Variation in the structure and function of deep-sea fish assemblages with depth and over time

Beth L. Mindel

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Contents

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Chapter 5: Abundance—occupancy relationships based on spatial and depth distribution in deep-sea fish

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Abstract

The deep sea is the largest environment on Earth, but has remained relatively under-studied due to its inaccessibility. In recent years however, technological advances have increased our understanding of this globally important system. In this thesis, I add to this understanding by examining fish assemblage structure along the environmental gradient of the continental slope at depths of 300–2000 m and over a time period (1998–2014) following a reduction in fishing pressure from previous levels. I show that body size is an important factor in structuring deep-sea assemblages along a depth gradient and that it increases at least up to 1500 m. A new metric, fractional size, builds on our knowledge of size structure by accounting for both intra- and interspecific variation in body size and also increases with depth. The Large Fish Indicator, the slope of the biomass spectrum and fractional size have increased over time, signifying recovery of the size structure of deep-sea assemblages, but this increase is depth-dependent. I reveal other depth-related changes by linking morphological traits that relate to function, such as caudal fin aspect ratio and gape size, to the shifting dominance of feeding guilds and patterns in functional diversity. I show that despite the uniqueness of deep-sea ecosystems, the general macroecological pattern of increasing regional occupancy with increasing local abundance still applies. I incorporate the all-pervading importance of depth into these abundance–occupancy relationships by calculating occupancy based on depth distribution as well as spatial distribution. This thesis reveals some surprising characteristics of deep-sea assemblages, such as high biodiversity and the ability to recover from fishing pressure. It further highlights the importance of body size in the marine environment and of depth resolution in deep-sea ecology.

1. Introduction

1.1. Background

The state of our oceans is increasingly being recognised as cause for concern by scientists and the general public. We are exploiting the seas at an often unsustainable level (Pauly 2008, 2009; Jackson 2010), as illustrated by the collapse of stocks such as cod in the Northwest Atlantic (Hutchings & Myers 1994; Myers et al. 1996). In recent years, this has also been true of the deep sea. As we have depleted fish stocks in shallower seas, fishermen have been forced to fish in deeper waters (Morato et al. 2006). This means that we are exploiting fish stocks of which we know very little in terms of their biology and ecology.

The deep sea encompasses depths from 200 m to 6000 m (Kaiser et al. 2011) and extends from the continental slope to the abyssal plain. It is the largest environment on earth and offers important ecosystem services such as fisheries and mining for minerals (Ramirez-Llodra et al. 2011). It is also important for carbon storage (Irigoien et al. 2014; Trueman et al. 2014), which is particularly relevant in this current era of climate change. The seafloor is punctuated by trenches that reach down to depths of 10 km, and seamounts and mid-ocean ridges that rise up several kilometres above the seabed without breaking the surface of the ocean (Kaiser et al. 2011). It is also now known that the deep-sea environment is much more varied than previously thought (Danovaro, Snelgrove & Tyler 2014) and species distributions may rely on habitats such as sponge fields or deep-sea coral banks (Ramirez-Llodra et al. 2010). The deep sea was once thought to be devoid of any life, however, new technology such as improved fishing gear, deep-sea submersibles and remote cameras has allowed us to start to understand its nature (Kaiser et al. 2011).

In the deep sea, the lack of light means there is no photosynthesis (Kaiser et al. 2011). Rather, all food webs are based on the detritus that sinks from the shallower ocean layers, such as faecal pellets, crustacean moults, and carcasses of larger organisms (Lalli & Parsons 1993), making for simplified energy pathways relative to shallower seas and the terrestrial environment (Tittensor et al. 2011). Other differences in deep-sea communities include the necessary adaptation to high pressure and low temperature (Carney 2005). Hydrostatic pressure increases by 10 atm for every 100 m in depth and adaptations such as the alteration of membrane structure (Hazel & Williams 1990) and the stabilisation of enzymes (Yancey & Siebenaller 1999) are needed to occupy these depths. Additionally, on the continental slope, depth changes rapidly for any unit change in horizontal distance. This means that it encompasses a very steep environmental gradient, changing in pressure, temperature, oxygen and salinity (Lalli & Parsons 1993; Carney 2005; Kaiser et al. 2011). Such a vast gradient would not be ignored in terrestrial ecology, and it cannot be assumed that communities will remain constant along the continental slope. Changes in species composition along this gradient have been well documented (e.g. Gordon & Bergstad 1992; Magnussen 2002; Carney 2005; Tolimieri & Levin 2006; Yeh & Drazen 2009), but more work is needed on understanding what this means for ecosystem function and how assemblages at different depths interact with one another.

Many deeper-living animals tend to be longer lived and reach sexual maturity at an older age relative to their shallow-dwelling counterparts (Koslow et al. 2000; Morato et al. 2006; Drazen & Haedrich 2012), resulting in an increase in vulnerability with depth (Norse et al. 2012). At one extreme, the orange roughy (*Hoplostethus atlanticus*) does not mature until around 30 years of age and may live to be nearly 150 years old (Fenton, Short & Ritz 1991), while one specimen of the black coral genus *Leiopathes* has been found to be over four thousand years old (Roark et al. 2009). This means that deep-sea creatures are likely to be particularly vulnerable to fishing pressure, as they will take longer to recover from disturbance due to the long time it takes them to grow and reproduce. Perhaps this explains why some deep-sea fisheries, despite their recent implementation, are already no longer economically sustainable (Norse et al. 2012).

This unsustainable level of exploitation (Norse et al. 2012) is occurring with very little knowledge of the ecology of the communities therein. We need to understand the potential for recovery of these systems, and how much fishing pressure they can withstand, in order to implement effective protection measures. In this thesis, I aim to combine traditional ecological methods with new trait-based approaches to provide an overview of deep-sea fish ecology along a depth gradient and over time. Not only will this give us a better understanding of deep-sea communities, it will also highlight the most appropriate methods to use in the future, for example when monitoring the impacts of exploitation and potential resilience of the system.

1.2. The trait-based approach

An approach that is becoming more prevalent in community ecology is to use traits, rather than species identities, to describe systems (McGill et al. 2006; Litchman et al. 2010; Webb et al. 2010). Traits can be any measurable property of an organism, for example size at maturity, fecundity, seed/egg/offspring size, metabolic rate, rate of carbon fixation and diet breadth. Taxonomic approaches can be useful, but findings based on species identity are not easily applicable to other communities. Conversely, if conclusions can be drawn about the impact of traits on the community, we may be able to assume that similar traits will cause similar responses in other communities, regardless of species identity (Bremner 2008). Trait-based approaches may therefore help to unify community ecology theory, not just across different communities, but also across multiple ecosystems. Traits also map onto function more directly than does taxonomic information. By examining functional traits, we can learn more about what aspects of a community are going to change in response to an environmental or anthropogenic driver (Webb et al. 2010; Enquist et al. 2015; Schmitz et al. 2015).

One trait that is particularly important for function in the marine environment is body size. In the past, food webs have been analysed in terms of interactions between species (May et al. 1979). However, in the marine environment, as fish grow they are able to eat a wider variety of prey sizes, so a predatory fish may feed on every level of the food chain in the course of its life. This means that body size is often a better predictor of trophic level than is species (Cohen et al. 1993; Scharf, Juanes & Rountree 2000; Jennings et al. 2001). This has led to the interpretation of marine food webs as groups of interacting individuals of different sizes, which are not specified as a certain species (Hall et al. 2006; Pope et al. 2006). The importance of body size has already been recognised in the deep sea, but variation in size with depth is not consistent. It has been found to increase (Polloni et al. 1979) or decrease (Stefanescu, Rucabado & Lloris 1992) along a depth gradient, and the pattern may vary for different functional groups (Collins et al. 2005). The body plan of deep-sea species also becomes more elongated with depth (Neat & Campbell 2013), possibly due to increased efficiency of swimming at high water pressure. Body size is also important in determining important life history characteristics such as maturity and fecundity (Winemiller & Rose 1992) and growth rate (Jobling 1983). It can therefore provide valuable information on both function and overall health of a community.

Traits other than body size will also affect the structure and function of the community, for example by determining what an individual can eat. Mouth size and shape, locomotion ability and eyesight will all impact what types of prey predators are able to catch, and morphological traits such as these have been used to develop functional groupings in fish (Sibbing & Nagelkerke 2001; Reecht et al. 2013). Reduced metabolism and locomotory capabilities have been attributed to the lack of light in the deep sea (Childress 1995), and scavengers have traits that allow them to exploit intermittent resources (Haedrich & Rowe 1977; Tamburri & Barry 1999; Collins et al. 2005). Differences in reproduction and development may also play a role in structuring deep-sea communities. Some species spawn in aggregations (Koslow et al. 2000) and some have seasonal reproduction, though the extent of this is poorly understood. Species also change their depth range as they age but whether the juveniles live in shallower waters and descend as they grow older and larger, or *vice versa*, varies between species (Gordon & Duncan 1985; 1987) and has not been revealed for most. Depth range will also vary within individuals as they move between depths to feed (Gordon & Duncan 1985; Bailey et al. 2009). This movement heavily impacts the interactions across communities in the deep sea and has important implications for the storage of carbon at depth (Trueman et al. 2014), and the propagation of the effects of fishing to areas outside those fished. Species living below the range of commercial fishing gear have been affected by fisheries (Bailey et al. 2009; Priede et al. 2011) and the movement of individuals may be responsible for transmitting these effects (Priede et al. 2011).

1.3. The effect of fishing

The impact of commercial fishing on species that live on the continental shelf has been well documented (Botsford, Castilla & Peterson 1997; Pauly 2008, 2009;

Jackson 2010). Despite the lack of study of the deep sea, this habitat provides a unique opportunity to examine the effect of fishing pressure in detail, due to the fact that commercial fishing has only been practised in the deep sea in recent decades (Morato et al. 2006). This means that there are data available for the state of deep-sea communities in a pristine, or close to pristine, condition (Gordon 2003). We will therefore be better able to document changes due to fishing than we can in for example, the North Sea, which has been exploited for centuries (Barrett, Locker & Roberts 2004; Kerby, Cheung & Engelhard 2012), making early environmental states hard to estimate.

One approach used to illustrate the effects of fishing is size-based indicators. Fishing impacts body sizes in a community because it is size-selective, harvesting individuals once they become a certain size, hence not allowing them to reach their full growth potential (Bianchi et al. 2000). This means that metrics based on body size tend to decrease under fishing pressure (Shin et al. 2005). Examples of such metrics include the Large Fish Indicator (LFI) and slope of the biomass spectrum (Shin et al. 2005; Greenstreet et al. 2011; Fung et al. 2012). The LFI is the proportion of biomass that is made up of individuals above a certain length, and it illustrates the health of an assemblage because larger individuals are more fecund (Winemiller & Rose 1992) and more likely to occupy a wider range of trophic levels (Scharf, Juanes & Rountree 2000). The LFI is therefore expected to decrease under fishing pressure. In the North Sea, a value of 0.3 has been suggested to represent a healthy LFI (ICES 2007; Greenstreet et al. 2011), but in recent years it has been as low as 0.1 (Fung et al. 2012). The expected value of the LFI in the deep sea is, to my knowledge, as yet undescribed. The other common indicator, the slope of the biomass spectrum, is based on the general macroecological pattern of fewer large organisms than smaller ones (Elton 1927). This produces a negative relationship between abundance and body mass that shows surprising regularity across many different types of ecosystems (Sheldon, Prakash & Sutcliffe 1972; Boudreau & Dickie 1992; Reuman et al. 2008). Fishing truncates the size spectrum by harvesting the larger individuals, resulting in a shift towards smaller body sizes (Bianchi et al. 2000; Jennings & Blanchard 2004; Shin et al. 2005), meaning that steeper (or more negative) size spectrum slopes are predicted under exploitation.

The impact of fishing pressure in the deep sea has already been investigated. A particularly well-studied area is the Rockall Trough in the Northeast Atlantic.

Basson et al. (2001) attempted to combine research survey data from this area in order to answer fundamental questions about the effect of fishing on body size and biomass. The authors could not always rule out an effect of the type of gear used in the survey, but the evidence points to declines in biomass of exploited and unexploited species, a change in species composition, and a steepening of the slope of the size spectrum (Basson et al. 2001). However, the change in the slope is weak, which the authors hypothesise may be due to the short timescale available for analysis or because the high mortality of by-catch means that large fish are not preferentially targeted (Basson et al. 2001).

Other studies in the same area have found that species abundances have declined significantly (Lorance & Dupouy 2001), even at depths greater than those commercially fished (Bailey et al. 2009; Priede et al. 2011) which may equate to an area 2.74 times greater than that directly impacted by fishing gear being affected by fishing activity (Priede et al. 2011). The deepest-living fish to decline significantly over time was the abyssal halosaur (*Halosauropsis macrochir*), which lives between 1750 m and 3500 m below sea level (Bailey et al. 2009). Thus, even those able to escape the range of fishing gears by moving to deeper waters are impacted by the presence of fisheries at shallower depths. In other areas, for example the Northwest Atlantic, these declines in deep-water fish abundances equate to the criteria set out by the International Union for the Conservation of Nature (IUCN) Red List as being Critically Endangered (Devine, Baker & Haedrich 2006). However, as yet, recorded extinctions are absent in deep-sea ecosystems, and diversity has remained constant in the Rockall Trough since the start of commercial fishing (Bailey et al. 2009; Campbell et al. 2010).

Not all species have shown decreases in abundance, and it is important to consider the timescale involved. Neat & Burns (2010) revealed that grenadiers (family Macrouridae) in the Rockall Trough have persisted at a stable abundance since 1998, probably due to the implementation of Total Allowable Catches (TACs) in 2003. Although it is encouraging that some deep-sea species may be able to be fished at sustainable levels, the population is showing no sign of recovery from the high levels of exploitation before the TACs were implemented (Neat & Burns 2010). Body size of grenadiers has also remained constant on average, but large individuals on the upper continental slope have increased in abundance, possibly due to decreased fishing pressure (Neat & Burns 2010).

The effect of fishing can also be seen in areas other than the Rockall Trough. The orange roughy (*Hoplostethus atlanticus*) fishery in New Zealand increased dramatically from 1979 to 1989 but catches have declined since 1990 due to the depletion of stocks and implementation of TACs (Clark 2001). Now many historical fishing grounds are closed in the region (Larcombe & Begg 2007; Hallett & Daley 2011). The slender armourhead (*Pseudopentaceros wheeleri*) is relatively short-lived for a deep-sea fish, and appears to be recovering from heavy overfishing up until the 1980s in the North Pacific, though the stock is still only a fraction of its original size (Norse et al. 2012). The black scabbardfish (*Aphanopus carbo*) has been fished sustainably around Madeira, North Atlantic, using longlines for more than 200 years (Noronha 1925), however, in other areas where trawling is permitted, stocks are declining (ICES 2008).

In some areas, the effect of recent commercial deep-sea fishing has been documented, but there are still gaps in our knowledge. We need to extend our study to encompass community-wide effects, rather than just changes in abundance and biomass. The use of size-based indicators in the deep sea would allow direct comparison with shelf seas. Reference directions (Jennings & Dulvy 2005; Shin et al. 2005) for these indicators are well documented in shallower waters, which would aid in interpreting how communities are responding to either relaxed or increased fishing pressure. Indicators based on size will also relate to the function of a community, allowing for predictions to be made on the impact that fishing will have on important aspects of an ecosystem.

1.4. Generality of macroecological patterns

Macroecology describes a suite of emergent patterns that seem to be very general properties of both marine and terrestrial ecosystems (Webb 2012). One pervasive macroecological pattern is the abundance–occupancy relationship (AOR): the generally positive relationship between average local abundance and proportional regional occupancy (Gaston et al. 2000), which has been demonstrated for a wide range of taxa and in many different ecosystems (Blackburn, Cassey & Gaston 2006). AORs can be fitted across species, with each species contributing a single mean abundance and proportional occupancy (the interspecific AOR), or within species, for instance by considering a time series of abundance and occupancy estimates for a single species (the intraspecific AOR). These two relationships are intimately linked (Webb, Noble & Freckleton 2007), although different mechanisms may drive them (Gaston et al. 2000; Borregaard & Rahbek 2010).

AORs are ecologically important because they link local- and regional-scale population processes, and have implications for monitoring and conservation of species (Webb, Noble & Freckleton 2007). For instance, it is easier to obtain information on the presence or absence of species than it is on their abundance, but positive AORs suggest that local abundances could be predicted from proportional occupancy (Gaston et al. 2000). A positive AOR also means that species can face a "double jeopardy" (Lawton 1993, 1996; Gaston 1999) whereby a population with a small geographic range and low local abundance can be easily wiped out, with no potential regional colonisers to reclaim the area lost. This is also true for the intraspecific relationship: in years where abundances are low, species are proportionally more vulnerable to local extinction because they are also likely to be occupying a small geographic space.

Despite the importance of AORs, to my knowledge only one study has so far applied abundance–occupancy theory to the deep sea. Using simulation modelling, Trenkel et al. (2013) found that fishing could potentially alter the form of the intraspecific AOR. However, only four species were described in the model, and the interspecific AOR was not included (Trenkel et al. 2013). If positive AORs can be shown empirically to be a general phenomenon in the deep sea, which is thought to differ in many ways to other marine ecosystems (Ramirez-Llodra et al. 2010), then this macroecological pattern would be shown to be even more widespread and consistent. In addition, the predictions made by Trenkel et al. (2013) on the effect of fishing could be tested using data from areas subjected to changing fishing pressure, which has previously been shown to alter the AOR in shallow marine environments (Fisher & Frank 2004). However, the response is not consistent across taxa, and the slope and strength of the AOR have been found both to increase and decrease in response to pressures, depending on the type of habitat occupied and the nature of human disturbance (Fisher & Frank 2004; Webb, Noble & Freckleton 2007). Furthermore, AORs can exhibit different characteristics depending on species traits. For example, intraspecific AORs and/or variation around interspecific AORs can depend on whether species are rare or common (Webb, Noble & Freckleton 2007), their aggregation behaviour (Frisk, Duplisea & Trenkel 2011), and their body size (Webb, Tyler & Somerfield 2009). It is therefore interesting to examine whether AORs can be used alongside size-based indicators to investigate the effect of fishing in the deep sea, and whether the unique characteristics of deep-sea systems and the traits of the species that live there can further increase our understanding of macroecological patterns and relationships.

1.5. Data and study site

My study site is the Rockall Trough, Northeast Atlantic, in ICES (International Council for the Exploration of the Sea) area VI at latitude 55° to 59°N and longitude approximately 9°W (Chapter 2: Fig. 1). This site is one of the best-studied deep-sea ecosystems in the world, with research surveys extending back to the 1970s (Gordon 2003). The dominant commercial fishery in the area is the French fleet, which has been exploiting the deep sea in the Rockall Trough since the 1970s, though only on a large scale in the past 20 years (Basson et al. 2001; Gordon 2003). TACs have been implemented and reduced year on year since 2003 (STECF 2013). The main target species are roundnose grenadier (*Coryphaenoides rupestris*) and blue ling (*Molva dipterygia*) though others commonly caught are the black scabbardfish (*Aphanopus carbo*), Baird's slickhead (*Alepocephalus bairdii*), Kaup's arrowtooth eel (*Synaphobranchus kaupii*), birdbeak dogfish (*Deania calceus*) and Portuguese dogfish (*Centroscymnus coelolepis*) (Gordon & Bergstad 1992; Gordon 2003). Although my work will be focussed on a particular study area, by using a trait-based framework, it is aimed that this approach will be applicable to other ecosystems.

The core dataset I will use is from fisheries-independent research monitoring surveys conducted by Marine Scotland, of the Scottish Government, since 1998 at depths of 300 m to 2067 m. The data consist of information on species, abundance, size and depth, for the demersal fish assemblage. Additional morphological trait data were collected on board the survey in the year 2013 which are used to examine functional changes. Where appropriate I also use stable isotope data supplied by the National Oceanography Centre, Southampton, to infer trophic level. Traits are also obtained from the online compendium FishBase (Froese and Pauly 2016).

1.6. Thesis structure

My thesis is centred around the following research questions.

Chapter 2: How do species composition and body size change with depth?

Depth is the most important driver of community structure in the deep sea, and the environmental gradient spanned by the continental slope is vast. We therefore must understand changes with depth before we can investigate the effects of fishing. I examine species composition in order to understand the natural history of the system. I then look at body sizes of assemblages as this is thought to be the most important trait in the marine environment. Specifically, I test:

- Whether a new metric, fractional size, can be used to illustrate variation in deep-sea assemblages along a depth gradient
- What changes in body size occur within and between species along a depth gradient
- Which descriptor of assemblage structure (species composition, fractional size, or size structure) explains the most variation along a depth gradient

Chapter 3: What do morphological traits tell us about functional changes with depth?

I then expand on my findings regarding body size to incorporate other traits that may be related to function. Morphological traits were available for some species that span the depth range of the study and account for 84% of the total biomass. These traits can be related to functions such as swimming speed and prey capture. I therefore use them to describe functional diversity in the system, and to explain these patterns by examining each trait separately along a depth gradient. I compare this trait-based approach to traditional taxonomic diversity, and use size diversity as an additional trait-based method. I aim to relate these traits to a specific function, feeding guild, using information from stable isotope data. Specifically, I test:

- How functional diversity changes with depth
- Whether size diversity and species richness show similar patterns to functional diversity
- Which traits can be related to patterns in functional diversity

- How the distribution of morphological traits links to variation in dominant feeding guilds

Chapter 4: Do size-based indicators show recovery due to relaxed fishing pressure?

Fishing pressure has been decreasing in the study area, however it is thought that deep-sea systems are slow to recover from exploitation. It is therefore important to discover whether size-based indicators show signs of recovery. I use the information from my first two data chapters to inform my implementation of these indicators, particularly in accounting for differences in response that may occur at different depths. Specifically I test:

- How size-based indicators have changed over time, and whether this pattern differs across depths
- Whether fractional size can be used as an indicator
- How fishing effort and temperature have changed over the timescale of the research survey

Chapter 5: What is the relationship between local abundance and regional occupancy in the deep sea?

One of the most general ecological rules is the positive relationship between abundance and occupancy, so I establish whether this holds in the deep sea, despite being thought of as fundamentally a very different ecosystem to coastal waters. Abundance–occupancy relationships can also have important implications for conservation and monitoring of species, which could be useful in this time of increasing exploitation in the deep sea. Furthermore, abundance–occupancy relationships are predicted to change in response to environmental pressures, so in looking at change over time in the form of this relationship, I am able to establish whether it is an indicator that could be applied to the deep sea, in addition to those based on body size. Specifically, I test:

- For relationships between abundance and occupancy in the deep sea, both across and within species
- Whether we can calculate the abundance–occupancy relationship based on depth distributions
- How the interspecific relationship has changed over time

- Whether we can attribute the form of the intraspecific relationship to species characteristics

In the final chapter, *General Discussion*, I synthesise these data chapters into a set of conclusions that can be applied to future work. I highlight the most important recurring themes in deep-sea fish assemblage variation and suggest why they are valuable insights in terms of the management and resilience of this ecosystem. I conclude by suggesting the next logical steps to be taken in the advancement of deep-sea ecology that can build on the work presented in this thesis.

2. A trait-based metric sheds new light on the nature of the body size—depth relationship in the deep sea

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2.1. Abstract

Variation within species is an often-overlooked aspect of community ecology, despite the fact that the ontogenetic structure of populations influences processes right up to the ecosystem level. Accounting for traits at the individual level is an important advance in the implementation of trait-based approaches in understanding community structure and function. I incorporate individual- and species-level traits into one succinct assemblage structure metric, fractional size, which is calculated as the length of an individual divided by its potential maximum length. I test the implementation of fractional size in demersal fish assemblages along a depth gradient in the deep sea. I use data from an extensive trawl survey at depths of 300–2030 m on the continental slope of the Rockall Trough, Northeast Atlantic, to compare changes in fractional size structure along an environmental gradient to those seen using traditional taxonomic and trait-based approaches. The relationship between fractional size and depth was particularly strong, with the overall pattern being an increase with depth, implying that individuals move deeper as they grow. Body size increased with depth at the intra-specific and assemblage levels. Fractional size, size structure and species composition all varied among assemblages, and this variation could be explained by the depth that the assemblage occupied. The inclusion of individual-level traits and population fractional size structure adds to our

understanding at the assemblage level. Fractional size, or where an individual is in its growth trajectory, appears to be an especially important driver of assemblage change with depth. This has implications for understanding fisheries impacts in the deep sea and how these impacts may propagate across depths.

2.2. Introduction

Identifying broad patterns in how community structure changes along an environmental gradient is central to ecology. Community composition tends to be quantified using the traditional taxonomic approach of listing species abundances. Community function, on the other hand, can best be explored in terms of the traits of the species or individuals therein, where the traits can be any measurable physiological or morphological feature that contributes to the function of the organism. Trait-based approaches, where organisms are described by their traits rather than species identity, are becoming more common in community ecology (McGill et al. 2006; Litchman et al. 2010; Webb et al. 2010; Mouillot et al. 2013). One advantage of trait-based approaches is that they may allow greater generalisations across systems, because traits are common to multiple ecosystems, even if these ecosystems do not share the same species (Keddy 1992; Weiher & Keddy 1995). Additionally, trait-based approaches can be applied in systems where detailed, species-specific information on changes in abundances do not exist, but the traits of the species are known due to studies on similar systems. However, even if trait-based approaches are giving more information than taxonomic descriptions, there is still a shortfall if traits can only be described at the species level, ignoring the substantial changes in function that can occur throughout ontogeny. It has been shown that variation within species alters community function and ecosystem processes, and that functional differences among species depend on the demographic structure of the populations of those species (Rudolf & Rasmussen 2013a, b), implying that individual traits must also be taken into consideration to accurately describe community function.

A trait that changes dramatically at the individual level is body size, and in the marine environment, where food webs are strongly size structured, it is the trait most responsible for determining interactions between individuals (Dickie, Kerr &

Boudreau 1987). In fish, size is often a better predictor than species identity of the trophic level of an individual (Cohen et al. 1993; Scharf, Juanes & Rountree 2000; Jennings et al. 2001), because as fish grow they can feed on increasingly large prey, gradually heightening their position in the food web. Closely related to individual size, another commonly used size-based trait in the marine environment is L_{max}. This is the potential maximum length of a species, and is an important life history trait. It can be used as a proxy for asymptotic size, size at maturity, fecundity, growth rate and longevity (Winemiller & Rose 1992; Froese & Binohlan 2000).

It is already known that in fish, body size changes with depth (Polloni et al. 1979; Macpherson & Duarte 1991; Collins et al. 2005). There is, however, little in the way of a consistent pattern; Polloni et al. (1979) reported a pattern of increased size with depth, Snelgrove & Haedrich (1985) found no relationship in all but two deep-sea fish and Stefanescu, Rucabado & Lloris (1992) reported the complete opposite. The relationship holds better within certain functional guilds, for example scavenging species (Collins et al. 2005), but even within scavengers it is not ubiquitous (Yeh & Drazen 2009). This suggests that there are many other factors at play including ontogenetic changes in behaviour and habitat preference that are more closely related to depth than body size *per se* (Stein et al. 1992).

These body size traits at the individual and species level (L_{max}) can be combined to better account for the structure of the community as a whole. I suggest that a new metric, fractional size, can be calculated by dividing the length of an individual by the L_{max} of that species. It resolves the demographic structure of populations and assemblages and signifies how far along an individual is in its growth trajectory. Fractional size captures intra- as well as interspecific variation in size; an aspect that is often ignored in ecology (Rudolf & Rasmussen 2013a, b).

