectors, displaying the significant linear regressions.

4 Results

4.1 Functional Diversity

The four functional diversity indices used in the study gave varying results for canyon and slope communities, the analysis constrained the 49 trait modalities to 10 PCO axes, explaining 62 % of the functional trait space within canyon and adjacent slope communities. Functional richness (FRic) varied across the depth gradient, with Baltimore Canyon and slope having visibly greater functional richness compared to Norfolk Canyon and slope (Figure 1a). However, only the upper Baltimore Slope showed significantly higher functional richness than the Norfolk slope (Figure 1a, Table 4), and no significant differences were detected within the Norfolk site (SM Table 2). Baltimore slope showed steady decrease in FRic with depth, with significantly lower functional richness below 900 m depth compared to the upper slope (Table SM 2). The pattern in Baltimore Canyon was more variable, with significantly suppressed functional richness within at 900 m compared to 180 and 1180 m (SM Table 2). Rao's Q, which weights modalities with biomass, demonstrated a more consistent pattern across the two sites when compared to FRic (Figure 1b). Canyons exhibited a significant suppression in Rao's Q functional richness at 900m in Baltimore Canyon (Figure 1b, Table 4, SM Table 2) and 190 m in Norfolk Canyon when compared to their respective slopes. Functional evenness (FEve) was significantly higher on the slopes than in the canyons, with the two deepest sites having a greater evenness than 180/190 m and 550/555 m (Figure 1c, Table 4, SM Table 2). Biomass-weighted functional divergence (FDiv) did not differ significantly across sites, habits or depths (Figure 1d, Table 4).

4.2 Biological Trait Analysis

4.2.1 Multivariate trait analysis

Multivariate community BTA revealed significant differences in community trait assemblages between canyons and slopes, and across the depth gradient (Figure 2, Table 5). Overall, the Norfolk area had greater community functional affinity than the Baltimore area, Baltimore Canyon had greater affinity than its adjacent slope and canyons had greater affinity than adjacent slope at depths 180/190 m and 800/900 m (SM Table 3). Slopes in contrast had greatest affinities at shallower depths (180/190 m and 550/555 m) compared to those deeper (800/900 m and 1110/1180 m). Cluster analysis identified 11 distinct groups of functional affinities that characterised the sampled communities. Four of which were associated with differences in functional assemblages between canyons, slopes and depth (Figure 2 denoted by A-D).

Cluster A was comprised of 8 trait modalities that typified surface-deposit bioturbating taxa (bSurfaceDeposit), that had exoskeletons (mExoskeleton), were free living (lhFreeLiving) and long lived (L3-10). This cluster can be defined as a surface-deposit bioturbating community. Members of this group were most common within canyons at 180/190 m and 550/555 m. Cluster B consisted of 5 trait modalities, which included soft-bodied taxa (mSoft) that lived in the upper sediment (spInfauna0-5), had direct benthic larval development (ldBenDirect) and had medium longevity (L1-3). These features define cluster B as a fast-growing shallow-living infauna community. The highest trait affinity associated with this group was found on slopes at 180/190 m and 550/555 m depths. Cluster C was comprised of 3 trait modalities, typified by deep sediment-dwelling taxa (spInfauna6-10), that suspension fed (fSuspension) and lived within burrows (lhBurrowDwelling). The cluster can be defined as a burrowing suspension feeding community, which had higher association with upper canyon communities compared to slope communities, although these communities were also found on the upper Norfolk slope. Finally, Cluster D was comprised of 6 trait modalities which typified, surface-deposit feeding taxa (fSurfaceDeposit) that were diffusive-mixing bioturbators (bDiffusiveMixing) and were mobile burrowers (mobBurrower). They were generally large (sr101-200) and also included subsurface-deposit feeders (fSubsurfaceDeposit) and tube-dwellers (lhTubeDwelling). Cluster D can be defined as a large burrowing and subsurface-feeding community. Cluster D had the lowest trait modality scores and were associated mostly with upper Norfolk slope assemblages.

4.2.2 Individual trait analysis

There was high variability in the distribution of biomass-weighted trait modalities across habitats and depth as indicated by univariate analysis (Figure 3, Table 6). Overall, between areas, Norfolk was represented by assemblages that had generally had a higher functional trait affinity for most of the individual traits; size range, longevity, larval development, egg development, life habit, sediment position and feeding mode compared to the Baltimore study site (Figure 3, SM Table 4). Within the two areas, Baltimore Canyon had communities with higher trait affinities compared to its adjacent slope (Figure 3, SM Table 4). Longevity generally decreased with depth across both study sites, particularity between upper Baltimore and Norfolk canyons (SM Table 4). Between slopes, Norfolk had larger longevity scores than

Baltimore slope. Pairwise tests revealed that only Baltimore Canyon 900 m communities had larger longevity trait scores compared to slope communities (SM Table 4), driven by the dominating long-lived bivalve taxa (Yoldiellinae and Thyasiridae). Feeding mode also changed across the depth gradient, with canyons generally having higher predatory feeding modality in middle canyon communities compared to the adjacent slopes (Figure 3). Feeding mode affinity differed in lower depth communities, specifically between and canyon and slope communities, but also among lower slopes. (Figure 3, SM Table 4). There was also greater incidence of bioturbation, including taxa that were classed as surface-deposition, modalities between lower Baltimore Canyon and slope but not for Norfolk Canyon and slope (Figure 3, SM Table 4).

4.2.3 Analysis of similarity

SIMPER analysis identified the community functional trait modalities that contributed to the similarity and dissimilarity between canyon and slope habitats and among depth groups (Table 7). The analysis identified modalities that mirrored those comprising the four functional clusters that were identified in multivariate analysis (Figure 3 and section 4.2.1). Both canyons shared similar functional assemblage similarity, although Baltimore Canyon 900 m communities showed the highest similarity (91 %) across the whole study. In contrast, Norfolk Canyon communities 555 and 800 m assemblages displayed the lowest similarities (Table 7). Differences in the top ranked (>4 %) trait modalities were evident between canyon and slope and along the depth gradient. In the lower Baltimore Canyon community (900 m), long lived (L3-10), surface-deposit feeding, sessile taxa (mobSessile), egg-brooding and planktotrophic larval development strategies (edSexualBroodEggs and ldPlanktotrophic) were widespread.

In other Baltimore Canyon depths, the most common trait modalities were planktotrophic larval development strategies, sessile taxa and surface-deposit bioturbators. In Norfolk Canyon, the most common modalities were similar, although long-lived taxa (L3-10) were most common, followed by planktotrophic larval development strategies, and surface-deposit bioturbators. This indicates that canyon functional assemblages are dominated by long-lived, sessile surficial-bioturbating taxa with planktotrophic larval dispersal methods, reflecting high species dominance (i.e. high biomass) of Lucinidae, Yoldiellinae and Thyasiridae bivalves and Ophiuroidea in Baltimore Canyon and the high dominance of Lucinidae and Ophioruidea in Norfolk Canyon (Table 7). Overall trait assemblage dissimilarity between canyons and the adjacent slopes was 45 % for Baltimore and 40 % for Norfolk (Table 7b). The surface-deposit bioturbation modality ranked highly at almost all depths and was the most commonly occurring modality contributing to the dissimilarity between canyons and slopes (Table 7b).

4.3 Bioturbation Potential

Analysis of the biomass-weighted community BP_c indicated a significant interaction between study sites, canyons and slope and the depth gradient for community BP_c (Table 4). Norfolk Canyon and slope communities exhibited significantly greater sediment bioturbation potential than in Baltimore Canyon and slope (with the exception of slope 800/900 m depth; Figure 4, SM Table 2). Generally, BP_c decreased across the depth gradient in both canyon and slope habitats, with the exception of a significant secondary peak at intermediate depth community in Baltimore Canyon (900 m; Figure 4, SM Table 2).

4.4 Functional assemblages across environmental gradients

Nine variables were used in distance based linear models (DISTLM) to test the influence of environmental variability on community functional trait assemblages. BP_c, sediment organic enrichment and depth all had significant effects on the functional traits exhibited by the communities (Tables 8 and 9, Figure 5). In both study sites BP_c was the most explanatory variable followed by depth and two organic enrichment variables; $\delta^{15}N$ for Baltimore (22.7 %) and % C for Norfolk (17.2 %). The multivariate regression model providing the best explanation for the observed differences in Baltimore functional traits between canyon and slope communities was a combination of BP_c, % C and sediment biological mixing depth, which explained 61 % of the total variation in community functioning among samples across two axes (Table 8b). The best explanatory model for the Norfolk study site was BP_c and $\delta^{15}N$ (62 %).

5 Discussion

It is generally accepted that changes in species diversity are associated with changes in the functioning of communities, but the relationship between these two aspects of community ecology remains largely unknown, especially in deep-sea ecosystems (Danovaro et al., 2008; Hooper et al., 2005; Naeem et al., 1994). This study examined, for the first time, the distribution of macrofaunal functional traits within two well-studied canyon and slope systems and provides an insight into how benthic community functional assemblages vary along disturbance and depth gradients. Overall, the findings indicate that substantial differences in macrofaunal functional diversity exist between canyons and adjacent slopes, with the most pronounced differences being evident in the shallower sampled communities. Community bioturbation potential (BP_c) was higher in canyon habitats than on slopes and represents a greater ability of canyon macrofauna to enhance sedimentary ecosystem processes. Higher benthic species richness has previously been shown to enhance functional richness (Danovaro et al., 2008), though increases in the expression of detritus ingestion, sediment reworking traits and hence enhancing organic matter remineralization (Solan et al., 2009).

5.1 Functional Diversity

Analysis of the functional diversity of the two canyons and their adjacent slopes revealed higher functional richness in upper and middle canyon communities compared to slope communities across the depth gradient. Higher upper canyon functional richness was attributed to the presence of large, long-lived, sediment-ingestion or filter feeding bioturbators, mainly via bivalves (Lucinidae and Periplomatidae), brittle-stars (Amphiuridae), sea-cucumbers (Phyllophoridae), and sea-stars (Astropectinidae). Lower canyon communities (800-900 m) were less functionally rich, a feature attributed to substantial biomass contribution of the opportunistic taxa Yoldiellinae and Thyasiridae bivalves and Cossuridae, Cirratulidae, Capitellidae polychaetes, which benefitted from the organically enriched sediment in the canyons. The measures of functional richness used in this study (FRic and Rao's Q) highlighted that despite their variability, some differences exist between the communities. Lower FRic at 900 m within Baltimore Canyon suggests some resource (likely organic matter) is not fully used (Mason et al., 2005), perhaps a result of the frequent replenishment of organic matter in lower canyon deposition areas (Harding and Dartmouth 1998; van Oevelen et al., 2011; Pusceddu et al., 2010). Additionally, this notion is mirrored by the depressed functional evenness in Baltimore Canyon (550-900 m), suggesting that the functional niche space, whilst occupied, is only partially filled and a portion of the space remains underutilised. Mason et al., (2005) noted that this can suggest a lowered state of competitive exclusion or community stability, which may allow for an increased risk of invasion by opportunists, a view supported in this study, by the high biomass and numerical dominance of the aforementioned, opportunistic taxa that thrive in disturbed areas (See Chapter 3).

5.2 Community functional assemblages

Our results provide an example of how community functional diversity contributes to ecosystem function across enrichment and depth gradients. Various studies have noted on the difficulty in making direct links between community biological trait expression and ecosystem processes in general, because of the lack of knowledge regarding the relationship between functional roles, abiotic and biotic interactions in benthic ecology (Bolam, 2013; Cadotte & Tucker, 2017; Gagic et al., 2015). Previous works have established that not all traits can be of equal importance (Bremner et al., 2003, Solan et al., 2004a, Frid et al., 2008). However, Frid et al. (2008) advocated the inclusion of all relevant traits in an analysis, although traits of particular reference to important functional processes for a habitat in question should be further interrogated. In this study, four distinct functional clusters were identified, that operated to various degrees, in different areas within the canyon and slope habitats (Figure 3).

Upper canyon assemblages were functionally distinct compared to the adjacent slope, especially at the Baltimore Canyon site. The four functional clusters (A-D, see Section 4.2.1 for description) describe the main community functional differences between canyons and slopes. Given that the trait modalities that made up these groups were not exclusively associated with any one particular taxon but were shared between many species present in the species pool, suggests some degree of functional redundancy, environmental filtering (Bremner et al., 2006a, 2006b) or inter-specific interaction (i.e. competition) may be prevalent within the sampled communities. Increased functional redundancy implies a more resilient and robust community, since high redundancy acts as a buffer against ecosystem function loss in the face of environmental disturbance (Folke et al., 2004). Recent work by Mori et al. (2013) recognises that differences in the trait vulnerability to environmental change can mean high redundancy does not necessarily ensure the preservation of ecosystem function and advocated the assessment of functional compensation in order to disentangle concepts of redundancy and insurance effects of biodiversity. Despite the complexity of multi-faceted functional ecology this study showed that functional community differences occur between canyons and adjacent slopes, and these functional differences are structured by sediment enrichment and depth gradients.

In most studies, surrogates of specific functions are applied due to incomplete knowledge of how traits link to processes (Violle et al., 2007). For example, bioturbation modalities are known to be associated with regulation of sediment nutrient fluxes and benthic-pelagic coupling (Volkenborn et al., 2007) and sediment pore-water oxygen fluxes (Widdicombe et al., 2000). This study focussed on traits that are known to be important in marine benthic processes, and thus are likely to capture traits that contribute to functions associated with soft sediments. The trait modalities operating within each functional cluster provided some insight into functions; however, the effective partitioning of traits into functional effect or functional response traits is difficult and remains a limitation in most marine BTA studies. Generally, traits associated with life history represent response traits (response to environmental changes), reflecting community colonisation, recruitment, dispersal and therefore community stability and resilience capabilities (Elmqvist et al., 2003; Folke et al., 2004). In contrast, traits associated with morphology, body size (Rakocinski, 2012) and behaviour (Bremner, 2008), represent effects traits (effect of ecosystem functioning), closely linked to ecosystem processes; a reflection of the ability of communities to utilise and augment environmental resources (Folke et al., 2004).

One confounding factor to note, is that the increased trait affinity in Baltimore slope 1180 m and Norfolk slope 800 m communities were the result of individual, large bodied Sipunculidae and Edwardsiidae species. This study utilised samples that were collected using a single model of box core. Several studies have highlighted that box cores under sample macrofaunal densities when compared to megacorers (Bett et al., 1994; Montagna et al., 2017), but they are capable of sampling far greater areas of seafloor and can capture the presence of larger and rarer taxa (Glover et al., 2008; Montagna et al., 2017). Such taxa may have substantial influence on ecosystem function, and their inclusion in such studies remains a topic of debate (Solan et al., 2004a; Hooper et al., 2005).

The BTA approach used in the present study utilised ten traits developed from shelf sea communities to characterise community function. This represents a good starting point in assessing functional ecology in the deep sea and performs better than single trait analytical approaches (e.g. feeding guilds). However, it is important to recognise that extensive sets of specific biological traits are needed to fully understand the functional nature of deep-sea communities, where species are often unique or ecologically specialised and may perform unknown functional roles. Furthermore, in establishing the functioning of deep-sea communities, as this study shows, it is important to demonstrate the environmental gradients that influence communities and how these correlate with community functioning and structure (e.g. Cadotte & Tucker 2017). Environmental filtering is often posited as a driving mechanism structuring communities and the presence or absence of species (Kraft et al., 2015; Mason et al., 2007; Mouchet et al., 2010). The differences between species niches and that inter-specific interactions such as competition, predation and growth rate (Cadotte & Tucker 2017) need to be accounted for, alongside underlying environmental conditions, before true assessment of community function can be attained.

5.3 Bioturbation Potential

The present study found that bioturbation traits were important aspects of canyon community functioning, differentiating between canyons and slopes across the depth gradient. Considerable differences in community bioturbation potential (BP_c) were found between canyon and slope habitats, which appear to be driven by observed enrichment and disturbance with canyons, particularly at 550 m and 900 m canyon communities. This was supported by sediment mixing depth (Z_{mix}), showing that deeper sediment mixing occurs in the canyons, likely due to coarser sediments and greater organic enrichment. Functional clusters A and B drove this higher bioturbation potential i.e. higher proportions of surface-sediment modifiers and sediment ingestion or filter feeding bioturbators. The mid-canyon areas (800-900 m), which were organically enriched, contributed to a secondary peak in BP_c and was most pronounced in Baltimore Canyon. The increased bioturbation was due to the high biomass and numerical dominance of taxa (i.e. Yoldiellinae, Thyasiridae) that expressed subsurface-dwelling sediment ingestion or filter-feeding bioturbating modalities. Norfolk Canyon enriched communities were also characterised by these trait modalities, however the main contributing taxa differed (i.e. Capitellidae and Yoldiellinae). Community traits present within deeper areas of the canyons suggest more quiescent environmental conditions, in alignment with sediment deposition areas (Chapter 2 and 3). The canyon community is actively reworking the sediment matrix to a greater depth and utilising a larger number of sediment modifying modalities, suggesting that these communities could have implications for enhanced nutrient fluxes, benthic-pelagic solute exchange and ultimately carbon storage through burrow ventilation and burial of accumulated organic matter (Aller, 1988; Teal et al., 2013; Volkenborn et al., 2007). Organic matter accumulation in the deep sea is associated with increased sediment working (DeMaster et al., 2002). However, this also increases sediment oxygen deficiency which in turn affects tube irrigation, vertical sediment position (Díaz & Rosenberg, 1995) as well as species richness, abundance and biomass (Gutierrez et al., 2000; Pearson & Rosenberg, 1978).

5.4 Conclusions

The deep-sea benthos is the most extensive of all habitats on Earth, occupying more than three quarters of the planet's surface, yet our knowledge of how benthic communities contribute to ecosystem processes is still in infancy. This study represents the first application of BTA and BP_c to benthic macrofauna communities within canyon and slope habitats. Our findings suggest that canyon ecosystems, as well as acting as centres of macrofaunal biomass, biodiversity, sediments and organic matter accumulation, foster communities that can enhance sediment reworking and hence, carbon storage within sediments. Applying BTA to such a system is strongly constrained by the amount of information available (Bolam, 2013; Gayraud et al., 2003). However, as evidenced, it can provide insight into types of functioning operating in the deep sea. Moreover, the method when applied to existing large-scale datasets and campaigns could substantially extend the amount of extractable knowledge yielded from traditional macrofaunal sampling efforts, furthering understanding of deep-sea ecosystem function.