Here I use this alternative measure of size to determine whether differences in fractional size structure exist along the depth gradient of the continental slope and compare these differences to those revealed by the traditional taxonomic and trait-based measures of fish community structure. Depth is the major environmental gradient driving changes in marine communities from the coast to the deep sea, and the taxonomic changes seen across this depth gradient have been well documented (e.g. Gordon & Bergstad 1992; Magnussen 2002; Carney 2005; Tolimieri & Levin 2006; Yeh & Drazen 2009). As depth increases, pressure increases, while temperature, salinity, oxygen concentration and food availability decrease before stabilising (Lalli & Parsons 1993; Kaiser et al. 2011). The changes in abiotic parameters resulting from a small change in vertical position can be equivalent to those observed over extensive latitudinal or longitudinal ranges (Angel 1993; Lalli & Parsons 1993; Kaiser et al. 2011).

Here I use data from a deep-water bottom trawl survey to analyse how changes in fractional size of individuals influence fish assemblage structure along a depth gradient. I compare these results with two traditional measures of assemblage structure: mean length of individuals in the assemblage, and species composition. This analysis allows the interpretation of intra- and interspecific variation in size, the comparison of taxonomic and trait-based approaches in understanding assemblage structure, and the understanding of a novel way of measuring the fractional size structure of fish assemblages.

2.3. Materials and methods

2.3.1. Data

The survey data used have been collected by Marine Scotland's *MRV Scotia* on a deep-water bottom trawl survey of demersal fish in September of the years 1998, 2000, 2002, 2004–2009, 2011 and 2012. The survey area is the Rockall Trough, Northeast Atlantic, within ICES (International Council for the Exploration of the Sea) area VIa, stretching along the continental slope at latitudes of 55° to 59°N and a longitude of approximately 9°W (Fig. 1). A BT184 bottom trawl was used with rockhopper ground gear and the mesh size at the cod end was 2 cm. Further trawl gear specifications are described in Neat & Burns (2010). Demersal fish only (those that live on or around the seabed, including those classified as benthopelagic) were included in the analysis due to the unreliability of catching benthic invertebrates and mesopelagic species that generally live higher in the water column.

In order to focus on depth-related trends in assemblage structure, time-averaged metrics were used to control for temporal variation. Three hundred and twenty one hauls were taken over the course of the survey, at depths ranging from 300 m to 2030 m, and these hauls were concatenated into stations that were re-sampled through time. Hauls were grouped into the same station if they were in the

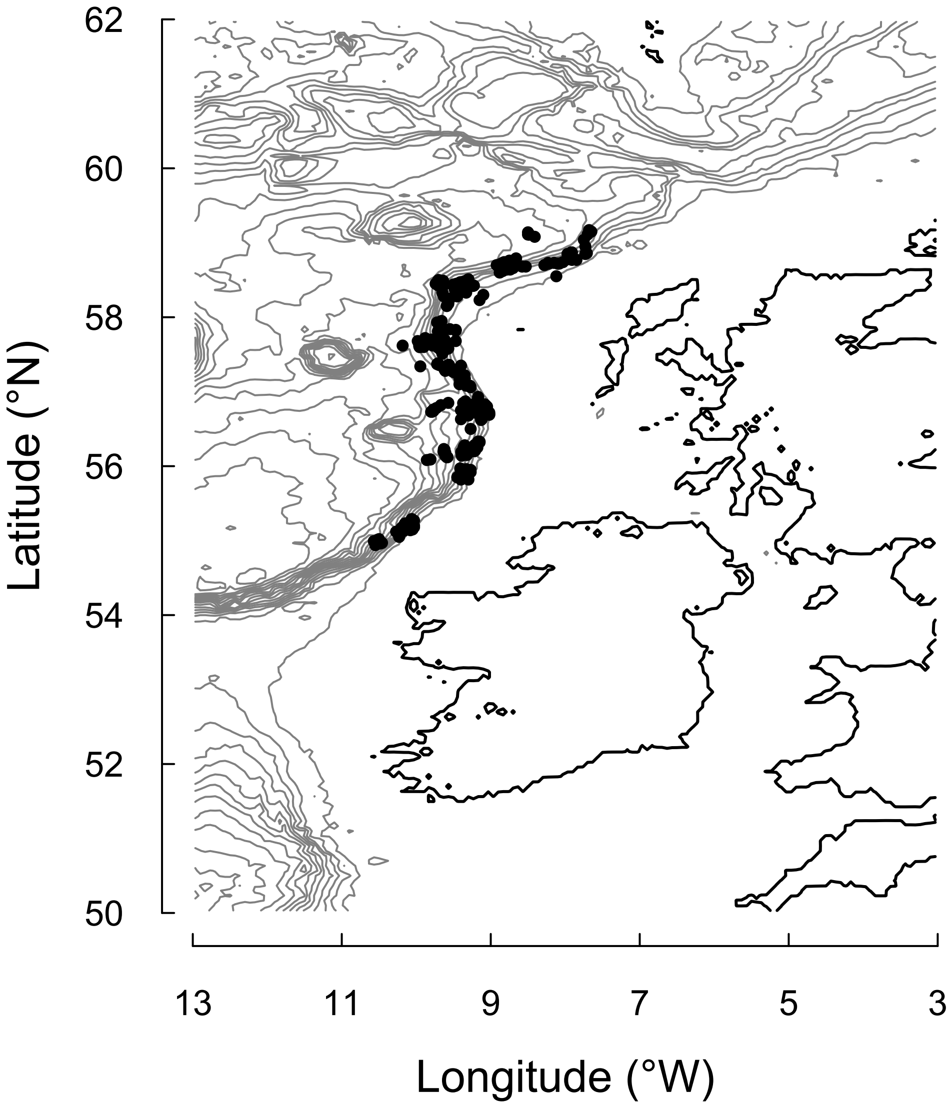

Fig. 1. Location of hauls of the Marine Scotland deep-water bottom trawl survey along the continental slope of the Rockall Trough from 1998–2012. The map was produced using the R package (R Core Team 2014) *marmap* (Pante & Simon-Bouhet 2013).

same ICES statistical rectangle (of area 1° longitude by 30' latitude) and within 100 m of each other in depth. The depth of the station was taken as the mean of the depths of the hauls in that station. Hauls that were not repeated across years were still included as they were assumed to occur randomly with respect to time and depth. The reduced dataset consisted of 72 stations (Table S1), including 15 stations with only one representative haul, and 57 stations where hauls were repeated over at least two years allowing them to be time-averaged.

Catch was identified to the finest taxonomic resolution possible, which was species level for 99.9% (of a total of 683319) of individuals caught. This resulted in the classification of 187 taxa (Table S2), of which 175 (93.6%) were species, six (3.2%) were genera, five (2.7%) were families and one (0.5%) was order. The full classification of these taxa was determined using the World Register of Marine Species (WoRMS Editorial Board 2013). Each individual's length was measured; for some species it was appropriate to measure standard length, pre-anal fin length, or pre-supra caudal fin length rather than total length, due to tails commonly breaking off in the net. In these instances, total length was determined using conversion factors calculated from a subset of the data (Table S2). This is standard practice in fisheries surveys (ICES 2012) because the ratio of the alternative measured lengths to total length can be assumed to be constant throughout growth. It was necessary to predict total length from other length measures for 38 (20%) taxa.

The measure of relative abundance derived from the survey was the biomass of individuals caught per hour spent trawling. Biomass could not always be recorded on the survey due to time constraints, so weight was predicted from the length of the individual. The relationship between length and weight was established for each species using a subset of the data for which length and weight were available. A linear model was performed on the $\log_{10}$-transformed variables for each species, and the coefficients from this model were used to predict missing weights.

Fractional size of an individual was calculated as its total length divided by the potential maximum length of that species (L_{max}). The value of L_{max} was set as the largest known length of any recorded individual. For most species, this value was downloaded from FishBase (Froese & Pauly 2014) using the R package (R Core Team 2014) *rfishbase* (Boettiger, Lang & Wainwright 2012). Individuals that were not able to be identified to species level on the survey were assigned the largest L_{max} of the species in that taxon caught on the survey. Only 0.29% (out of a total of 683319) individuals caught throughout the course of the survey had to be assigned their L_{max} from a related species so the method is unlikely to be biasing the results. For 60 (32%) taxa, observed lengths on the survey exceeded the values listed on FishBase. This is expected, as a comprehensive survey of a poorly known assemblage such as deep-sea fish is likely to expand the known range of sizes of some species beyond that previously recorded in a global compendium of data such as FishBase. In these cases, I used the size of the largest recorded specimen from the survey as L_{max}, such that

L_{max} consistently equates to the size of the largest known individual (Appendix 1). To determine whether there were any depth-related biases produced by using this method, I analysed the difference between FishBase L_{max} and observed maximum size with respect to depth. The relationship was statistically significant, but had low explanatory power (LM: F = 22.1, d.f. = 1, 185, $R^2 = 0.1$, $p < 0.001$), with the pattern being determined by a small number of species living at around 1500 m in depth. In support of this, a further analysis performed only on those species with L_{max} values taken directly from FishBase produced statistically identical relationships to those obtained when all species were included (Appendix 1). I therefore propose that combining FishBase L_{max} values and maximum observed size provides the most comprehensive method for indicating the true genetic growth potential of a species, while allowing the metric of fractional size to be widely applicable to all areas of the ocean, including shelf waters, on a global scale.

2.3.2. Analysis

The data were manipulated in three ways to describe assemblage structure using fractional size structure, size structure, and species composition. For fractional size structure, the mean total length was calculated across individuals in each station for each species, then this was divided by the L_{max} of each species (Appendix 1), giving mean fractional size for each species in each station. For size structure, the mean individual length for each species in each station was used. For species composition, the survey-derived relative abundance of each species in each station was standardised using the Hellinger transformation (Legendre & Gallagher 2001), whereby the species abundances were divided by the total abundance in that station, then square-root transformed. Changes in each of these three metrics along a depth gradient were analysed using Redundancy Analysis (RDA; Legendre & Legendre 2012) in the *vegan* package (Oksanen et al. 2013) in R (R Core Team 2014), whereby depth was the predictor and the values of assemblage structure at the station level, calculated as described above, was the response. RDA is a multivariate statistical technique that allows the analysis of multiple species and their assemblage metric values simultaneously. By taking depth as a predictor variable, RDA quantifies its effect on assemblage structure, revealing how much variation in the dataset can be apportioned to changes in depth. For fractional size and size structure, if a species was absent from a station it was said to have a fractional size or length of zero in order to signify that it was not caught and to be analogous to the measure of species composition. The fit of the RDA model was assessed using adjusted R-squared and statistical significance was established using a permutation test.

Overall assemblage structure was examined by averaging the fractional sizes and individual lengths across species for each station, and fourth root transforming the time-averaged total biomass in each station. The averages were calculated as weighted means, where the weighting of each species was the fourth root-transformed biomass of that species. In each of these instances, the fourth root transformation was chosen in order to downweight common species, as is often desired in abundance and biomass data (Clarke & Warwick 2001; Wilding & Nickell 2013; Rutterford et al. 2015). These assemblage level metrics could then be analysed with respect to the depth of the station using Generalised Additive Models (GAM), which were implemented with the R package (R Core Team 2014) *mgcv* (Wood 2011). A smoother function of depth was the predictor variable, and the upper limit of the degrees of freedom associated with the smooth (value of *k* in the model) was set as five in order to balance smoothness and complexity. The values for the test statistic, its significance, R-squared, and effective degrees of freedom were extracted from the model summary.

To compare intra- and interspecific changes in body size with depth in more detail, general linear models of the relationship between the mean length of individuals within a station and the depth of that station were fitted for each species. The coefficients of the relationship were extracted and used to calculate a mean slope weighted by 1/(standard error) such that slopes that were estimated with more accuracy were given a higher weighting. The standard error around this weighted mean was calculated using the method proposed by Cochran (1977) and described by Gatz & Smith (1995). Interspecific changes in size were analysed by fitting a general linear model to the relationship between the length of the largest individual of a species caught throughout the course of the survey, and the maximum depth at which that species occurred.

To visualise changes in the three measures of assemblage structure, hauls were grouped into 100 m depth bands and the metrics were averaged across the hauls in each depth band. As 187 taxa were present in the dataset, for ease of visualisation, only the most common species were plotted. Common species were defined as those that exhibited a relative abundance over 10 kg. These 38 species accounted for 95% of the total biomass caught so were determined to be a good representation of the study system. Relative abundance was plotted after a fourth root transformation. For the fractional size and size structure metrics, the 'Other' category was calculated by averaging the values for each species not plotted individually. For the species composition metric, the remaining species were grouped in the 'Other' category by summing their abundances in each depth band and taking the fourth root of this value.

2.4. Results

2.4.1. *Fractional size structure*

There was a statistically significant effect of depth on the fractional size of individuals within hauls, as measured by the mean lengths of species divided by their L_{max} (RDA: Pseudo-F = 25.5, d.f. = 1, 70, $R^2 = 0.26$, $p < 0.001$). There was a marked relationship between mean fractional size and depth (GAM: F = 50.4, e.d.f. = 3.9, $R^2 = 0.74$, $p < 0.001$), which was characterised by an overall increase in fractional size with depth, but with a roughly constant fractional size between 500-1000 m, and the suggestion of a decline beyond the range of depths considered here (Fig. 2b).

2.4.2. *Size structure*

There was a statistically significant effect of depth on size composition of hauls, as measured by mean lengths of individuals within each species (RDA: Pseudo-F = 24.0, d.f. = 1, 70, $R^2 = 0.24$, $p < 0.001$). There was also a relationship between mean body size and depth (GAM: F = 19.1, e.d.f. = 3.7, $R^2 = 0.51$, $p < 0.001$), which was characterised by an overall increase in body size with depth, but with a potential decline starting at the deepest end of the study site (Fig. 3b).

The depiction of changing size structure with depth in Fig. 3a allowed the examination of both intra- and interspecific variation in size. Some species were very large at all depths (e.g. the black scabbardfish, *Aphanopus carbo*, and the small-eyed rabbitfish, *Hydrolagus affinis*; Fig. 3a) while some were very small at all depths (e.g. the blackbelly rosefish, *Helicolenus dactylopterus*, and the hollowsnout grenadier,

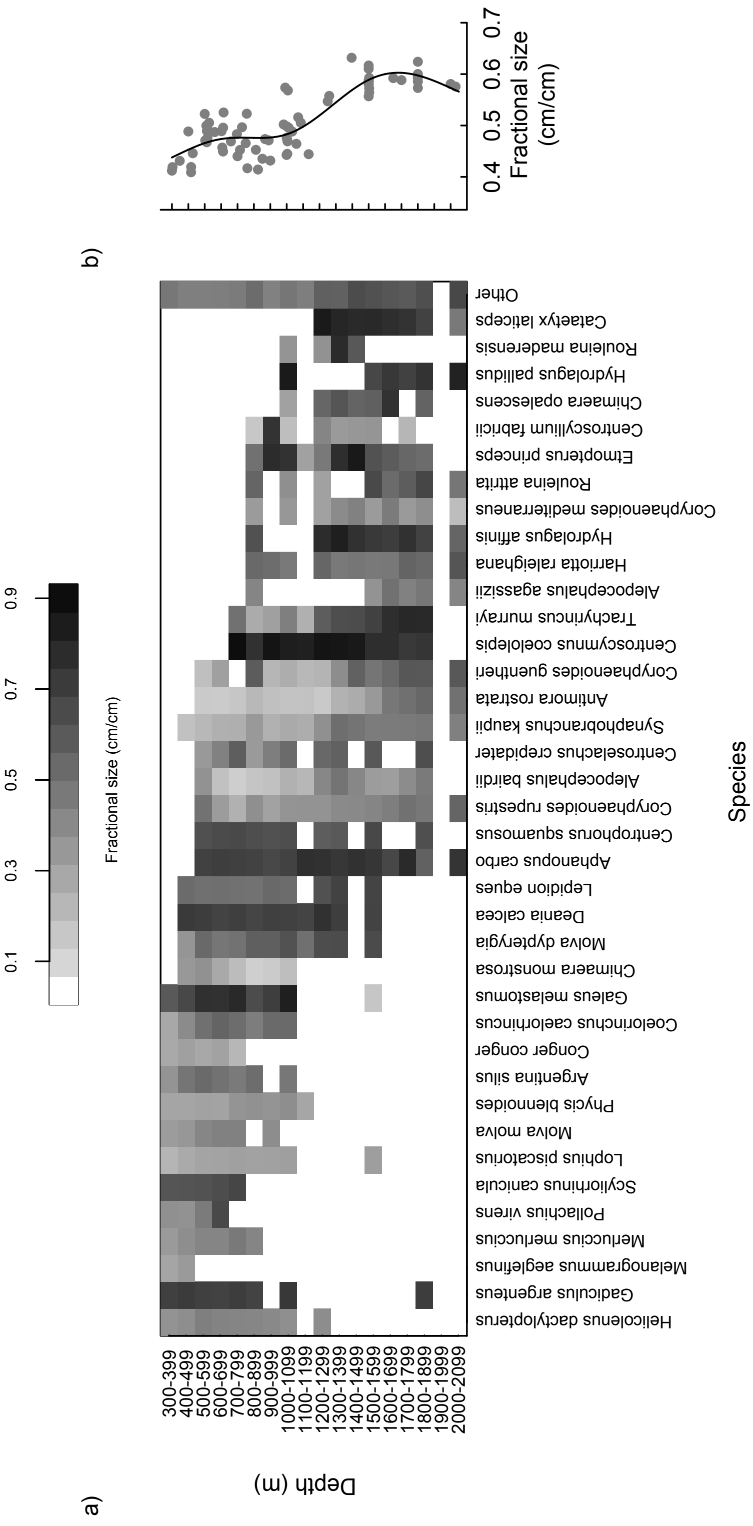

Fig. 2. Fractional size structure of assemblages along a depth gradient. *a)* For each depth band, fractional size was calculated by dividing the mean observed length for each species by the potential maximum size of that species (see Methods for details). Species with relative abundance greater than 10 kg are plotted individually, and the remaining species' mean fractional size values are averaged and plotted as 'Other'. *b)* Fractional size of the assemblage as a whole across a depth gradient, calculated as the mean fractional size value, weighted by species abundances, of the species present in each station.

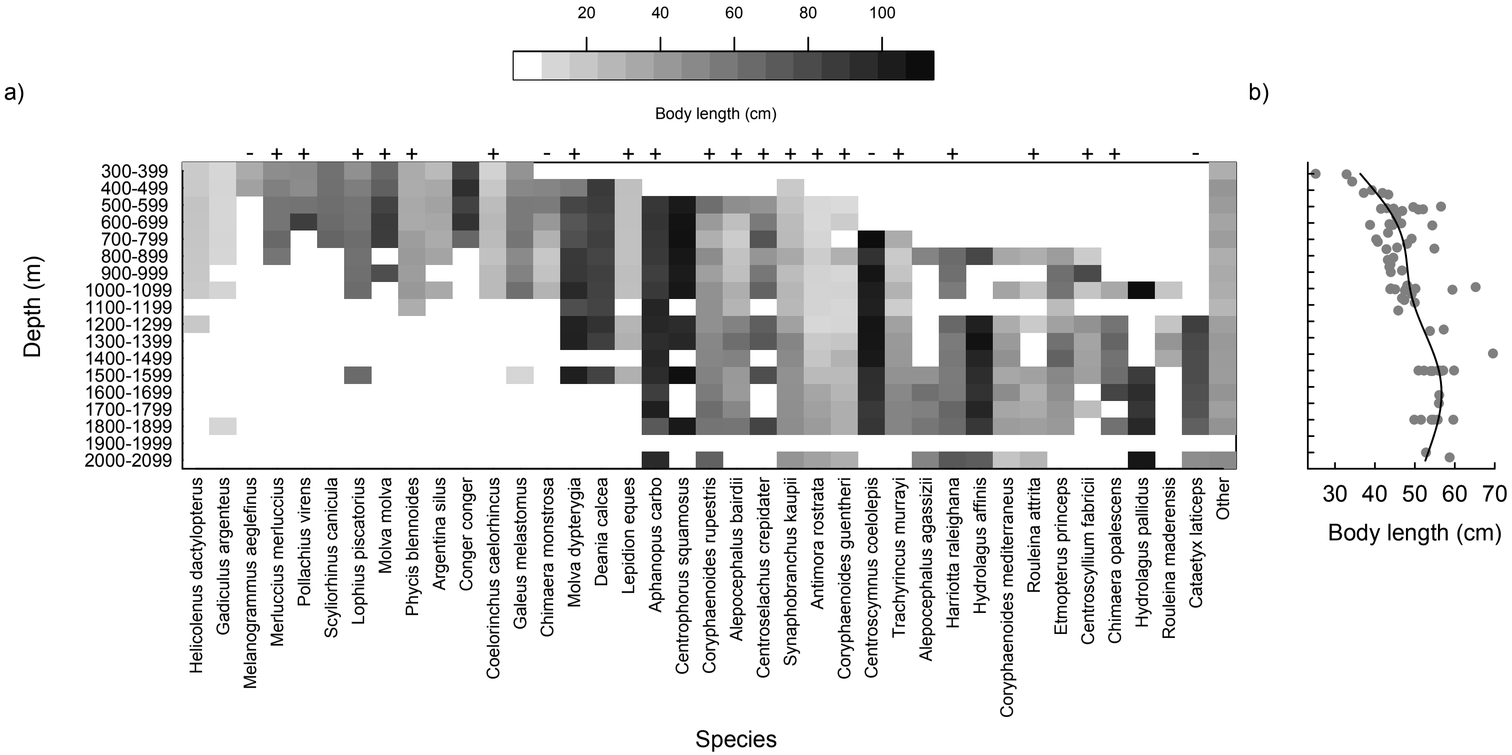

Fig. 3. Size structure of assemblages along a depth gradient. *a)* For each depth band, mean observed length was calculated from the total lengths of all individuals of that species. Species with relative abundance greater than 10 kg are plotted individually, and the remaining species' mean lengths are averaged and plotted as 'Other'. A '+' indicates a statistically significant positive relationship between body length and depth for that species; a '-' indicates a statistically significant negative relationship. *b)* Observed size of the assemblage as a whole across a depth gradient, calculated as the mean length, weighted by species abundances, of the species present in each station.

Coelorinchus caelorhincus; Fig. 3a). For those species whose sizes change with depth, there was mostly an increase in length with depth (e.g. Kaup's arrowtooth eel, *Synaphobranchus kaupii*; Fig. 3a); species that are larger in shallower waters were rare (e.g. the rabbitfish, *Chimaera monstrosa*; Fig. 3a). This conclusion that intraspecific changes in size tend to lead to bigger individuals in deeper waters was supported by the analysis of the slopes of the relationships between length and depth for each species. Of the 38 common species visualised in Fig. 3a, 20 (53%) exhibited statistically significant positive relationships between length and depth (illustrated by a '+' in Fig. 3a), four (11%) exhibited statistically significant negative relationships (illustrated by a '-' in Fig. 3a), and the weighted mean slope for all common species was 0.008 cm/m (SE: $6.9*10^{-6}$). The interspecific relationship between maximum observed length and maximum depth of occurrence was statistically significant, but had very low explanatory power, when fitted to all 187 taxa (LM: $F = 5.5$, d.f. = 1, 185, $R^2 = 0.02$, $p = 0.02$) and this relationship disappeared entirely when only the common species were included in the analysis (LM: $F = 0.2$, d.f. = 1, 36, $R^2 = -0.02$, $p = 0.65$).

2.4.3. Species composition

There was an effect of depth on the species composition of hauls (RDA: Pseudo-$F = 30.6$, d.f. = 1, 70, $R^2 = 0.29$, $p < 0.001$). The relative abundance of the assemblage as a whole showed a peak in biomass at around 1500 m and was relatively constant throughout other depths (Fig. 4b; GAM: $F = 5.9$, e.d.f. = 3.5, $R^2 = 0.25$, $p < 0.001$).

A visual inspection of assemblage structure reveals a change in taxonomy at approximately 1100 m where shallow-living species disappear, such as *H. dactylopterus*, *C. caelorhincus*, and the greater argentine, *Argentina silus* (Fig. 4a). Up to this depth, abundances tended to decrease as depth increased. Deeper than 1100 m, species with particularly large depth ranges started to dominate, such as *S. kaupii, A. carbo*, the roundnose grenadier, *Coryphaenoides rupestris*, and Baird's slickhead, *Alepocephalus bairdii* (Fig. 4a). These deeper-living species with larger depth ranges showed a variety of patterns in abundance (Fig. 4a).

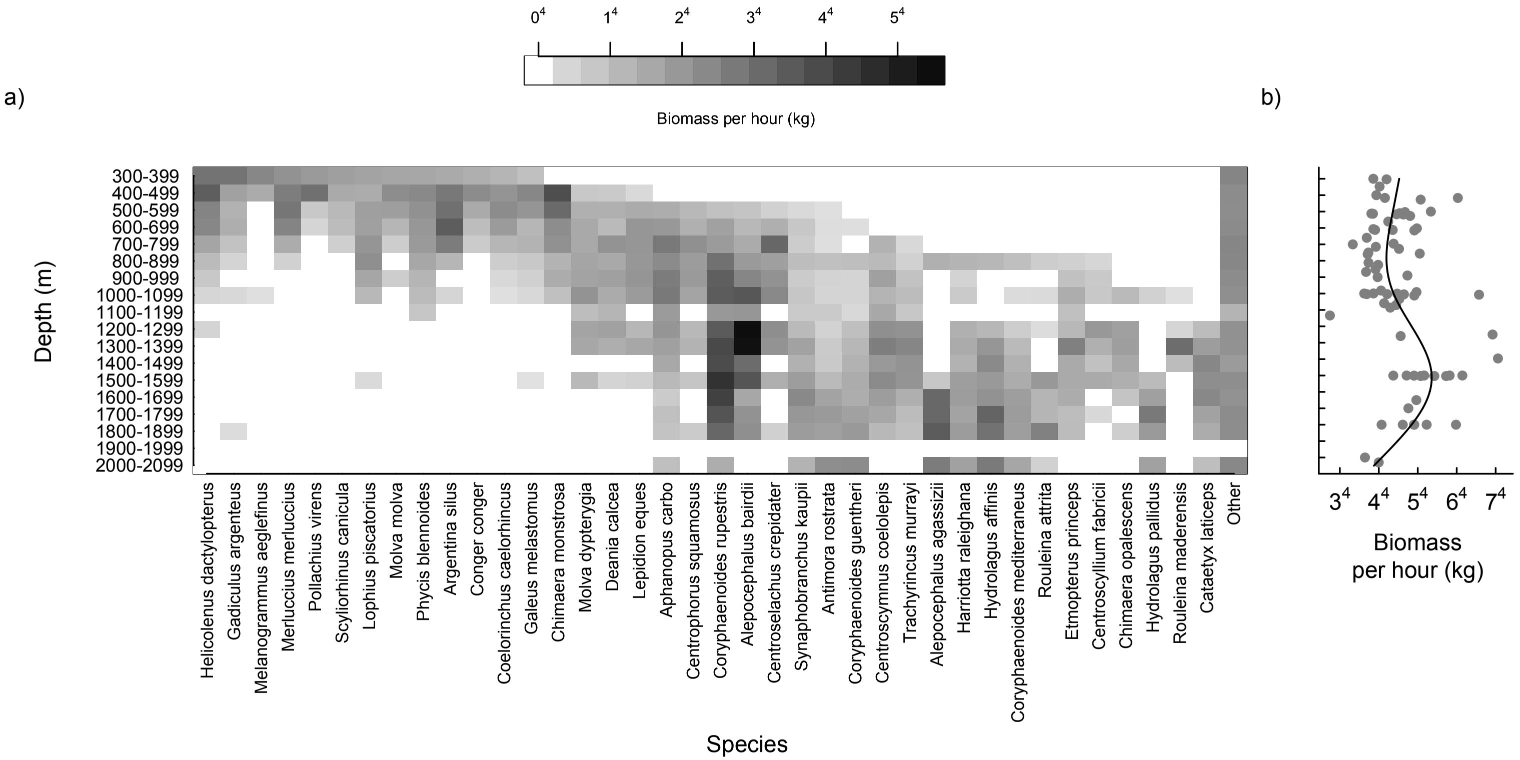

Fig. 4. Species composition of assemblages along a depth gradient. *a)* For each depth band, relative abundance was calculated for each species as the fourth root of mean biomass caught per hour. Species with relative abundance greater than 10 kg are plotted individually, and the remaining species' abundances are averaged and plotted as 'Other'. *b)* Biomass abundance of the assemblage as a whole across a depth gradient, calculated as the fourth root of the total biomass of individuals caught per hour in each station.

2.5. Discussion

Accounting for the fractional size and size structure of assemblages provides insight on change along an environmental gradient. The derivation of the fractional size metric shows that individuals that live deeper are further along in the growth trajectory of that species than individuals that live in shallower waters. However, this pattern may start to reverse at approximately 1700 m, but more data are needed for depths beyond the study site considered here in order to determine the robustness of this decrease. The changes in fractional size correspond to an increase in body length of fish as depth increases, at both the individual and assemblage levels. However, importantly, fractional size explained more variation in assemblage structure than body size alone, because the two metrics capture different qualities of the individual. By only capturing the absolute size of an individual at any one time, body size is not necessarily comparable among species that vary in maximum size. Important life history characteristics, such as size at maturity, are related to the maximum size of a species (Froese & Binohlan 2000), implying that it may be more informative to examine how close an individual is to this size, rather than the observed length of an individual which can make an individual appear 'large' or 'small' depending on what species it is and to what it is being compared. Fractional size combats this problem and can be applied globally, to all types of ocean environment.

The changes in fractional size seen with depth can be explained in three ways. The first is that the long lifespans documented in the deep sea (Koslow et al. 2000; Morato et al. 2006; Drazen & Haedrich 2012) do not manifest themselves in terms of larger potential maximum sizes, but rather an increased likelihood of the fish reaching their maximum size, which would be observed as an increase in the number of individuals with a high fractional size. Such an ability to reach maximum size may be due to the relatively constant environmental conditions and lack of disturbance in the deep (Lalli & Parsons 1993; Kaiser et al. 2011). The second explanation is that deep-living species start life in shallower waters due to food supply and temperature, then descend as they grow. Indeed it has been found that some deep-living fish spawn near the seabed, the eggs float to much shallower waters, then the juveniles move deeper as they age, either through the water column (Lin et al. 2012; Trueman, Rickaby & Shephard 2013), or down the continental slope after they have settled in the demersal environment (Magnússon 2001; Lin et al. 2012). Thirdly, there is a depth-related trend in fishing pressure, whereby effort is reduced in waters deeper than 1200 m (Neat & Burns 2010). Fishing effects may prevent individuals from growing large in shallow waters due to harvesting them once they become a certain size (Bianchi et al. 2000; Hsieh et al. 2010), resulting in reduced fractional sizes in those assemblages. However, the effect of fishing in the deep sea has been found to extend beyond the depth range of the fishing vessels themselves (Bailey et al. 2009), meaning that it is not necessarily possible to draw conclusions about the effect of fishing along a depth gradient using solely the depths fished as the predictor. This is particularly true for mobile species that may move in and out of fished areas over the course of their lives. The potential decline in fractional size at particularly deep depths could suggest that there is a depth limit to the benefits of a stable environment. For example, food availability may be too low to support large individuals, which has been found to be the case for certain functional groups (Collins et al. 2005).

Accounting for the population fractional size structure by including observed length of individuals as well as their potential length at the species level allows a more accurate description of the function of the assemblage as a whole. One example of this is that higher fractional sizes are likely to mean that a larger proportion of the assemblage is comprised of mature individuals (Froese & Binohlan 2000). Maturation size is thought to decline due to the genetic and phenotypic effects of fishing as well as potentially in response to environmental change (Marshall & Browman 2007), and the fractional size metric provides insight into the population and community size structure. Protecting the mature, larger, more fecund individuals is paramount in fisheries management (Law, Plank & Kolding 2012). Fractional size may also be related to average growth rate of individuals within the assemblage as smaller, younger individuals grow faster than older ones that are additionally allocating energy to reproduction (Jobling 1983). Faster relative growth rates, from reduced size and age structure, typify populations impacted by fishing and are linked with lower resilience to environmental perturbations that can result in higher variability in abundance through time (Hsieh et al. 2006; Anderson et al. 2008). The observed smaller fractional size in the shallows may therefore indicate a more heavily impacted assemblage due to fishing that could be less resilient to environmental variation, as the proportion of reproducing individuals is lower than in the deep, where fractional size is high. Alternatively, if the shallow assemblages are being replenished by recruitment from the mature individuals in the deep, as may be the case for several species in this system (Magnússon 2001; Lin et al. 2012; Trueman, Rickaby & Shephard 2013), then that would allow for increased resilience.

The interpretation of fractional size, however, is limited by the efficacy of using a maximum trait value to describe that trait. Maximum values will vary depending on sample size (Head, Hardin & Adolph 2012; Moorad et al. 2012), or may only illustrate the characteristics of a few anomalous individuals, rather than the species as a whole. However, L_{max} is correlated with important life history traits (Winemiller & Rose 1992; Froese & Binohlan 2000) and has been widely used in size-based fish ecology (e.g. Nicholson & Jennings 2004; Daan et al. 2005; Piet & Jennings 2005; Houle et al. 2012; Le Quesne & Jennings 2012) so still has a place in the computation of fractional size. An alternative trait metric to incorporate into fish ecology, and into large databases such as FishBase where possible, is the value of a trait at which only 10% of individuals exceed it. This approach has been applied as an alternative to maxima for studies using longevity (Moorad et al. 2012) and physiological performance (Head, Hardin & Adolph 2012) and as trait databases such as FishBase continue to develop, it may become possible to apply such a method in a comparative macroecological context.

The mean length of individuals also increased as depth increased when looking at the assemblage as a whole. This increase results in functional differences in assemblages along the environmental gradient, as larger individuals often occupy higher trophic levels than smaller individuals, regardless of species identity (Jennings et al. 2001), and body size influences diet breadth and type of prey consumed (Cohen et al. 1993; Scharf, Juanes & Rountree 2000). The increase in body length with depth held when species were analysed separately, with over half of common species increasing in size with depth. Conversely, interspecific analysis showed that there was no relationship between maximum observed length and maximum depth of occurrence for this same set of common species which exhibited increases at the individual level, implying that changes in body size of individuals can be masked when patterns are only analysed at the species level. By only using one value for each species, the changes in the course of an individual's life are disregarded, and as is shown by my analysis of fractional size structure, this is a particularly important factor in the description of assemblages along a depth gradient. Analysing fractional size instead of size structure captures the differing intra- and interspecific changes in size using just one metric.

Species composition also changes along a depth gradient, as has been widely documented (e.g. Gordon & Bergstad 1992; Magnussen 2002; Carney 2005; Tolimieri and Levin 2006; Yeh & Drazen 2009). The most visually striking change in species composition appears to occur at around 1100 m (Fig. 4a), where species with very large depth ranges start to dominate, broadly agreeing with previous work on depth zonation in the area (Gordon & Bergstad 1992). Several environmental variables change at around 1000 m in depth: light is available for vision up to 1000 m (Kaiser et al. 2011), and there is rapidly decreasing salinity above 1000 m, but constant salinity below 1000 m (Lalli & Parsons 1993). The dominance of species with large depth ranges below 1100 m, such as the roundnose grenadier *C. rupestris*, and Baird's slickhead *A. bairdii*, may be due to these stabilising environmental conditions at depth (Lalli & Parsons 1993; Kaiser et al. 2011). The species composition metric explained more variation between stations than fractional size or size structure. However, the difference was slight, and it is difficult to map taxonomic changes onto functional roles; the species composition and size structure metrics also fail to resolve demographic changes and the role of an individual (Rudolf & Rasmussen 2013a, b) with respect to both its observed traits and species-level life history characteristics. Thus, fractional size structure, by incorporating species, individual lengths and L_{max}, represents more information than species composition or size structure about the assemblage as a whole and illustrates changes along a depth gradient with particularly high explanatory power.

The relative biomass abundance of the assemblage as a whole was highest at 1500 m, and relatively constant throughout the rest of the depth range. This peak in biomass can be explained by an assemblage of bentho-pelagic-feeders that dominates at this depth (Trueman et al. 2014). The lack of variation in total biomass at other depths implies that the increase in body size with depth is accompanied by a decrease in numerical abundance (Sheldon, Prakash & Sutcliffe 1972) so that total biomass remains relatively constant. This is to be expected if individuals move deeper as they grow because some individuals die while others become large. It is generally accepted that biomass decreases with depth on a global scale (Carney 2005) so it is possible that this relationship was not captured in this study due to being limited to 2000 m in depth, and only sampling the demersal fish community.

It must be noted that in order to explore depth-related trends in assemblage structure, metrics were averaged over time. This is not to dismiss the potential temporal effects on community structure, but rather to summarise the variation that occurs along the environmental gradient before attempting to untangle temporal variation. I assume that over the course of this medium-term survey, any changes that may have occurred in assemblage metrics will not be large enough to impact the relationships with depth presented here, which are determined by an extreme environmental gradient that cannot, within this timescale, be outweighed by potential temporal variation in local environmental conditions. It is shown here that assemblages vary dramatically along the continental slope, and these results will need to be taken into consideration and controlled for when investigating other changes in deep-sea communities.

The three measures of community structure discussed here shed light on taxonomic and trait-based changes in fish assemblages in the deep sea. Depth explained the most variation in assemblage structure when the traditional metric, species composition, was used. However, mean fractional size changed along a depth gradient with unprecedented significance, supporting the idea that community ecologists need to move beyond species abundances, towards the inclusion of the functional role of the individual. The ability to examine the metrics at both the population and assemblage level is an advantage of the approach presented in this paper. Panel a) of figures 2, 3 and 4 show both levels of organisation simultaneously, allowing us to unpack the assemblage metric and deduce the relative influence of different species on the assemblage as a whole. Understanding the distribution of different sizes of fish and where along a depth gradient different fractional sizes are situated will help in understanding the resilience of deep-sea communities and their sustainable harvesting (Bailey et al. 2009). Relatively larger fish are more likely to be mature and here appear to be distributed in deeper waters, particularly at around 1500 m. Larger individuals, with higher fecundity, are widely acknowledged as being important to support the spawning stock biomass (Law, Plank & Kolding 2012; Hixon, Johnson & Sogard 2014). How fishing impacts propagate throughout depths in the deep sea needs more study, and this research into the taxonomy and traits of these assemblages can feed into this understanding. The trait-based approaches presented here will also be of relevance to other aspects of continental slope communities, such as pelagic species and marine invertebrates, for which it would be interesting to examine fractional size along a depth gradient in order to establish the generality of these findings. These approaches can also be used in alternative systems where body size is of importance in structuring assemblages, and in order to understand community variation across a changing environmental gradient such as temperature due to climate change.

2.6. Supporting information

Table S1. Concatenation of hauls into stations (survey data 1998–2012).

Table S2. Conversion of lengths measured on the survey to total length.

Appendix 1. The robustness of L_{max} allocation.

3. Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea

3.1. Abstract

Biodiversity is well studied in ecology and the concept has been developed to include traits of species, rather than solely taxonomy, to better reflect the functional diversity of a system. The deep sea provides a natural environmental gradient within which to study changes in different diversity metrics, but traits of deep-sea fish are not widely known, hampering the application of functional diversity to this globally important system. I used morphological traits to determine the functional richness and functional divergence of demersal fish assemblages along the continental slope in the Northeast Atlantic, at depths of 300–2000 m. I compared these metrics to size diversity based on individual body size and species richness. Functional richness and size diversity showed similar patterns, with the highest diversity at intermediate depths; functional divergence showed the opposite pattern, with the highest values at the shallowest and deepest parts of the study site. Species richness increased with depth. The functional implications of these patterns were deduced by examining depth-related changes in morphological traits and the dominance of feeding guilds as illustrated by stable isotope analyses. The patterns in diversity and the variation in certain morphological traits can potentially be explained by changes in the relative dominance of benthic and pelagic feeding guilds. All measures of diversity examined here suggest that the deep areas of the continental slope may be equally or more diverse than assemblages just beyond the continental shelf.

3.2. Introduction

Understanding biotic responses to environmental change remains a major challenge in ecology. Increasingly, approaches based on quantifying the functional traits of species are seen as a useful way to meet this challenge (e.g. Harfoot et al. 2014; Violle et al. 2014; Pawar, Woodward & Dell 2015). Over the last decade, trait-based approaches have thus become central to ecology in both terrestrial and marine systems (McGill et al. 2006; Bremner 2008; Litchman et al. 2010; Webb et al. 2010; Tyler et al. 2012; Mouillot et al. 2013). Using traits, rather than taxonomy, to describe communities confers several benefits, such as being more widely applicable to other ecosystems that may share function even with no taxonomic overlap, reducing the number of variables from hundreds of species down to only a few traits, and having a clearer connection to the function and properties of the system than do taxonomic lists (Bremner 2008; Enquist et al. 2015; Schmitz et al. 2015). However, the extent to which we can predict the response of ecosystems to environmental change based on the traits of species remains a fundamental question in ecology (Sutherland et al. 2013), and more studies on how different dimensions of diversity vary across environmental gradients are needed.

A trait-based approach that has often been applied to marine systems, including the deep sea, uses size-based metrics (e.g. Blanchard et al. 2005a; Collins et al. 2005; Piet & Jennings 2005; Mindel et al. 2016). Body size is important in the oceans because fish grow several orders of magnitude over the course of their lives, and size, rather than species identity, often determines what prey is consumed (Cohen et al. 1993; Scharf, Juanes & Rountree 2000; Jennings et al. 2001). Body size can be used to calculate a distinct measure of diversity, based solely on the range of individual sizes present in an assemblage, irrespective of species identity (e.g. Ye et al. 2013; Rudolf et al. 2014; Quintana et al. 2015). The diversity of individual sizes present could give more information about the range of size-based niches a fish community is occupying than does a mean or a maximum size. Leinster & Cobbold (2012) proposed a measure of diversity based on Hill numbers (Hill 1973) that allows traditional measures of diversity based on richness and evenness to be adjusted to account for the relative similarity of the biological units of assessment. Similarity can be based on any trait, and although typically the biological units will be species, the method can be generalised to any biologically meaningful group, including size classes.

Traits other than body size also impact assemblage function. For example, gape size can be used as a proxy for what prey are consumed (Boubee & Ward 1997) and tail measurements can be used to estimate swimming capabilities (Fisher et al. 2005). In the deep sea, variation in some morphological characteristics has been attributed to the habitat occupied. For example, species that aggregate at seamounts are deep-bodied to cope with the strong currents in these areas (Koslow 1996; Koslow et al. 2000) and deeper-living species have more elongated body plans to increase swimming efficiency at high hydrostatic pressure (Neat & Campbell 2013). Locomotory capacity also declines with depth, which is likely a response to decreased light for vision that relaxes the demand for high activity levels needed to obtain prey or escape predation (Childress 1995). Age at maturity increases with depth while fecundity and potential rate of population growth decrease (Drazen & Haedrich 2012), ultimately having important implications for the productivity and resilience of deep-sea populations. Traits also predict where or on what a species is feeding. Species that vertically migrate through the water column to feed on pelagic prey have worldwide impacts for carbon storage in the deep sea (Trueman et al. 2014). Furthermore, scavengers exhibit different traits to non-scavengers due to the high-energy reward of carrion compared to the low food availability for predators in the deep (Haedrich & Rowe 1977; Collins et al. 2005). Large food falls are an important resource in the deep sea (Hilario et al. 2015) and scavengers that exploit this resource must possess traits such as the ability to undergo prolonged starvation, recognition of carrion odours, and sufficient motility to locate and reach the carcass (Tamburri & Barry 1999).

Thus, traits determine what individuals feed on, where they live, and ultimately the function of deep-sea ecosystems. How communities function is not constant throughout the deep sea, as it is now known to be a diverse environment (Danovaro, Snelgrove & Tyler 2014). The continental slope, which links shallow waters to the abyssal plain, experiences profound environmental changes due to depth, such as increased pressure and decreased temperature, light and food availability (Lalli & Parsons 1993; Kaiser et al. 2011). These changes mean that assemblage structure varies more on a vertical gradient than it does horizontally (i.e. spatially; Angel 1993; Lalli & Parsons 1993; Kaiser et al. 2011), but what these structural changes mean in terms of distribution of traits and function is not yet known.

A popular approach that uses traits as building blocks is functional diversity (Tilman 2001; Petchey & Gaston 2002), which aims to quantify differences and similarities in function and role between species. Higher species richness may not necessarily confer a more diverse ecosystem if species overlap in the roles they perform (Walker 1992); functional diversity aims to address this by quantifying the distinctness of different species based on biological traits. How traits are partitioned among groups of co-occurring species is debated. The 'limiting similarity' hypothesis predicts that species that occupy similar niches will not be able to co-exist due to interspecific competition (MacArthur & Levins 1967), resulting in high diversity of traits (Mouillot, Dumay & Tomasini 2007). The 'environmental filtering' hypothesis states that species must adapt in similar ways to local abiotic conditions, resulting in the co-existence of similar species (Keddy 1992; Violle et al. 2007) and hence low trait diversity (Mouillot, Dumay & Tomasini 2007). Alternatively, under the neutral hypothesis (Hubbell 2001, 2005), no species are at a competitive advantage or disadvantage, so assemblages are formed by stochastic processes. Along the depth gradient of the continental slope, resource availability declines and environmental conditions become more extreme (Carney 2005). It could therefore be expected that functional diversity will be highest in the shallowest areas where 'limiting similarity' causes species to occupy different niches (MacArthur & Levins 1967), while in the deepest areas, the harsh conditions result in 'environmental filtering' (Keddy 1992; Violle et al. 2007) and hence a reduction in functional diversity.

I use the depth gradient of the continental slope to compare the trait-based approaches of functional diversity calculated using species-level morphological traits, and size diversity calculated using individual body size data, to a simple measure of taxonomic diversity, species richness. I relate these changes in diversity to patterns in dominant morphological traits and the relative dominance of feeding guilds. Feeding guilds were established using stable isotope analysis, which reveals the position of an individual in the food chain from the relative concentrations of light and heavy isotopes of nitrogen and carbon in body tissue (e.g. Michener & Schell 1994). I use this combination of taxonomic and trait-based approaches to answer for the first time in deep-sea fish assemblages the following key questions: i) How does functional diversity based on species-level traits vary along a depth gradient? ii) How does this compare to depth-dependent changes in species richness and the diversity of individual body sizes? iii) What traits are driving these relationships, and how can they be related to assemblage function as illustrated by feeding guilds?

3.3. Materials & methods

3.3.1. Study site

Data were collected on Marine Scotland's deep-water bottom trawl survey of demersal fish using *MRV Scotia* in September 1998, 2000, 2002, 2004–2009 and 2011–2013 (Neat & Burns 2010). The study area is within ICES area VIa at latitude of 55° to 59°N and a longitude of approximately 9°W (Fig. 5), along the continental slope of the Rockall Trough in the Northeast Atlantic, at depths of 300–2067 m. Mesopelagic fish (those that live in the water column) and invertebrates were excluded from the analysis due to the gears being adapted to sample only demersal fish (those that live on or around the seabed, including those classified as benthopelagic).

In order to focus solely on depth-related trends, I controlled for temporal variation by pooling hauls into stations that were re-sampled through time. I then used metrics that were averaged over time within each station in all analyses. Hauls were grouped into the same station if they were in the same ICES statistical rectangle (of area 1° longitude by 30' latitude) and within 100 m of each other in depth. The depth of the station was taken as the mean of the depths of the hauls in that station. Hauls that were not repeated across years were still included as they were assumed to occur randomly with respect to time and depth. The dataset consisted of 80 stations, including 22 stations with only one representative haul, and 58 stations where hauls were repeated over at least two years allowing for time-averaging (Table S5).

3.3.2. Data collection

During the survey, catch was identified to the finest taxonomic resolution possible, which was species level for 99.9% individuals caught. The full classification of taxa was determined using the World Register of Marine Species (WoRMS

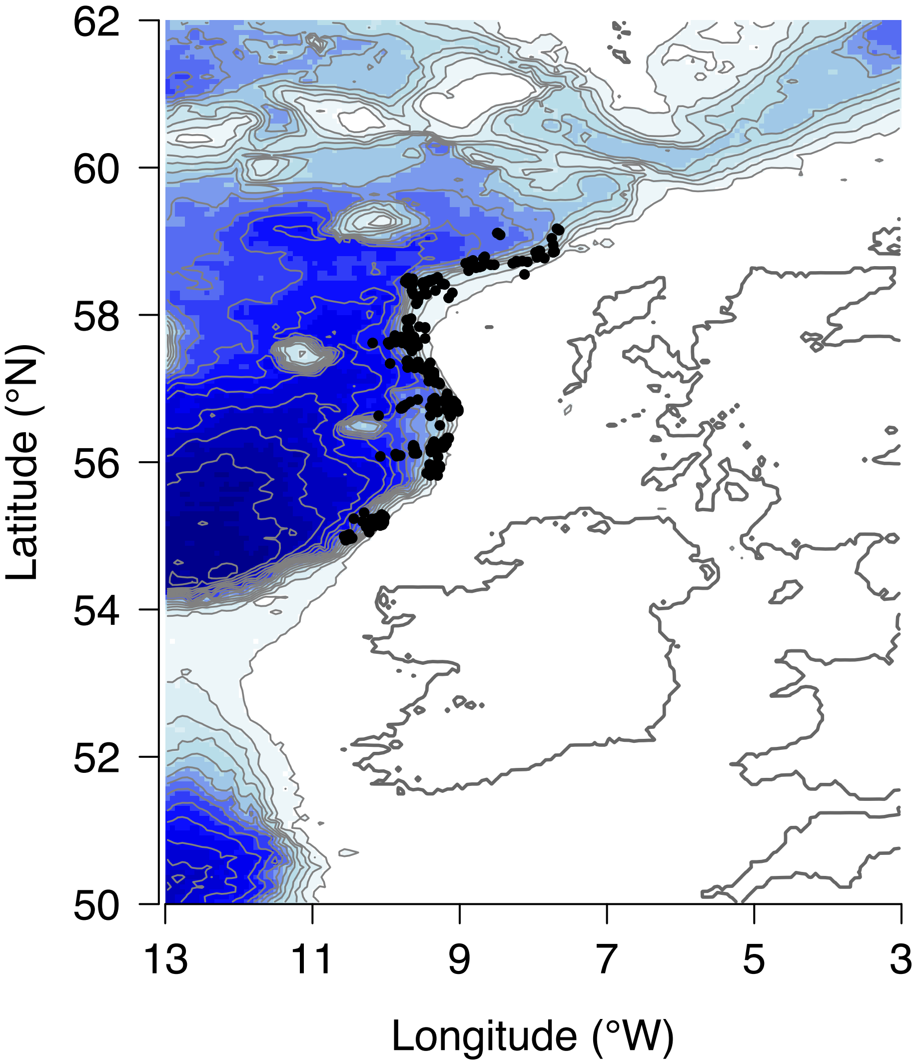

Fig. 5. Location of hauls of the Marine Scotland deep-water bottom trawl survey along the continental slope of the Rockall Trough from 1998-2013. Shading indicates depth, with white representing the shallowest, and dark blue representing the deepest areas.

Editorial Board 2013). Photographs taken on board in 2013 were used for subsequent morphological measurements using the measuring software ImageJ (Schneider, Rasband & Eliceiri 2012). Morphological data were collected for 31 species (Table 1) that together account for 84% of all biomass caught over the duration of the survey. These species were selected for their abundance and in order to include species that span all depths. Data for additional species could not be collected due to time constraints in photographing individuals on the survey. Measurements were replicated by using photographs of multiple individuals; the number of replicates differed among species (Table 1).

The morphological measurements taken using photographs were total length, head length, tail height, tail surface area, eye size, eye position, angle of mouth in

Table 1. Species-level trait data for the 31 species for which morphological measurements were collected. L_{max} was downloaded from FishBase (Froese & Pauly 2016) or calculated from the survey data (please see Methods for details), feeding guild classification was based on stable isotope analyses, and all other traits were measured from photos taken on Marine Scotland's deep-water trawl survey in 2013. Please refer to Fig. 6 and Table 2 for definitions and calculations of traits.

Species	Number of individuals measured	Relative head size (cm/cm)	Caudal fin aspect ratio ($cm^2/cm^2/cm$)	Relative eye size (cm/cm)	Eye position	Angle of mouth in relation to lateral line (°)	Relative surface area of mouth protrusion (cm^2/cm)	Relative gape size (mm^2/cm)	Feeding guild	L_{max} (cm)
Alepocephalus agassizii	22	0.29	3.11	0.074	Side	25.6	0.34	75.7	Pelagic	123.0
Alepocephalus bairdii	19	0.21	5.29	0.065	Side	23.3	0.19	43.8	Pelagic	127.4
Antimora rostrata	16	0.21	2.77	0.044	Side	16.5	0.17	58.2	Unknown	87.0
Aphanopus carbo	19	0.19	3.09	0.032	Side	16.9	0.00	55.8	Pelagic - high	129.0
Apristurus aphyodes	13	0.24	0.38	0.013	Side	9.3	0.00	20.4	Benthic	85.0
Argentina silus	20	0.19	3.53	0.087	Side	26.5	0.13	14.9	Pelagic	81.1
Bathypterois dubius	18	0.16	3.10	0.010	Side	21.1	0.17	24.8	Unknown	29.0
Bathysaurus ferox	6	0.14	2.19	0.018	Side	28.8	0.00	97.2	Unknown	74.2
Beryx decadactylus	17	0.24	3.93	0.111	Side	35.1	1.30	93.4	Unknown	100.0
Cataetyx laticeps	10	0.21	NA	0.020	Top	28.2	0.51	101.1	Benthic - suspension	101.0
Centroscymnus coelolepis	1	0.15	2.58	0.021	Side	NA	NA	35.5	Benthic	122.0
Chimaera monstrosa	19	0.15	NA	0.037	Side	48.3	0.08	7.9	Benthic	150.0
Coelorinchus caelorhincus	16	0.18	NA	0.045	Side	50.9	0.10	10.2	Benthic - low	48.0
Coelorinchus labiatus	20	0.26	NA	0.046	Side	57.7	0.12	5.9	Unknown	50.0
Coryphaenoides guentheri	21	0.17	NA	0.044	Side	35.6	0.06	6.7	Benthic	55.3
Coryphaenoides mediterraneus	19	0.10	NA	0.023	Side	47.5	0.19	19.8	Benthic - low	105.8
Coryphaenoides rupestris	29	0.15	NA	0.038	Side	56.0	0.27	25.4	Pelagic	127.7
Halargyreus johnsonii	20	0.22	2.72	0.061	Side	42.7	0.22	27.9	Unknown	56.0

Table 1. Continued.