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8 Tables and Figures

Table 1. Locations of sampling stations (decimal degrees) for samples collected in (a) Baltimore Canyon, (b) Baltimore Slope, (c) Norfolk Canyon and (d) Norfolk Slope. * = Boxcore reserved for geological / biogeochemical assessment in Baltimore. In Norfolk, a subcore was taken for these variables out of the macrofauna boxcore due to logistical constraints.

(a)

Baltimore Canyon

Date	Station	Depth (m)	Latitude	Longitude
19/08/12	NF-2012-019	189	38.243217	-73.8436
19/08/12	NF-2012-020*	189	38.243183	-73.84353
20/08/12	NF-2012-028	191	38.242817	-73.84352
20/08/12	NF-2012-029	191	38.242833	-73.84352
20/08/12	NF-2012-030	563	38.1661	-73.85018
21/08/12	NF-2012-032	563	38.166183	-73.85018
21/08/12	NF-2012-034	565	38.166217	-73.85007
21/08/12	NF-2012-035*	567	38.166267	-73.84998
22/08/12	NF-2012-046*	844	38.11722	-73.83532
22/08/12	NF-2012-045	840	38.11722	-73.8358
22/08/12	NF-2012-047	848	38.1174	-73.8348
23/08/12	NF-2012-049	844	38.11752	-73.83453
23/08/12	NF-2012-053*	1120	38.0709	-73.7783
23/08/12	NF-2012-055	1179	38.0724	-73.7732
23/08/12	NF-2012-056	1179	38.0724	-73.7732
24/08/12	NF-2012-062	1180	38.0721	-73.77337

(b)

Baltimore Slope

Date	Station	Depth (m)	Latitude	Longitude
24/08/12	NF-2012-064	168	38.06258	-73.86562
24/08/12	NF-2012-065*	170	38.06258	-73.86558
25/08/12	NF-2012-066	170	38.06258	-73.86562
25/08/12	NF-2012-067	168	38.06258	-73.86562
25/08/12	NF-2012-070*	515	38.04352	-73.80347
25/08/12	NF-2012-072	514	38.04352	-73.80344
25/08/12	NF-2012-076	510	38.04352	-73.80344
26/08/12	NF-2012-088	502	38.0436	-73.8032
26/08/12	NF-2012-082	990	38.01388	-73.7535
26/08/12	NF-2012-084*	990	38.013883	-73.7534
26/08/12	NF-2012-085	991	38.0139	-73.7534
26/08/12	NF-2012-087	991	38.0139	-73.7534
27/08/12	NF-2012-090	1185	37.9774	-73.6694
27/08/12	NF-2012-091*	1185	37.997383	-73.66938
27/08/12	NF-2012-092	1187	37.97742	-73.6694
27/08/12	NF-2012-093	1186	37.97742	-73.6694

Table 1 cont…

(c)

Norfolk Canyon

Date	Station	Depth (m)	Latitude	Longitude
11/05/13	RB-2013-046*	195	37.09475	-74.74658
11/05/13	RB-2013-047	195	37.09478	-74.74657
11/05/13	RB-2013-048	195	37.09478	-74.74657
11/05/13	RB-2013-043*	559	37.07597	-74.66063
11/05/13	RB-2013-044	557	37.07597	-74.66058
11/05/13	RB-2013-045	558	37.07595	-74.66058
10/05/13	RB-2013-040*	805	37.04273	-74.62917
10/05/13	RB-2013-041	803	37.04275	-74.6292
10/05/13	RB-2013-042	804	37.0428	-74.62925
10/05/13	RB-2013-038*	1110	37.03863	-74.57986
10/05/13	RB-2013-039	1110	37.03868	-74.57995
15/05/13	RB-2013-077*	1108	37.03875	-74.57964

(d)

Norfolk Slope

Date	Station	Depth (m)	Latitude	Longitude
11/05/13	RB-2013-049*	187	37.02307	-74.64577
11/05/13	RB-2013-050	187	37.02445	-74.64729
11/05/13	RB-20 13-051	187	37.02415	-74.64594
12/05/13	RB-2013-054*	549	37.0158	-74.5782
12/05/13	RB-2013-055	549	37.0158	-74.57815
12/05/13	RB-2013-056	548	37.0158	-74.57817
13/05/13	RB-2013-059	790	37.00903	-74.56478
12/05/13	RB-2013-060	790	37.00905	-74.56472
14/05/13	RB-2013-069*	804	37.00902	-74.56496
14/05/13	RB-2013-071*	1118	37.00577	-74.53373
15/05/13	RB-2013-073	1105	37.00577	-74.5337
15/05/13	RB-2013-075	1103	37.00588	-74.53365

Table 2. Traits and associated modalities used in biological trait analysis of canyon and adjacent slope macrofauna communities (Adapted where required from Bolam et al. (2014)). † indicates behavioural traits thought to be directly related to ecosystem processes (i.e. functional effect traits). Size range is included given its influence on bioturbation processes in soft sediments.

Trait	**Modality code and values**	**Definition and *significance***
Size range †	sr<10 sr11-20 sr21-100 sr101-200 sr201-500 sr>500	Maximum size (mm) that the taxon has been reported to reach during adult stage (as individuals or colonies). *Size has a direct influence on the movement of organic matter within the benthos. Larger bodied organisms retain a greater amount of organic material (i.e. low turnover) compared with those with smaller bodies (high turnover) (Pearson & Rosenberg, 1978).*
Morphology	mSoft mTunic mExoskeleton mCrustose mCushion mStalked	The external morphological characteristics of the taxon. Soft: External tissue is soft and not covered by any form of protective casing. Tunic: Body is covered by a protective outer tissue made up of, for example, cellulose, e.g., tunicates. Exoskeleton: Body is covered or encased in either a thin chitinous layer or calcium carbonate shell. Crustose: Body is hard and forms a thin layer over either the substratum and/or flora/fauna. Cushion: Body is soft and forms a cushion-like layer over the substratum and/or flora/fauna. Stalked: Typically attached and erect. *Morphology has an influence on multiple levels of function, ranging from the behaviour, feeding and position of organisms within an ecosystem, as well as their ability to tolerate disturbance.*
Longevity	L1 L1-3 L3-10 L>10	The maximum reported lifespan of the adult stage (years). *Longevity typically reflects the level of investment into somatic growth, over reproductive or defensive resource allocation (Pearson & Rosenberg, 1978). Longevity is also linked to the age of sexual maturity.*

Larval Development	ldPlanktotrophic ldLecithotrophic ldBenDirect	The strategy of larval dispersal. Planktotrophic: larvae feed and grow in the water column. Lecithotrophic: larvae grow in the water column and feed on yolk reserves during early stages. Benthic (direct): larval stage missing (eggs develop into juvenile forms) or larvae are limited to the seabed. *The type of larval development affects the ability of taxa to recover from disturbance, planktonic recruitment may lead to faster recolonisation following longer periods in the water column than lecithotrophic (typically only a short pelagic phase) and direct development which only has limited dispersal range (Thrush & Whitlatch, 2001).*
Egg Development	edAsexualBudding edSexualShedEggsPelagic edSexualShedEggsBenthic edSexualBroodEggs	The means of dispersal according to egg stage and reflects the potential for damage due to disturbance. Asexual Budding: Species that can reproduce asexually (e.g. fragmentation, budding, epitoky), often in addition to some form of sexual reproduction. These species can often increase in number rapidly following disturbance. Sexual Shed Eggs Pelagic: Eggs are released into the water column, and have the potential to disperse widely. Sexual Shed Eggs Benthic: Eggs are released onto or into the bed, and can be either free or maintained on bed by mucous or other means. These eggs would be more concentrated over a smaller spatial area. Sexual Brood Eggs: Eggs are maintained by adult for protection, either within parental tube or within body cavity and have limited dispersal range beyond the movement of the adult. *Egg development strategy influences rates of recruitment, colonisation of a community and is an important aspect as to how a community will recover after a disturbance.*
Life Habit †	lhTubeDwelling lhBurrowDwelling lhFreeLiving lhCreviceHoleUnder lhEpiEndoZoicPhytic lhAttachedSubstratum	The exposure of the adult stage to the environment, may also indicate potential for evading disturbance. Tube Dwelling: Tube may be lined with sand, mucus or calcium carbonate. Burrow Dwelling: Lives within a permanent or temporary burrow. Free Living: Not limited to any restrictive structure at any time. Able to move freely within and/or on the sediments. Crevice Hole Under: Adults are typically cryptic, predominantly found inhabiting spaces made available by coarse/rock substrate and/or tubes made by other fauna. Epi Endo Zoic Phytic: Lives on other organisms. Attached Substratum: Attached to larger substrata or rock.

		Life habits typically influence nutrient cycling and oxygen exchange that results from sediment reworking by organisms, e.g. enhanced exchange between the pore water and the overlying water column owing to burrow flushing (Volkenborn et al., 2007).
Sediment Position †	spInfaunaSurface spInfauna0-5 spInfauna6-10 spInfauna>10	Typical living position within the sediment (cm). Infauna Surface: Found on or just above the seabed. Infauna 0-5: Shallow macrofauna taxa whose bodies are found almost exclusively below sediment surface between 0 and 6 cm sediment depth. Infauna 6-10: Mid-depth macrofauna taxa whose bodies are partly or exclusively found below sediment surface at a depth generally between 6 and 10 cm sediment depth. Infauna > 10: Deep macrofauna taxa whose bodies are partly or exclusively found below sediment surface at a depth greater than 10 cm sediment depth. *Sediment position has implications for nutrient cycling oxygen exchange and sediment biogeochemistry through the burrowing of fauna at sediment depth. Sediment position impacts sediment mobility through behaviours such as bio-irrigation of burrows which impacts on sediment oxygen profiles. Sediment position impacts sediment vertical profiles.*
Feeding Mode †	fSuspension fSurfaceDeposit fSubsurfaceDeposit fScavengerOpportunist fChemo fPredator fParasite	How the taxa feeds. Suspension: Taxa that remove particulate food taken from the water column, generally via filter feeding. Surface Deposit: Taxa that actively remove detrital material from the sediment surface. Subsurface Deposit: Taxa that remove detrital material from within the sediment matrix. Scavenger Opportunist: Taxa that feed upon dead animals. Chemo: Taxa that have complete or partial chemosynthetic autotrophy. Predator: Taxa that actively predate upon other animal taxa (including the predation on smaller zooplankton). Parasite: Taxa that have a parasitic mode of life on other invertebrate species. *Feeding mode has links with inter-specific interactions such as competition and predation, as well as ecosystem processes, such as carbon transfer, sediment-water exchange and sediment biogeochemistry.*

Mobility †	mobSessile mobSwim mobCrawlCreepClimb mobBurrower	How the taxa moves. Sessile: Taxa in which the adults have no, or very limited, mobility either because they are attached or are limited to a (semi) permanent tube or burrow. Swim: Taxa in which the adults actively swim in the water column (many usually return to the bed when not feeding). Crawl Creep Climb: Taxa capable of some, generally limited, movement along the sediment surface or rocky substrata. Burrower: Taxa in which adults are capable of active movement within the sediment. *Mobility typically has influence on nutrient cycling and oxygen exchange that results from sediment reworking by organisms. E.g. The enhanced exchange between the pore water and the overlying water column owing to burrow flushing (Volkenborn et al., 2007).*
Bioturbation †	bDiffusiveMixing bSurfaceDeposition bUpwardConveyor bDownwardsConveyer bNone	The ability of the taxa to rework sediment. Diffusive Mixing: Vertical and/or horizontal movement of sediment and/or particulates. Surface Deposition: Deposition of particles at the sediment surface resulting from e.g., defecation or egestion (pseudofaeces) by, for example, filter and surface deposit feeding organisms. Upward Conveyor: Translocation of sediment and/or particulates from depth within the sediment to the surface during subsurface deposit feeding or burrow excavation. Downwards Conveyer: The subduction of particles from the surface to some depth by feeding or defecation. None: Does not perform any of the above and/or not considered as contributing to sediment reworking. *Activities such as burrowing, reworking and displacing of sediment particles, bio-irrigation and bio-deposition influences related functions ranging from alteration of sediment biogeochemistry, organic matter regeneration and nutrient cycling to the provision and maintenance of habitats for other organisms (Birchenough et al., 2012).*

Table 3. Summary of mean (± 1 SE) macrofaunal standing stock (g Wwt m^{-2}), diversity *H'*($\log_e$) and trait derived community bioturbation potential (BP_c) obtained from boxcore samples collected in Baltimore and Norfolk canyons and adjacent slopes. Sediment accumulation rates (ω, g cm^2 yr^{-1}) and. Z_{mix} (g cm^{-2}, the depth to which biological mixing occurs) were calculated from cores taken for biogeochemical analysis.

Location	**Biomass**	***H'***	***BP_c***	**Z_{mix}**	**ω**
Baltimore Canyon					
180 m	30.70 ± 8.56	3.11 ± 0.05	2,589.89 ± 200.39	14.7	0.051
550 m	20.82 ± 9.36	3.15 ± 0.09	772.85 ± 165.93	7.5	0.075
900 m	8.19 ± 0.10	2.17 ± 0.09	1,890.18 ± 130.60	8.7	0.032
1180 m	5.10 ± 0.61	3.25 ± 0.12	1,053.60 ± 146.85	7.7	0.11
Mean	**16.22 ± 4.66**	**2.92 ± 0.09**	**1,576.62 ± 443.80**	**9.65 ± 1.48**	**0.067 ± 0.01**
Baltimore Slope					
180 m	14.29 ±3.97	2.71 ± 0.05	1,675.91 ± 330.07	0	0.21
550 m	7.54 ± 1.24	2.80 ± 0.27	872.84 ± 202.98	6.4	0.25
900 m	2.94 ± 0.59	3.24 ± 0.047	589.29 ± 37.20	0.44	0.064
1180 m	21.23 ± 15.24	3.19 ± 0.04	591.89 ± 213.87	4.3	0.036
Mean	**11.50 ± 5.26**	**2.98 ± 0.1**	**587.76 ± 339.34**	**2.66 ± 1.31**	**0.191 ± 0.037**
Norfolk Canyon					
190 m	30.71 ± 11.61	2.62 ± 0.12	5,595.27 ± 2,577.80	12.9	0.55
555 m	31.66 ± 21.31	2.73 ± 0.03	3,056.51 ± 1,594.23	1	0.19
800 m	7.27 ± 2.62	1.89 ± 0.45	1,778.10 ± 351.15	4	0.22
1110 m	7.16 ± 0.70	2.73 ± 0.01	632.46 ± 40.06	2	0.66
Mean	**19.20 ± 9.06**	**2.49 ± 0.15**	**2,765.59 ± 1,860.82**	**2.33 ± 0.72**	**0.357 ± 0.12**

Table 3 cont…

Norfolk Slope					
190 m	21.80 ± 0.22	2.73 ± 0.07	4048.99 ± 97.32	3.9	0.2
555 m	14.19 ± 5.05	2.12 ± 0.05	2,157.36 ± 720.39	3.1	0.13
800 m	110.99 ± 88.380	2.61 ± 0.20	1,010.91 ± 427.16	0.00	0.14
1110 m	7.90 ± 1.23	3.17 ± 0.03	1,038.79 ± 155.43	0.00	0.16
Mean	**38.72 ± 23.72**	**2.66 ± 0.09**	**2,064.01 ± 832.37**	**1.75 ± 0.89**	**0.158 ± 0.01**

Table 4. Univariate PERMANOVA 3-factor models analysing differences in functional diversity indices (Functional Richness, Rao's Q, Functional Evenness and Functional Divergence), within the canyons and adjacent slope community using biomass-weighted biological traits, and differences in macrofaunal community derived bioturbation potential (BP_c). Bold text indicates significant differences ($p < 0.05$), ‡ = $log(x+1)$ transformed, † = square–root transformed.

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Functional Richness (FRic) ‡						
Habitat (*ha*)	1	0.01699	0.01699	0.02406	0.8799	9828
Site (*si*)	1	4.2238	4.2238	5.9803	**0.0173**	9831
Depth (*de*)	3	10.221	3.4069	4.8238	**0.007**	9948
ha x *si*	1	0.38688	0.38688	0.54777	0.4743	9828
ha x *de*	3	1.1085	0.36951	0.52318	0.6688	9934
si x *de*	3	0.23018	0.07673	0.10864	0.9565	9948
ha x *si* x *de*	3	8.212	2.7373	3.8757	**0.0184**	9947
Residual	32	22.601	0.70628			
Total	47	47				
Functional Diversity (RaoQ)						
Habitat (*ha*)	1	1.6256	1.6256	2.0102	0.1621	9845
Site (*si*)	1	0.90003	0.90003	1.1129	0.298	9848
Depth (*de*)	3	0.66372	0.22124	0.27358	0.8363	9950
ha x *si*	1	0.59867	0.59867	0.74028	0.3968	9839
ha x *de*	3	4.4364	1.4788	1.8286	0.1623	9951
si x *de*	3	2.385	0.79501	0.98307	0.4167	9971
ha x *si* x *de*	3	10.512	3.5041	4.333	**0.0114**	9967
Residual	32	25.878	0.8087			
Total	47	47				
Functional Evenness (FEve)						
Habitat (*ha*)	1	6.4118	6.4118	9.9848	**0.0044**	9830
Site (*si*)	1	0.00757	0.00757	0.01179	0.9158	9838
Depth (*de*)	3	11.212	3.7372	5.8198	**0.0024**	9938
ha x *si*	1	0.99902	0.99902	1.5557	0.2212	9837
ha x *de*	3	1.0594	0.35314	0.54993	0.649	9951
si x *de*	3	3.4009	1.1336	1.7654	0.1755	9951
ha x *si* x *de*	3	3.3609	1.1203	1.7446	0.1814	9958
Residual	32	20.549	0.64215			
Total	47	47				

Table 4 cont…

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Functional Divergence (FDiv) ‡						
Habitat (*ha*)	1	0.25451	0.25451	0.25399	0.626	9836
Site (*si*)	1	1.3923	1.3923	1.3894	0.2506	9835
Depth (*de*)	3	1.5263	0.50876	0.50771	0.6791	9967
ha x *si*	1	1.9338	1.9338	1.9298	0.1769	9822
ha x *de*	3	1.4266	0.47554	0.47456	0.7034	9958
si x *de*	3	6.6116	2.2039	2.1994	0.1054	9958
ha x *si* x *de*	3	1.7891	0.59636	0.59514	0.6302	9951
Residual	32	32.066	1.0021			
Total	47	47				
Bioturbation Potential (BP_c) †						
Habitat (*ha*)	1	4,597.60	4,597.60	6.1228	**0.0001**	9913
Site (*si*)	1	4,444.70	4,444.70	5.9192	**0.0001**	9890
Depth (*de*)	3	20,865	6,955.10	9.2625	**0.0001**	9896
ha x *si*	1	3,950.90	3,950.90	5.2616	**0.0001**	9910
ha x *de*	3	8,499.90	2,833.30	3.7732	**0.0001**	9859
si x *de*	3	7,455.80	2,485.30	3.3098	**0.0001**	9864
ha x *si* x *de*	3	8,815.70	2,938.60	3.9134	**0.0001**	9853
Residual	32	24,029	750.89			
Total	47	82,658				

Table 5. Multivariate PERMANOVA 3-factor model analysing patterns in macrofauna community biological traits (square–root transformed) within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), after transformation all factors met the assumptions of the permutations of dispersions test (PERMDISP $p > 0.05$).