Species	Number of individuals measured	Relative head size (cm/cm)	Caudal fin aspect ratio (cm²/cm²/cm)	Relative eye size (cm/cm)	Eye position	Angle of mouth in relation to lateral line (°)	Relative surface area of mouth protrusion (cm²/cm)	Relative gape size (mm²/cm)	Feeding guild	L_{max} (cm)
Halosauropsis macrochir	11	0.13	NA	0.012	Side	44.7	0.08	15.9	Benthic - high	90.0
Harriotta raleighana	9	0.30	NA	0.027	Side	NA	NA	6.6	Unknown	120.0
Helicolenus dactylopterus	20	0.31	2.27	0.076	Side	46.5	0.67	76.3	Benthic	47.0
Hoplostethus atlanticus	15	0.30	3.82	0.067	Side	40.2	0.82	140.8	Benthic	75.0
Hydrolagus affinis	9	0.20	0.49	0.029	Side	NA	NA	19.3	Unknown	131.6
Lepidion eques	20	0.20	0.92	0.061	Middle	42.9	0.16	27.0	Benthic - low	44.0
Merluccius merluccius	6	0.20	1.41	0.036	Middle	26.7	0.50	85.0	Benthic - high	140.0
Mora moro	20	0.18	1.89	0.064	Middle	32.6	0.37	66.8	Unknown	80.0
Nezumia aequalis	17	0.16	NA	0.057	Middle	31.0	0.06	7.6	Benthic - high	37.8
Phycis blennoides	20	0.19	1.33	0.048	Mixed	33.6	0.55	49.8	Benthic	110.0
Spectrunculus grandis	14	0.16	NA	0.024	Mixed	32.9	0.24	30.5	Unknown	147.3
Synaphobranchus kaupii	20	0.11	NA	0.013	Side	50.4	0.00	9.6	Benthic - low	100.0
Trachyrincus murrayi	20	0.20	NA	0.036	Side	54.1	0.15	17.7	Benthic - low	66.7

relation to lateral line and surface area of mouth protrusion if present (Table 2; Fig. 6A, B, C). Mouth height and mouth width were measured on board due to the difficulty of photographing the mouth. Gape size was then calculated as the area of an oval with mouth height and mouth width as the diameters (Table 2; Fig. 6D). The tail measurements were used to calculate the aspect ratio of the fish, which can be used to deduce activity levels (Table 2; Fig. 6A; Pauly 1989). Head, eye, surface area of mouth protrusion and gape size were divided by total length in order to calculate relative trait values (Table 2). Relative traits were used in all analyses because body size varies substantially within species. By controlling for body size, the relative trait value can be assumed to be constant throughout an individual's life because it represents an inherent body plan. Relative traits represent differences in function between species regardless of body size (Table 2 and references therein). The individual correlations between each of the continuous traits can be found in Fig. S2.

Total length was measured on board the survey for all individuals caught, in addition to the measures taken using the photographs of subsets of individuals. For

Table 2. The morphological traits used in the calculation of functional diversity, how they were calculated from the measurements depicted in Fig. 6, and their predicted link to function.

Morphological trait	**Calculation**	**Figure 6 panel**	**Function/Strategy**	**Reference**
Relative head size	$\frac{HL}{TL}$	A	Approach to prey; use of space	Reecht et al. (2013)
Caudal fin aspect ratio	$\left(\frac{TH^2}{SAT}\right)/TL$	A	Swimming speed; correlates with life history and physiological characteristics	Pauly (1989); Fisher et al. (2005)
Relative eye size	$\frac{ED}{TL}$	A	Visual sensitivity and/or acuity	Sibbing & Nagelkerke (2001)
Eye position	EP	B	Vertical position in the water column	Clavel et al. (2013)
Angle of mouth in relation to lateral line	MA	C	Prey capture mode; vertical position in the water column of prey	Piet (1998); Sibbing & Nagelkerke (2001)
Relative surface area of mouth protrusion	SAM/TL	C	Prey capture mode and speed	Sibbing & Nagelkerke (2001)
Relative gape size	$\left(\pi\frac{MH*MW}{2}\right)/TL$	D	Size of prey targeted	Boubee & Ward (1997)
L_{max}	See Methods	NA	Correlates with size at maturity, fecundity, growth rate and longevity	Winemiller & Rose (1992); Froese & Binohlan (2000)

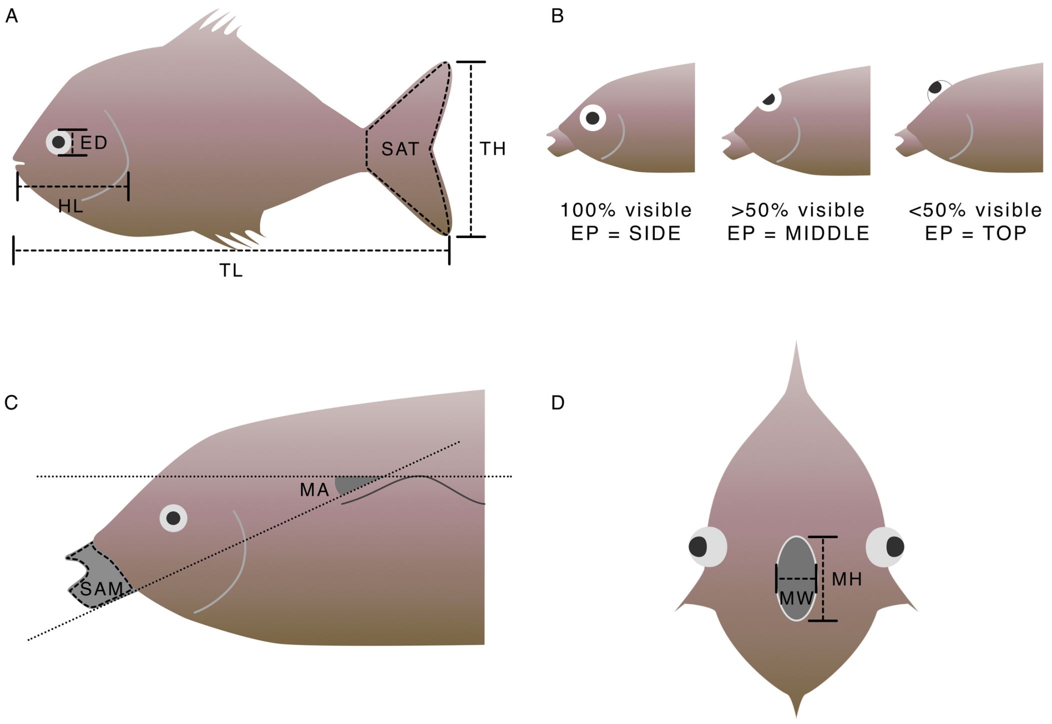

Fig. 6. How morphological measurements were taken using photographs (panels A, B and C) and on board the survey (panel D). Morphological traits were calculated from these measurements using the formulae in Table 2. A) TL = total length; HL = head length; ED = eye diameter; SAT = surface area of tail; TH = tail height. B) EP = eye position. C) SAM = surface area of mouth protrusion; MA = mouth angle. D) MW = mouth width; MH = mouth height.

12 (39%) of the 31 species for which morphological measurements were taken (hence the species on which most analyses presented here focus), it was inappropriate to measure total length due to tails commonly breaking off in the net, so alternative measurements were taken and converted to total length using conversion factors calculated from a subset of the data (Table S6).

Subsets of the survey data were used to calculate conversion factors for translating the total length measurements to weight. Predicted weights were then standardised by controlling for the duration of time spent trawling. This measure of biomass caught per hour of trawling was used in all further analyses as the measure of abundance. The species-level measure of body size to be included in the calculation of functional diversity was the maximum recorded length of a species, or L_{max}. L_{max} was set as the maximum length listed on FishBase (Froese & Pauly 2016) or the maximum length recorded on the survey, whichever was the greater (Mindel et al. 2016). Of the 31 species for which morphological data were available, one (*Apristurus aphyodes*) did not have an L_{max} listed on FishBase. Therefore its L_{max} was set as that of the largest species of that genus caught on the survey (*Apristurus manis*). Standard Lengths on FishBase were converted to Total Length using conversion factors calculated from the survey data where possible (Table S6).

Stable isotope data were available for 21 of the species for which morphological data were collected. The stable isotope analyses are described in Trueman et al. (2014; data are available at Dryad Digital Respository doi: 10.5061/dryad.n576n). The isotopic dataset was compared to a meta-dataset of diet studies based on stomach content analyses (Trueman et al. 2014). Where species were present in both datasets, stable isotope compositions clearly distinguished between species categorised as feeding on either benthic (seabed) or pelagic (water column) prey (Trueman et al. 2014). Stable isotope compositions were subsequently used to assign feeding guild to species and individuals lacking reliable stomach content data (Trueman et al. 2014). The distinction between benthic and pelagic feeders was less pronounced in the assemblage at 500 m, as the diets of the two guilds are similar at this depth. However, species could still be assigned to a feeding guild based on their relative isotope signatures throughout the rest of their depth range. Specialised signatures within these two feeding guilds could be established in some cases: if the smallest individual sampled for that species was in the upper half of stable isotope space for that category, the species was defined as high trophic level; if the largest individual sampled was in the lower half of stable isotope space, the species was defined as low trophic level; fish that feed on benthic suspension feeding prey have a noticeably enriched isotope signature for a given body size, depth and feeding guild, so were categorised separately.

3.3.3. Data analysis

Diversity was calculated in four ways: 1) functional richness, 2) functional divergence, 3) size diversity and 4) species richness. The two measures of functional diversity are described by Villéger, Mason & Mouillot (2008) and were calculated using the R (R Core Team 2015) package *FD* (Laliberté & Shipley 2011). Functional richness is an estimate of the degree to which the assemblage fills functional space

(Fig. 7A; Villéger, Mason & Mouillot 2008) and functional divergence measures how abundance is distributed within the volume of functional trait space occupied by species (Fig. 7B; Villéger, Mason & Mouillot 2008). The traits included in the calculation of functional diversity were relative head size, aspect ratio of the caudal fin, relative eye size, eye position, angle of mouth in relation to lateral line, relative surface area of mouth protrusion if present, relative gape size, and L_{max} (Table 2). A species-level mean was calculated from the relative trait values for all continuous traits (Table 1). Functional richness does not include species abundances in its calculation; functional divergence includes a weighting of traits by species abundance, which in this case was biomass caught per hour of trawling. Due to only having trait data for a maximum of 31 species, functional diversity was only calculated using those species and their biomasses, and the rarer species were not considered. As these 31 species accounted for 84% of all biomass caught on the survey and spanned the entirety of the depth range studied, they were considered to be a good representation of the study system.

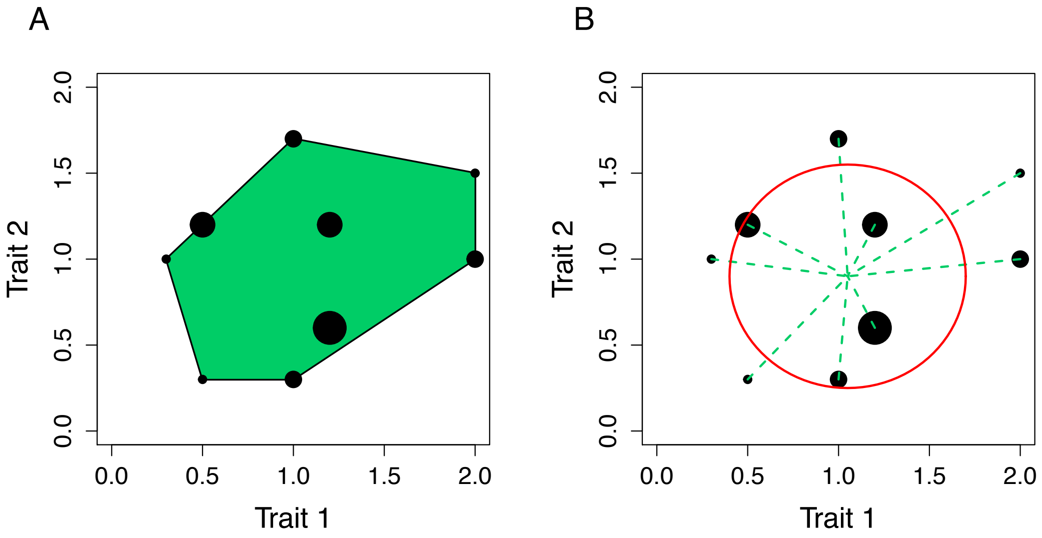

Fig. 7. Toy example using only two traits of the calculation of A) functional richness and B) functional divergence. Each black point represents a species that exhibits trait values indicated by their positioning within the axes, and the size of the point represents the abundance of that species. A) Functional richness is represented by the green shaded area, corresponding to the volume of trait space occupied by the species. B) Functional divergence is determined by species abundances, how far those species are from the centre of gravity as determined by the species traits (illustrated by dotted lines), and how this distance compares to the mean distance to the centre of gravity (illustrated by the circle). Figures are adapted from Villéger, Mason & Mouillot (2008).

Size diversity was calculated using the generalised measure of diversity proposed by Leinster & Cobbold (2012). In this index, abundance of biologically meaningful groups and similarities between them are accounted for. Here the groups were size classes each of 10 cm in width and abundance was calculated as the proportional biomass per hour that each size class accounts for in each station, when only the species for which morphological data were known were included. The Euclidean distance matrix (d) between the mid-points of size classes was converted to similarities using the formula suggested by Leinster & Cobbold (2012): $\mathit{Similarity} = e/(\log(2)*d)$. The final input for the Leinster-Cobbold measure of diversity is the sensitivity parameter, q, which determines how much emphasis is given to rare species (or in this case, size classes; Leinster & Cobbold 2012). Here a value of q = 1.1 was used in order to balance the richness (lower q) and evenness (higher q) components of diversity, and to be comparable to the widely used Shannon index (Shannon 1948; Leinster & Cobbold 2012).

Species richness was calculated using only hauls that were of 120 ± 5 minutes in duration in order to control for sampling effort. For this subset of hauls, the number of species present was averaged across hauls in each station. All species were included in the calculation of species richness, not just those with morphological data available. This is because calculating species richness using only the morphological subset would merely be a count of the number of species for which morphological data were available and not be meaningful in a diversity context.

The four diversity measures were calculated for each station and then analysed with respect to the depth of that station with Generalised Additive Models (GAMs) using the R (R Core Team 2015) package *mgcv* (Wood 2011). A smoother function of depth was used as the predictor, and the values for the test statistic, significance, R-squared, and effective degrees of freedom (e.d.f.; the flexibility of the fitted model; Wood 2006) were extracted from the model summary.

Abundance-weighted station means were calculated for each continuous morphological trait included in the functional diversity metric and analysed with respect to the depth of the station using GAMs. The weighted mean was said to be the mean value across species, where values were weighted by the biomass caught per hour of trawling for each species. The mean observed size of individuals, irrespective of species identity, was also calculated for comparison. This value was not included in the functional diversity metric because a species-level measure of body size (L_{max}) was needed. The station mean body size was therefore calculated as the average length across individuals in a station, when only individuals of species for which morphological data were obtained were included, in order to be comparable to the measures of functional and size diversity. The standard deviation of each continuous trait at each station was also calculated and analysed with respect to depth using GAMs in order to relate variation in traits to patterns seen in functional diversity. The Pearson's product-moment correlation coefficient was calculated for the relationships between the means and standard deviations of each of the traits, and each measure of diversity.

The isotopic feeding guild data (Table 1) were interpreted using the percentage of biomass that each guild accounted for in depth bands of 200 m in width. The percentage was calculated as a proportion of the biomass accounted for by the species for which there were morphological data.

All data manipulation and analysis was performed using R version 3.1.2 (R Core Team 2015) and figures were produced using the packages *ggplot2* (Wickham 2009), *gridExtra* (Auguie 2016) and *marmap* (Pante & Simon-Bouhet 2013).

3.4. Results

Functional richness was low in the shallowest and deepest depths, and high at around 800 m (Fig. 8A; GAM: F = 14.1, e.d.f. = 3.8, $R^2 = 0.40$, $p < 0.001$). Functional divergence was high at both the shallow and deep ends of the depth gradient, with lowest values at around 1300 m (Fig. 8B; GAM: F = 10.4, e.d.f. = 2.9, $R^2 = 0.31$, $p < 0.001$). Size diversity increased to a peak at roughly 900 m, then declined as depth increased further, but remained higher in the deepest areas than in the shallowest ones (Fig. 8C; GAM: F = 10.8, e.d.f. = 3.5, $R^2 = 0.33$, $p < 0.001$). Species richness increased significantly with depth (Fig. 8D; GAM: F = 34.2, e.d.f. = 1.9, $R^2 = 0.61$, $p < 0.001$).

Abundance-weighted station means and the standard deviation of continuous morphological variables changed with depth and all statistics are reported in Table 3. The mean and standard deviation of relative head size exhibited strong relationships with depth (Table 3), where heads were larger in proportion to body size, and more varied, in the shallowest and deepest parts of the study site (Fig. 9A;

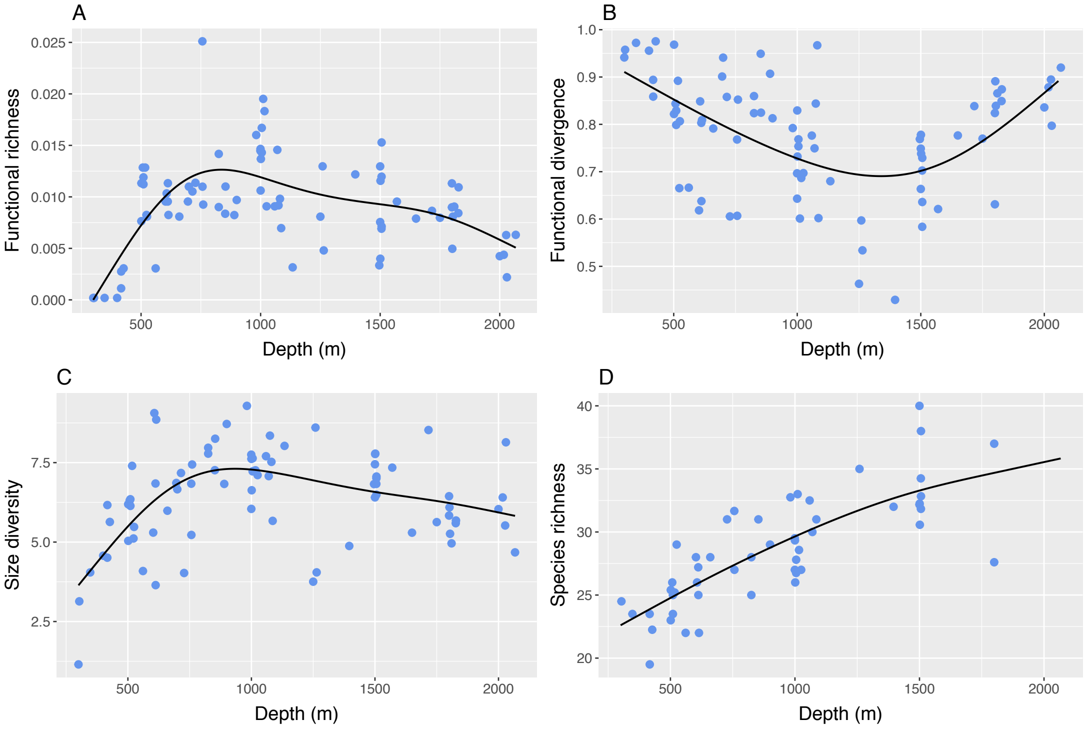

Fig. 8. The relationship between depth and A) functional richness, B) functional divergence, C) size diversity and D) species richness. Curves represent the fitted Generalised Additive Model.

Fig. 10A). Mean and standard deviation of aspect ratio also varied strongly with depth (Table 3), showing peaks at 1000-1500 m (Fig. 9B; Fig. 10B). Depth did not explain as much variation in relative eye size as it did relative head size (Table 3), but there was still a significant relationship and eye size was largest at the shallowest depths (Fig. 9C). Variation in eye size was highest at the deepest depths (Fig. 10C). The mean angle of the mouth in relation to the lateral line varied with depth but the variance explained was low (Table 3). However, the standard deviation of the mouth angle showed a highly significant pattern with depth (Table 3), with the highest variation at intermediate depths (Fig. 10D). The mean and standard deviation of the relative surface area of the mouth protrusion exhibited strong relationships with depth (Table 3) where both values were high in the shallows then decreased and remained constant from 1000-2000 m (Fig. 9E; Fig. 10E). Depth explained an intermediate amount of variation in mean relative gape size (Table 3), which showed a pattern similar to that of head size, with the highest values at the shallowest and deepest parts of the study site (Fig. 9F). The standard deviation of relative gape size showed a similar pattern with depth (Fig. 10F), but the variance explained was much higher than for mean gape size (Table 3). The mean of L_{max} increased to approximately 1000 m then remained high (Table 3; Fig. 9G). Depth explained less variation in the standard deviation of L_{max} than its mean (Table 3) but it did show a peak at around 800 m (Fig. 10G). Station mean body size, which was calculated at the individual level rather than by weighting by species abundances, increased up to 1500 m and then declined (Table 3; Fig. 9H).

Pearson's product-moment correlation coefficients are reported for all diversity metrics and traits in Table S7. Functional richness was particularly correlated with the standard deviation of the aspect ratio (R = 0.54) and the standard

Table 3. Statistics extracted from Generalised Additive Models on the relationships between trait means and trait variances in a station, and the depth of that station. e.d.f. = effective degrees of freedom; the flexibility of the fitted model (Wood, 2006). Please refer to Fig. 6 and Table 2 for calculations and definitions of traits.

Trait	**Calculation**	**F**	**e.d.f.**	**R^2**	**p**
Relative head size (cm/cm)	Mean	37.6	3.9	0.65	<0.001
	SD	33.6	3.3	0.62	<0.001
Caudal fin aspect ratio ($cm^2/cm^2/cm$)	Mean	34.7	3.8	0.63	<0.001
	SD	36.7	3.4	0.64	<0.001
Relative eye size (cm/cm)	Mean	10.5	2.3	0.28	<0.001
	SD	9.4	2.9	0.29	<0.001
Mouth angle (°)	Mean	7.3	3.7	0.28	<0.001
	SD	39.0	3.4	0.65	<0.001
Relative surface area of mouth protrusion (cm^2/cm)	Mean	46.6	3.8	0.70	<0.001
	SD	81.4	3.8	0.80	<0.001
Relative gape size (mm^2/cm)	Mean	14.9	3.9	0.42	<0.001
	SD	40.1	3.0	0.65	<0.001
L_{max} (cm)	Mean	31.8	2.5	0.56	0.004
	SD	10.7	3.5	0.34	<0.001
Individual body size (cm)	Mean	35.4	3.6	0.64	<0.001

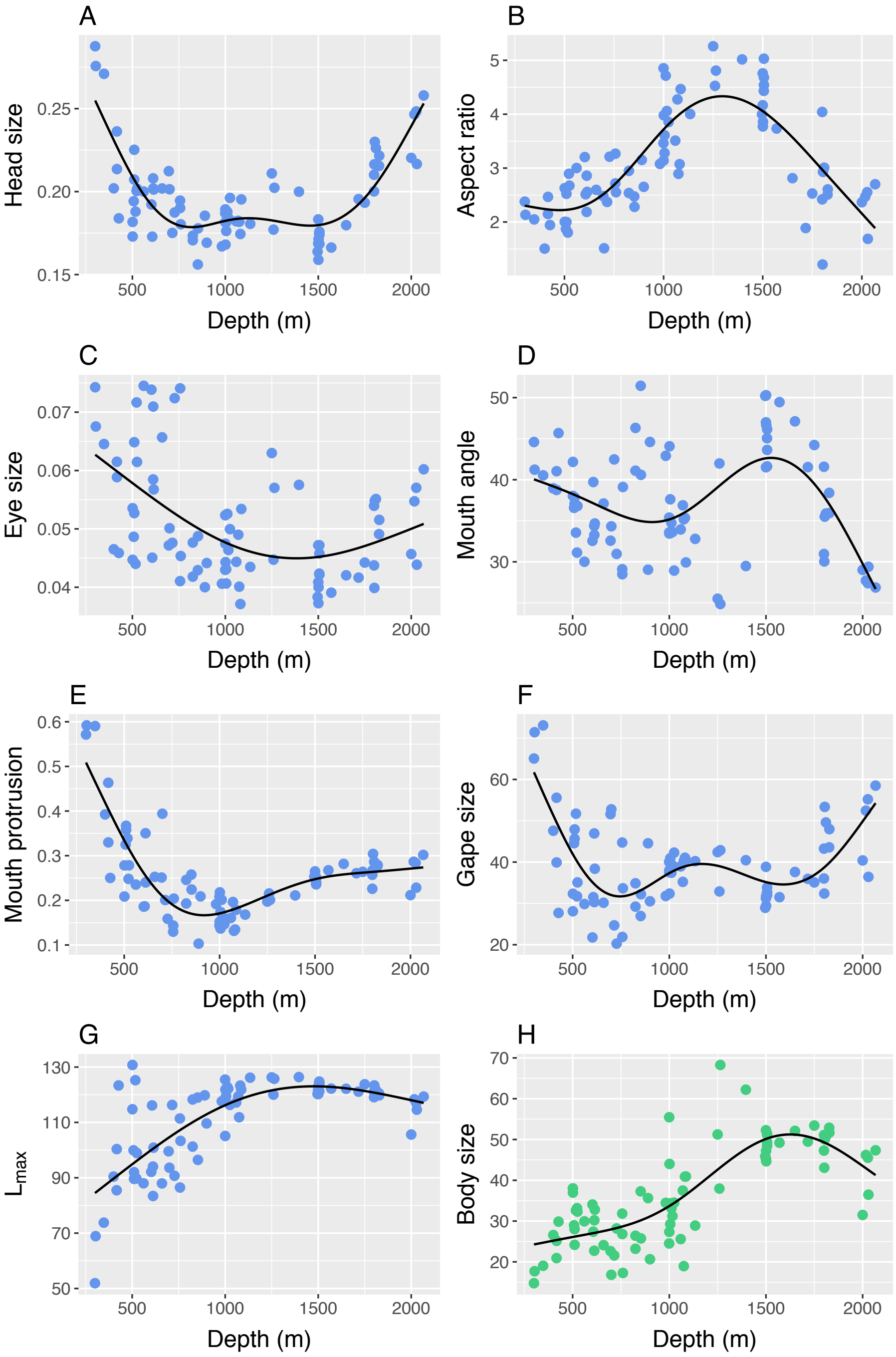

Fig. 9. The relationship between depth and the abundance-weighted station means of continuous morphological traits. Traits that were used in the calculation of functional diversity are represented by blue points and station mean body size is represented by green points. The traits were A) relative head size (cm/cm); B) caudal fin aspect ratio ($cm^2/cm^2/cm$); C) relative eye size (cm/cm); D) angle of mouth in relation to lateral line (°); E) relative surface area of mouth protrusion (cm^2/cm); F) relative gape size (mm^2/cm); G) L_{max} (cm); H) body size (cm). Please see Fig. 6 and Table 2 for definitions and calculations of traits.