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Habitat (*ha*)	1	2,145.80	2145.8	3.8282	**0.0121**	9936
Site (*si*)	1	769.77	769.77	1.3733	0.2258	9940
Depth (*de*)	3	15,018	5006.1	8.9313	**0.0001**	9945
ha x *si*	1	2,016.40	2016.4	3.5974	**0.018**	9946
ha x *de*	3	3,250.90	1083.6	1.9333	**0.0467**	9918
si x *de*	3	2,947.60	982.53	1.7529	0.069	9913
ha x *si* x *de*	3	2,807.10	935.69	1.6693	0.0823	9920
Residual	32	17,937	560.52			
Total	47	46,892				

Table 6. Univariate PERMANOVA 3-factor models analysing patterns in macrofaunal community biological traits and bioturbation potential (BP_c) within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), † = square–root, * = weighted dispersion transformed.

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Size range †						
Habitat (*ha*)	1	369.09	369.09	1.8534	0.1336	9948
Site (*si*)	1	328.10	328.10	1.6475	0.1771	9943
Depth (*de*)	3	6,065	2,021.50	10.151	**0.0001**	9952
ha x *si*	1	678.78	678.78	3.4085	**0.0278**	9960
ha x *de*	3	1,153.50	384.49	1.9307	0.0623	9936
si x *de*	3	935.67	311.89	1.5661	0.1287	9940
ha x *si* x *de*	3	982.10	327.37	1.6439	0.1164	9940
Residual	32	6,373	199.15			
Total	47	16,884				
Longevity †						
Habitat (*ha*)	1	718.86	718.86	3.9302	**0.0251**	9966
Site (*si*)	1	584.71	584.71	3.1968	**0.0416**	9955
Depth (*de*)	3	6,895	2,298.30	12.566	**0.0001**	9958
ha x *si*	1	852.35	852.35	4.66	**0.0153**	9954
ha x *de*	3	565.98	188.66	1.0315	0.4177	9949
si x *de*	3	2,221.50	740.49	4.0485	**0.001**	9945
ha x *si* x *de*	3	1,751.30	583.76	3.1916	**0.0028**	9943
Residual	32	5,853	182.91			
Total	47	19,443				
Larval development *						
Habitat (*ha*)	1	774.41	774.41	5.8608	**0.0059**	9953
Site (*si*)	1	386.52	386.52	2.9251	0.0622	9959
Depth (*de*)	3	4,272	1,424.10	10.778	**0.0001**	9948
ha x *si*	1	1,002.50	1,002.50	7.5871	**0.0029**	9950
ha x *de*	3	1,322.20	440.74	3.3355	**0.0052**	9947
si x *de*	3	491.53	163.84	1.24	0.292	9955
ha x *si* x *de*	3	516.87	172.29	1.3039	0.2753	9952
Residual	31	4,096	132.14			
Total	46	12,990				

Table 6 cont…

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Egg development (ed) †						
Habitat (*ha*)	1	554.02	554.02	3.0433	0.0526	9958
Site (*si*)	1	551.55	551.55	3.0297	**0.043**	9946
Depth (*de*)	3	5,272	1,757.20	9.6522	**0.0001**	9939
ha x *si*	1	914.20	914.20	5.0218	**0.013**	9965
ha x *de*	3	1,338.00	445.99	2.4499	**0.0265**	9954
si x *de*	3	1,138.00	379.32	2.0836	0.0632	9948
ha x *si* x *de*	3	939.02	313.01	1.7194	0.1109	9940
Residual	32	5,826	182.05			
Total	47	16,532				
Life History (lh) †						
Habitat (*ha*)	1	631.60	631.60	3.0563	**0.036**	9948
Site (*si*)	1	642.93	642.93	3.1112	**0.0321**	9959
Depth (*de*)	3	5,604	1,868.00	9.0392	**0.0002**	9944
ha x *si*	1	901.02	901.02	4.3601	**0.0132**	9949
ha x *de*	3	1,273.50	424.51	2.0542	**0.0498**	9945
si x *de*	3	1,669.50	556.52	2.693	**0.0123**	9942
ha x *si* x *de*	3	1,066.70	355.56	1.7205	0.0905	9929
Residual	32	6,613	206.65			
Total	47	18,402				
Sediment position (sp) †						
Habitat (*ha*)	1	833.90	833.90	4.5192	**0.012**	9961
Site (*si*)	1	305.85	305.85	1.6575	0.1883	9947
Depth (*de*)	3	4,892	1,630.60	8.8369	**0.0001**	9945
ha x *si*	1	700.27	700.27	3.795	**0.0329**	9963
ha x *de*	3	1,018.60	339.52	1.84	0.0981	9939
si x *de*	3	1,588.00	529.33	2.8686	**0.0122**	9948
ha x *si* x *de*	3	598.87	199.62	1.0818	0.3904	9946
Residual	32	5,905	184.52			
Total	47	15,842				

Table 6 cont…

Factor	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Feeding Guild (f) †						
Habitat (*ha*)	1	754.37	754.37	4.1773	**0.0173**	9962
Site (*si*)	1	393.68	393.68	2.1799	0.1046	9961
Depth (*de*)	3	6,260	2,086.60	11.554	**0.0001**	9951
ha x *si*	1	953.23	953.23	5.2784	**0.0094**	9952
ha x *de*	3	1,004.50	334.84	1.8541	0.0985	9950
si x *de*	3	980.87	326.96	1.8105	**0.0953**	9950
ha x *si* x *de*	3	1,339.20	446.42	2.472	0.0222	9952
Residual	32	5,779	180.59			
Total	47	17,464				
Bioturbation (b) †						
Habitat (*ha*)	1	624.48	624.48	2.8726	**0.0463**	9960
Site (*si*)	1	468.99	468.99	2.1574	0.0961	9946
Depth (*de*)	3	5,882	1,960.60	9.0188	**0.0001**	9930
ha x *si*	1	1,123.60	1,123.60	5.1686	**0.0057**	9958
ha x *de*	3	1,542.10	514.04	2.3646	**0.0209**	9916
si x *de*	3	1,725.50	575.18	2.6458	**0.0097**	9919
ha x *si* x *de*	3	1,381.00	460.35	2.1176	**0.0421**	9933
Residual	32	6,957	217.39			
Total	47	19,704				

Table 7. Similarity Percentage (SIMPER) analysis for macrofauna functional traits at canyon and adjacent slope habitats, showing Families (Total ≥ 40%) contributing the most to (a) average similarity differences within canyon and slope depth groups, and (b) average dissimilarity between canyon and slope habitat.

(a)

Baltimore Canyon (64.5%)							
180 m (76.5%)		**550 m (56.7%)**		**900 m (91.0%)**		**1180 m (76.3%)**	
mobSessile	7.4	L3-10	7.4	L3-10	8.6	mSoft	7.6
ldPlanktonic	6.9	ldPlanktotrophic	7.3	mobSessile	6.5	ldPlanktotrophic	5.5
bSurfaceDeposition	6.5	mSoft	7.1	mExoskeleton	5.6	L1-3	5
sr21-100	6.5	edSexualShedEggsPelagic	6	ldPlanktotrophic	5.5	mobSessile	4.9
lhBurrowDwelling	5.4	mobSessile	5.9	spInfauna0-5	5.4	L3-10	4.6
spInfauna6-10	5.3	bSurfaceDeposition	5.5	bSurfaceDeposition	5.3	spInfauna0-5	4.4
mExoskeleton	5.3	spInfauna0-5	5.1	edSexualBroodEggs	4.5	fSubsurfaceDeposit	4.3
						sr21-100	4.2
Baltimore Slope (54.1%)							
180 m (64.4%)		**550 m (72.8%)**		**900 m (79.7%)**		**1180 m (59.6%)**	
mSoft	8.9	mExoskeleton	7.8	mSoft	6.9	mobSessile	7.2
ldBenDirect	6.7	bSurfaceDeposition	7.2	ldPlanktotrophic	6.6	ldPlanktotrophic	6.6
spInfauna0-5	6	L3-10	6	mobSessile	6.5	bSurfaceDeposition	6.1
edSexualBroodEggs	5.1	ldDirect	5.9	L1-3	5.6	L3-10	5.9
L3-10	4.9	lhFreeLiving	5.8	spInfauna0-5	5.2	lhBurrowDwelling	5.5
L1-3	4.8	edSexualShedEggsBenthic	5.8	bSurfaceDeposition	5	mSoft	5.3
sr101-200	4.3	mobSessile	5	L3-10	4.6	edSexualBroodEggs	4.6

Table 7 cont…

Norfolk Canyon (61.4%)							
190 m (74.5%)		**555 m (57.4%)**		**800 m (55.7%)**		**1110 m (78.9%)**	
L3-10	8.2	mSoft	6.2	ldPlanktotrophic	8.1	L3-10	9.2
ldPlanktotrophic	7.8	spInfauna0-5	5.9	bSurfaceDeposition	7.8	mobSessile	8.1
bSurfaceDeposition	7.8	mobSessile	5.5	mExoskeleton	6.3	spInfauna0-5	7.7
edSexualShedEggsPelagic	7.1	ldPlanktotrophic	5.5	L3-10	6.2	mSoft	7.3
mExoskeleton	6.4	L3-10	5.4	mobSessile	5.6	fSurfaceDeposit	6.1
sr21-100	6.3	bSurfaceDeposition	4.7	spInfauna0-5	5.2	ldBenDirect	5.1
		edSexualBroodEggs	4.7	mSoft	4.7		
		L1-3	4.6				
Norfolk Slope (58.5%)							
190 m (89.4%)		**555 m (55.2%)**		**800 m (57.3%)**		**1110 m (79.5%)**	
mSoft	7.2	mSoft	8.7	edSexualBroodEggs	7.2	mSoft	8.2
spInfauna0-5	6.9	mobSessile	7.3	lhFreeLliving	6.7	ldBenDirect	5.7
L1-3	5.5	spInfauna0-5	7	L3-10	6.5	L1-3	5.6
ldBenDirect	5.4	L3-10	5.2	mExoskeleton	5.6	mobSessile	5.3
L3-10	5	L1-3	4.9	ldBenDirect	5.5	L3-10	5
edSexualBroodEggs	4.5	ldPlanktotrophic	4.7	mSoft	5.2	ldPlanktotrophic	5
bSurfaceDeposition	4.5	bSurfaceDeposition	4.7	ldPlanktotrophic	4.7	spInfauna0-5	4.7
mobSessile	4.4					edSexualBroodEggs	4.6

Table 7 cont…

(b)

Baltimore (44.9%) Canyon vs Slope		**Norfolk (40.3%) Canyon vs Slope**		**Canyons (36.3%) Baltimore vs Norfolk**		**Slopes (45.8%) Baltimore vs Norfolk**	
ldPlanktotrophic	5.2	mSoft	5.9	ldPlanktotrophic	6.1	mSoft	6.8
mSoft	5.1	ldPlanktotrophic	5	bSurfaceDeposition	5.7	spInfauna0-5	5.3
L3-10	5	L3-10	4.9	mExoskeleton	5.1	ldBenDirect	4.7
bSurfaceDeposition	4.9	bSurfaceDeposition	4.8	edSexualShedEggsPelagic	5	L1-3	4.6
mobSessile	4.7	edSexualShedEggsPelagic	4.7	L3-10	4.9	mobSessile	4.4
mExoskeleton	4.7	spInfauna0-5	4.6	mobSessile	4.2	L3-10	4.2
sr21-100	4.1	mobSessile	4.3	mSoft	4.2	edSexualBroodEggs	4.1
edSexualShedEggsPelagic	3.6	L1-3	4.1	sr21-100	4.2	bSurfaceDeposition	3.8
ldBenDirect	3.5	mExoskeleton	3.9	lhBurrowDwelling	4.1	sr21-100	3.7

Table 8. Distance-based linear modelling (DISTLM) on species abundances at Baltimore Canyon and adjacent slope based on Euclidean distance similarity, showing (a) the proportion of macrofaunal biological trait patterns explained by each explanatory variable and (b) the most explanatory models using the *BEST* selection procedure.

(a)

Variable	**SS(trace)**	**Pseudo-F**	**P**	**Prop. (%)**
BP_c	30.526	12.669	**0.0001**	36.5
Depth	28.556	11.426	**0.0001**	34.2
$\delta^{15}N$	19.036	6.493	**0.0036**	22.7
% C	12.750	3.963	**0.0187**	15.3
ω	8.353	2.444	0.0728	10.0
W	2.447	0.664	0.5399	2.9
$\delta^{13}C$	5.987	1.698	0.1532	7.2
Z_{mix}	5.973	1.694	0.1565	7.2
Chl *a*	4.561	1.271	0.2464	5.5

(b)

AICc	**R^2**	**RSS**	**Selections**
17.53	0.609	32.7	BP_c, % C, Z_{mix}
17.69	0.656	28.8	BP_c, % C, Z_{mix}, ω
17.95	0.602	33.3	BP_c, % C, ω
18.22	0.648	29.4	BP_c, % C, Z_{mix}, Depth
18.30	0.647	29.5	BP_c, % C, $\delta^{13}C$, ω
18.47	0.644	29.7	BP_c, % C, $\delta^{13}C$, Z_{mix}
18.51	0.644	29.8	BP_c, % C, $\delta^{15}N$, Z_{mix}
18.53	0.693	25.6	BP_c, % C, $\delta^{13}C$, $\delta^{15}N$, ω
18.60	0.692	25.7	BP_c, % C, $\delta^{15}N$, Z_{mix}, ω
18.63	0.692	25.8	BP_c, % C, Z_{mix}, ω, Depth
Total SS (Trace):		83.536	

Table 9. Distance-based linear modelling (DISTLM) on species abundances at Norfolk Canyon and adjacent slope based on Euclidean distance similarity, showing (a) the proportion of macrofaunal biological trait pattern explained by each explanatory variable and (b) the most explanatory models using the *BEST* selection procedure.

(a)

Variable	**SS(trace)**	**Pseudo-*F***	**P (perm)**	**Prop. (%)**
BP_c	46.616	27.063	**0.0001**	55.2
Depth	26.537	10.07	**0.0005**	31.4
% C	14.535	4.5699	**0.0192**	17.2
Z_{mix}	12.777	3.9186	**0.0274**	15.1
Chl *a*	5.1054	1.4145	0.208	6.0
$\delta^{15}N$	4.965	1.3734	0.2357	5.9
ω	3.1825	0.8609	0.4002	3.8
$\delta^{13}C$	3.5863	0.9749	0.3429	4.2
W	1.9802	0.5278	0.6073	2.3

(b)

AICc	$\boldsymbol{R^2}$	**RSS**	**Selections**
14.13	0.621	32.03	BP_c, $\delta^{15}N$
14.30	0.618	32.26	BP_c, Chl *a*,
14.83	0.698	25.55	BP_c, % C, Z_{mix}, ω
14.88	0.653	29.28	BP_c, $\delta^{15}N$, ω
14.93	0.653	29.28	BP_c, $\delta^{15}N$, Z_{mix}
15.08	0.653	29.34	BP_c, $\delta^{13}C$, $\delta^{15}N$
15.10	0.651	29.54	BP_c, Chl *a*, ω
15.21	0.649	29.69	BP_c, Chl *a*, Z_{mix}
15.24	0.648	29.73	BP_c, $\delta^{15}N$, Depth
15.31	0.647	29.81	BP_c, % C, $\delta^{15}N$
Total SS (Trace): 84.510			

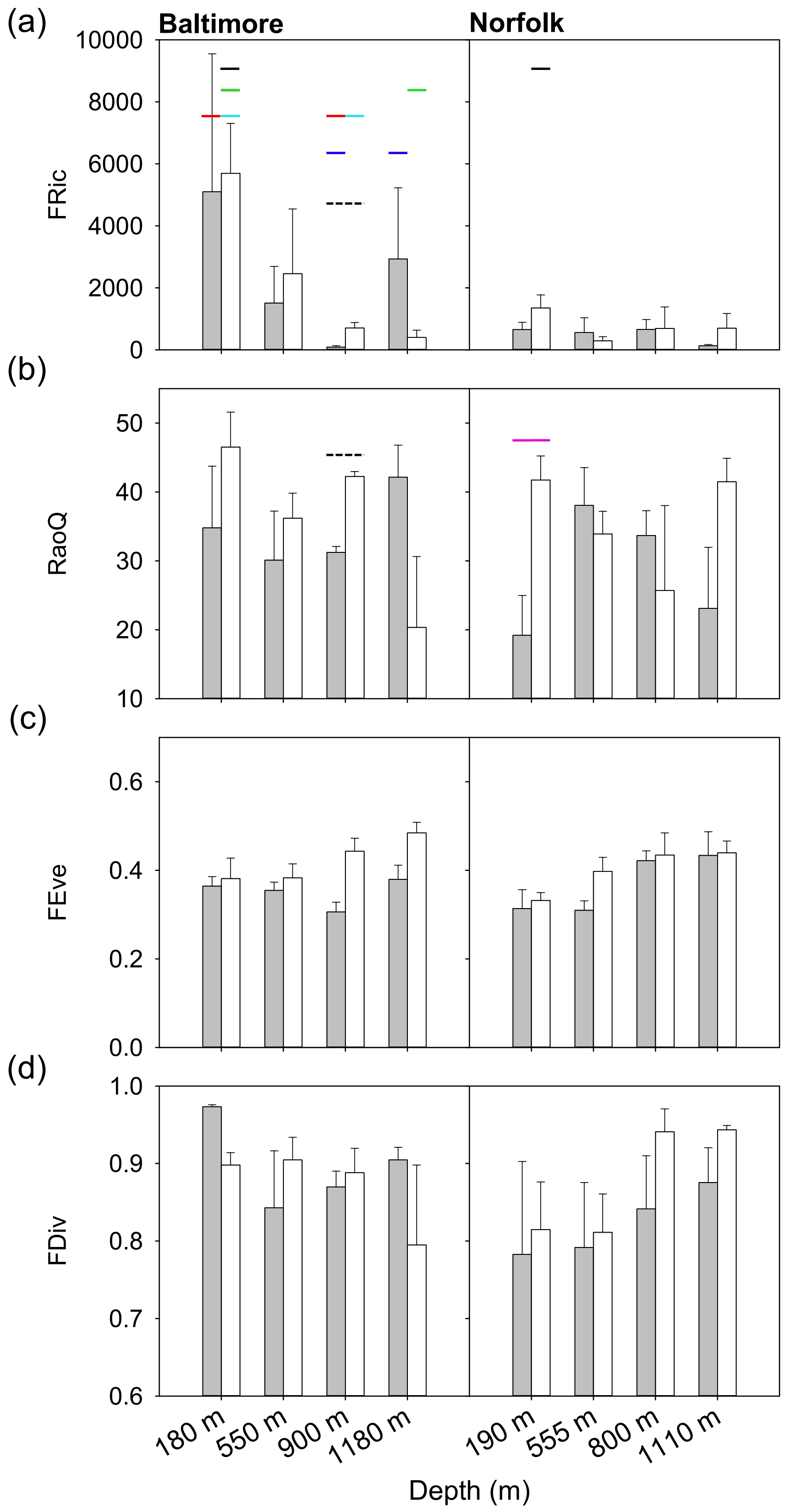


Figure 1. Mean (± 1 SE) functional diversity indices of macrofauna communities at Baltimore and Norfolk canyons (grey bars) and their adjacent slopes (white bars). FRic, functional richness; RaoQ, Rao's quadratic entropy; FEve, functional evenness; FDiv functional divergence. Coloured bars indicate significant pairwise (*ha* x *si* x *de*) comparisons at $p <$ 0.05.