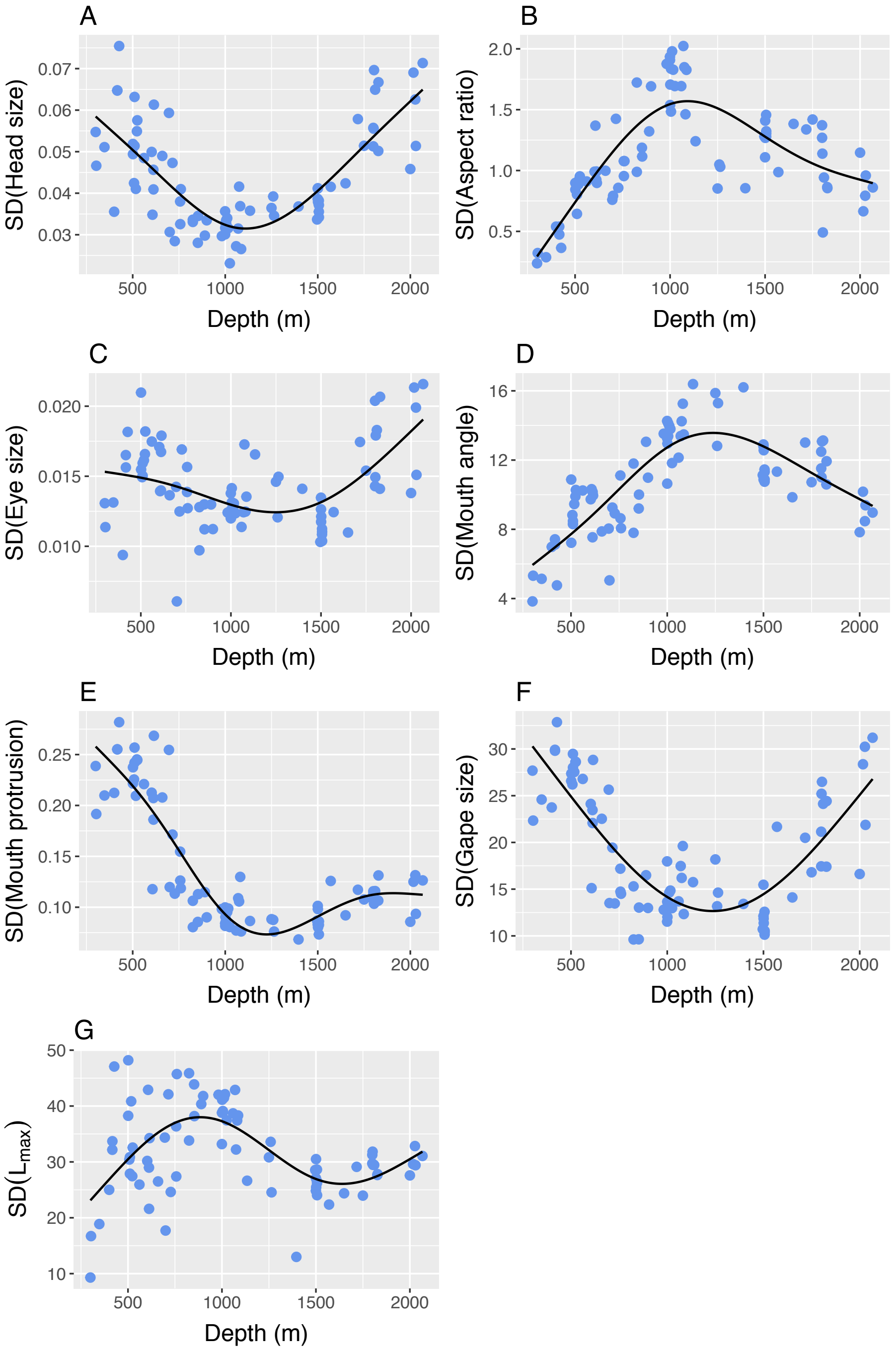

Fig. 10. The relationship between depth and the standard deviation of the continuous morphological traits used in the calculation of functional diversity. The traits were A) relative head size (cm/cm); B) caudal fin aspect ratio ($cm^2/cm^2/cm$); C) relative eye size (cm/cm); D) angle of mouth in relation to lateral line (°); E) relative surface area of mouth protrusion (cm^2/cm); F) relative gape size (mm^2/cm); G) L_{max} (cm). Please see Fig. 6 and Table 2 for definitions and calculations of traits.

deviation of the angle of mouth in relation to lateral line (R = 0.57). Functional divergence was particularly correlated with the standard deviation of the surface area of the mouth protrusion (R = 0.54), standard deviation of relative gape size (R = 0.51), and mean of the mouth protrusion (R = 0.53). Size diversity was particularly correlated with standard deviation of aspect ratio (R = 0.56), standard deviation of L_{max} (R = 0.54) and mean of L_{max} (R = 0.52). Functional richness was associated with size diversity (R = 0.42) and inversely related to functional divergence (R = -0.38).

Relative contributions of feeding guilds to total biomass changed with depth (Fig. 11). Benthic feeders were the largest component of biomass up to 700 m then declined as depth increased. The benthic feeders that were of particularly high or low trophic levels followed the same pattern, but those of a high trophic level virtually disappeared at around 1100 m. The specialised fish that feed on benthic suspension feeders lived mainly at 1300–1900 m. Generalist pelagic feeders increased with depth and dominated the biomass from 700 m, then started to decline in dominance at particularly deep depths. The high trophic level pelagic feeders were abundant only from 500–1100 m. The biomass accounted for by species for which

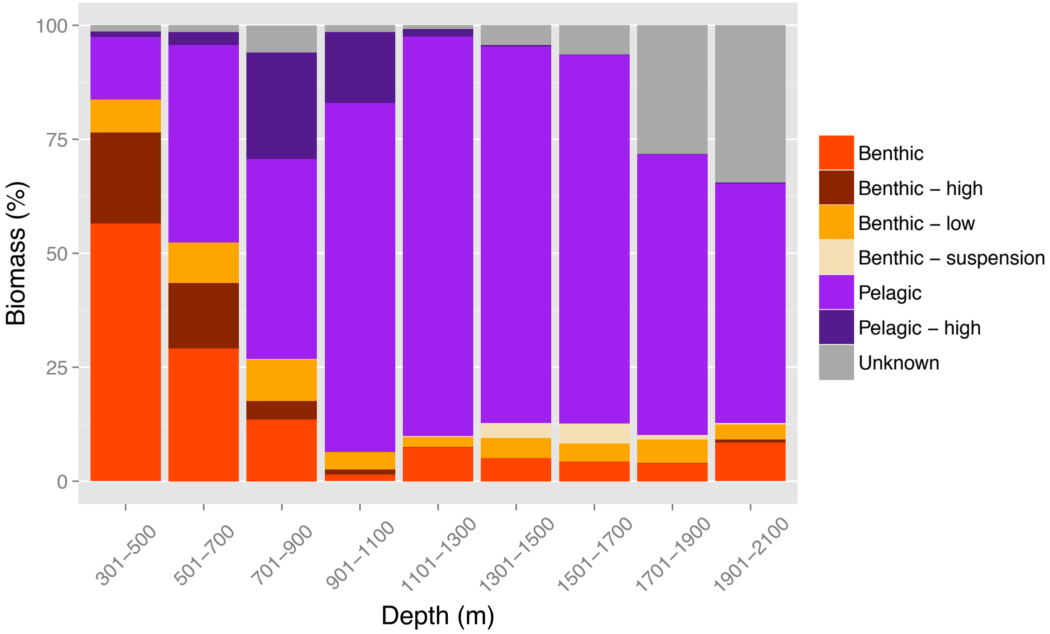

Fig. 11. Biomass accounted for by each feeding guild in 200 m depth bands, as a percentage of the biomass accounted for by species for which morphological data were known. 'Benthic' refers to species feeding in the benthic environment. If they could be assigned specifically to high or low trophic levels (see Methods for details) then they are listed as 'Benthic – high' or 'Benthic – low' accordingly. Species that feed on benthic suspension feeders exhibit a distinct isotope signature so are presented as 'Benthic – suspension'. 'Pelagic' refers to species feeding in the pelagic environment and 'Pelagic – high' represents those that could be distinguished as high trophic level.

isotopic signatures were not known increased with depth.

3.5. Discussion

The four measures of diversity examined here exhibit different patterns along a depth gradient, but all show intermediate or high values in the deepest part of the study site (Fig. 8). At the shallower end of the continental slope, functional richness, size diversity and species richness indicate low levels of diversity, but functional divergence is high. This implies that species are widely and unevenly distributed around the small amount of trait-space occupied (Fig. 7). The deepest areas exhibit similar patterns but functional richness and size diversity are higher than in the shallowest areas. Functional richness and size diversity are both highest at around 800-1000 m in depth where functional divergence is low, implying that species are evenly distributed around a wide range of trait space. The conflicting patterns of the two different measures of functional diversity have been found previously in a global analysis of reef fish communities, and it has been suggested that including the abundance of species in the calculation of functional diversity (as is the case for functional divergence, but not functional richness) is particularly important in understanding patterns (Stuart-Smith et al. 2013). The similarities between functional richness and size diversity are striking as they are calculated using completely different information: functional richness uses species-level traits that have been controlled for body size, and size diversity uses variation in individual body sizes. That they correlate highly could imply that size-based metrics capture much of the information that is conveyed by species-level functional traits. Species richness increases with depth up to 1500 m; data beyond this depth are missing due to the reduced dataset of hauls that were equal in duration not spanning the entire depth range.

The low values of functional richness, size diversity and species richness at the shallowest areas of the study site is surprising as it is often thought that diversity is higher in shallower waters where primary production is higher and there is more variation in environmental conditions (Price, Keeling & O'Callaghan 1999; Ellingsen 2002; Zintzen et al. 2011). Conversely, the deep sea has only been colonised recently in terms of geological time and there is a global decrease in species richness up to

8000 m (Priede & Froese 2013). However, alternative patterns of species richness have been postulated in the deep sea. A unimodal relationship where species richness is highest between 1000–3000 m has been found (Priede et al. 2010; Brown & Thatje 2014) and the increase in species richness seen in my study could be consistent with this pattern if depths beyond the study site were to be sampled.

The high species richness, high functional divergence, and intermediate to high values of size diversity seen in the deepest part of this study site can be explained in three ways. Firstly, biodiversity and functional diversity are influenced by the range and quality of food sources, as well as total productivity (Gambi et al. 2014), implying that even if quantity of resources is lower in the deep (Carney 2005), functional divergence could still be high if there is a heterogeneous food supply. This is consistent with the 'limiting similarity' hypothesis (MacArthur and Levins 1967) whereby high trait diversity results from interspecific competition preventing species from occupying similar niches. In contrast, the declining functional richness at depth supports the 'environmental filtering' hypothesis (Keddy 1992; Violle et al. 2007), perhaps because species share similar traits to cope with the extreme environmental conditions. Secondly, fishing in this study region mostly occurs above 1200 m in depth so the deepest fish assemblages are not harvested. Human exploitation has been known to decrease diversity (de Boer & Prins 2002; Tittensor et al. 2007; Nanola, Alino & Carpenter 2011), which may explain the high diversity in areas outside of human impacts. Fishing pressure is also likely to have supressed size diversity in the shallower areas due to its well-known impact on body sizes (Bianchi et al. 2000). Thirdly, it is hypothesised that the peak in species richness generally found at 1000–3000 m is due to a peak in speciation rates that occurs at the physiological boundary where shallow-living species became adapted to the low temperature and high pressure beyond these depths (Brown & Thatje 2014).

The patterns in functional and size diversity can also be examined within the context of the distribution of individual functional traits (Fig. 9). Body size is known to be a particularly important functional trait in marine species (Winemiller & Rose 1992; Froese & Binohlan 2000; Cohen et al. 1993; Scharf, Juanes & Rountree 2000; Jennings et al. 2001), but as most other continuous morphological traits were calculated relative to body size, their individual relationships with depth illustrate that functional traits of an assemblage are not solely determined by body size. For example, in the shallowest areas, observed body size is small while relative gape size is high. This means that for their size, the species that occupy shallower depths will have relatively larger gapes, even if this does not necessarily equate to them having the largest observed gape of all individuals in the study system.

The links between trait values and function can be observed by using stable isotope data to illustrate the relative dominance of different feeding guilds across depths (Fig. 11). Benthic feeders dominate in the shallowest areas of the slope and then drop off sharply to remain low in abundance from 900 m. This pattern mirrors that shown by the relative surface area of the mouth protrusion, which is used to suck up prey from the benthos. Similarly, the dominance of pelagic feeders at 900-1700 m (in this study: the greater argentine, *Argentina silus*; Agassiz's slickhead, *Alepocephalus agassizii*; Baird's slickhead, *Alepocephalus bairdii*; the roundnose grenadier, *Coryphaenoides rupestris*; the black scabbardfish, *Aphanopus carbo*) is mirrored by several traits. The high aspect ratios of the caudal fin at these depths equate to increased swimming capabilities and are common in species that live or feed in the pelagic ocean (Pauly 1989; Sambilay 1990). These species also have small heads and gapes in relation to their body length (Fig. 9). As they feed mainly on planktonic invertebrates (Froese & Pauly 2016), aside from the black scabbardfish, which is a top predator, it is unnecessary for them to have large mouths. The weighted mean head and gape size are highest in the shallowest and deepest areas (Fig. 9A, F), where a wider range of prey sources are utilised (Fig. 11).

Variation in traits generally mirrors the patterns seen in the means of those traits (Fig. 10), aside from relative gape size and angle of mouth in relation to lateral line, which show lower correlations between the mean and the standard deviation than in other traits (Table S7). Despite the low correlation for relative gape size, both the mean and standard deviation are highest at the shallow and deep areas of the study site. Mouth angle shows an inconclusive relationship with depth when the mean is used, but a very strong relationship when the standard deviation is used. The high variation at intermediate depths is perhaps more informative than the mean because it could be explained by the dominance of pelagic feeders in a similar way to the aforementioned traits. It may be that there is no particular mouth angle that is selected for in pelagic feeders, hence species show a wider range of angles. In comparison, the shallowest and deepest areas exhibit lower variation because a certain mouth angle is selected for in the benthic feeders in the shallows, and potentially in the unknown feeders in the deep (Fig. 11).

Depth-dependent patterns in the variation of all traits can be linked to diversity metrics, apart from relative head size and eye size, which show lower correlations with diversity (Table S7). The mean and variation in L_{max} are linked to patterns in size diversity, implying that variation in observed individual sizes is at least partially explained by the potential maximum sizes of the species present. It may therefore be possible to use this species-level measure of potential size as a proxy for variation in observed sizes in data-poor scenarios. Functional divergence is particularly associated with relative gape size and the surface area of the mouth protrusion, and aspect ratio of the caudal fin links highly with functional richness and size diversity. Higher aspect ratios have been found to associate with depth generalist species in coral reefs (Bridge et al. 2016), further highlighting this trait's role in many aspects of community assembly, and the aforementioned potential link between high aspect ratios and the dominance of pelagic feeders over a wide depth range.

The dominance of pelagic feeders at intermediate depths is mainly due to the presence of a community of Diel Vertical Migrators (DVM; Mauchline & Gordon 1991; Trueman et al. 2014), otherwise known as the deep scattering layer. This is a mesopelagic community containing fish, invertebrates and zooplankton, which has recently been found to be particularly important for global biogeochemical cycles and carbon storage in the oceans (Irigoien et al. 2014; Trueman et al. 2014). Its relative positioning could potentially explain the patterns that we see in the two measures of functional diversity examined here. At the shallow end of the continental slope (< 500 m), the DVM community is close to the seabed, so both benthic- and pelagic-feeding demersal fish are able to exploit it. This could be consistent with the low functional richness that we see in this area, if all species are occupying similar functional space in order to exploit the same resources, and the high functional divergence, because multiple species could co-exist through fine partitioning of resources in-line with the 'limiting similarity' hypothesis (MacArthur & Levins 1967). With increasing depth, the distance of the DVM community from the seabed also increases, meaning that benthic feeders are no longer able to exploit it (1000-1500 m). The dominance of pelagic-feeders here, and the related traits of those species, may therefore be caused by their competitive release. The low functional divergence seen at these depths may be due to the dominance of only a few species, all with similar traits that are adapted to feeding on pelagic prey, such as small gapes and high aspect ratio as discussed above. The co-existence of species with similar traits, exploiting similar resources, may be maintained by an assembly rule termed 'emergent neutrality' (Scheffer & van Nes 2006). This is when species aggregate in certain areas of a niche axis and has been supported by studies on marine phytoplankton (Vergnon, Dulvy & Freckleton 2009), pollinators (Fort 2014) and beetles (Scheffer et al. 2015). Beyond 1500 m, the DVM community is too far above the seabed for even the pelagic-feeding demersal fish to reach. Less is known about the feeding habits of fish species at these depths, but the high functional divergence could illustrate a high level of specialisation and exploitation of different resources among the benthic- and pelagic- feeders.

Here I have shown that there are non-linear patterns in functional and size diversity of a deep-sea demersal fish assemblage. Functional richness and size diversity are lowest at the shallowest (< 500 m) and deepest (~ 2000 m) parts of the continental slope studied; functional divergence is the opposite, with the lowest values seen at 1000-1500 m. Species richness increases linearly along the depth gradient, at least up to 1500 m. Changes in functional diversity appear to be driven by traits such as caudal fin aspect ratio and relative surface area of mouth protrusion, which can in turn be linked to the dominance of different feeding guilds along the slope. Functional richness and size diversity show similar depth-dependent patterns, despite accounting for different morphological traits. Future work could incorporate individual-level traits, rather than the species-level traits used here, and could investigate the different drivers of community assembly along the continental slope.

3.6. Supporting information

Table S5. Concatenation of hauls into stations (survey data 1998–2013).

Fig. S2. The relationships between each of the continuous trait variables included in the calculation of functional diversity.

Table S6. The species caught on the survey, their conversion factors and maximum lengths.

Table S7. The Pearson's product-moment correlation coefficient between each measure of diversity, mean trait values, and standard deviation of trait values.

4. Size-based indicators show depth-dependent recovery from fishing pressure in the deep sea

4.1. Abstract

Size-based indicators are well established as a management tool in coastal seas as they respond to changes in fishing pressure and describe important aspects of community function. However, they have not yet been applied to the deep sea with the same rigour, despite the increasing exploitation pressure on this ecosystem. I use data from a deep-water bottom trawl survey in the Northeast Atlantic, at depths of 300–2000 m, to test whether size-based indicators show recovery from exploitation over a 16-year period during which fishing pressure has decreased. I apply five indicators to these data: mean body length, mean maximum length, Large Fish Indicator, slope of the biomass spectrum, and fractional size. Patterns were analysed within four different depth bands. The Large Fish Indicator, slope of the biomass spectrum and fractional size showed positive change over time, suggesting recovery from fishing pressure. This response was generally most apparent in the shallowest depth band, where most fishing activity has been distributed. Values of the Large Fish Indicator were much higher overall than in coastal seas, so the same reference points cannot be applied to all marine ecosystems. These findings imply that size-based indicators can be applied to the deep sea with the same efficacy as in coastal waters, and that deep-sea fish assemblages are able to recover from fishing pressure in the medium-term.

4.2. Introduction

The deep sea is the largest ecosystem on the planet (Ramirez-Llodra et al. 2011), but due to its inaccessibility, we have known very little about it until recent decades. However, as our exploitation of the deep sea increases, due to activities such as fishing (Morato et al. 2006) and mining for minerals (Ramirez-Llodra et al. 2011), it is becoming more important that we understand how the ecosystem is responding to human pressures and how to manage these pressures. The relatively recent start to deep-sea exploitation gives us an opportunity to better monitor ecosystem changes than is possible in heavily exploited coastal waters, and to manage fisheries accordingly, before they become unsustainable.

One way to monitor these changes in fish communities is to use size-based indicators. These indicators represent the health of communities by summarising their size structure. Body size is particularly relevant when examining impacts of fishing for two main reasons. Firstly, fishing is size-selective, meaning that it is likely to produce a change in size structure by removing large individuals from the system (Bianchi et al. 2000). Secondly, these changes are important for understanding how fishing impacts ecosystem structure and because of the role that body size plays in virtually all aspects of a fish's life: namely trophic level (Jennings et al. 2001), diet breadth and choice (Scharf, Juanes & Rountree 2000), maturity and fecundity (Winemiller & Rose 1992), growth (Jobling 1983) and survival (Pauly 1980). The use of size-based indicators is well established in coastal waters and they are used to compute reference values to monitor impact and recovery of fishing in areas such as the North Sea (e.g. Jennings & Dulvy 2005; Greenstreet et al. 2011) and the Celtic Sea (e.g. Blanchard et al. 2005a; Shephard et al. 2013). However, this same success has not yet been translated to the deep sea. Deep-sea species are still poorly known, prohibiting the use of indicators based on life history or ecological traits, but as deep-sea research increases, body size data are becoming more available, allowing the application of size-based indicators to deep-sea fish for the first time.

The continental slope of the Rockall Trough in the Northeast Atlantic provides an excellent study site to examine the effect of fishing pressure in the deep sea (300–2067 m) using size-based indicators. Fishing pressure has been decreasing in the area since the early 2000s due to the introduction and subsequent decline of

Total Allowable Catches (TACs). The area has been monitored during this time period of decreasing fishing pressure by Marine Scotland's deep-water trawl survey, allowing the use of size-based indicators to establish whether these deep-sea stocks have been able to recover from fishing pressure in the medium-term.

In order to fully understand any changes that occur in this study site, we must also account for the depth of the assemblages. Due to the large environmental differences between sites of different depths (namely water pressure, temperature and oxygen levels; Lalli & Parsons 1993; Kaiser et al. 2011), species composition changes across depths (e.g. Gordon & Bergstad 1992; Carney 2005; Yeh & Drazen 2009) as does body size (e.g. Polloni et al. 1979; Macpherson & Duarte 1991; Collins et al. 2005; Mindel et al. 2016). Additionally, fishing pressure in the area only occurs at depths up to 1200 m, although it has been found that the effects of fishing can propagate deeper than the areas fished (Bailey et al. 2009). Thus, effects may be masked if depths are not analysed separately.

In this study I use five indicators, including four that are well-established in shallow seas: 1) mean body length, 2) mean maximum length, 3) Large Fish Indicator, 4) slope of the normalised biomass spectrum; and one experimental indicator: 5) fractional size. Mean body length illustrates the average observed size of individuals and decreases as increasing fishing pressure removes large individuals (Shin et al. 2005). Mean maximum length gives an alternative perspective on body size by calculating an average based on the largest individuals caught at a site, in order to not be unduly influenced by abundant, small individuals, and is also expected to decrease as fishing pressure increases (Shin et al. 2005). The Large Fish Indicator is calculated as the proportion of biomass at a site that is made up of individuals over 40 cm in length (Greenstreet et al. 2011; Fung et al. 2012; ICES 2013). This indicator was developed due to the importance of large individuals in marine assemblages and high values indicate a healthy system. The normalised biomass spectrum is important in the marine environment because it symbolises how all individuals are arranged along a size axis (Sheldon, Prakash & Sutcliffe 1972). The slope of the descending right-hand side of the spectrum becomes steeper under fishing pressure because large individuals are removed (Bianchi et al. 2000; Blanchard et al. 2005a). Fractional size is a recently developed metric (Mindel et al. 2016) that is calculated by dividing individual body size by the potential maximum size of that species (L_{max}). It illustrates how far along an individual is in the growth trajectory of that species, and could be a proxy for age and maturity. It has been found to exhibit a particularly strong relationship with depth in the deep sea (Mindel et al. 2016) and is predicted to be negatively impacted by fishing pressure, as is the case for the established size-based indicators.

I analyse trends in these five indicators over time from 1998–2013 in each of four depth bands. I test the hypothesis that all five indicators show recovery from fishing pressure (i.e. an increase in the values of the indicators) due to decreasing levels of exploitation throughout the study period. I predict that the two shallower depth bands show the biggest change, as these are the depths at which fishing occurs. I aim to test the efficacy of fractional size as a new indicator.

4.3. Materials & methods

4.3.1. Data

A deep-water bottom trawl survey was conducted by Marine Scotland's *MRV Scotia* in September 1998, 2000, 2002, 2004–2009 and 2011–2013 along the continental slope of the Rockall Trough in the Northeast Atlantic (Fig. 12; ICES area VIa, latitude 55° to 59°N, longitude approximately 9°W) at depths of 300–2067m (Neat & Burns 2010). The gear was adapted to sampling demersal fish (those that live on or around the seabed, including those classified as benthopelagic) so mesopelagic fish (those that live in the water column) and invertebrates were excluded from the analysis. Sea bottom temperature was recorded on the survey at the depth of the haul from 2005 onwards, for 205/325 hauls.

During the survey, catch was identified to the finest taxonomic resolution possible (which was species level for 99.9% individuals caught) and the lengths of individual fish were measured. Where applicable, standard length, pre-anal fin length or pre-supra caudal fin length were converted to total length (ICES 2012) using conversion factors calculated from a subset of the survey data (Table S6). Species-specific conversion factors established from survey data were also used to convert lengths to weights in order to calculate the indicators that are based on biomass. The full taxonomy of species was determined using the World Register of Marine Species (WoRMS Editorial Board 2013).

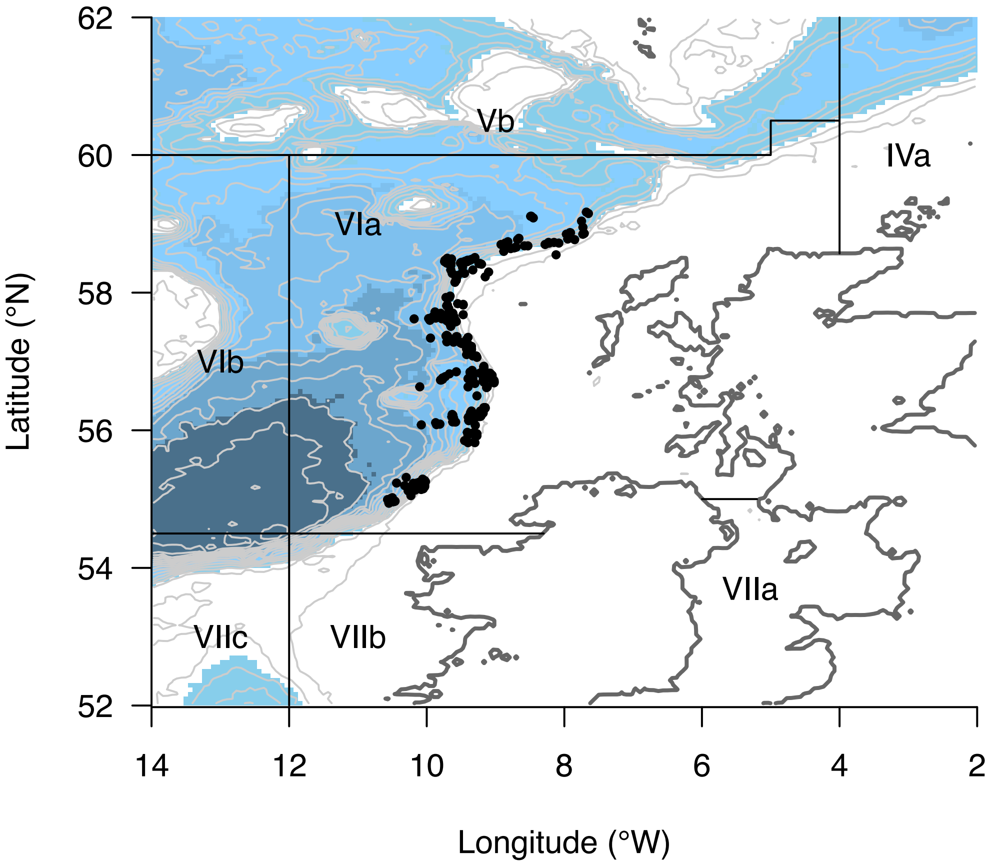

Fig. 12. Location of hauls of the Marine Scotland deep-water bottom trawl survey in the Northeast Atlantic from 1998-2013. Coloured shading indicates depth, with white being the shallowest areas and dark blue representing the deepest areas. Labelled sections represent ICES statistical areas.