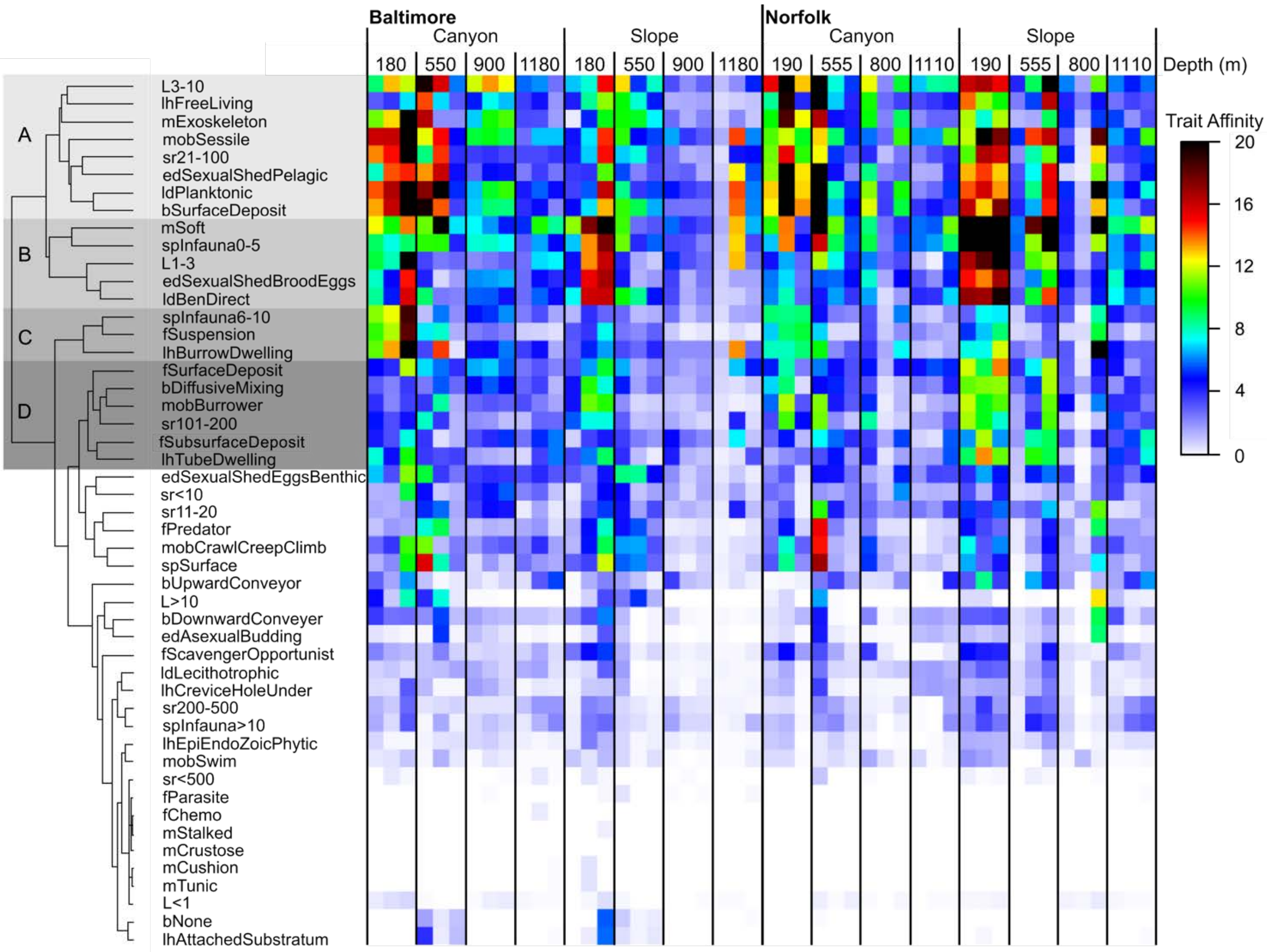


Figure 2. The distribution of functional traits in Baltimore and Norfolk canyons and adjacent slopes, across the depth gradient. Trait modalities (*y*-axis) are based on Euclidean distance hierarchical clustering and ordered based on Whittaker's index of association among pairs of modalities. Samples (*x*-axis) are sorted by location and along the depth gradient. The colour scheme indicates the affinity of various traits. Several significant functional groups were identified and are indicated by the letters A-D and shaded regions on the *y*-axis.

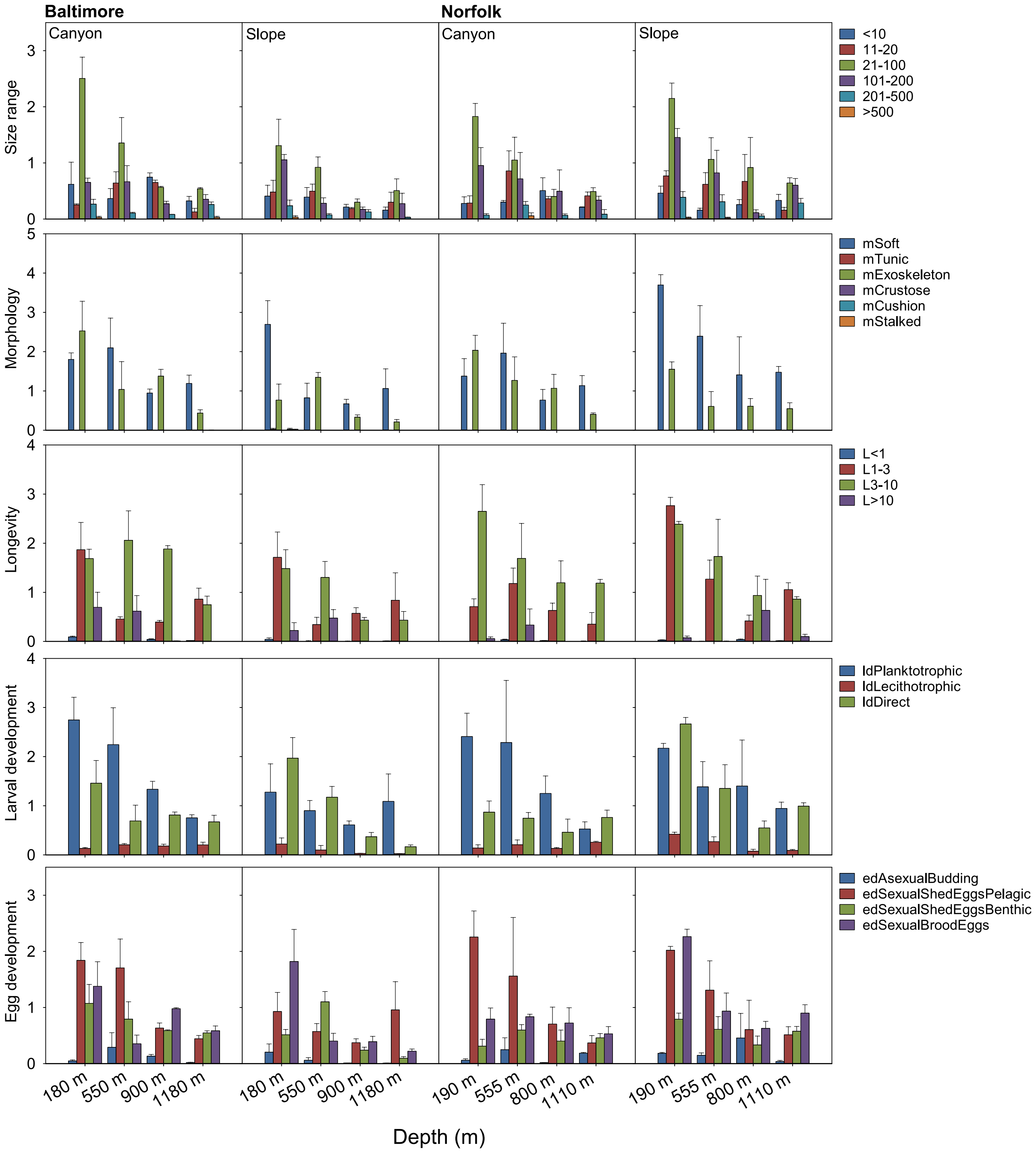
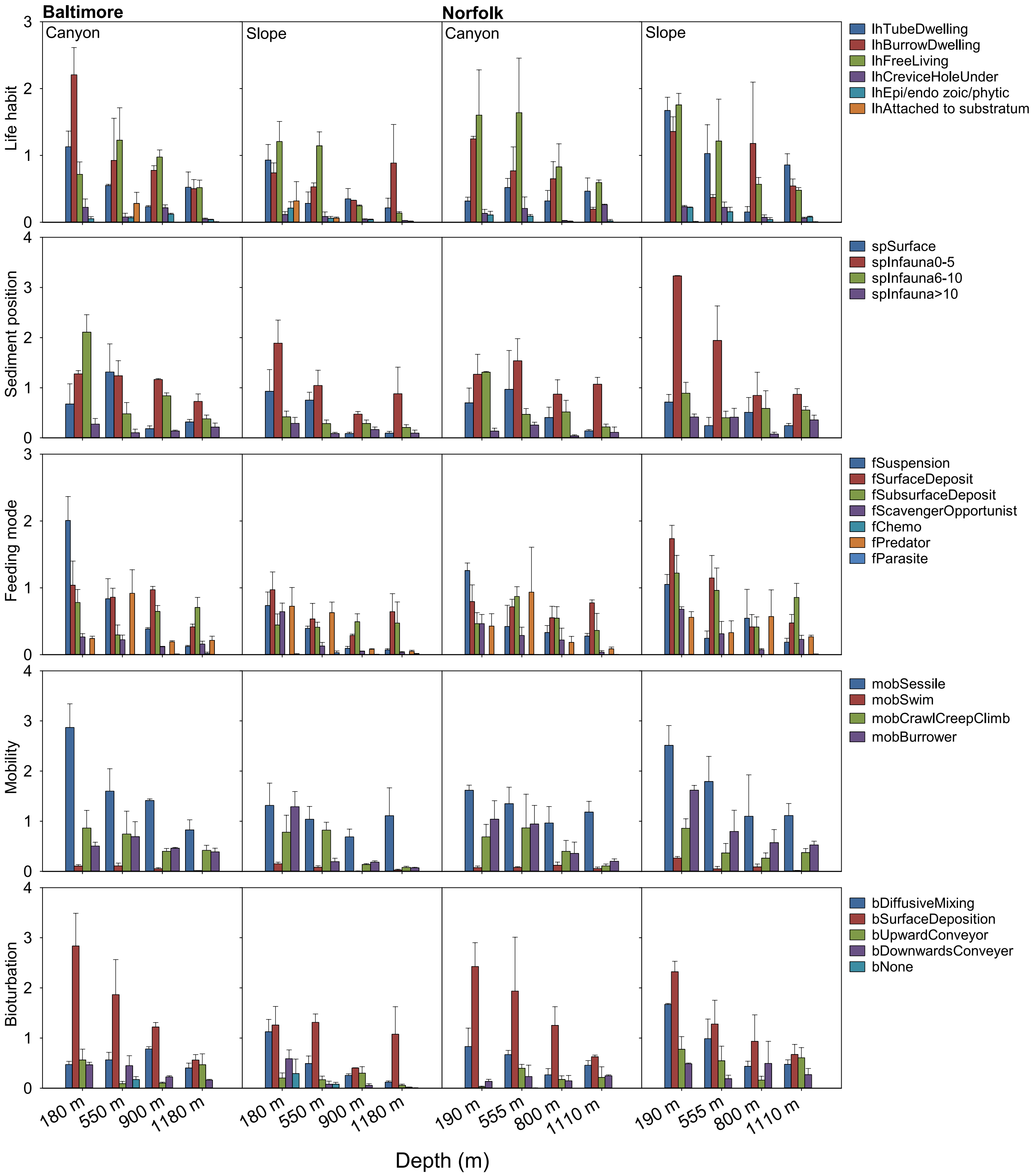


Figure 3. Distribution of biomass-weighted modality scores within benthic macrofaunal community traits in Baltimore and Norfolk canyons and adjacent slopes for each individual trait used (See *y*-axis labels for traits).

Figure 3 cont…



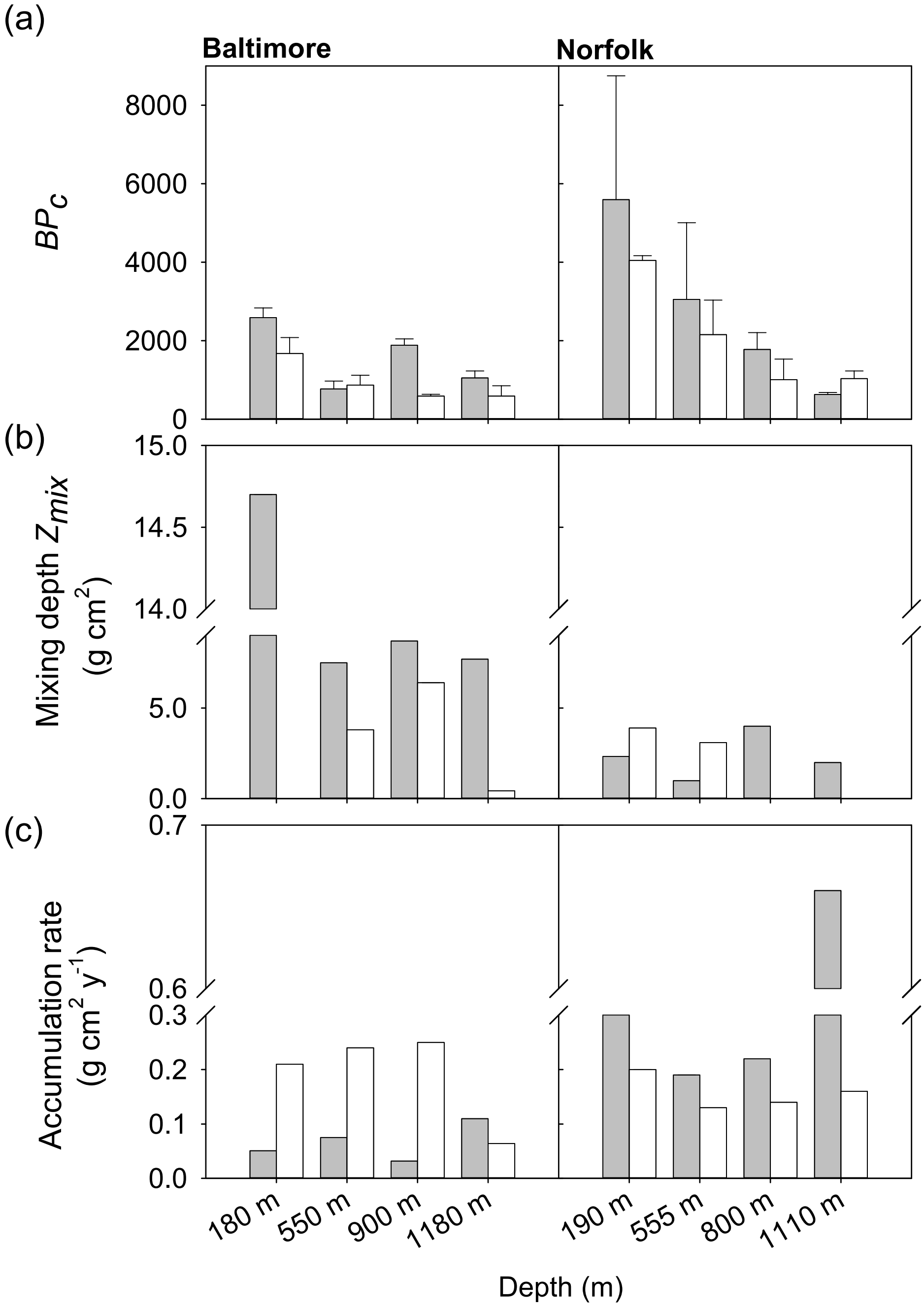


Figure 4. Mean bioturbation potential (a) (±1 SE, BP_c) and the derived sediment characteristics (b) sediment biological mixing depth (Z_{mix} g cm^2), based on ^{210}Pb data and (c) sediment accumulation rate (ω, g cm^2 yr^{-1}) for Baltimore and Norfolk canyons (grey bars) and adjacent slopes (white bars).