Depth-specific trends were analysed by separating hauls into four depth bands: Shallow (S) = ≤ 750 m (minimum depth = 300 m); Medium (M) = 751–1200 m; Deep (D) = 1201–1650 m; Very deep (V) = > 1650 m (maximum depth = 2067m). There is a consistent increase over time in the number of hauls taken in the deepest depth band (Table 4) so the results from this depth band are interpreted with caution.

The Scientific, Technical and Economic Committee for Fisheries (STECF 2013) reported on fishing effort in the deep sea of ICES area VI by ICES (International Council for the Exploration of the Sea) member states. As these data are not depth-resolved, I only use them for illustrative purposes, rather than to quantify the impact of fishing. Here I present bottom trawl effort data, in order to focus on demersal fish, from the EU waters of ICES area VI, which equates to area

Table 4. Number of hauls taken in each year of the survey from each depth band.

Year	≤ 750 m	751-1200 m	1201-1650 m	> 1650 m
1998	10	9	0	0
2000	13	11	9	0
2002	15	8	7	1
2004	12	8	5	1
2005	5	8	5	1
2006	11	10	7	1
2007	6	6	6	1
2008	8	9	8	3
2009	8	16	7	4
2011	7	6	9	4
2012	7	8	8	6
2013	7	8	8	8
Total	**109**	**107**	**79**	**30**

VIa (Fig. 12). I exclude 2002 as recommended in the report due to the unreliability of that year's data (STECF 2013).

4.3.2. Indicators

Due to the unreliability of catching very small individuals on the survey, all individuals of ≤ 32g were excluded from the calculation of indicators. This value was suggested by Jennings & Dulvy (2005) as a potentially optimal cut-off point, and from examination of the data used in the present study, it captures the sizes of fish that are consistently caught by the Marine Scotland survey.

Mean body length of the community was the mean total length across all individuals caught in a haul.

Mean maximum length of the community was calculated by assigning each individual the largest length of its species in that haul, and averaging this across individuals. In other words, the maximum length of a species per haul was averaged across species, weighting by species abundances.

The Large Fish Indicator (LFI) was calculated as the proportion by weight of individuals greater than 40 cm in length per haul (ICES 2013).

The slope of the size spectrum was calculated using a normalised biomass spectrum (Platt & Denman 1977). This was calculated for each combination of year and depth band, rather than for each haul, as hauls did not represent enough data to create a reliable biomass spectrum. Individuals were separated into weight classes that were of equal widths on a $\log_2$ scale. Biomass caught per hour of trawling in each weight class was summed across hauls within each year and depth band. These values of biomass were divided by the width of the weight class to give an estimate of the abundance density of organisms in each weight class (Platt & Denman 1977). The slope of the normalised size spectrum was then derived from the relationship between $\log_{10}$ of the mid-point of the weight class versus $\log_{10}$ of the normalised biomass in that weight class, for each year and depth band combination. The slope was established by fitting a linear regression to the descending section of the relationship (Blanchard et al. 2005a), which was judged to start from the weight class 2^5–2^6g.

Fractional size was the observed length of an individual divided by its potential maximum size (Mindel et al. 2016). Potential maximum size, or L_{max}, was set as the maximum length listed on FishBase for that species (Froese & Pauly 2016), or the maximum length recorded on the deep-water trawl survey, whichever was the greater (Table S6). This approach was chosen so that L_{max} consistently equates to the largest known length for that species (Mindel et al. 2016). Fractional size of the assemblage was calculated as the mean fractional size across species in a haul, weighted by the fourth root of the biomass of that species (Mindel et al. 2016). This transformation was chosen in order to down-weight the influence of abundant species, as is common in biomass data (Clarke & Warwick 2001; Wilding & Nickell 2013; Rutterford et al. 2015).

4.3.3. Analysis

General linear models (LM) were fitted to the relationships between indicator values and year, including the interaction between time and depth band. For mean body length, mean maximum length, LFI and fractional size, the haul was the unit of analysis. For the slope of the size spectrum, the unit of analysis was year. Post-hoc multiple comparison Tukey tests were performed for the indicators without significant interactions using the R package (R Core Team 2015) *multcomp* (Hothorn, Bretz & Westfall 2008). The relationship between sea bottom temperature and year was analysed for each depth band using general linear models. All analyses were performed using R version 3.2.3 (R Core Team 2015); figures were produced using the packages *ggplot2* (Wickham 2009), *gridExtra* (Auguie 2016) and *marmap* (Pante & Simon-Bouhet 2013).

4.4. Results

For mean body length in the community, there was no interaction between year and depth band (ANOVA: F = 1.3, p = 0.29) so the model was fitted without the interaction, and this model had high explanatory power (LM: F = 74, d.f. = 4, 320, R^2 = 0.47). There was no significant change in mean body length over time, but the trend was increasing (Fig. 13A; LM: b = 0.13, S.E. = 0.092, p = 0.17). There were significant differences in mean body length between depth bands: Shallow (S) differed from all other depth bands and Medium (M) and Deep (D) differed from each other (Fig. 13A; Table 5).

For mean maximum length in the community, there was no interaction between year and depth band (ANOVA: F = 2.0, p = 0.12) so the model was fitted without the interaction, and this model had high explanatory power (LM: F = 168, d.f. = 4, 320, R^2 = 0.67). There was no significant change in mean maximum length

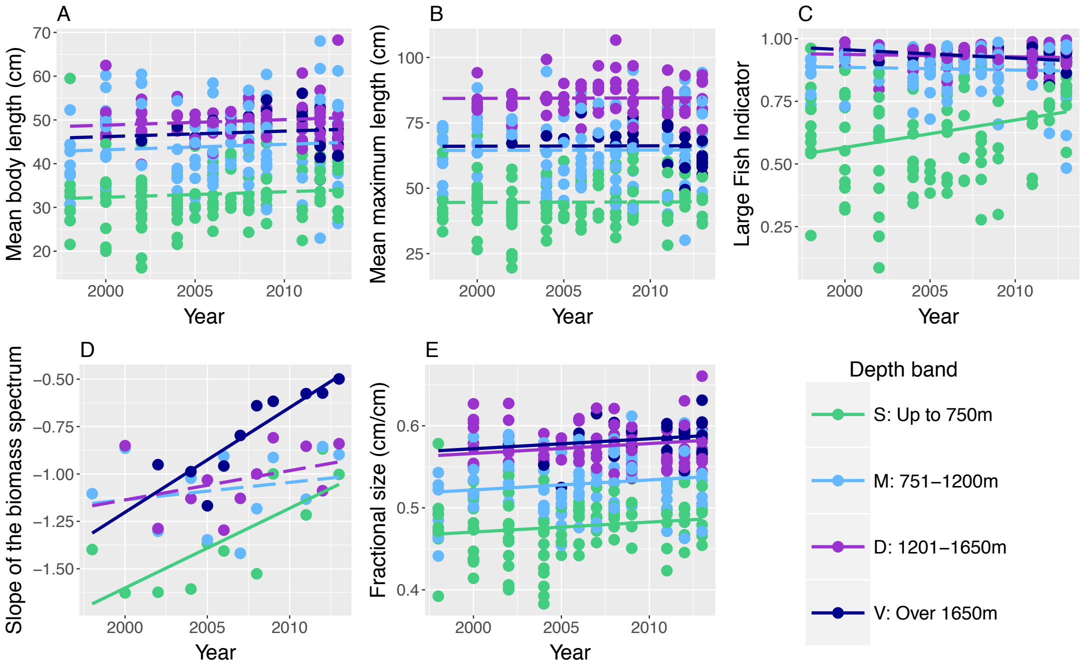

Fig. 13. Change over time in the indicators A) mean body length, B) mean maximum length, C) Large Fish Indicator, D) slope of the normalised biomass spectrum and E) fractional size, in each of four depth bands. Lines represent the fitted general linear model; significant changes over time are depicted as solid lines, non-significant relationships are dotted lines.

Table 5. Statistical results of post-hoc multiple comparison Tukey tests for indicators not found to have a significant interaction. Estimates represent the differences in intercept between depth bands. Models were implemented using the R package *multcomp* (Hothorn, Bretz & Westfall 2008). S = shallow, up to 750 m; M = medium, 751–1200 m; D = deep, 1201–1650 m; V = very deep, over 1650 m.

Indicator	Depth bands	Estimate	Standard error	p value
Mean body length	S-M	10.9	1.0	< 0.001
	S-D	16.5	1.1	< 0.001
	S-V	13.9	1.5	< 0.001
	M-D	5.6	1.1	< 0.001
	M-V	3.0	1.5	0.19
	D-V	-2.6	1.5	0.32
Mean maximum length	S-M	19.9	1.4	< 0.001
	S-D	39.8	1.6	< 0.001
	S-V	21.5	2.3	< 0.001
	M-D	19.9	1.6	< 0.001
	M-V	1.6	2.2	0.89
	D-V	-18.3	2.3	< 0.001
Fractional size	S-M	0.051	0.0044	< 0.001
	S-D	0.096	0.0048	< 0.001
	S-V	0.102	0.0070	< 0.001
	M-D	0.044	0.0048	< 0.001
	M-V	0.050	0.0069	< 0.001
	D-V	0.006	0.0070	0.84

over time (Fig. 13B; LM: b = 0.016, S.E. = 0.14, p = 0.91). Overall mean maximum length differed significantly between all depth bands apart from M and Very deep (V) (Fig. 13B; Table 5).

For the Large Fish Indicator, there was a significant effect of year (ANOVA: F = 34, $p < 0.001$), depth band (ANOVA: F = 110, $p < 0.001$), and their interaction (ANOVA: F = 4.3, p = 0.005), and the model had high explanatory power (LM: F = 54, d.f. = 7, 317, $R^2 = 0.53$). The LFI increased over time in depth band S (Fig. 13C; LM: b = 0.011, S.E. = 0.0027, $p < 0.001$), but did not change over time in any of the other depth bands (Fig. 13C; LM: M: b = -0.0011, S.E. = 0.0038; D: b = -0.001, S.E. = 0.0044; V: b = -0.0031, S.E. = 0.0082).

For the slope of the biomass spectrum, the interaction between year and depth band was very close to significant at the 5% confidence threshold (ANOVA: F = 2.7, p = 0.058), so it was decided that the interaction should remain in the model in order to retain as much information as possible, and it had good explanatory power (LM: F = 12, d.f. = 7, 37, $R^2 = 0.64$). There was a significant effect of year (ANOVA: F = 29, $p < 0.001$) and depth band (ANOVA: F = 16, $p < 0.001$) on the slope of the biomass spectrum. The slope increased significantly over time (in other words, became less negative, so the biomass spectrum became more shallow) in depth band S and V, but did not change over time in depth bands M and D (Fig. 13D; LM: S: b = 0.042, S.E. = 0.011, $p < 0.001$; M: b = 0.0092, S.E. = 0.016; D: b = 0.015, S.E. = 0.017; V: b = 0.055, S.E. = 0.02).

For fractional size, there was no interaction between year and depth band (ANOVA: F = 2.1, p = 0.1) so the model was fitted without the interaction, and the new model had good explanatory power (LM: F = 135, d.f. = 4, 320, $R^2 = 0.62$). There was a significant increase in fractional size over time (Fig. 13E; LM: b = 0.0012, S.E. = 0.00042, p = 0.004), and as there was no significant interaction, this increase was the same in all depth bands. There were significant differences in overall fractional size among depth bands, apart from between D and V (Fig. 13E; Table 5).

There was no significant change in sea bottom temperature from 2005 onwards for any depth band, though in the shallowest depth band there was a minor increasing trend (Fig. 14; LM: S: b = 0.041, S.E. = 0.022, p = 0.06; M: b = -0.019, S.E. = 0.045, p = 0.67; D: b = 0.023, S.E. = 0.016, p = 0.15; V: b = -0.0065, S.E. = 0.01, p = 0.54).

Bottom trawling effort according to STECF (2013) has decreased over the study period (Fig. 15).

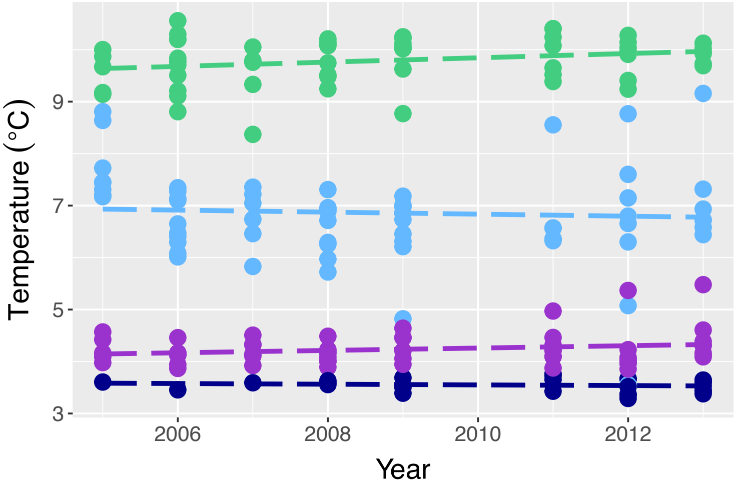

Fig. 14. Temperature of hauls from the period 2005–2013 in the four depth bands used throughout the manuscript: S (green) ≤ 750 m; M (light blue) 751–1200 m; D (purple) 1201–1650 m; V (dark blue) > 1650 m. None of the relationships over time were significant.

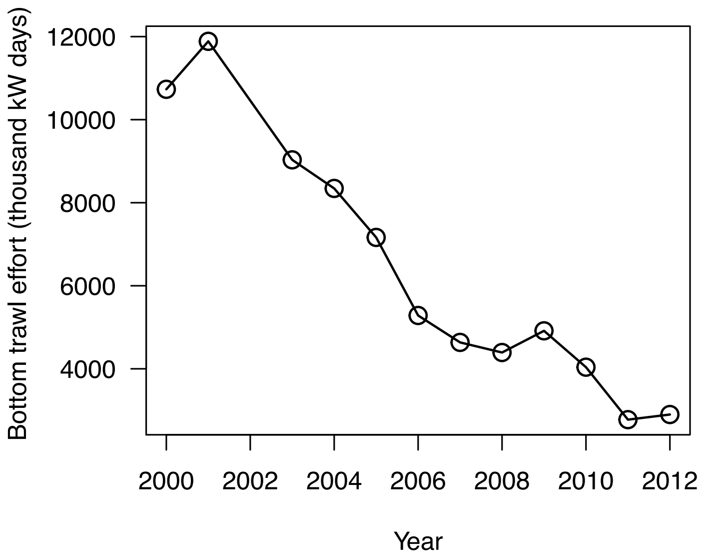

Fig. 15. Bottom trawl effort in the deep sea of ICES area VIa by ICES member states from 2000–2012, as reported by STECF (2013).

4.5. Discussion

Out of the five size-based indicators examined here, three (LFI, slope of the biomass spectrum and fractional size) show change over time in the demersal fish community of the Rockall Trough. All of the significant trends are positive, indicating recovery. Depth has an impact on the values of size-based indicators, and of the three indicators that show significant relationships, the pattern over time in two of them (LFI and slope of the biomass spectrum) varies with depth.

The indicator that shows the most striking pattern is the Large Fish Indicator. There is a significant increase over time in the LFI in depth band S (≤ 750 m), but not in any other depth band. The values of the LFI in the shallowest depth band were much lower than in any other depth band at the start of the study period, but by the most recent year surveyed, the values were approaching those in the other depth bands. This implies that in depth band S, the fish assemblages are recovering due to the relaxed fishing pressure in recent years, while in the deeper depths, the assemblages were not originally as impacted by fishing as were the other depth bands, as fishing pressure is likely to be at its highest levels at the shallowest end of the study site.

Similarly, the slope of the biomass spectrum increases (i.e. the slope becomes shallower) in depth band S, but not in depth bands M (751–1200 m) or D (1201–1650 m). In depth band V (> 1650 m) there is also an increase in the slope over time, however this must be interpreted with caution as sampling effort at those depths has increased markedly over time. Thus, the main conclusions that can be drawn are similar to those seen in the LFI, and the size spectrum has been recovering from relaxed fishing pressure in the shallowest depth band. This is because as fishing pressure decreases, individuals are able to grow larger and the bias towards highly abundant small individuals decreases, resulting in a shallower slope of the size spectrum (Nicholson & Jennings 2004; Piet & Jennings 2005; Blanchard et al. 2005a; Blanchard et al. 2009). As fishing pressure goes as deep as 1200 m in the area, the lack of response in depth band M is likely to be because assemblages therein are slower to recover from fishing pressure than in depth band S. However in the Deep depth band, where there is little or no fishing pressure, the lack of change implies that they were not impacted by exploitation, despite there being the potential for fishing effects to propagate through depths (Bailey et al. 2009).

Fractional size is the only indicator to show a significant change over time in all depth bands. This is the first time that fractional size has been used as an indicator, and these results imply that it can successfully capture recovery of an assemblage. The increase in fractional size in response to fishing pressure occurs because as exploitation decreases, fish are able to grow for longer, allowing them to reach nearer their potential maximum size. This indicates a healthier system because as individuals get closer to their L_{max}, their fecundity and likelihood of being mature increases (Froese & Binohlan 2000). Fractional size captures intra- and interspecific variation in body size (Mindel et al. 2016), which may be why it responds faster to relaxed fishing pressure than does mean body length. By including species-level traits and weighting species by their fourth root-transformed biomass, fractional size accounts for information about species without being unduly influenced by a small number of highly abundant species. Even disregarding the patterns seen in the deepest depth band due to increasing sampling effort over time at those depths, fractional size shows a significant increase in depth bands M and D, unlike the relationships seen in the LFI or the slope of the biomass spectrum. Even if fishing pressure is lower or non-existent in depth bands M and D, it may have still had an impact on those assemblages due to the effects propagating to deeper waters (Bailey et al. 2009). The increase in fractional size could suggest that this indicator is able to capture the recovery of these assemblages earlier than the other indicators, which do not show significant relationships in these depth bands. Alternatively, fractional size may be capturing other changes in assemblages, such as shifting species composition, because it is able to capture both intra- and interspecific information.

Mean body length, on the other hand, may not be responding to relaxed fishing pressure because it is highly influenced by large numbers of small individuals (Shin et al. 2005). If decreased exploitation has led to higher recruitment success, then this could manifest itself as an influx of small individuals, hence causing mean body length to remain low (Shin et al. 2005; Houle et al. 2012). Mean maximum length also does not show a change in response to relaxed fishing pressure. It may be that the timescale considered in this study is not long enough for these indicators to show a response (Nicholson & Jennings 2004).

The recovery of size-based indicators in the Rockall Trough can be qualitatively related to the decreasing fishing pressure as reported by the Scientific, Technical and Economic Committee for Fisheries (STECF 2013). However, these fishing effort data are not thorough enough to be used to quantify the impact of fishing. The first main issue with fishing effort data is that they are not depth-resolved. Thus, the different patterns within different depth bands cannot as yet be fully ascribed to either varying fishing pressures in the depth bands, or varying patterns of recovery. Additionally, although the area included by STECF (2013) and the present study site overlap, I cannot know the precise effort at the Rockall Trough only. I must also use the report's definition of deep-sea species and which fishing fleets have provided data for that report (STECF 2013).

Despite the issues with the fishing effort data, I can assume with some confidence that the change in size-based indicators over time is due to this relaxed fishing pressure. I am able to rule out the effect of temperature over the timescale of this study, as there was no change over time in temperature for any of the depth bands. However, it should be noted that over a longer timescale (1975–2013), temperature and salinity have increased over time in upper waters (30–800 m) and stayed roughly constant in Labrador Sea Water (> 1200 m) in the Rockall Trough (Holliday et al. 2015). These water masses cannot necessarily be translated directly onto the depth bands used here, and do not always equate to sea bottom temperature, so it would be unwise to interpret the alternative patterns in different depth bands using this information alone. However, it is important to recognise that long-term environmental changes could be impacting overall indicator values, because temperature affects body size (e.g. Angilletta, Steury & Sears 2004). This impact must be considered when interpreting baseline, historical or expected values of indicators, because it may be that even if an ecosystem has recovered from fishing pressure, its indicator values are lower overall due to an increase in temperature favouring smaller species and individuals (Genner et al. 2010).

For all of the indicators used here, only individuals above a predicted weight of 32 g were included. This is in order to exclude small individuals that are caught unreliably by the survey gear and the value was chosen based on recommendations by Jennings & Dulvy (2005). As this limit was applied consistently in all of the analyses used here, I do not believe that it can be affecting the trends shown. However, discrepancies could arise when comparing specific indicator values among studies that do not use the same methods. This is one of the reasons why it has been suggested that 'reference directions' (suggested trends that indicators will show in response to recovery) rather than 'reference points' (suggested values of indicators in healthy assemblages) are more suitable for use in fisheries management (Jennings & Dulvy 2005; Shin et al. 2005). Reference directions are expected to be consistent across surveys, areas, and different marine ecosystems, while reference points are much harder to establish (Shin et al. 2005). This issue is illustrated here, as the values of the LFI seen in the deep sea, even before fishing pressure started to reduce, are extremely high in comparison to the value of 0.3 that has been suggested to equate to a healthy ecosystem in the North Sea (ICES 2007; Greenstreet et al. 2011). The high values in the deep, even in the depth band ≤ 750 m, show that there are more large fish in proportion to small fish in the deep sea than in coastal waters. One reason for this may be that some fish species spawn in shallow waters and move deeper as they grow (Lin et al. 2012; Trueman, Rickaby & Shephard 2013). Additionally, the value of a healthy LFI for the North Sea was set as 0.3 using data from the 1920s–1980s (ICES 2007), a time period in which coastal seas were already being exploited. Thus, it may be that in the deep sea we are able to see true pre-exploitation values of the LFI, a feat that has not been possible in shallower waters. It is clearly then wrong to use the same reference point for all marine ecosystems, whereas reference directions would perform in the same way in response to the same pressures on a global scale. In order to produce values in the deep-sea assemblages studied here similar to the coastal reference point of 0.3, the calculation of the LFI would need to be changed to the proportion of fish at least over 60 cm in length (Fig. S3). If this alternative calculation is used, the overall patterns remain the same: recovery is shown in the shallowest depth band and all other depth bands show no change (Fig. S3).

The slope of the biomass spectrum also suggests that the expected values for coastal seas cannot be applied to the deep sea. In recent years, the three shallowest depth bands show slopes of around -1, which is in the range of what is expected for coastal size spectra (Blanchard et al. 2005a; Jennings & Dulvy 2005). However, in the deepest depth band, during the most recent years when data collection for these depths was at its highest, the slope approaches values of -0.5. It may be that over a longer time period the other three depth bands also reach this value, indicating a particularly healthy size spectrum. Alternatively, depth bands could naturally differ in the shapes of their size spectra, regardless of fishing, and indeed it has been shown that functional differences within communities result in different values for the slope of the spectrum (Blanchard et al. 2009).

My results suggest that relaxed fishing pressure in the deep sea of the Rockall Trough has allowed assemblages to recover, as shown by positive responses of the Large Fish Indicator, slope of the biomass spectrum, and a new indicator known as fractional size, and that the recovery is most apparent at the shallowest depths. Mean body length and mean maximum length did not show signs of recovery, perhaps because they do not respond to changes in fish assemblages over medium timescales, or because they are unduly influenced by recruitment events that keep body size values low. I suggest that size-based indicators can be applied to the deep sea with the same success that they have achieved in coastal waters, but that the same reference points cannot be used for these different ecosystems. Depth must also be accounted for when analysing trends in the deep sea. It is encouraging that even in the medium-term, deep-sea fish assemblages show positive signs of recovery, implying that they may be more resilient than previously thought (Koslow et al. 2000; Norse et al. 2012), which is just one of many paradigms that are now being questioned in the deep sea (Drazen & Haedrich 2012; Danovaro, Snelgrove & Tyler 2014). Future work is needed to establish historical baselines in the deep sea, which could then be related to long-term environmental changes such as those seen in data collected from the Extended Ellett Line in the Northeast Atlantic (Holliday et al. 2015). Non-size-based indicators such as mean trophic level, biodiversity indicators and those based on life histories, should also be applied to the deep sea where there is sufficient information on the relevant traits of these poorly known species.

4.6. Supporting information

Table S6. The species caught on the survey, their conversion factors and maximum lengths.

Fig. S3. Large Fish Indicator calculated as the proportion of fish over 60 cm in length (LFI60).

5. Abundance—occupancy relationships based on spatial and depth distribution in deep-sea fish

5.1. Abstract

Abundance–occupancy relationships are one of the most robust general rules of ecology, whereby increasing local abundance accompanies increasing regional occupancy, both across and within species. Here, I examine inter- and intraspecific abundance–occupancy relationships in deep-sea fish and expand on this macroecological pattern by applying occupancy to depth ranges to produce what I call the bathymetric abundance–occupancy relationship. I use data from a deep-water bottom trawl survey in the Northeast Atlantic, from 1998–2014, at depths of 300–2000 m. I find that the positive relationship between abundance and occupancy across species holds for deep-sea fish when occupancy is calculated based on both spatial and depth distribution. The form and strength of the interspecific abundance–occupancy relationship remained constant over time despite relaxed fishing pressure in the area. Intraspecific abundance–occupancy relationships were mostly positive when occupancy was calculated based on both space and depth, though few species exhibited significant relationships. Deeper-living species were more likely to have positive abundance–occupancy relationships, potentially making them more vulnerable to environmental or anthropogenic change. I have shown that the abundance–occupancy relationship remains positive in the under-studied deep sea, hence increasing its generality across a variety of ecosystems and over a time period of decreasing exploitation. I argue that depth distributions should not be ignored in the three-dimensional marine environment, as species that have a high local abundance and wide spatial distribution will also occupy a wider range of depths, adding another layer to this macroecological principle.

5.2. Introduction

Understanding the abundance and distribution of species has always been important in ecology, but in this time of rapid environmental change, there is increased focus on being able to predict how these ecological attributes will respond to human exploitation or climate change (Møller 2013; Poloczanska et al. 2013). Predictions of this nature are inherently difficult to make, especially when trying to generalise across taxa. However, one macroecological pattern that appears to hold across many different species and ecosystems is the positive relationship between local abundance and regional occupancy (Gaston, Blackburn & Lawton 1997; Gaston et al. 2000; Blackburn, Cassey & Gaston 2006). This can be analysed both across and within species. The interspecific abundance–occupancy relationship (AOR) tests whether species that are locally more abundant also tend to be regionally more widespread. In contrast, intraspecific AORs usually represent temporal trends in individual species, documenting whether species tend to be more widespread in years in which they are also more abundant locally.