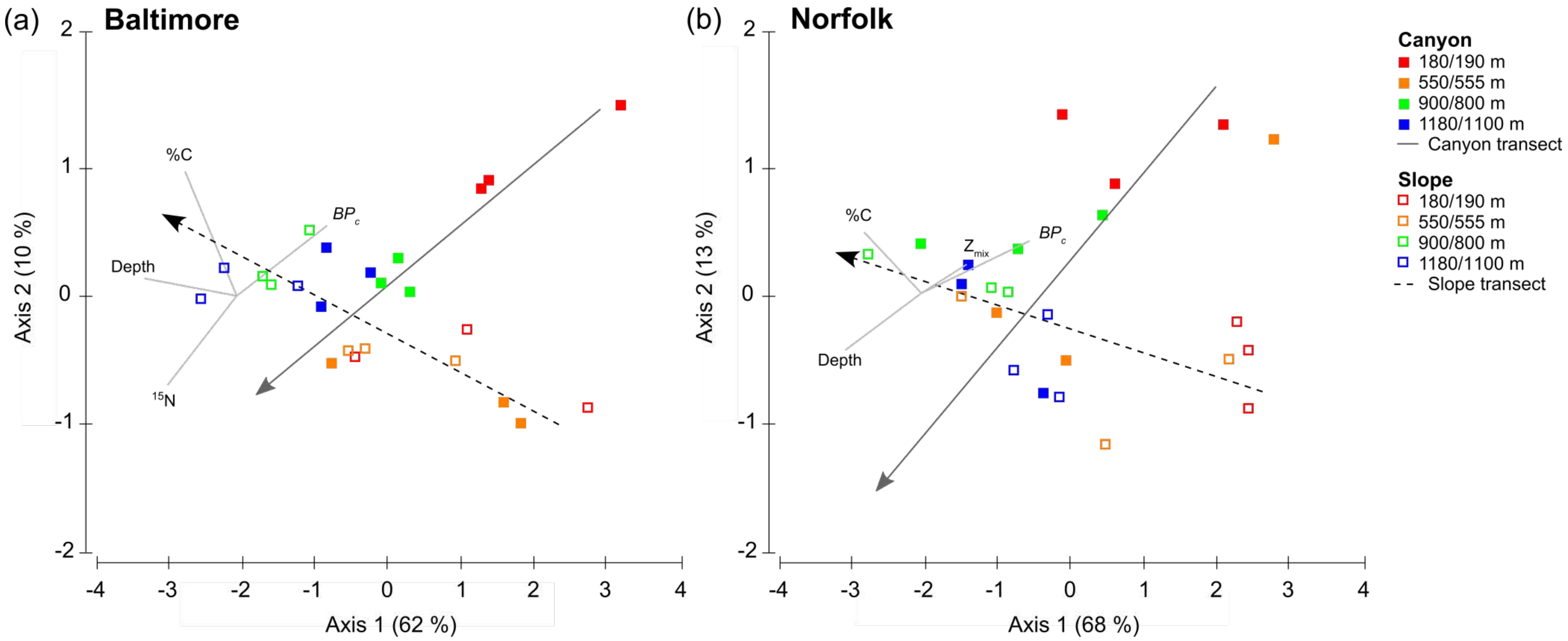


Figure 5. Principal Coordinate Ordination (Euclidean Distance) for Log(x+1) transformed community biological traits from Baltimore and Norfolk canyons and adjacent slopes, including significant explanatory variable as Eigenvectors.

9 Supplementary Materials

SM Table 1. List of taxa substitutions for study taxa not represented in the traits database from Bolam & Eggleton (2014), that were used in BTA. * = traits and modalities assigned based on primary literature and best professional judgement.

Database Taxa	**MAB Taxa**
Achelia	Ammotheidae *Paranymphon spinosum*
Chaetoderma	Aplacophora
Colus	Buccinidae
Spiochaetopterus	Chaetopteridae *Spiochaetopterus costarum*
Buccinum	Columbellidae
Unciola	Corophidae *Jassa spp.*
Cirratulidae	Cossuridae *Cossura longocirrata*
Cirratulidae	Ctenodrillidae *Ctenodrilus serratus*
Antalis	Dentaliidae
Isopoda	Desmosomatidae
Amphipoda	Dulichiidae *cf. Dulichia* spp.
Isopoda	Eurycopeinae
Emarginula	Fissurellidae
Nereididae	Gymnonereidinae *Ceratocephale loveni*
Isopoda	Halicharidae
Isopoda	Haploniscidae *Haploniscus* spp. cf.
Hemichordata	Hemichordata Enteropneusta
Turbellaria	Heterobranchia cf. *Turbellaria*
Spionidae	Heterospionidae indet.
Isopoda	Ilyarachnidae
Isopoda	Ilyarachnidae
Ischyroceridae	Ischnomesidae
Kellia	Lasaeidae
Listriella	Liljeborgidae
Limaria	Limopsidae *Limopsis sulcata*
Isopoda	Macrostylidae *sp.*1 cf. *Macrostylis* / Nannoniscidae
Hyas	Majidae Hyas spp.
Kurtiella	Malletidae cf.
Ampharetidae	Melinninae Melinna spp.
Vesicomyidae	Neilonellidae *Neilonella* spp.
Eunereis	Nereiidae
Protodrilidae	Nerillidae *Paranerilla* spp.
Arciodea	Noetiidae *Striarca / Bathyarca* spp.
Nereiphylla	Notophyllinae
Jupiteria	Nuculanidae
Anthozoa	Octocorallia
Grania	Oligochaeta

SM Table 1 cont…

Database Taxa	**MAB Taxa**
Retusa	Opistobranchia
Munna	Paramunnidae Pleurogonium sp2.
Nicippe	Pardaliscidae
Cochlodesma	Periplomatidae *Periploma* spp.
Harpinia	Phoxocephalidae
Thyone	Phyllophoridae *Thyone*
Glyphohesione	Pilargidae
Similipecten	Propeamussidae
Orbiniidae	*Questa* cf.
Alvania	Retusidae *Retusa obtusa*
*	Siboglinidae
*	Solemyidae *Solemya velum*
Parametopa	Stenothoidae
Tiron	Synopidae *Syrrhoe crenulata*
Terebellides	Trichobranchinae
Margarites	Trochidae *Margarites / Solariella* spp.
*	Tunicata indet.
Unciola	Unciolidae *Unciola laticornis / irrorata*
Vesicomyidae	Vesicomyidae indet.
Vesicomyidae	Vesicomyidae indet.
Vesicomyidae	Vesicomyidae indet.
*	Xenophyophore Astrorhiza type cf.
*	Yoldiellinae

SM Table 2. Univariate PERMANOVA pairwise comparisons for significant terms (see Tables 4 and 5) for macrofaunal community functional diversity indices (functional richness, Rao's quadratic entropy, functional evenness, functional divergence and bioturbation potential (BP_c), within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), ‡ = *log*(*x*+1) transformed. * = square-root transformed.

Pairwise tests	**Source**	**df**	***t*-statistic**	***P* (perm)**	***P* (MC)**	**Unique Perms**
Functional richness (FRic)‡						
ha x *si* x *de*	BC x NC (1)	4	1.0666		0.3583	10
	BC x NC (2)	4	0.94937		0.3998	10
	BC x NC (3)	4	2.5336		0.0661	10
	BC x NC (4)	4	2.6277		0.063	10
	BS x NS (1)	4	3.0685		**0.039**	10
	BS x NS (2)	4	1.3002		0.2626	10
	BS x NS (3)	4	1.474		0.2098	10
	BS x NS (4)	4	0.59291		0.5811	10
	BC x BS (1)	4	1.0007		0.3735	10
	BC x BS (2)	4	0.19639		0.8553	10
	BC x BS (3)	4	4.2567		**0.0131**	10
	BC x BS (4)	4	1.4904		0.204	10
	NC x NS (1)	4	1.2623		0.2698	10
	NC x NS (2)	4	0.05617		0.9584	10
	NC x NS (3)	4	1.3117		0.2542	10
	NC x NS (4)	4	1.5881		0.1893	10
	BC (1 x 2)	4	0.66905		0.5331	10
	BC (1 x 3)	4	2.8201		**0.0457**	10
	BC (1 x 4)	4	0.18941		0.8566	10
	BC (2 x 3)	4	2.4379		0.0737	10
	BC (2 x 4)	4	0.52544		0.6308	10
	BC (3 x 4)	4	2.9921		**0.0432**	10
	BS (1 x 2)	4	1.678		0.1706	10
	BS (1 x 3)	4	5.465		**0.0058**	10
	BS (1 x 4)	4	3.2973		**0.0272**	10
	BS (2 x 3)	4	0.3781		0.7192	10
	BS (2 x 4)	4	1.127		0.3185	10
	BS (3 x 4)	4	1.1811		0.3063	10
	NC (1 x 2)	4	0.80583		0.4651	10
	NC (1x 3)	4	0.12257		0.912	10
	NC (1 x 4)	4	2.4934		0.0682	10
	NC (2 x 3)	4	0.68824		0.5234	10
	NC (2 x 4)	4	0.61789		0.5635	10
	NC (3 x 4)	4	2.0582		0.1099	10

SM Table 2 cont…

	NS (1 x 2)	4	2.7256	0.0522	10
	NS (1x 3)	4	1.7122	0.1593	10
	NS (1 x 4)	4	1.2856	0.2717	10
	NS (2 x 3)	4	1.0279	0.3638	10
	NS (2 x 4)	4	0.6759	0.539	10
	NS (3 x 4)	4	1.2319	0.2937	10
Functional diversity (Rao's Q)					
ha x *si* x *de*	BC x NC (1)	4	1.4665	0.2169	10
	BC x NC (2)	4	0.88657	0.4232	10
	BC x NC (3)	4	0.66031	0.5463	10
	BC x NC (4)	4	1.8978	0.1346	10
	BS x NS (1)	4	0.77309	0.4833	10
	BS x NS (2)	4	0.47252	0.6548	10
	BS x NS (3)	4	1.3398	0.2542	10
	BS x NS (4)	4	1.9518	0.1221	10
	BC x BS (1)	4	1.138	0.318	10
	BC x BS (2)	4	0.76469	0.4883	10
	BC x BS (3)	4	9.8303	**0.001**	10
	BC x BS (4)	4	1.9302	0.1233	10
	NC x NS (1)	4	3.3517	**0.0301**	10
	NC x NS (2)	4	0.65226	0.5497	10
	NC x NS (3)	4	0.6201	0.5755	10
	NC x NS (4)	4	1.9329	0.1182	10
	BC (1 x 2)	4	0.41086	0.6998	10
	BC (1x 3)	4	0.39742	0.7174	10
	BC (1 x 4)	4	0.72659	0.5128	10
	BC (2 x 3)	4	0.15693	0.8818	10
	BC (2 x 4)	4	1.4135	0.2288	10
	BC (3 x 4)	4	2.3011	0.0868	10
	BS (1 x 2)	4	1.649	0.1771	10
	BS (1x 3)	4	0.83023	0.4425	10
	BS (1 x 4)	4	2.281	0.087	10
	BS (2 x 3)	4	1.6356	0.1787	10
	BS (2 x 4)	4	1.4559	0.2198	10
	BS (3 x 4)	4	2.1252	0.0944	10
	NC (1 x 2)	4	2.3743	0.0753	10
	NC (1x 3)	4	2.1314	0.0993	10
	NC (1 x 4)	4	0.36838	0.731	10
	NC (2 x 3)	4	0.66962	0.541	10
	NC (2 x 4)	4	1.4346	0.2137	10
	NC (3 x 4)	4	1.1037	0.3297	10

SM Table 2 cont…

	NS (1 x 2)	4	1.6389		0.1791	10
	NS (1x 3)	4	1.2525		0.2832	10
	NS (1 x 4)	4	0.0542		0.9563	10
	NS (2 x 3)	4	0.6418		0.5515	10
	NS (2 x 4)	4	1.6018		0.1834	10
	NS (3 x 4)	4	1.2338		0.2886	10
Functional evenness (FEve)						
ha	Canyon x Slope	32	3.16	**0.0039**		9826
de	1 x 2	16	0.6199	0.5285		9816
	1 x 3	16	2.2487	**0.0399**		9817
	1 x 4	16	3.4844	**0.0036**		9836
	2 x 3	16	1.8953	0.0776		9850
	2 x 4	16	3.2778	**0.0068**		9851
	3 x 4	16	1.3569	0.1967		9856
Bioturbation potential (*BP_c*) *						
ha x *si*	C (B x N)	16	2.4414	0.0001		9938
	S (B x N)	16	2.2907	0.0001		9891
	B (C x S)	16	2.3538	0.0001		9925
	N (C x S)	16	2.4111	0.0001		9933
ha x *de*	C x S (1)	8	2.4033	**0.0019**		8881
	C x S (2)	8	2.1671	**0.0017**		8890
	C x S (3)	8	1.9423	**0.0022**		8906
	C x S (4)	8	1.8745	**0.0027**		8892
	Canyon (1 x 2)	8	2.4739	**0.0026**		8919
	Canyon (1 x 3)	8	2.9220	**0.0026**		8906
	Canyon (1 x 4)	8	3.0988	**0.0026**		8913
	Canyon (2 x 3)	8	2.3772	**0.0024**		8922
	Canyon (2 x 4)	8	2.5129	**0.0025**		8853
	Canyon (3 x 4)	8	1.8906	**0.0054**		8886
	Slope (1 x 2)	8	3.0223	**0.0018**		8921
	Slope (1 x 3)	8	3.1141	**0.0027**		8938
	Slope (1 x 4)	8	3.4362	**0.0015**		8861
	Slope (2 x 3)	8	1.9406	**0.0053**		8933
	Slope (2 x 4)	8	2.4867	**0.0022**		8920
	Slope (3 x 4)	8	1.0215	0.4106		8912
si x *de*	1 (Baltimore x Norfolk)	8	2.5139	**0.0032**		8861
	2 (Baltimore x Norfolk)	8	2.1228	**0.0026**		8875
	3 (Baltimore x Norfolk)	8	1.6788	**0.0020**		8890
	4 (Baltimore x Norfolk)	8	1.6648	**0.0065**		8844
	Baltimore (1 x 2)	8	2.7827	**0.0029**		8882
	Baltimore (1 x 3)	8	3.7058	**0.0019**		8914
	Baltimore (1 x 4)	8	3.1224	**0.0030**		8888

SM Table 2 cont…

	Baltimore (2 x 3)	8	2.6349	**0.0026**		8869
	Baltimore (2 x 4)	8	2.4980	**0.0025**		8871
	Baltimore (3 x 4)	8	2.0652	**0.0021**		8906
si x *de*	Norfolk (1 x 2)	8	2.3629	**0.0027**		8900
	Norfolk (1 x 3)	8	2.5857	**0.0024**		8931
	Norfolk (1 x 4)	8	3.3892	**0.0022**		8854
	Norfolk (2 x 3)	8	1.7198	**0.0111**		8927
	Norfolk (2 x 4)	8	2.2336	**0.0020**		8928
	Norfolk (3 x 4)	8	1.0837	0.3335		8953
ha x *si* x *de*	BC x NC (1)	4	2.4217		**0.0194**	10
	BC x NC (2)	4	1.9717		**0.0335**	10
	BC x NC (3)	4	2.2957		**0.0252**	10
	BC x NC (4)	4	2.1566		**0.0235**	10
	BS x NS (1)	4	2.1013		**0.0277**	10
	BS x NS (2)	4	2.0420		**0.0342**	10
	BS x NS (3)	4	1.5710		0.1052	10
	BS x NS (4)	4	1.8650		**0.0430**	10
	BC x BS (1)	4	2.4417		**0.0155**	10
	BC x BS (2)	4	2.0226		**0.0294**	10
	BC x BS (3)	4	2.9646		**0.0090**	10
	BC x BS (4)	4	2.0841		**0.0230**	10
	NC x NS (1)	4	2.0163		**0.0407**	10
	NC x NS (2)	4	2.0315		**0.0336**	10
	NC x NS (3)	4	1.6047		0.0834	10
	NC x NS (4)	4	2.0930		**0.0255**	10
	BC (1 x 2)	4	2.7322		**0.0086**	10
	BC (1x 3)	4	4.2579		**0.0015**	10
	BC (1 x 4)	4	3.0086		**0.0060**	10
	BC (2 x 3)	4	3.0902		**0.0057**	10
	BC (2 x 4)	4	2.3686		**0.0180**	10
	BC (3 x 4)	4	2.8918		**0.0091**	10
	BS (1 x 2)	4	2.4692		**0.0196**	10
	BS (1x 3)	4	2.5115		**0.0138**	10
	BS (1 x 4)	4	2.4764		**0.0128**	10
	BS (2 x 3)	4	2.0439		**0.0316**	10
	BS (2 x 4)	4	2.2256		**0.0169**	10
	BS (3 x 4)	4	1.2635		0.2136	10
	NC (1 x 2)	4	2.0147		**0.0423**	10
	NC (1x 3)	4	1.7755		0.0663	10
	NC (1 x 4)	4	2.4211		**0.0168**	10
	NC (2 x 3)	4	1.3978		0.1501	10
	NC (2 x 4)	4	2.0152		**0.0372**	10

SM Table 2 cont…

	NC (3 x 4)	4	1.5003	0.1143	10
	NS (1 x 2)	4	2.3697	**0.0211**	10
	NS (1x 3)	4	2.5055	**0.0150**	10
	NS (1 x 4)	4	3.0976	**0.0068**	10
	NS (2 x 3)	4	1.7757	0.0626	10
	NS (2 x 4)	4	2.1610	**0.0249**	10
	NS (3 x 4)	4	1.1289	0.3085	10

SM Table 3. Multivariate PERMANOVA pairwise comparisons for significant terms (see Table 5) for macrofauna community functional traits (square–root transformed). Bold text indicates significant differences ($p < 0.05$), for explanation of the codes used see methods.

Factors	**Comparison**	**df**	***t*-statistic**	***P*(perm)**	***P* (MC)**	**Unique Perms**
ha x *si*	C (B x N)	16	0.9390	0.4168		9946
	S (B x N)	16	1.9883	**0.0176**		9950
	B (C x S)	16	2.6489	**0.0012**		9948
	N (C x S)	16	1.1261	0.2646		9946
ha x *de*	C v S (1)	8	1.9455	**0.0186**		8907
	C v S (2)	8	0.7782	0.5428		8888
	C v S (3)	8	2.0281	**0.0341**		8906
	C v S (4)	8	1.6016	0.0647		8903
	Canyon (1 x 2)	8	1.3578	0.1807		8897
	Canyon (1 x 3)	8	2.4810	**0.0084**		8872
	Canyon (1 x 4)	8	4.1301	**0.0028**		8880
	Canyon (2 x 3)	8	1.1735	0.2480		8914
	Canyon (2 x 4)	8	1.8414	0.0707		8856
	Canyon (3 x 4)	8	1.6238	0.0638		8889
	Slope (1 x 2)	8	1.9334	0.0517		8910
	Slope (1 x 3)	8	4.0600	**0.0035**		8908
	Slope (1 x 4)	8	3.7246	**0.0028**		8943
	Slope (2 x 3)	8	2.1512	**0.0252**		8863
	Slope (2 x 4)	8	1.9067	**0.0350**		8899
	Slope (3 x 4)	8	0.8769	0.4837		8893

SM Table 4. Univariate PERMANOVA pairwise comparisons for significant terms (see Table 6) for macrofaunal community biological traits and bioturbation potential (BP_c) within the canyons and adjacent slopes. Bold text indicates significant differences ($p < 0.05$), † = square–root, * = weighted dispersion transformed.