Both of these classes of AOR have potential implications for conservation and monitoring of populations (Lawton 1993; Gaston 1999). For example, presence-absence data are often easier to obtain than abundance data, so consistently positive AORs could allow for a prediction of abundance based on a species' occupancy (Gaston 1999). Additionally, the positive interspecific relationship between abundance and occupancy implies that there are sets of species that are both abundant and widespread, and sets of species that are the opposite. Having low abundance and a small geographical range results in potential "double jeopardy" where the species could be easily wiped out from its narrow range, with no potential colonisers in the region to replace the local losses (Lawton 1993, 1996; Gaston 1999). The same is true for positive intraspecific AORs: if a species contracts its range due to environmental or anthropogenic pressure, this tends to result in a reduced mean density at the remaining sites that it occupies. This means that the decline in abundance is of a higher magnitude than would be expected merely from the loss of individuals that would occur when certain sites become unoccupied, and that extinction risk increases both from the loss of abundance and the reduced range size (Gaston et al. 2000; Freckleton et al. 2005).

Abundance–occupancy relationships can also illustrate temporal trends in pressures on assemblages, though patterns are not consistent. For fish, the strength of the correlation between abundance and distribution increased over three decades due to exploitation (Fisher & Frank 2004). However for birds, the correlation decreased, with farmland birds showing a decrease in slope of the AOR, and woodland birds an increase in slope, throughout a time of habitat alteration (Webb, Noble & Freckleton 2007). These differences in dynamics could be due to how individual species respond to changes in their environment or in what way environmental change occurs (Fisher & Frank 2004; Webb, Noble & Freckleton 2007; Fisher, Frank & Leggett 2010).

To my knowledge, only one study has described AORs in the deep sea, which mainly focused on modelling the effects of fishing on the relationship (Trenkel et al. 2013). It only reported on the empirical AOR in four species, none of which showed significant relationships (Trenkel et al. 2013), so an interspecific analysis and large-scale implementation of intraspecific AORs are still required for deep-sea fish. Study of the deep sea is now increasing, but it is still not well known, despite being the largest environment on earth and providing important services such as carbon storage (Irigoien et al. 2014; Trueman et al. 2014) and fisheries (Ramirez-Llodra et al. 2011). The continental slope is the area that links the shallow waters of the continental shelf to the deep seas of the abyssal plain. This area is important for trawl fisheries and it covers a vast environmental gradient as light, temperature and resources decrease with depth, while pressure increases (Lalli & Parsons 1993; Kaiser et al. 2011). Assemblages along the slope therefore vary in terms of species composition, feeding behaviour, and traits such as body size (Carney 2005; Collins et al. 2005; Mindel et al. 2016; *Chapter 3: Functional, size and taxonomic diversity of fish along a depth gradient*). This means that it would be wrong to assume that all continental slope communities can be grouped together and interact equally throughout the depth gradient.

I therefore propose a new way of examining AORs in the marine environment, where occupancy is based on depth distribution rather than horizontal spatial distribution. I call this the bathymetric abundance–occupancy relationship. The oceanic environment is three-dimensional and the vertical aspect of space should not be ignored. By calculating occupancy based on depth, I can establish whether locally abundant species also exhibit large depth ranges. If a rare species is also found to have a narrow spatial range and a narrow depth range, this could add a third layer to the concept of "double jeopardy"; for example, a rare species could be easily wiped out by a fishery that targets the specific area and/or depth which that species occupies. An intraspecific bathymetric AOR would also be of potential interest, as a species should not necessarily be able to expand its depth range if it is constrained by its physiology (Carney 2005; Yancey et al. 2014), regardless of how abundant it is. Thus, a positive intraspecific bathymetric AOR would imply that in low abundance years, species are prevented from occupying their full potential depth ranges and may be more vulnerable to external pressures.

Here, using data from a deep-water bottom trawl survey that has been conducted regularly between 1998–2014, I investigate both inter- and intraspecific abundance–occupancy relationships to establish whether the general ecological pattern of positive correlations apply to deep-sea fish. I repeat these analyses in a novel way, by calculating occupancy based on the range of depths a species occupies. I examine whether either the spatial or bathymetric interspecific AORs have changed over time, potentially due to relaxed fishing pressure in the area over the duration of the study period (STECF 2013). I relate intraspecific patterns to the abundance, occupancy, depth distribution and body size of each species. The mean and variation in abundance and occupancy were examined in relation to the slope of the AOR, because positive AORs are more common in species where one of the variables has the capacity to change over time (Gaston et al. 2000). Depth variables were included in order to establish whether AORs affect species equally along the continental slope. Body size was examined because it has been found to affect the AOR in the marine environment (Webb, Tyler & Somerfield 2009).

5.3. Materials & methods

5.3.1. Data

Data were collected on Marine Scotland's deep-water bottom trawl survey in September 1998, 2000, 2002, 2004–2009 and 2011–2014 using the vessel *MRV Scotia*. The study site was the continental slope of the Rockall Trough in the Northeast Atlantic (Fig. 16) at latitude 55° to 59°N, longitude approximately 9°W,

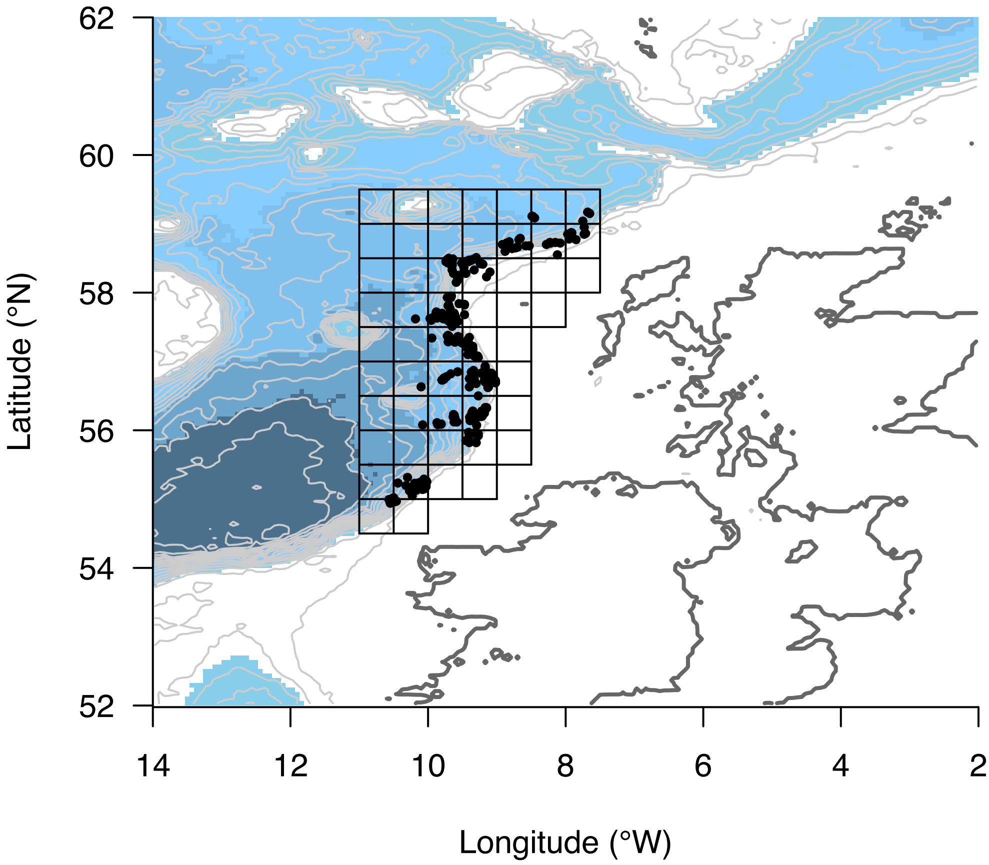

Fig. 16. Location of hauls of the Marine Scotland deep-water trawl survey from 1998–2014. Coloured shading indicates depth, with white being the shallowest areas and dark blue representing the deepest areas. Boxes are the spatial sampling units (0.5 x 0.5 decimal degrees).

and depth 300–2067m. Only demersal fish (those that live on or around the seabed, including those classified as benthopelagic) were sampled effectively by the gear, so mesopelagic fish (those that live in the water column) and invertebrates were not included in the analysis.

Fish were identified to the finest taxonomic resolution possible (which was species level for 99.9% individuals caught) and their taxonomic classification was verified using the World Register of Marine Species (WoRMS Editorial Board 2013). Body lengths of individual fish were measured on board during the survey. As recommended by ICES (2012), standard length, pre-anal fin length or pre-supra caudal fin length was used rather than total length for some species. These measurements were then converted to total length using conversion factors calculated from a subset of the survey data (Table S6).

All data manipulation and analysis was performed using R version 3.2.3 (R Core Team 2015), and graphs were produced using the packages *ggplot2* (Wickham 2009), *gridExtra* (Auguie 2016) and *marmap* (Pante & Simon-Bouhet 2013).

5.3.2. Interspecific abundance–occupancy relationships

Abundance was calculated in the same way for both spatial and bathymetric AORs: the number of individuals caught per hour of trawling was averaged across hauls, excluding those hauls where the species in question had an abundance of zero. Numbers per hour equate to a measure of local population density. Hauls varied in duration from 12 to 180 minutes, with most at 60 or 120 minutes. As haul duration was controlled for in calculating abundance and haul duration did not vary systematically with space, the full range of haul durations was used. Occupancy was taken as the proportion of sampled units that were occupied. For the spatial AOR, these units were squares of 0.5 x 0.5 decimal degrees (Fig. 16), and for the bathymetric AOR, the units were depth bands of 50 m.

For the overall interspecific AOR, the abundance of a species was defined by calculating its mean density across all hauls in which it occurred, over all years. Occupancy was the proportion of units sampled over all years in which that species had been recorded. The relationships between abundance and spatial or bathymetric occupancy were analysed using a binomial Generalised Linear Model (GLM) of the form proportional occupancy ~ a + b*log(abundance), using the number of sampled units (spatial squares or depth bands) as model weights.

To quantify temporal change in the interspecific AOR, I defined annual abundance for a species as its mean density across all of the hauls in which it occurred separately for each year. Annual occupancy was the proportion of units sampled in each year that a species occupied. Annual AORs were fitted using separate binomial GLMs for each year, of the form annual proportional occupancy ~ a + b*log(annual abundance), using the number of units sampled in each year as model weights. From each annual model I extracted the model coefficient b as a measure of the form of the relationship between annual abundance and annual occupancy. I also calculated the correlation between log(annual abundance) and annual occupancy as a measure of the strength of the relationship. Temporal trends in both the AOR coefficient and correlation were analysed over 13 years using linear models, for both spatial and bathymetric AORs.

5.3.3. Intraspecific abundance–occupancy relationships

Annual intraspecific abundance and occupancy were calculated as for the annual interspecific relationships calculated above. For intraspecific AORs, however, temporal relationships were calculated separately from the time series of annual abundance and occupancy estimates for each species. These relationships were fitted as binomial GLMs of the form: annual proportional occupancy[species$_i$] ~ a_i + b_i*log(annual abundance[species$_i$]), where model weights were the number of units sampled each year (spatial squares or depth bands). The model coefficient b_i was extracted for all species that occurred in > 6 years (93 taxa). This was used to examine the relationship between the slope of the spatial AOR and the slope of the bathymetric AOR for each species. I also tested separately for spatial and bathymetric AORs for associations between the species-level AOR coefficient and seven species characteristics, calculated from the survey data: mean abundance, variation in abundance, occupancy, range in occupancy, depth range, mean depth, and body size (Table 6).

Table 6. Variables calculated for each species to examine the relationships between the slope of the abundance–occupancy relationship and species characteristics.

Variable	**Definition**
Mean abundance	Log(mean(abundance))
Variation in abundance	Log(standard deviation(abundance))
Occupancy	Proportion of sampled units occupied
Range in occupancy	Max(occupancy per year) – min(occupancy per year)
Depth range	Max(depth occupied) – min(depth occupied)
Mean depth	Mean(depths occupied)
Body size	Mean(body lengths)

5.4. Results

5.4.1. Interspecific abundance–occupancy relationships

Using data from all 13 years, there was a significant positive spatial AOR across all species (Fig. 17A; GLM: b = 0.47, S.E. = 0.020, d.f. = 192, $p < 0.001$). The bathymetric AOR was also significantly positive (Fig. 17B; GLM: b = 0.46, S.E. = 0.018, d.f. = 192, $p < 0.001$).

Neither spatial nor bathymetric interspecific AORs changed systematically over time (Fig. 18), either in terms of their general form (measured using the model coefficient; relationship between spatial AOR coefficient and year, LM: b = 0.0042, S.E. = 0.0047, R^2 = 0.07, d.f. = 11, p = 0.39; relationship between bathymetric

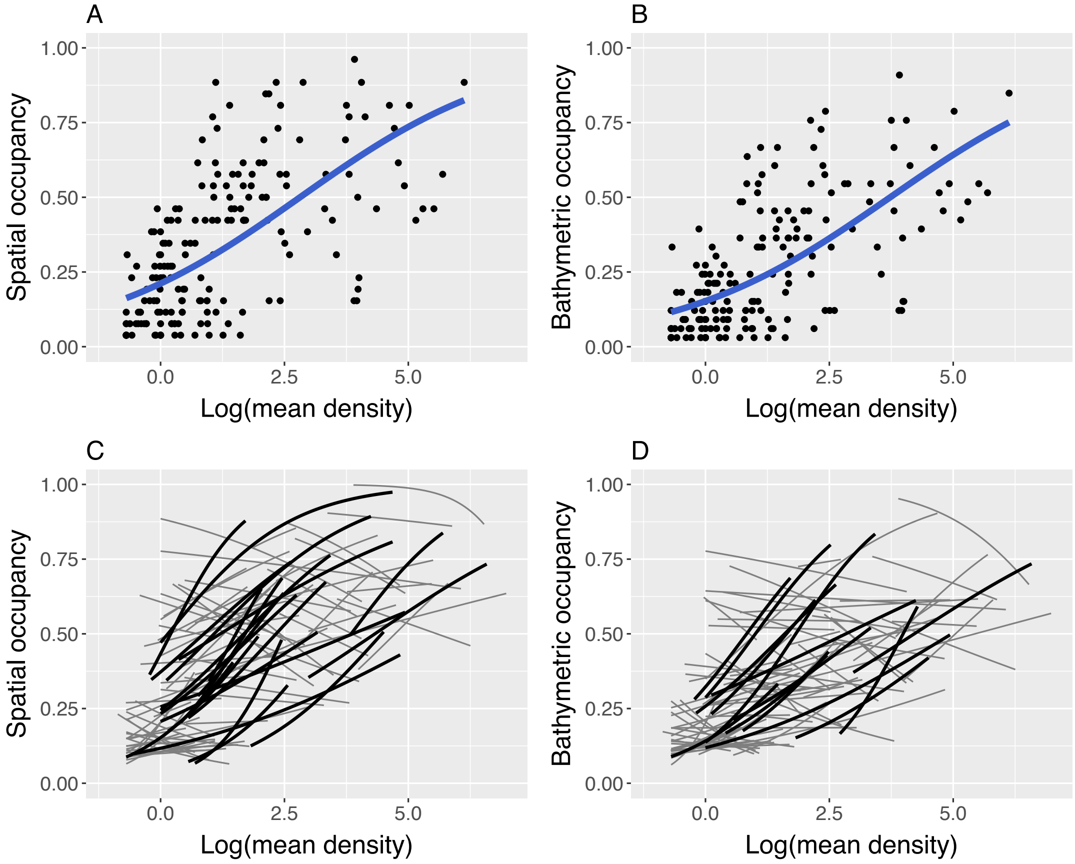

Fig. 17. Inter- and intraspecific abundance–occupancy relationships (AOR) for space and depth. A) Overall interspecific spatial AOR; curve is the fitted binomial Generalised Linear Model (GLM). B) Overall interspecific bathymetric AOR; curve is the fitted binomial GLM. C) Intraspecific spatial AORs. D) Intraspecific bathymetric AORs. For panels C) and D), each line represents the fitted binomial GLM for each species; thick, black lines represent statistically significant relationships; thin, grey lines represent non-significant relationships.

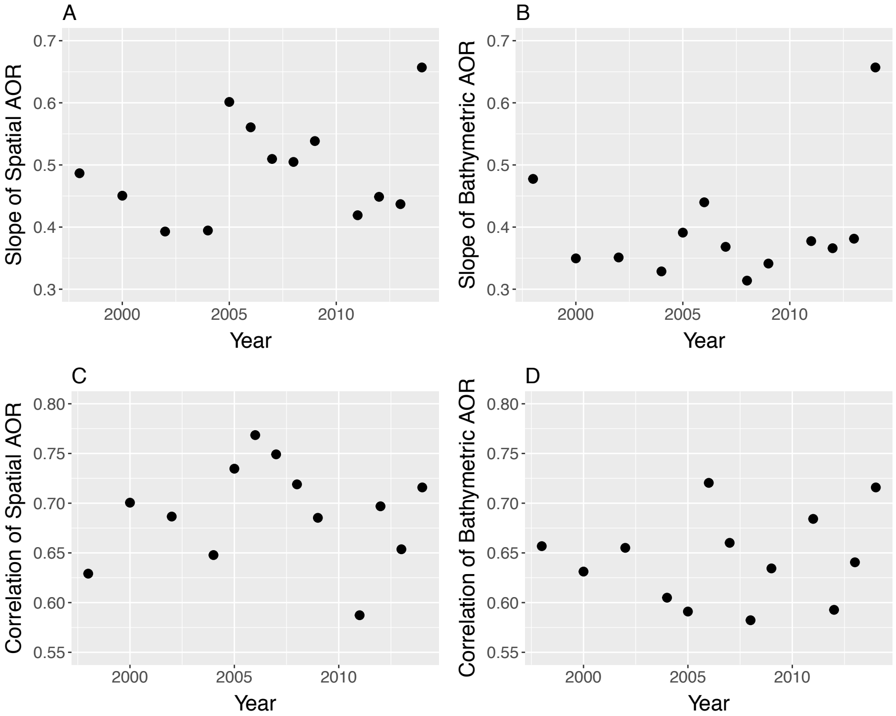

Fig. 18. Change over time in characteristics of yearly interspecific AORs. A) Model coefficient of yearly spatial AORs; B) model coefficient of yearly bathymetric AORs; C) correlation of yearly spatial AORs; D) correlation of yearly bathymetric AORs.

AOR coefficient and year, LM: b = 0.0044, S.E. = 0.0053, R^2 = 0.06, d.f. = 11, p = 0.43), or their strength (relationship between spatial AOR correlation and year, LM: b = 0.00019, S.E. = 0.0031, R^2 = 0.00, d.f. = 11, p = 0.95; relationship between bathymetric AOR correlation and year, LM: b = 0.0012, S.E. = 0.0027, R^2 = 0.02, d.f. = 11, p = 0.65).

5.4.2. Intraspecific abundance–occupancy relationships

The spatial AOR was positive in 65 out of 93 taxa that occurred in > 6 years, and 21 of these relationships were statistically significant (Fig. 17C; Fig. 19; Table S8). Twenty-eight taxa exhibited negative relationships, but none of these were significant (Fig. 17C; Fig. 19; Table S8). The bathymetric AOR was positive in 58 out of the 93 taxa with reliable estimates of the coefficient, and 14 of these were statistically significant (Fig. 17D; Fig. 19; Table S8). The bathymetric AOR was negative in 35 species, but none of these relationships were significant (Fig. 17D; Fig. 19; Table S8). Coefficients were positive on average and significantly different to zero for the species that occurred in > 6 years, for both spatial and bathymetric

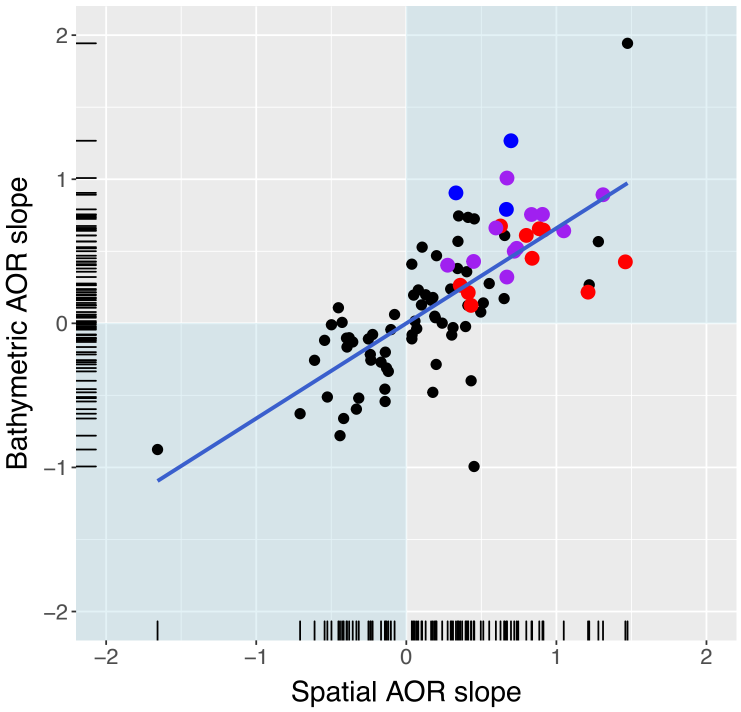

Fig. 19. Relationship between model coefficients of spatial and bathymetric intraspecific AORs for each species. Larger points signify species that had significant relationships in spatial and/or bathymetric AORs. Purple points = species was significant in both spatial and bathymetric AORs; red points = species was significant in spatial AOR only; blue points = species was significant in bathymetric AOR only. Rug plots represent the distribution of coefficients and light blue quadrants highlight the areas where the slopes are both above or both below zero. Line represents the general linear model fitted to all data points.

AORs (Fig. 19; spatial AOR LM: b = 0.24, S.E. = 0.055, $p < 0.001$; bathymetric AOR LM: b = 0.16, S.E. = 0.050, p = 0.002).

There was a significant, positive relationship between the slope of the spatial AOR and the slope of the bathymetric AOR when all species that occurred in > 6 years were included (Fig 19; LM: b = 0.66, S.E. = 0.065, $R^2 = 0.52$, d.f. = 91, p < 0.001) but not when only species that exhibited positive intraspecific AORs were included (Fig 19; LM: b = 0.13, S.E. = 0.19, $R^2 = 0.02$, d.f. = 22, p = 0.51).

Intraspecific spatial AORs were largely unrelated to the species-level traits I considered, except for mean depth (deeper-living species have more strongly positive AORs; Fig. 20F; LM: b = 0.00046, S.E. = 0.00012, $R^2 = 0.14$, d.f. = 91, p < 0.001), and a weak trend for species with more variable occupancies across years to have more strongly positive AORs (Fig. 20D; LM: b = 0.60, S.E. = 0.31, $R^2 = 0.03$, d.f. = 91, p = 0.056). Intraspecific bathymetric AORs were also unrelated to species-level

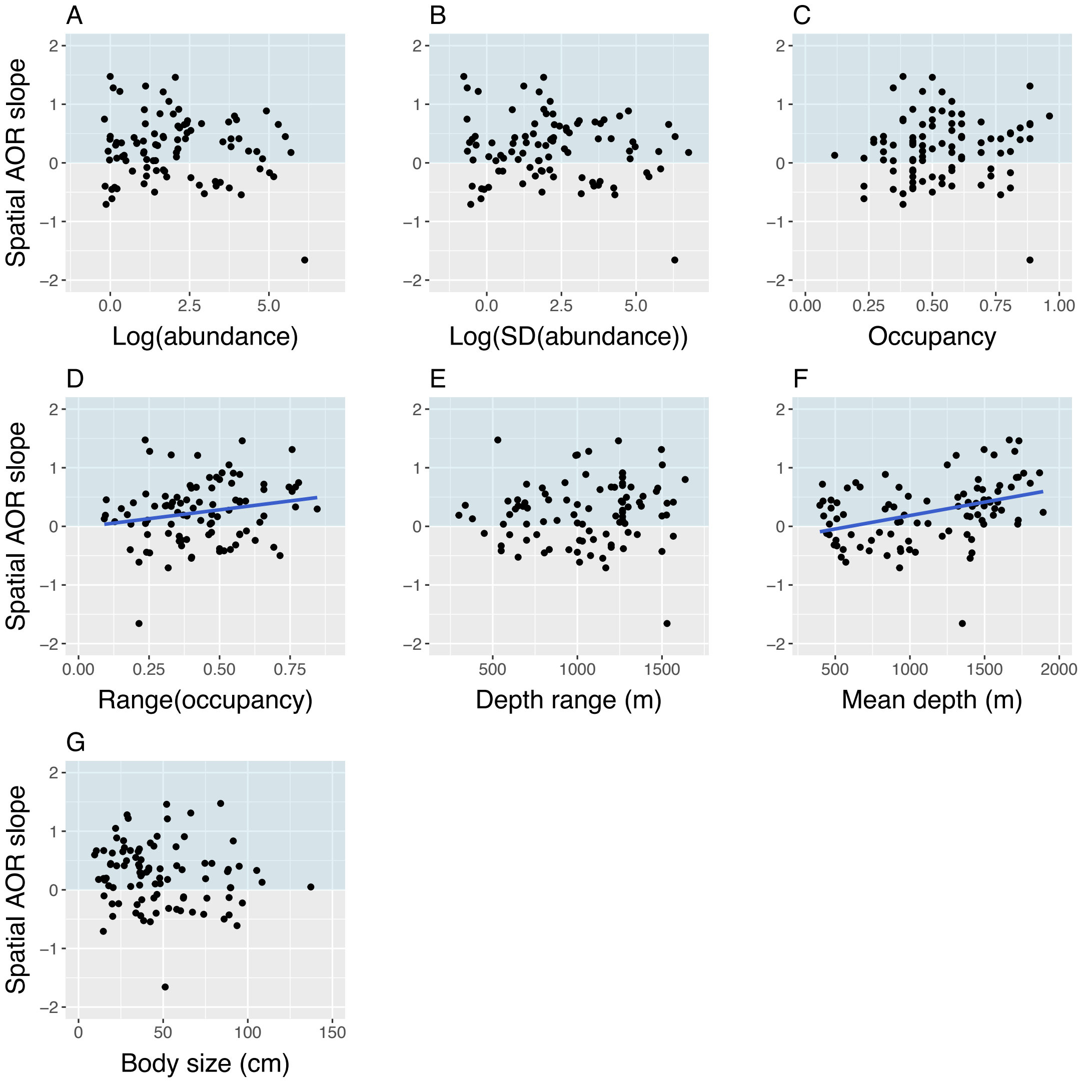

Fig. 20. The relationships between the model coefficients of intraspecific spatial AORs and species characteristics. A) Mean abundance; B) Standard deviation of abundance; C) Mean occupancy; D) Range in occupancy; E) Depth range; F) Mean depth; G) Body size. Lines represent the fitted general linear model if the relationship was significant or borderline significant (see main text). Light blue areas highlight where slopes are positive.

traits apart from mean depth, with again a trend for more strongly positive AORs in species living at deeper depths, though the variance explained was low (Fig. 21F; LM: b = 0.00035, S.E. = 0.00011, R^2 = 0.09, d.f. = 91, p = 0.0016).