Factors	**Source**	**df**	***t*-statistic**	***P* (perm)**	***P* (MC)**	**Unique Perms**
Size Range (sr) †						
ha x *si*	C (B x N)	16	1.3108	0.1744		9940
	S (B x N)	16	1.7725	**0.0472**		9958
	B (C x S)	16	2.5001	**0.0063**		9953
	N (C x S)	16	0.5976	0.7878		9949
Longevity (L) †						
ha x *si*	C (B x N)	16	1.5364	0.1116		9960
	S (B x N)	16	2.3406	**0.0135**		9955
	B (C x S)	16	2.7279	**0.0028**		9958
	N (C x S)	16	1.3401	0.1658		9953
si x *de*	1 (Baltimore x Norfolk)	8	2.0786	**0.0207**		8948
	2 (Baltimore x Norfolk)	8	2.1648	**0.0231**		8925
	3 (Baltimore x Norfolk)	8		*negative*		
	4 (Baltimore x Norfolk)	8	2.4559	**0.0154**		8908
	B (1 x 2)	8	2.2401	**0.0158**		8867
	B (1 x 3)	8	4.305	**0.003**		8895
	B (1 x 4)	8	4.3143	**0.0041**		8823
	B (2 x 3)	8	3.7136	**0.0023**		8878
	B (2 x 4)	8	3.8714	**0.0027**		8851
	B (3 x 4)	8	1.8693	0.0647		8945
	N (1 x 2)	8	1.5226	0.1505		8936
	N (1 x 3)	8	3.628	**0.0027**		8891
	N (1 x 4)	8	4.2922	**0.0019**		8914
	N (2 x 3)	8	1.7165	0.0999		8928
	N (2 x 4)	8	1.3853	0.1823		8875
	N (3 x 4)	8	1.5088	0.1571		8919
ha x *si* x *de*	BC x NC (1)	4	2.7259		**0.0224**	10
	BC x NC (2)	4	1.2113		0.2892	10
	BC x NC (3)	4	1.3088		0.2415	10
	BC x NC (4)	4	2.1049		0.095	10
	BS x NS (1)	4	1.2649		0.2665	10
	BS x NS (2)	4	2.1108		**0.048**	10
	BS x NS (3)	4	1.1096		0.3331	10
	BS x NS (4)	4	3.3801		**0.0172**	10
	BC x BS (1)	4	1.0085		0.3769	10
	BC x BS (2)	4	0.69074		0.6671	10

SM Table 4 cont…

	BC x BS (3)	4	5.6169		**0.0005**	10
	BC x BS (4)	4	1.9861		0.083	10
	NC x NS (1)	4	2.8191		**0.0226**	10
	NC x NS (2)	4	0.63656		0.6237	10
	NC x NS (3)	4	0.8869		0.4582	10
	NC x NS (4)	4	3.106		**0.0184**	10
	BC (1 x 2)	4	1.7706		0.1016	10
	BC (1x 3)	4	3.8669		0.1033	10
	BC (1 x 4)	4	3.3933		0.1036	10
	BC (2 x 3)	4	1.8237		0.0998	10
	BC (2 x 4)	4	2.6305		0.099	10
	BC (3 x 4)	4	3.1798		0.1083	10
	BS (1 x 2)	4	1.5805		0.1995	10
	BS (1x 3)	4	2.963		0.1034	10
	BS (1 x 4)	4	3.0225		0.0992	10
	BS (2 x 3)	4	3.835		0.0982	10
	BS (2 x 4)	4	2.9558		0.0995	10
	BS (3 x 4)	4	1.3581		0.2971	10
	NC (1 x 2)	4	1.1296		0.4033	10
	NC (1x 3)	4	1.6763		0.2023	10
	NC (1 x 4)	4	2.6098		0.0991	10
	NC (2 x 3)	4	1.0828		0.5047	10
	NC (2 x 4)	4	1.6939		0.1955	10
	NC (3 x 4)	4	1.3365		0.2034	10
	NS (1 x 2)	4	1.9601		0.0947	10
	NS (1x 3)	4	3.6576		0.1034	10
	NS (1 x 4)	4	5.9062		0.1024	10
	NS (2 x 3)	4	1.6217		0.2991	10
	NS (2 x 4)	4	1.3371		0.2931	10
	NS (3 x 4)	4	2.0537		0.0992	10
Larval development (ld) *						
ha x *si*	C (B x N)	16	0.66127	0.6739		9961
	S (B x N)	16	3.1824	**0.0047**		9947
	B (C x S)	16	3.6083	**0.0011**		9965
	N (C x S)	16	1.2934	0.1935		9970
ha x *de*	C x S (1)	8	2.1128	**0.0176**		8874
	C x S (2)	8	1.3933	0.1855		8924
	C x S (3)	7	2.1536	**0.0342**		8944
	C x S (4)	8	2.972	**0.0034**		8886
	Canyon (1 x 2)	8	1.1848	0.2773		8895
	Canyon (1 x 3)	8	2.3311	**0.0185**		8952
	Canyon (1 x 4)	8	4.3794	**0.0022**		8912

SM Table 4 cont…

	Canyon (2 x 3)	8	1.0559	0.3491	8934
	Canyon (2 x 4)	8	2.0769	**0.0488**	8936
	Canyon (3 x 4)	8	1.9658	**0.035**	8943
	Slope (1 x 2)	8	1.8643	0.0909	8899
	Slope (1 x 3)	7	5.3437	**0.004**	8886
	Slope (1 x 4)	8	5.115	**0.0022**	8883
	Slope (2 x 3)	7	2.0961	0.0653	8953
	Slope (2 x 4)	8	2.4243	**0.0283**	8939
	Slope (3 x 4)	7	1.057	0.3538	8914
Egg development (ed)					
ha x *si*	C (B x N)	16	1.1746	0.2688	9960
	S (B x N)	16	2.5034	**0.0074**	9957
	B (C x S)	16	2.9681	**0.0022**	9946
	N (C x S)	16	0.72308	0.6166	9954
ha x *de*	C x S (1)	8	1.7511	**0.0585**	8901
	C x S (2)	8	0.94245	0.4372	8937
	C x S (3)	7	1.87	**0.0523**	8919
	C x S (4)	8	2.16	**0.021**	8945
	Canyon (1 x 2)	8	1.1059	0.3449	8911
	Canyon (1 x 3)	8	2.4582	**0.0097**	8960
	Canyon (1 x 4)	8	4.1963	**0.0014**	8885
	Canyon (2 x 3)	8	1.3167	0.2216	8881
	Canyon (2 x 4)	8	1.916	0.0641	8865
	Canyon (3 x 4)	8	1.4464	0.1537	8919
	Slope (1 x 2)	8	2.323	**0.0206**	8924
	Slope (1 x 3)	7	3.9959	**0.0022**	8919
	Slope (1 x 4)	8	4.2882	**0.0029**	8896
	Slope (2 x 3)	7	2.3184	**0.0272**	8892
	Slope (2 x 4)	8	2.213	**0.0336**	8894
	Slope (3 x 4)	7	0.62372	0.7765	8949
Life habit (lh) *					
ha x *si*	C (B x N)	16	1.4698	0.0953	9958
	S (B x N)	16	2.302	**0.0111**	9943
	B (C x S)	16	2.3956	**0.0058**	9956
	N (C x S)	16	1.4509	0.1142	9947
ha x *de*	C x S (1)	8	1.7285	0.0708	8932
	C x S (2)	8	0.96782	0.4322	8908
	C x S (3)	7	1.7171	0.0719	8915
	C x S (4)	8	1.8722	**0.0281**	8906
	Canyon (1 x 2)	8	1.6351	0.0912	8917
	Canyon (1 x 3)	8	2.1095	**0.0175**	8873
	Canyon (1 x 4)	8	3.0213	**0.0025**	8942

SM Table 4 cont…

	Canyon (2 x 3)	8	1.4701	0.1161	8884
	Canyon (2 x 4)	8	1.8357	**0.026**	8896
	Canyon (3 x 4)	8	1.5125	0.1132	8910
	Slope (1 x 2)	8	1.8192	0.0769	8865
	Slope (1 x 3)	7	3.8504	**0.0034**	8893
	Slope (1 x 4)	8	4.473	**0.0027**	8871
	Slope (2 x 3)	7	2.0076	**0.0477**	8911
	Slope (2 x 4)	8	2.3973	**0.0245**	8925
	Slope (3 x 4)	7	0.9875	0.3854	8890
si x *de*	1 (Baltimore x Norfolk)	8	1.4067	0.1384	8915
	2 (Baltimore x Norfolk)	8	1.5495	0.0776	8926
	3 (Baltimore x Norfolk)	8	1.3857	0.2237	8886
	4 (Baltimore x Norfolk)	8	2.4653	**0.0112**	8883
	B (1 x 2)	8	1.878	**0.0262**	8881
	B (1 x 3)	8	3.1836	**0.0061**	8914
	B (1 x 4)	8	3.5401	**0.0047**	8920
	B (2 x 3)	8	2.3414	**0.0028**	8922
	B (2 x 4)	8	2.7236	**0.0058**	8861
	B (3 x 4)	8	2.1413	**0.0108**	8896
	N (1 x 2)	8	1.6543	0.0824	8959
	N (1 x 3)	8	3.0146	**0.0055**	8955
	N (1 x 4)	8	4.2809	**0.0019**	8904
	N (2 x 3)	8	1.7849	0.0786	8903
	N (2 x 4)	8	1.3365	0.1895	8906
	N (3 x 4)	8	1.5695	0.1178	8921
Sediment position (sp)					
ha x *si*	C (B x N)	16	0.79971	0.5413	9960
	S (B x N)	16	2.1828	**0.0243**	9951
	B (C x S)	16	2.8756	**0.0022**	9959
	N (C x S)	16	1.2238	0.2065	9955
si x *de*	1 (Baltimore x Norfolk)	8	1.1744	0.2694	8940
	2 (Baltimore x Norfolk)	8	1.4717	0.137	8812
	3 (Baltimore x Norfolk)	8	1.6171	0.1057	8909
	4 (Baltimore x Norfolk)	8	2.0852	**0.0318**	8925
	B (1 x 2)	8	1.8523	0.061	8968
	B (1 x 3)	8	3.4797	**0.0055**	8908
	B (1 x 4)	8	3.6186	**0.0052**	8982
	B (2 x 3)	8	3.0807	**0.004**	8940
	B (2 x 4)	8	2.7121	0.0118	8942
	B (3 x 4)	8	1.8824	0.0537	8860
	N (1 x 2)	8	1.8012	0.0813	8926
	N (1 x 3)	8	3.0642	**0.0046**	8911

SM Table 4 cont…

	N (1 x 4)	8	4.1264	**0.0023**		8889
	N (2 x 3)	8	1.7286	0.0793		8891
	N (2 x 4)	8	1.1392	0.2739		8849
	N (3 x 4)	8	1.3089	0.2371		8898
Feeding mode (f)						
ha x *si* x *de*	BC x NC (1)	4	1.0994		0.3393	10
	BC x NC (2)	4	1.083		0.3479	10
	BC x NC (3)	4	0.90949		0.4634	10
	BC x NC (4)	4	2.5177		**0.0358**	10
	BS x NS (1)	4	1.4306		0.193	10
	BS x NS (2)	4	1.2529		0.2603	10
	BS x NS (3)	4	0.9004		0.4831	10
	BS x NS (4)	4	2.8609		**0.0148**	10
	BC x BS (1)	4	1.621		0.1291	10
	BC x BS (2)	4	1.1347		0.3144	10
	BC x BS (3)	4	4.7162		**0.0028**	10
	BC x BS (4)	4	2.6566		**0.0252**	10
	NC x NS (1)	4	1.9474		0.0986	10
	NC x NS (2)	4	0.50502		0.753	10
	NC x NS (3)	4	0.84614		0.4888	10
	NC x NS (4)	4	2.4706		**0.0467**	10
	BC (1 x 2)	4	1.4926		0.1564	10
	BC (1x 3)	4	3.0455		**0.0107**	10
	BC (1 x 4)	4	3.2096		**0.0093**	10
	BC (2 x 3)	4	1.5549		0.174	10
	BC (2 x 4)	4	2.2901		0.0509	10
	BC (3 x 4)	4	2.5098		**0.0193**	10
	BS (1 x 2)	4	1.4443		0.1796	10
	BS (1x 3)	4	3.7068		**0.0074**	10
	BS (1 x 4)	4	3.42		**0.0122**	10
	BS (2 x 3)	4	2.8321		**0.0157**	10
	BS (2 x 4)	4	2.856		**0.0201**	10
	BS (3 x 4)	4	1.5139		0.1504	10
	NC (1 x 2)	4	1.3029		0.2368	10
	NC (1x 3)	4	1.6271		0.1351	10
	NC (1 x 4)	4	2.7405		**0.0177**	10
	NC (2 x 3)	4	0.89572		0.4531	10
	NC (2 x 4)	4	1.8577		0.0919	10
	NC (3 x 4)	4	0.90292		0.5007	10
	NS (1 x 2)	4	1.682		0.1504	10
	NS (1x 3)	4	3.6875		**0.0092**	10
	NS (1 x 4)	4	3.5409		**0.0037**	10

SM Table 4 cont…

	NS (2 x 3)	4	1.3045	0.2382	10
	NS (2 x 4)	4	0.73971	0.6167	10
	NS (3 x 4)	4	1.466	0.1663	10
Bioturbation (b)					
ha x *si* x *de*	BC x NC (1)	4	2.0668	0.052	10
	BC x NC (2)	4	1.6356	0.1246	10
	BC x NC (3)	4	1.4598	0.1878	10
	BC x NC (4)	4	1.2534	0.2628	10
	BS xNS (1)	4	1.3796	0.2083	10
	BS xNS (2)	4	1.3034	0.2291	10
	BS xNS (3)	4	0.68713	0.61	10
	BS xNS (4)	4	2.8094	**0.0153**	10
	BC x BS (1)	4	1.4477	0.1699	10
	BC x BS (2)	4	1.2496	0.2584	10
	BC x BS (3)	4	4.8226	**0.0023**	10
	BC x BS (4)	4	2.4482	**0.0264**	10
	NC x NS (1)	4	2.5105	**0.0263**	10
	NC x NS (2)	4	0.72296	0.6187	10
	NC x NS (3)	4	1.0191	0.3901	10
	NC x NS (4)	4	1.3152	0.2348	10
	BC (1 x 2)	4	1.7972	0.0944	10
	BC (1x 3)	4	3.5732	**0.0065**	10
	BC (1 x 4)	4	2.5908	0.0183	10
	BC (2 x 3)	4	1.7199	0.0939	10
	BC (2 x 4)	4	2.2328	**0.0438**	10
	BC (3 x 4)	4	2.5143	0.0533	10
	BS (1 x 2)	4	1.6211	0.1234	10
	BS (1x 3)	4	2.8065	**0.0154**	10
	BS (1 x 4)	4	3.0581	**0.013**	10
	BS (2 x 3)	4	2.6723	**0.0199**	10
	BS (2 x 4)	4	2.6858	**0.0266**	10
	BS (3 x 4)	4	1.8286	0.0792	10
	NC (1 x 2)	4	1.7811	0.0857	10
	NC (1x 3)	4	1.6508	0.1157	10
	NC (1 x 4)	4	2.4578	**0.0196**	10
	NC (2 x 3)	4	1.1512	0.3051	10
	NC (2 x 4)	4	1.7502	0.1029	10
	NC (3 x 4)	4	1.4918	0.1426	10
	NS (1 x 2)	4	1.564	0.1728	10
	NS (1x 3)	4	3.2132	**0.0192**	10
	NS (1 x 4)	4	2.7098	**0.0158**	10
	NS (2 x 3)	4	1.1607	0.3104	10

SM Table 4 cont…

NS (2 x 4)	4	0.44487	0.884	10
NS (3 x 4)	4	1.2096	0.2821	10

Chapter 5

Synthesis and conclusions

Robertson CM

1 Introduction

In this chapter, the main findings of this thesis are discussed, providing an overview of the hydrodynamic, sedimentary and organic enrichment gradients that were found within the Baltimore and Norfolk canyons. These data underpin the observed benthic community structure and the estimated ecosystem functioning of the two canyons and their adjacent slopes. Such a complete and multidisciplinary dataset across two almost adjacent canyons is relatively rare in canyon studies, and it allows for the proposal of a holistic conceptual model that describes the role the physical environment plays in determining the structure and functioning of benthic communities. This concluding chapter also explores the study's limitations and future research directions.

2 The physical oceanography of Mid-Atlantic Bight canyons

Canyons are famed for their dynamic topographies, hydrodynamic and sedimentological variability which promotes unique and complex habitats (De Leo et al., 2010). Yet, our understanding of the environmental parameters that govern most canyon-related ecosystem processes is still emerging and although much progress has been made, there are few projects working on integrated multidisciplinary approaches to canyon ecosystem ecology. Chapter two provided an oceanographic context for canyon-specific hydrodynamic conditions in Baltimore and Norfolk canyons, designed to extend our understanding of the conditions within the MAB. These canyons are relatively understudied compared to the MAB shelf break (Beardsley & Winant, 1979; Castelao et al., 2010; DeMaster et al., 2002; Houghton et al., 1994), but through the use of ship-based hydrographic surveys of the water column and long-term *in situ* seafloor monitoring of canyon bottom currents and turbidity, the study characterised the oceanographic drivers within the two canyon systems.

Three hypotheses were posited, which addressed water mass characteristics, and sediment resuspension of canyon and slope habitats and canyon bottom current velocities. On account of the observation that Baltimore and Norfolk canyons are in close proximity of each other, incising the MAB shelf and far from the coastline, it was clear that the two canyons shared the same regional water masses, with similar temperature and salinity patterns throughout. This leads to a natural question, which formed the latter hypotheses, were the two canyons distinct with respects to their conditions if they reside within the same water masses? Submarine canyons can differ substantially in terms of their oceanography, sedimentary regimes, habitats and biota (Levin & Sibuet, 2012), especially when compared with the adjacent slope habitats. The topographic variability of canyons has been shown to generate areas of distinct and enhanced interaction with local hydrodynamics and sediment regimes, again when compared to the surrounding slopes (Amaro et al., 2016; Levin & Sibuet, 2012). But is this a true test of the distinctiveness of canyons? Should we not be attempting to compare conditions between different canyons to help address major conservation and management priorities regarding questions related to the uniqueness of habitats within the deep sea? (e.g. Auster et al., 2011; Fernandez-Arcaya et al., 2017).

2.1 Are MAB canyons hydrodynamically distinct?

In this thesis, the MAB shelf-slope front was prominent in the upper water column within the two MAB canyons and their adjacent slopes, below which, the two deep water masses (WNACW and WASIW) occurred, the latter in contact with the bed. However, one key finding was the difference in current velocities between the two canyons. Current velocities were twice as high in Norfolk as in Baltimore, at all locations and may be related to the orientation of the canyon-head, relative to the prevailing south-westerly shelf boundary current (See Obelcz et al., 2014 for canyon geomorphological description). These data suggest a greater potential for disturbance, particularly with resuspension events, in Norfolk Canyon compared to Baltimore Canyon. This is likely reflected by the differences in the distributions of the nepheloid layers and sediment organic enrichment between the two canyons. Both canyons had strong intermediate and benthic nepheloid layers, likely originating in the upper reaches, as a result of tidally-driven bottom currents, perhaps related to the interaction between steep-sided topography and the focusing of internal waves.

The nepheloid layer structure, water mass features and water column flow direction were described based on a single synoptic 'snap shot' of the entire water column within the two canyons. Although the findings imply differences in turbidity regime features between the canyons, a cautionary approached should be taken when inferring turbidity differences due to the timing of surveys. Rarely applied to canyon studies, the analysis of water masses was useful in that it revealed only minor differences between the canyons and slopes, indicating that in some respects, adjacent canyons may share similar environmental conditions. From the data collected, it was also possible to apply an estimation of the overall flow throughout the water column (not including the bottom 200 m, and unfortunately, the Norfolk field campaign was not able to replicate all the required across-canyon water profiling needed to compare water column flow between the two canyons). Baltimore Canyon exhibited a strong down-canyon flow within the upper and intermediate water column, but in contrast, long-term *in situ* data from the seafloor showed the net transport of bottom water was up-canyon at all lander and mooring locations. Gardner (1989a and 1989b) found evidence for the presence of a water mass convergence zone in Baltimore Canyon (~500 m) and suggested that down-canyon currents in the upper reaches meet up-canyon current flow in the mid canyon. From the intensive observations in Chapter 2, it was possible to identify the water masses forming the convergence zone and show that water flow through the canyon was interacting with the tide.

The study differed from the previous study in that bottom water was shown to flow up the canyon and that the layers of the intermediate water masses flow down the canyon, presumably sliding over the top of the canyon boundary layer water mass at an undetermined depth. In defining the stratified layer of the water column it was noted that the density surface (27 σ_θ) separating the shelf-slope front from intermediate WNACW and lower WASIW water, were closely coincident with the upper limits of the nepheloid layers (Figure 2a). Furthermore, Baltimore Canyon showed evidence of active advection of suspended particle nepheloid packages along the density surface, presumably deposited further down the canyon or dispersed onto the adjacent lower continental slope. Norfolk Canyon shared the same density structure, although lacked any evidence of advection of nepheloid packages, which may be a consequence of the weakly stratified water column during the spring season. In terms of canyon benthic communities, the persistent up-canyon current flow may have implications for the supply of organic matter to canyon benthic communities, an aspect which remains unresolved. It is not clear whether resuspension of organic matter from the enriched lower canyon is transported to upper canyon habitats during up-canyon flow events, providing further interesting research avenues. Similar up-canyon flow has been reported in previous studies, e.g. Whittard Canyon (Amaro et al., 2016) and in the Bay of Biscay (Mulder et al., 2012). Prouty et al., (2017) confirmed that MAB canyons, particularly Baltimore, act as conduits of marine and terrestrial derived organic matter, are likely key contributors to benthic biomass and productivity in the region.

2.2 Improving physical observations within canyons

In order to capture the three-dimensional movement of the water column, an improved approach to capturing the nepheloid structures and water masses of the canyons, would be to have repeated synoptic measures simultaneously between different canyons or at least conducted during the same season. Higher resolution, both in space and time, would also allow for a fuller characterisation of the nepheloid layer generation within canyons, as well as establishing how various hydrographic features interact to drive such patterns. However, such an approach would require substantial ship time, and even the use of several research vessels. Recently developed technology that could provide such detail, but are not yet a standard compliment of oceanographic research ships are gliders, which have been shown to capture various canyon processes in great detail (e.g. Hall et al., 2017; Porter et al., 2016). Despite the limitations within this study, the *in situ* long-term lander and mooring data confirmed temporal peaks and troughs in turbidity within both canyons. These were much smaller in magnitude and frequency in lower reaches of Baltimore than Norfolk Canyon, but appeared to be present throughout the different seasons.

2.3 Summary

To summarise and to an extent generalise the physical oceanographic conditions within the two MAB canyons, a schematic representation of the environmental conditions and their drivers is proposed in Figure 1. The simplistic model does omit some known drivers from canyon systems, for example, interactions between wind driven currents, prevailing continental slope currents, Gulf Stream eddies and storm events, which differ spatially and temporally. However, the proposed mechanism, based on our current knowledge of canyon hydrodynamics, illustrates how down-canyon movement from the surface and intermediate water masses can converge against the relatively slower up-wards flowing bottom water. Internal waves are focussed within the complex topography of the canyon (Cacchione et al., 2002), and density gradients entrain nephels to certain areas of the canyons (Gardner, 1989a; Figure 1). In this study it was thought the internal waves that enter Baltimore and Norfolk Canyon travel along density surface between water masses and at the point of contact with bed, generates the suspended material forming the nepheloid layer. Similar processes have been reported for Hudson Canyon (Hotchkiss & Wunsch, 1982; Keller and Shepard, 1978) in the northern MAB region, Whittard Canyon in the eastern North Atlantic (Wilson et al., 2015b) and in the Mediterranean Sea (Canals et al., 2006; Palanques et al., 2006).

3 Macrofaunal community patterns

Ecological research has shown the importance of canyons as hotspots of biodiversity and biomass on continental margins. Emerging trends suggest that canyons are also highly variable and sustain unique habitats with associated species which are often not present on adjacent slopes (Levin & Sibuet, 2012; Ramirez-Llodra et al., 2010). Over the last two decades, an important conclusion has been that the significant heterogeneity of canyons, especially along the sides where vertical cliffs are common and offer refuge to important species and habitats, such as cold-water corals and sponges (Huvenne et al., 2011). Several studies have also shown that enhanced and highly distinctive canyon macrofaunal communities, abundance and biomass patterns are structured by canyon-specific environmental conditions (Cúrdia et al., 2004; De Leo et al., 2014; Escobar Briones et al., 2008; García et al., 2010; Paterson et al., 2011).

Chapter Three investigated the macrofaunal diversity, density, biomass and community structure of the two canyons and adjacent slopes and related this to environmental gradients. The study utilised a combination of faunal and biogeochemical cores to assess differences in macrofaunal community, sediment grain-size and sediment organic enrichment, aiming to better understand the 'canyon effect' on community structure. Four hypotheses were tested: Firstly, canyon macrofaunal community assemblages differed in abundance, diversity, biomass and community composition from those found on adjacent slopes. Secondly, that canyon axis and slope macrofauna communities were structured by the same set of environmental parameters. Thirdly, those macrofauna communities exhibiting signatures of disturbance would be more prevalent within canyons than on slopes. Finally, this chapter asked whether canyon and slope communities followed the unimodal relationship in diversity with depth, as expected for deep-sea environments.

3.1 Do communities differ in canyons?

One of the key findings of this study was that MAB canyons support macrofaunal communities that were distinct from the adjacent slopes, supporting the first hypothesis of Chapter Three. Slope macrofauna density decreased with depth. However, canyon densities were supressed at 550-555 m followed by a sharp rise at 800-900 m, forming a distinct bimodal density distribution along the canyon axis. Communities in the canyons were generally dominated by opportunistic species that were able to take advantage of organic enrichment. In Norfolk, these were generally polychaetes (Capitellidae and Cirratulidae), whereas in Baltimore, the bivalves Lucinidae and Periplomatidae were found at the canyon heads and the bivalves Yoldiellinae and Thyasiridae in the secondary peak (800-900 m), reflecting depth preferences for these families. This study did not find enhanced biomass within these canyons when compared to the adjacent slope, contradicting previous observations (Cunha et al., 2011; Escobar Briones et al., 2008; Vetter & Dayton, 1998). The organically enriched areas of the canyons contained macrofauna that had smaller body sizes than slope habitats, reflecting communities dominated by smaller opportunistic species (Pearson & Rosenberg, 1978).

3.2 Are MAB canyons centres of benthic disturbance?

Altered hydrodynamics, especially when compared to adjacent slopes and as discussed above, are known factors influencing the biological communities within canyons (Cunha et al., 2011; Cúrdia et al., 2004; Vetter & Dayton, 1998). In this study, clear differences in macrofauna diversity, density and community compositional were attributed to disturbance originating from sediment organic enrichment patterns within the canyons. Such disturbance-food supply gradients have been repeatedly suggested as primary factors in explaining patterns of species diversity and richness across multiple habitats including canyons (Huston, 1979; Kadmon & Benjamini, 2006; Kondoh, 2001; Paterson & Lambshead, 1995; Paterson et al., 2011; Rex et al., 1993). Sedimentary organic enrichment was a significant factor in the structuring of canyon macrofaunal communities. Abundance-biomass *k*-dominance curves confirmed that deeper canyons communities (800-1180 m) were dominated by smaller and more opportunistic taxa, which were able to take advantage of the high levels of accumulated organic matter.

Disturbed community structure was also observed on the upper slopes at both study sites, but these sites were characterised by lower organic matter enrichment, suggesting a different disturbance mechanism in operation compared to lower canyon habitats. One may speculate, that upper slope habitats are subject to frequent high current speeds, as reflected in the grain-size data. Another may be that anthropogenic disturbance plays a role. The MAB region is known to support large demersal fisheries. According to the Mid-Atlantic Ocean Data Portal, the MAB shelf adjacent to the two canyons were subjected to moderate-high levels of bottom trawling in 2012 and 2013 (based on Federal reports for vessels > 20 m). Recently studies have shown that commercial trawling fleets can have significant effect, particularly with respect to sediment movement, when fishing around the rim of canyons in Mediterranean (Martín et al., 2014) and Celtic margin canyons (Wilson et al., 2015a).

Abundance and biomass in the deep sea generally follows an exponentially decreasing relationship with depth (McClain et al., 2009b), due to the decline in the availability of high quality food (Rex & Etter, 2010). This study found that accumulation of organic matter occurred in both canyons and was greater than found on the adjacent slopes. Both canyon habitats demonstrated significant changes in macrofaunal communities, which were attributed to organic enrichment and depth gradients. The distribution of organic matter did differ between the canyons; in Baltimore Canyon a distinct deposition centre was observed in the lower reaches of the canyon. By contrast, Norfolk Canyon were had higher levels of enrichment, distributed evenly along the canyon thalweg, a likely consequence of the far higher current speeds within the canyon. Both canyon communities exhibited a bimodal abundance relationship with depth with a secondary peak occurring in the deeper regions (Figure 2a). Canyons clearly disrupt expected patterns in abundance and biomass in the deep sea largely due to a high level of disturbance, whilst slopes followed the expected decline in abundance and biomass (Figure 2a).

3.3 Sampling limitations

This study does suffer from some design, logistic and equipment limitations. Many of which are similar to those found within many deep-sea studies (Rex & Etter, 2010). In particular, the sampling design was built around the collection of three true replicates at four depth zones, which limited the potential understanding of the distribution of sediment and organic enrichment patterns, as well as abundance, biomass and community patterns, particularly in the deeper reaches of the canyons. In future, fewer replicates covering a larger depth range would give a stronger insight into changes in communities along the full length of the canyon thalweg and deeper channels. There was also no replication of the various sedimentological or organic enrichment sampling, largely due to the amount of time available on the research vessel, and no independent biogeochemical cores were taken in Norfolk Canyon. These constraints were largely driven by the limited time available on the research cruises. The daily program was largely dominated by ROV operations, leaving only limited time to collect bottom samples.

The choice of sampling equipment in the deep sea is of much debate (Bett et al., 1994; Blomqvist, 1991; Montagna et al., 2017), with boxcores being the choice for many. Yet the adoption of multicorers is rapidly increasing, and within a few years it will certainly be the most accepted (See Chapter One). In this study, the NIOZ boxcore was used consistently throughout all sampling operations (Gage & Bett, 2005). The corer has several advantages over multicorers, in that it is highly robust and simple to deploy, it also collects a far greater area of sediment, which has been acknowledged as a requirement for sampling diversity. Indeed, some of the species found are highly unlikely to have been collected with a multicorer (i.e. large large-bodied individuals of Sipunculidae and Edwardsiidae). Boxcores are often cited as underestimating abundance and biomass of various components of the macro- and meiofauna (Montagna et al., 2017), however, the NIOZ designed device has made some attempts to limit the typical "bow wave" effect that can affect the sampling accuracy of such devices (See Chapter 1). Whilst it would be preferable to have used a multicorer for the benthic sampling in this study, the consistent use of the boxcore allows for within study comparisons and does not invalidate the data collected.

3.4 Summary

Overall, the chapter supported the importance of canyon-related accumulation of organic sediment enrichment as a key disturbance factor impacting MAB macrofaunal community assemblages. Various models have been proposed to understand the relationship between species richness, productivity and depth. In canyon studies, Paterson et al. (2011) used the Dynamic Equilibrium Model (DEM) to understand polychaete species richness across enrichment regimes in the Iberian margin canyons. The model predicts diversity is a function of the interaction between productivity and disturbance (Kondoh, 2001; McClain & Schlacher, 2015; Svensson et al., 2009), in this case organic enrichment. Paterson et al. (2011) suggested the high diversity at mid-canyon depths (3400 m) of Cascais Canyon was due to the balance between productivity and disturbance. In the present study, high diversity occurred at mid-canyon depths, followed by depressed diversity in the lower canyon. The DEM predicts a positive relationship between disturbance and diversity, when productivity is high. This suggests that the observed high diversity in MAB canyons is driven by the optimal levels of sediment organic enrichment and fast current speed disturbance regimes at mid-canyon depths (~550 m). In lower canyon depths, where depressed diversity occurred, high organic matter accumulation may exceed the optimal productivity balance, resulting in a negative productivity-diversity relationship and a shifting of the convex diversity curve to the right as sediment enrichment increases with depth (Figure 2b).

4 Macrofaunal community ecosystem function

Deep-sea sediments are one of the largest biomes on the planet and it is likely that the contribution of the soft sediment macrofauna to deep-sea ecosystem processes such as nutrient cycling and carbon burial is substantial (Leduc & Pilditch, 2013). Yet, our understanding of how these systems and the organisms within function remains poor and we need to establish the scale and resilience of services provided by them for conservation and management purposes (Leduc et al., 2013; Mengerink et al., 2014; Thurber et al., 2014). The study of the biological traits within marine environments is in its infancy (Bremner, 2008) but has proved promising in shallow-water ecosystems, particularly in relation to anthropogenic impact from fishing (Bolam, 2013). Ecologists have increasingly realised that the properties of species are essential in the promotion and maintenance of ecosystem functioning (Pawar et al., 2015). The ability of species to affect ecosystem properties and processes can be assessed through analyses of their functional traits, which reflect behaviour and morpho-physiology (Díaz & Cabido, 2001; Pawar et al., 2015). As such, methods that can generalise species to a number of traits or functions offer encouraging insights into community function and can be used to improve our ability to understand the ecosystem functioning of the deep sea.

Chapter Four sought to quantify the range of traits expressed by canyon and slope communities in order to determine specific behaviours that were related to the observed environmental gradients. The study focused on three questions: Firstly, to assess functional diversity differences across canyons and adjacent slopes. Secondly, the study assessed whether the proportions of biological traits differed between canyon and slope community assemblages. And finally, the study investigated the relationship between bioturbation potential and community trait assemblages across organically enrichment gradients.

4.1 Canyons as diverse functional habitats

In terms of functional diversity, this study established differences in functional richness and evenness between canyons and slopes, along the depth gradient. Two measures of functional richness were used. The non-weighted functional richness metric FRic showed higher functional richness in Baltimore Canyon compared to Norfolk Canyon, whereas Rao’s Q showed depressed functional richness in disturbed canyon communities. Functional diversity indices describe specific facets of the complex functional aspects of community structure (Cadotte, 2011; Magurran & McGill, 2011, Mason et al., 2005). Currently, there is no consensus on a preferred index, or one that captures all aspects of functional ecology, and there remains an ongoing debate as to which functional diversity measures best reflect ecosystem functioning (Cadotte, 2011). It is recognised, however, that weighted functional richness indices are particularly important in understanding community functional patterns (Mindel et al., 2016; Stuart-Smith et al., 2013). This study chose to use a biomass-weighted approach in the calculation of functional diversity on account of the closer relationship between biomass and ecosystem function, compared to abundance-weighted measures (Bolam & Eggleton, 2014; Bremner, 2008 Gagic et al, 2015). It should be noted that a comparison with abundance-weighted functional indices may add further insight into the functional dynamics of the soft sediment canyon communities.

The study showed the proportions of exhibited traits differed between Baltimore and Norfolk canyons and adjacent slopes. The study identified four functional cluster groups separating canyon and slope communities. Groups A and C, although common to both habitats, occurred more in canyon communities than slope communities. Groups B and D, were more associated with slopes than canyons. An enhanced affinity for canyon communities to utilise traits involved in the active reworking and movement of the canyon sediments was highlighted (Figure 3). Bioturbation is the biogenic modification of sediments through particle reworking and burrow ventilation and is known to be a key mediator of many important geochemical processes in marine systems (Meysman et al., 2006; Queirós et al., 2013; Teal et al., 2008). Canyon communities had enhanced soft-sediment functioning, with respects to community bioturbation potential, especially in upper canyons communities. This was driven by the large biomass of surface deposit-ingesting bivalves, ophiuroids and large polychaetes (Figure 3). The lower canyon had disturbed communities, which also showed higher bioturbation potential, in association with the high levels of organic enrichment, driven by the large dominant stands of surface and subsurface deposit-ingesting opportunistic bivalves and polychaetes (Figure 3).

4.2 Limitations of the functional approach

It should be noted however, that functional analyses are not, at present, a panacea for ecosystem function in the deep sea. The approaches are limited due to the unquantified relationships between biological traits and meaningful ecosystem functional indicators

(Bolam, 2013). Furthermore, there is a lack of taxonomic expertise and understanding of the general ecology of many species which is needed for assigning potential functional traits to most deep-sea taxa groups (Bremner et al., 2003; Solan et al., 2009). The approach used in the present study utilised ten traits developed from shelf sea communities to characterise community function. Whilst this represents a good starting point in assessing continental margin functional ecology and performs better than single-trait approaches (e.g. feeding guilds), future studies should develop specific sets of deep-sea traits in order to fully understand the functional nature of deep-sea communities, where species are often unique and may perform unknown functional roles.

Ultimately, the validation of functional roles will require autoecological and community manipulative experiments involving, for example, community responses to sediment enrichment, community recruitment and succession. Such experiments would provide *a priori* knowledge of which traits or combinations of traits are most important for ecosystem functions. The potential for trait-based studies in explaining and predicting biodiversity-ecosystem function relationships is clear (Gagic et al., 2015), and has been shown to perform better than traditional diversity-abundance metrics commonly used by researchers and policy makers. The present study used 10 traits consisting of 49 trait modalities. While it is advocated to include all traits deemed important, more research is needed to ascertain the best method appropriate for benthic communities. Recent works (Gagic et.al., 2015) suggest that statistical approaches (e.g. jackknife or step-wise) can be used to exclude or weight traits that contribute little to predicting functioning.

Clearly, research in deep-sea functional ecology is lagging behind that of the freshwater and terrestrial research areas. However, advances made in these fields can be transferred to the marine environment, as shown by the development of the biological traits approach in this study. Even with the limited data available, such approaches can provide a general understanding about the relationships between traits, species and their environment. Whilst our understanding of deep-sea functional ecology is currently emerging for many species, these approaches could be applied retrospectively to the abundance of large deep-sea community datasets. Ultimately, informing new avenues of research and the development of tools for use in marine conservation, management (Bremner, 2008) and assessments of ecosystem services (Thurber et al., 2014).

4.3 Summary

Overall, this study found substantial differences in macrofaunal functional diversity between canyons and adjacent slopes, with the most pronounced differences evident in shallower communities and represents the first such study for submarine canyon macrobenthic communities. Functional differences centred on sediment reworking traits, which were important within the macrofaunal communities and may have important implications for nutrient cycling and carbon burial in canyon habitats. Community bioturbation potential (BP_c) was higher in canyon habitats than on slopes and represents the greater ability of canyon macrofauna to enhance sedimentary ecosystem processes. The results are promising, especially for the first application of such approaches to a deep-sea system, but they are not without limitation and at best, this is an approximation of how communities could function in the canyons. Further research is needed to develop an accurate understanding of what various species and community types do and how they interact with their environmental gradients.

5 Concluding remarks

In conclusion, the thesis described the differences in species diversity, density, community structure and function in MAB canyons, compared to the adjacent slopes. In relating these differences to the environmental gradients, the thesis confirmed that the benthic macrofauna community structure and function are structured by depth, sediment type and organic enrichment gradients, and indirectly by the interaction of canyon-specific oceanographic regimes. These drivers are suggested to work in synergy shaping community patterns that were recognised as sources of disturbance to the sediment and benthic communities. Overall, the investigations of this thesis have enhanced current knowledge of the benthic ecology of MAB canyons and also provides a stronger understanding of wider submarine canyon and adjacent slope ecosystem ecology. This thesis shows that MAB canyons, like many others remain dynamic, unique and complex habitats, making it difficult to generalise on canyon processes. There are still a plethora of questions to be answered before a full characterisation of canyon ecosystem ecology can be made, especially when only few studies have looked at neighbouring canyons with the view to investigating the possible regional scale canyon-specific mechanisms. This thesis highlights the value of holistic multidisciplinary approaches in the study of deep-sea habitats.

In terms of the oceanography of MAB canyons, the study’s findings are aligned with other canyon studies from the North Atlantic. Amaro et. al., (2016) noted similar nepheloid layer structures and tidal current regimes in the well-studied Whittard Canyon in the eastern North Atlantic. However the present study adds to the standard modes of canyon study by attempting to conclusively link water mass dynamics with turbidity regimes, sediment organic enrichment processes and disturbance gradients. Moreover, the study contributes two high resolution long-term datasets which are can be applied to other studies within the MAB region. Most eastern Atlantic studies have been undertaken with single geological or oceanographic objectives in mind. Few studies have linked benthic soft sediment macrofauna with simultaneous measurements of sediment and biogeochemical parameters (except, De Leo et al., 2014; Gunton et al., 2015; Paterson et al., 2011). In the western North Atlantic, even fewer canyon macrofaunal studies have been undertaken (Houston & Haedrich, 1984; Rowe et al., 1982), highlighting the need for the data presented in this thesis. Furthermore, of the several Federal research efforts undertaken in the canyons off the U.S. coast, the present study represents the only robust macrofaunal study. These recent studies have not routinely included soft sediment communities in their assessment of canyon habitats; favouring instead to focus on megafauna and sensitive canyon coral habitats. This likely reflects the difficultly, costly and time-consuming nature of macrobenthic analyses, as well as the loss of identification skills in the field.

The study utilised abundance biomass curves, first developed to detect how pollution effects benthic assemblages in coastal areas, to assess community disturbance. Canyons are known to harbour distinctly different communities compared to surrounding slopes and although many studies recognise sedimentary disturbance as a key factor structuring benthic communities, few have sought to quantify community disturbance. The thesis established MAB canyons as centres of benthic disturbance, a stressor that strongly structures canyon communities, due to the interaction between disturbance food availability and depth. The study is the first to apply the method in deep-sea studies in the western North Atlantic.

Although functional ecological theory suggests a direct link between functional diversity and ecosystem functions, such study has rarely been attempted in the deep sea (Gambi et al., 2014). The thesis contributes much needed knowledge on the functioning roles of canyon communities and deep-sea macrofauna in general. Given that the majority of the deep-sea floor is soft sediment, the impact these communities are likely to have on global nutrient cycling and carbon sequestration is vast. In the face of continued biodiversity loss, increased anthropogenic and climatic threats, the imperative for understanding what preserves ecosystem service, stability and resilience continues to grow. These are important questions for deep-sea research and this thesis may lay the foundation for such work. The thesis established for the first time that submarine canyons, as well as being biodiversity hotspots, may act as centres of enhanced functioning and bioturbation. In the future, effort should be made to uncover the relationship between functional diversity and ecosystem functions in the deep sea.

6 Future work

Overall the conclusions of this thesis provide a basis for further work investigating the ecosystem ecology along outer continental margins. The work has inspired new questioning as to the ultimate contribution submarine canyons play in the overall productivity of continental margins. Future works are likely to follow similar lines, seeking to further relate estimations of bottom shear stress in canyon habitats to disturbance regimes and community functioning. Including, for example, the long-term oceanographic data in the validation of ROMS hydrostatic models (new work being conducted with C. Mohn, Denmark). The model allows for the extension of oceanographic regimes to the adjacent slopes. The aim is to extract approximate current speed, bottom shear stress, Froude number, and internal wave crucial slope values for canyon and slope macrofauna communities at the four depths (30 day models, Baltimore August 2012; Norfolk May 2013). These values will give further insight into the relationship between canyon macrofaunal communities and currents/bottom shear stress and could also be applied to the functional trait approach.

Future work on the functional traits of canyon macrofauna communities could include an assessment of the variance of response traits and effect traits across the studies gradients. In functional ecology ‘response diversity’, describes the variation of responses (response traits) to environmental change among species of a particular community (Elmqvist et al., 2003; Folke et al., 2004). Response diversity may also be a key determinant of ecosystem resilience in the face of anthropogenic pressures and environmental uncertainty (Díaz & Cabido, 2001; Mori et al., 2013). Applying this to deep-sea benthic communities may provide insights into how resilient a community is to environmental change and regime shifts. However, current understanding of response diversity is poor and there is an urgent need to disentangle the conceptual strands that pervade studies of the relationship between biodiversity and ecosystem functioning (Mori et al., 2013). Combined with traditional taxonomic methods and new experimentation, investigating functional diversity relationships will help improve our understanding of how biodiversity interacts with ecosystem processes and environmental constraints.

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8 Tables and Figures

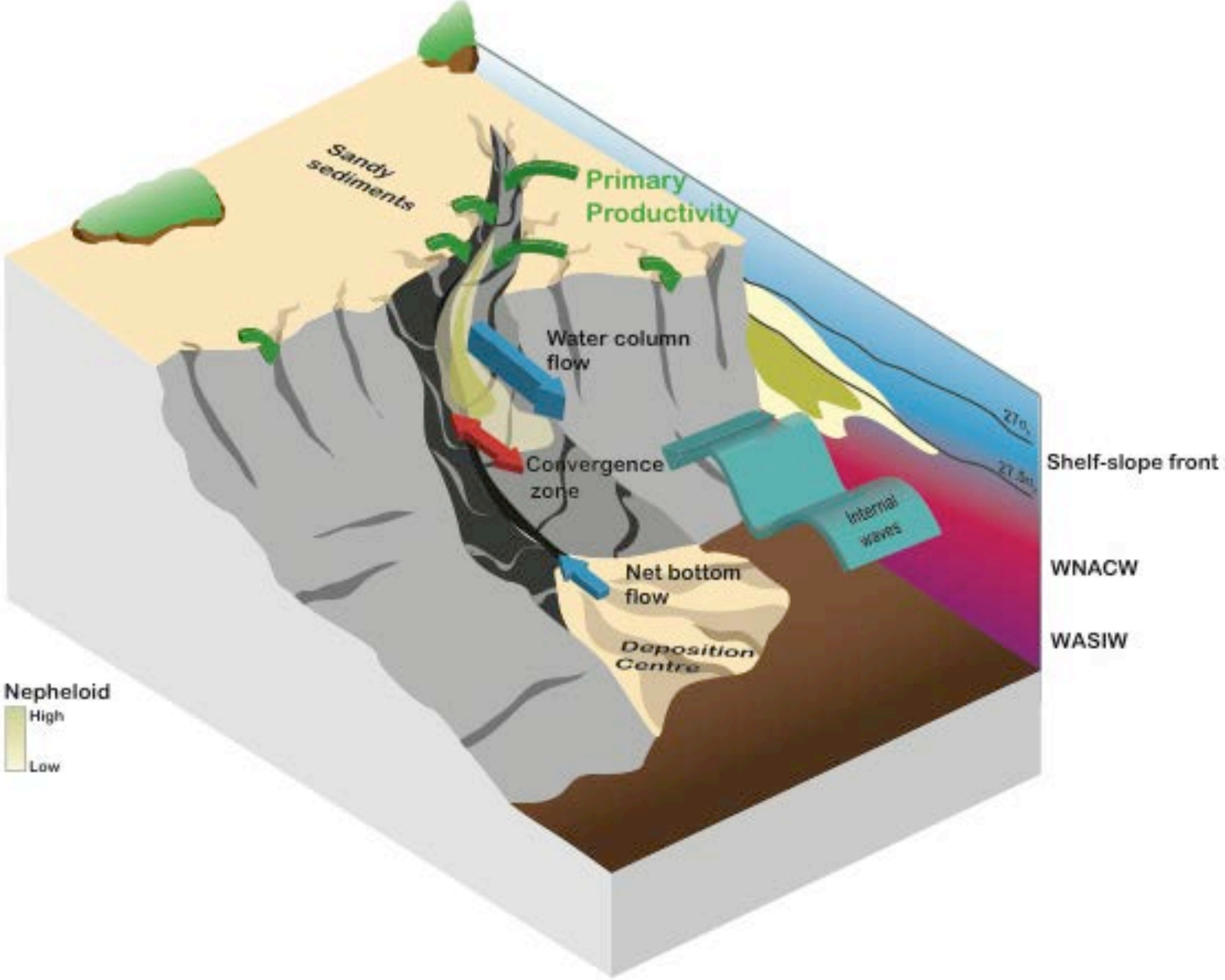

Figure 1. Three-dimensional generalised schematic of the physical oceanographic processes found within MAB canyons.

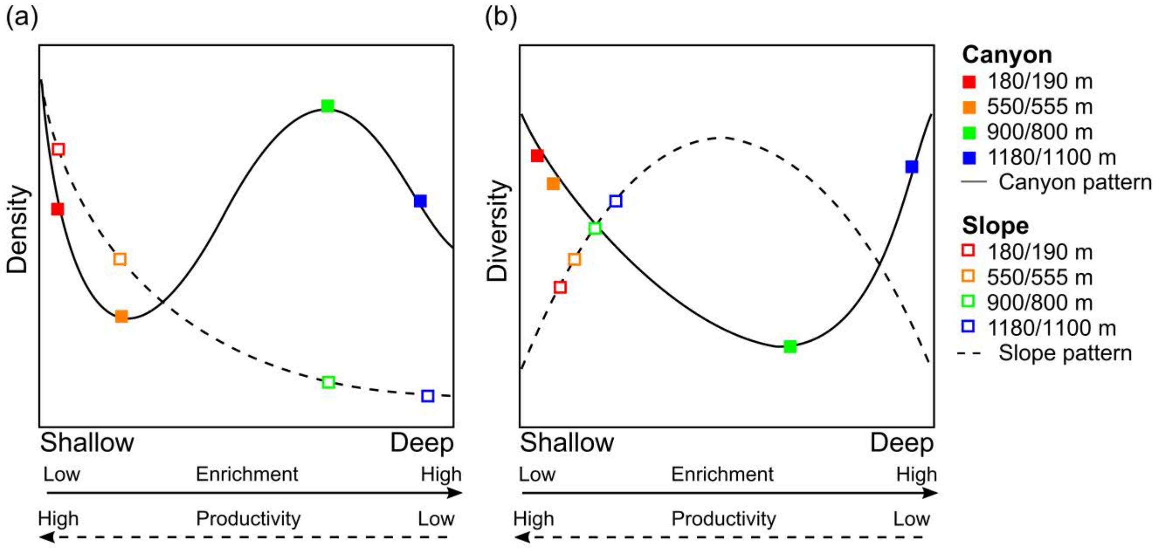

Figure 2. The density-depth and diversity-depth conceptual models adapted from Rex and Etter (2010) and repeated from Chapter 3 of this thesis for convenience. (a) Shows macrofaunal density and (b) species richness against productivity and enrichment. The dashed lines on both plots refer to the expected pattern (Rex and Etter, 2010), which in this study, the adjacent slopes followed (canyon and slope are conceptually placed as opposed to statistically fitted). The solid line reflects the divergent pattern that was observed in the Baltimore and Norfolk canyons.

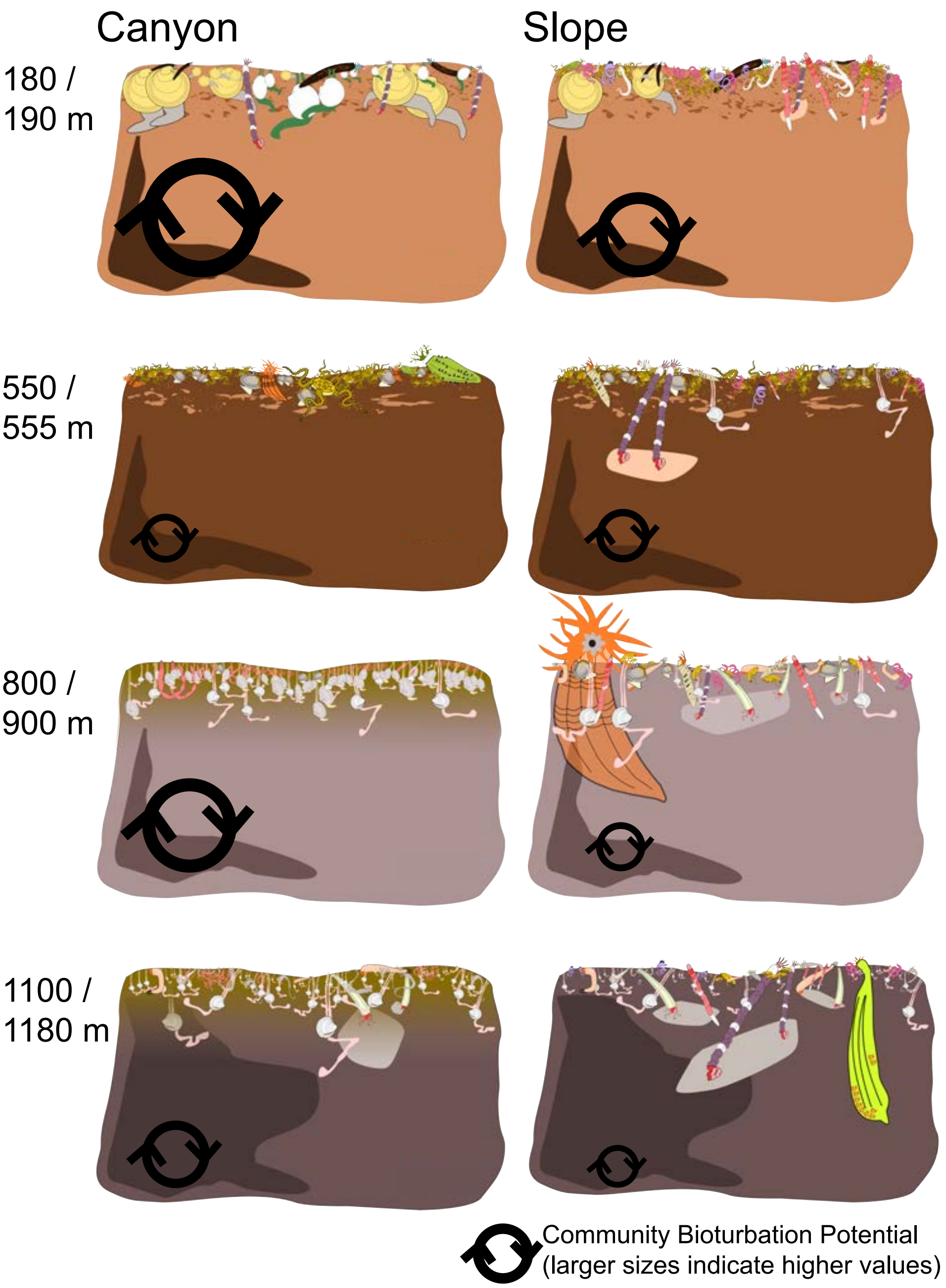

Figure 3. Schematic representation of biological communities found within the study, throughout the canyons and slopes. Higher bioturbation potential is represented by the cycling symbol and organic enrichment by green shading within surface layers of sediment. Lower canyon communities are dominated by small-bodied opportunistic taxa (Yoldiellinae, Thyasiridae, Captiellidae). Slope communities are characterised by greater faunal diversity (mainly polychaetes) and communities with greater range of the size of taxa, especially in lower slope communities (Sipunculidae and Edwardsiidae).