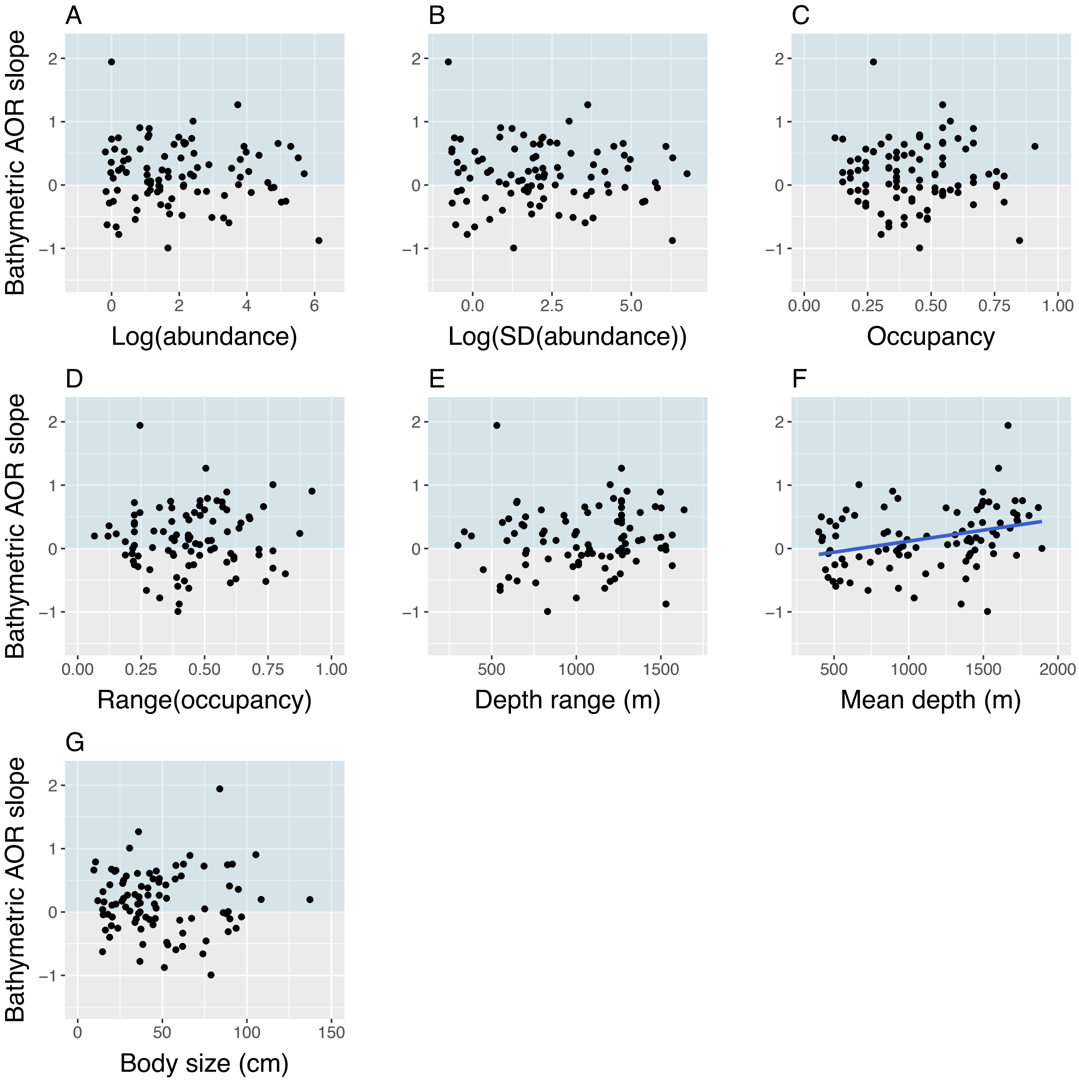

Fig. 21. The relationships between the model coefficients of intraspecific bathymetric AORs and species characteristics. A) Mean abundance; B) Standard deviation of abundance; C) Mean occupancy; D) Range in occupancy; E) Depth range; F) Mean depth, line represents the significant fitted general linear model; G) Body size. Light blue areas highlight where slopes are positive.

5.5. Discussion

Deep-sea demersal fish uphold the ecological principle of increasing proportional occupancy of a region with increasing average local abundance. In the marine environment, the habitat occupied is three-dimensional, so the abundance–occupancy relationship (AOR) can also be addressed within vertical space. The positive interspecific AOR is upheld when occupancy is classified in terms of 50 m depth bands. The positive relationships in both spatial and bathymetric AORs mean that species with high average abundance are more likely to occupy more areas within a geographic region, and more depths along the continental slope.

There are several explanations for the positive spatial AOR that may all act synergistically (reviewed in Gaston et al. 2000; Holt, Gaston & He 2002; Borregaard & Rahbek 2010), and which could all apply to the deep sea. The first is that if the study site does not encompass the entire range of all species, then some species will be caught that are at the edge of their range, while some species are caught that are at the core of their range. This could apply here as it is unlikely that any species caught on this survey live solely in the Rockall Trough and the gear is adapted to sampling demersal fish only, potentially excluding part of the community. This means that a positive AOR could be produced naturally when core populations with high abundance and periphery populations with low abundance are sampled for different species (Gaston & Blackburn 1996). However, the positive AOR persists even when entire geographical ranges are surveyed, so range position is unlikely to explain the phenomenon as a whole (Gaston, Blackburn & Lawton 1997; Gaston et al. 2000). The second explanation is that species are influenced by their resources, such that species are abundant and widespread if they are able to utilise abundant and widespread resources (Brown 1984). Baird's slickhead (*Alepocephalus bairdii*) may be an example of one such species as it feeds on gelatinous zooplankton (Froese & Pauly 2016), which is likely to be found throughout the study site. Alternatively, the AOR may be determined by population dynamics such that local abundance affects processes of colonisation and extinction of patches (Gonzalez et al. 1998). Positive AORs are expected in species with high colonisation ability and large areas of continuous habitat (Freckleton et al. 2005), which can be said to apply to a substantial proportion of marine species (Powles et al. 2000).

The bathymetric AOR could be influenced by similar mechanisms to the spatial AOR but with some additional considerations. The range position hypothesis may apply to depth ranges because some species occupy depths outside of the study range. However, this effect is likely to be much reduced than for the spatial AOR, because only species at the very edge of the depth ranges studied here could be occupying alternative depths. The resource availability hypothesis may apply equally to the bathymetric and spatial AORs. Resources along the continental slope are depth-dependent: influx of detritus from surface productivity generally decreases with depth (although local oceanographic factors can alter this pattern; Carney 2005), but additional resources are supplied to certain depths through an assemblage of Diel Vertical Migrators (or the 'deep scattering layer'). This is a vertically moving layer of organisms, and at the depths where it can be best exploited, a few species that feed on the species therein dominate the demersal fish community both in terms of abundance and in their distribution across the depth range (Trueman et al. 2014; *Chapter 3: Functional, size and taxonomic diversity of fish along a depth gradient*).

Population dynamics may also influence the bathymetric AOR if some species are restricted to certain depths due to anthropogenic effects or biotic interactions, rather than their physiology. If a species is physiologically capable of living at a certain depth, then the typical rules of colonisation and extinction of patches could apply. However, physiology is an additional consideration when interpreting the bathymetric AOR because of the adaptations that are required to occupy deep water, such as the alteration of membrane structure (Hazel & Williams 1990) and the stabilisation of enzymes (Yancey & Siebenaller 1999). The ability to regulate one of these stabilising agents (trimethylamine N-oxide or TMAO) with depth may determine the depth range of a species (Yancey et al. 2014). Being adapted to only a small depth range may impact a species' overall abundance if it links to other characteristics such as generalist resource use and the ability to outcompete others. The widespread and continuous habitat that increases the likelihood of a positive AOR (Freckleton et al. 2005) and is often associated with the marine environment cannot be applied to vertical space if some depths (i.e. habitats) cannot be occupied by certain species due to their physiology. This is true for abyssal depths (Yancey et al. 2014), but specific physiological limitations for individual species within the continental slope are still speculative (Carney 2005).

Fishing pressure in my study region has decreased since the early 2000s due to the introduction and subsequent reduction of Total Allowable Catches (STECF 2013). Exploitation has previously been shown to affect AORs in fish (Fisher & Frank 2004) so we may expect the relationship to show recovery from fishing pressure over time in the Rockall Trough. However, neither the spatial nor bathymetric AORs show any systematic temporal change in either their form or strength. Conversely, the reduction in exploitation has been of sufficient magnitude to promote recovery in size-based indicators such as the Large Fish Indicator in this area (*Chapter 4: Size-based* *indicators show depth-dependent recovery from fishing pressure in the deep sea*). The AOR was therefore either not as impacted by fishing as are size-based aspects of the community, or it was impacted, but it is recovering more slowly than are body sizes. Both of these scenarios imply that over the medium-term, the AOR is not a good indicator of deep-sea fish community recovery. As some AORs appear very stable over time (Blackburn et al. 1998; Zuckerberg, Porter & Corwin 2009), and contrasting responses to pressure have been observed in others (Fisher & Frank 2004; Webb, Noble & Freckleton 2007; Guedo & Lamb 2013; Bulafu 2015), more work is needed to establish robust predictions of how AORs will respond to different kinds of environmental change.

Intraspecific relationships between abundance and occupancy in both space and depth are positive for 70% and 62% of taxa (that occurred in > 6 years) respectively, and the model coefficients are significantly positive on average. These positive trends in the intraspecific AOR could be explained by variations in the hypotheses suggested for interspecific relationships (Gaston et al. 2000). Range position could explain the relationship if distributions are shifting over time, such that in some years the sampled areas become representative of a core range, while in some years they are part of the periphery. Habitat selection can depend on abundance in fish (Marshall & Frank 1995; Blanchard et al. 2005b), and range shifts are already occurring in shallower marine environments due to climate change. These shifts may be through space or through depth (Heath et al. 2012; Rutterford et al. 2015), potentially applying to both forms of the AOR I study here. However, such changes in range position due to human impacts may not manifest themselves in the deep sea for several years (Glover & Smith 2003). Resource utilisation may also play a role if resource availability varies temporally, such as the dynamics seen in Particulate Organic Carbon supply to the seafloor (Ruhl 2008; Lampitt et al. 2010) and infaunal polychaetes (Soto et al. 2010; Laguionie-Marchais et al. 2013), while species with no relationship between abundance and occupancy may be exploiting constant resources. Population dynamics can also be viewed in a similar way to the interspecific explanation, where patches are colonised, grow, or go extinct, according to a metapopulation model (Gaston et al. 2000). The deep-sea floor is more heterogeneous than previously suggested (Danovaro, Snelgrove & Tyler 2014) so it may be that species form metapopulations due to congregation at features such as seamounts, canyons, sponge fields or deep-sea coral banks (Ramirez-Llodra et al. 2010).

Despite the positive slopes on the whole, the intraspecific relationships are only statistically significant in 23% species for the spatial AOR, and 15% species (that occurred in > 6 years) in the bathymetric AOR. This implies that deep-sea species have a tendency towards the generalised positive AOR, but there may not be enough variation in the study period considered for many relationships to be statistically significant. The species considered may be relatively stable over time in both range size and location, and in abundance. Although this would be unexpected due to a history of exploitation and then recovery of fish in this area (*Chapter 4: Size-based indicators show depth-dependent recovery from fishing pressure in the deep sea*), it could be possible if only a few species were particularly targeted by the fishery, or if the period of exploitation was not sufficiently covered by the survey. An additional explanation for the lack of relationship in the bathymetric intraspecific AORs is that of physiological constraints, similar to the effects discussed above in relation to the interspecific AOR. Adaptations to depth are unlikely to have changed over the time period studied, therefore if a species' abundance was higher in one year, it does not necessarily follow that it would be able to expand its depth range. For those species that do exhibit positive bathymetric AORs, the ability to expand the depth range in years of high abundance could result from that species being constrained in low abundance years by fishing pressure or interspecific competition.

The difference between species that exhibited a positive relationship and those with no relationship, represented by the slope of the AOR, can be partially explained by the mean depth occupied by that species. Species that live deeper show more positive relationships between abundance and both spatial and bathymetric occupancy. A possible explanation for this pattern is that of resource supply in the deep. Resources can often be patchy across space and time, for example the fall of a whale carcass (Hilario et al. 2015). This variable resource supply could cause changes in occupancy of both spatial and bathymetric areas, in turn allowing for higher abundance in the years where occupancy can increase. Additionally, deeper-living species tend to have wider depth and latitudinal ranges (Macpherson 2003). This could allow for a greater likelihood of exhibiting a positive intraspecific AOR because in years that are good for abundance, the species could expand into a wider range of depths or geographical space, resulting in an increase in occupancy. There is also a borderline significant positive relationship between range in occupancy and the slope of the spatial AOR. This is to be expected as the more one variable (abundance or occupancy) changes, the more the other will have the potential to change. The high variation in occupancy in some species could potentially be explained by any of the main hypotheses behind the AOR: shifts in range position, changes in resource availability, or population dynamics.

The form of the intraspecific AOR cannot be explained by mean or variation in abundance, mean occupancy, depth range, or body size. Body size could potentially alter the AOR because size impacts abundance: as fish age they increase continuously in size, but not all will survive, resulting in decreased abundance of individuals of those sizes (Webb et al. 2011). The lack of relationship found here could mean that body size affects characteristics of the AOR other than the slope, or that mean body size is not a sufficient measure to capture the disparity. Species characteristics that consistently determine the form of the AOR have remained elusive, but future work could examine behavioural traits such as aggregation (Frisk, Duplisea & Trenkel 2011), or ecological traits such as niche breadth and habitat preference (Frost et al. 2004; Faulks et al. 2015).

The generally positive bathymetric AOR could potentially imply a shift from the currently described “double jeopardy” (Lawton 1993, 1996; Gaston 1999) to a “triple jeopardy”, where a species could decrease in abundance, geographic range and depth range in response to a pressure, making it harder to monitor but potentially easier to obliterate. Three such species are identified in this study as they have strong, positive intraspecific AORs when occupancy is calculated based on both space and depth (Fig. 22; Table S8): the abyssal halosaur (*Halosauropsis macrochir*), the small-eyed rabbitfish (*Hydrolagus affinis*) and the stout sawpalate (*Serrivomer beanii*). For species such as this, any activity or environmental change that impacts on one aspect of their distribution (local abundance, spatial distribution or depth distribution) is likely to propagate through to the other variables, causing a disproportionate effect on total population size. These three species are found in the deepest part of the study site, which supports the finding that deeper-living species are more likely to have positive intraspecific spatial and bathymetric AORs. This potentially adds a macroecological element to the notion that deeper-living species are more vulnerable than coastal species due to their life histories (Drazen & Haedrich 2012; Norse et al. 2012).

Deep-sea species are under-studied and different in many ways to shallow-living species, for example in their life histories (Drazen & Haedrich 2012), morphology (Neat & Campbell 2013) and ecology (Ramirez-Llodra et al. 2010). In this study I have shown that despite this, general ecological principles hold across the marine environment. The generality of the positive AOR also applies to vertical space as well as horizontal space. Depth should not be ignored in any marine environment as species have differing depth ranges, and can move among depths

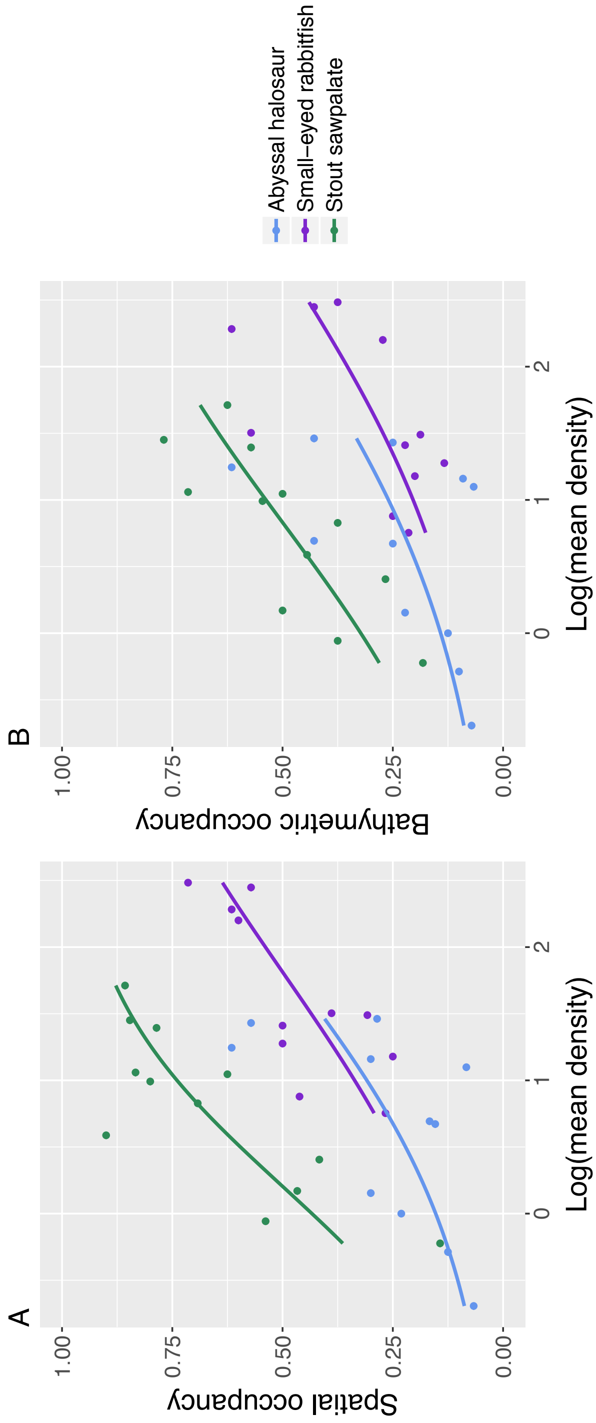

Fig. 22. Intraspecific relationships between abundance and A) spatial occupancy, and B) bathymetric occupancy, for three species potentially at risk from "triple jeopardy". Species were said to be at risk if the coefficients of the binomial Generalised Linear Models, fitted to both the spatial and bathymetric abundance–occupancy relationships, were greater than 0.7 and the p values were less than 0.05 (Table S8). Species are the abyssal halosaur *Halosauropsis macrochir*, the small-eyed rabbitfish *Hydrolagus affinis*, and the stout sawpalate *Serrivomer beanii*.

daily or during their development and growth (Magnússon 2001; Lin et al. 2012; Trueman, Rickaby & Shephard 2013). I show that deeper-living species have more positive intraspecific AORs, potentially making them more vulnerable than those in shallower waters. This study further highlights the importance of considering the three dimensions of the ocean when exploring marine ecology and establishing protection measures for the species therein.

5.6. Supporting information

Table S6. The species caught on the survey, their conversion factors and maximum lengths.

Table S8. The statistical output from intraspecific abundance–occupancy relationships.

6. General Discussion

Over the course of this work I have investigated change in deep-sea fish assemblages across a depth gradient and over time during a period of reduced fishing pressure. Here I summarise my key findings, then explore the explanations behind, and relevance of, the patterns I have found. I also outline the limitations of this work and recommend future directions for deep-sea ecological research.

6.1. Key findings

I. Species composition changes along the continental slope (Chapter 2). From 300–1000 m, many species have narrow depth ranges and this area is characterised by species such as the blackbelly rosefish (*Helicolenus dactylopterus*), the European hake (*Merluccius merluccius*) and the common ling (*Molva molva*). From 1000 m, species composition changes markedly, and some species are highly dominant over a wide depth range such as the roundnose grenadier (*Coryphaenoides rupestris*), Baird's slickhead (*Alepocephalus bairdii*) and the black scabbardfish (*Aphanopus carbo*). No species were found solely in the deepest parts of the study site, but Agassiz's slickhead (*Alepocephalus agassizii*) and the pale ghost shark (*Hydrolagus pallidus*) are mainly abundant below 1600 m. The shifts in community composition are accompanied by an increase in species richness with depth.

II. Assemblage structure can also be examined in terms of body size (Chapters 2 and 3). Average size increases with depth up to 1500 m and could potentially start to decline beyond the depth range of the study site. I propose that an alternative measure of body size provides more information about assemblage structure by combining intra- and interspecific variation in body size. It is calculated as observed body size divided by potential maximum size and I call this metric fractional size. It increases with depth to approximately 1800 m. A third body size metric, size diversity, aims to account for variation in size as well as the mean. Size diversity shows a peak at approximately 800 m, beyond which it remains fairly high.

III. Functional changes were deduced using morphological traits and isotopic signatures (Chapter 3). Functional richness mirrors the patterns seen in size diversity and is highest at 800 m. Functional divergence is highest at the shallowest and deepest parts of the study site. Functional traits such as caudal fin aspect ratio and surface area of the mouth protrusion vary substantially with depth and can be linked to patterns in the relative dominance of benthic and pelagic feeders.

IV. In the shallowest areas, where fishing pressure mainly occurs, some size-based indicators show recovery from fishing pressure (Chapter 4). The Large Fish Indicator and slope of the biomass spectrum are recovering at depths up to 750 m, whereas fractional size shows an increase at all depths over the timescale of the survey.

V. The general ecological pattern of increasing regional occupancy with increasing local abundance remains true in deep-sea fish at an interspecific level (Chapter 5). The positive trend is also true for most species when abundance and occupancy are calculated yearly. The interspecific trend does not change over the timescale of the study. Abundance–occupancy relationships are also positive when occupancy is calculated based on depth distribution, meaning that species that are low in average abundance occupy fewer areas both in horizontal and vertical space.

6.2. Assemblage structure along a depth gradient

Traditionally, changes in communities along environmental gradients have been studied using species composition and even in the current modern era of ecology, species abundance lists are common. Although in certain circumstances this approach is desirable, for example in documenting changes in abundance of commercially important species, it has been argued that to move forward in ecology we must embrace the 'trait-based approach' (McGill et al. 2006; Litchman et al.

2010; Webb et al. 2010; Mouillot et al. 2013; Pawar, Woodward & Dell 2015). This is a suite of methods that aim to extract the function of a community using the traits of the species therein. Once function has been established, we are in a better position to predict the effects of human activity, such as climate change or exploitation, on ecosystems.

A trait-based approach that is already widely used in the marine environment is the use of metrics based on body size. Body size is a particularly important trait in fish as they grow indeterminately, meaning that size can often be a better predictor than species identity of trophic level and diet choice (Scharf, Juanes & Rountree 2000; Jennings et al. 2001). Body size also influences maturity and fecundity (Winemiller & Rose 1992), growth rate (Jobling 1983) and mortality (Pauly 1980). Here, I investigate changes along the continental slope in multiple size-based metrics.

The first of these metrics is a novel method that I term fractional size (Chapter 2). It is calculated as observed body size divided by the potential maximum size of that species, hence illustrating where an individual is in the growth trajectory of that species. It combines intra- and interspecific variation in size, meaning that it captures more information than body size alone. I believe this is why, when all other methodological details were equivalent, fractional size explained more variation along a depth gradient than average body size. It increased along the slope to approximately 1800 m, where it may start to decline beyond the depth range of the study site. The increase seen in fractional size could be explained in three ways: i) the increased lifespans of deep-living species (Koslow et al. 2000; Morato et al. 2006; Drazen & Haedrich 2012) allow them more time to reach their potential maximum sizes; ii) some species' eggs float to shallower waters then juveniles move deeper as they grow (Magnússon 2001; Lin et al. 2012; Trueman, Rickaby & Shephard 2013); iii) fishing pressure in the shallower areas of the slope prevents individuals from reaching their maximum sizes (Bianchi et al. 2000; Hsieh et al. 2010). By accounting for maximum size, which relates to important life history characteristics of a species (Froese & Binohlan 2000), fractional size allows for comparisons across individuals of different species, and could be applied globally to fish and marine invertebrates.

However, the efficacy of the fractional size method may currently be limited by our knowledge of maximum size (L_{max}). Maximum values of any trait are skewed by sample size (Head, Hardin & Adolph 2012; Moorad et al. 2012) or can be representative only of a few individuals rather than the species as a whole. An alternative approach that has been applied in studies using longevity (Moorad et al. 2012) and physiology (Head, Hardin & Adolph 2012), is to use a trait value that only 10% of individuals exceed. This value is possible to compute from a dataset such as the one used in this thesis, where the sizes of all individuals are known. However, the L_{max} listed on the global compendium FishBase (Froese & Pauly 2016) was used here in order to make the values of fractional size globally applicable. By using maxima obtained directly from the survey data, any variation between the study site and other regions would be lost. For example, if no individuals in the study site reached close to their maximum size, this could be not because the maximum was taken from an anomalous individual, but rather because that species moves elsewhere to mature and breed (Gordon & Duncan 1987). This is a valid finding that would be lost in using a maximum value calculated from the survey data, however, it may be that the chosen method for the calculation of fractional size will vary depending on the hypotheses being tested. In the future, as compendiums such as FishBase (Froese & Pauly 2016) develop, it may be possible to collate global values for maxima using the 90th percentile method which could be a more robust way of illustrating maximum size.

Observed body size also increased with depth, and this held true for two methods: averaging across species, weighting by the biomass of those species (Chapter 2); averaging across all individuals present (Chapter 3). Both methods showed an increase in body size to 1500–1800 m, then the beginnings of a decline that may persist outside of the depth range considered here. This pattern also broadly agreed with what was seen in fractional size and may also be explained by depth-dependent patterns in fishing pressure, or individuals moving deeper as they grow. Whether or not body size does start to decrease beyond the depth ranges studied here has important implications for our general knowledge of the body size—depth relationship. Body size has been found to increase up to depths of 5000 m (Polloni et al. 1979; Collins et al. 2005), or decrease in non-scavenging species over the same depth range (Collins et al. 2005). The potential decline seen here at 2000 m may therefore just be an artefact of sampling effort at these depths, or it may be due to responses of certain functional groups.

The third size-based metric I used to examine changes along a depth gradient was size diversity (Chapter 3). In this calculation, species identity was ignored and individuals were instead separated into size classes. The diversity measure developed by Leinster & Cobbold (2012) took into account the number of individuals in each size class and the difference between them in terms of their body size. Size diversity was found to peak at around 800 m, unlike the other size-based metrics. Size diversity can therefore provide additional information to mean body size. At 800 m, body size on average is low, but size diversity is high, so a range of sizes must still be present. Alternatively, at 1500 m where average body size is high, there is an intermediate amount of spread around this average size. Size diversity can be associated with predation pressure and resource availability (Quintana et al. 2015) so may be an important indicator in itself. However, the relationship between depth and body size was much more pronounced than for size diversity, implying that average body size may be a better representative of functional changes along the slope.

Functional implications can also be established using morphological traits other than body size (Chapter 3). For example, caudal fin aspect ratio determines swimming capacity (Pauly 1989; Fisher et al. 2005) and the surface area of the mouth protrusion is related to prey capture mode (Sibbing & Nagelkerke 2001). I found that the average value of certain morphological traits within an assemblage could potentially be mapped onto whether the species in that assemblage fed in the benthic or pelagic environment, and in turn could link this to the positioning of Diel Vertical Migrators (DVM, or deep scattering layer; Trueman et al. 2014). Pelagic feeders are able to dominate from 900 m to at least 1700 m because they are exploiting the DVM community, which, at these depths, is too far above the seabed for the benthic feeders to reach. The dominance of the pelagic feeders results in high aspect ratios and small gapes because they need to swim effectively but mainly feed on planktonic invertebrates (Froese & Pauly 2016), hence do not require large gapes. At shallower depths, the DVM community can be reached by the benthic feeders, and their dominance is illustrated by large mouth protrusions which they use to feed on the seabed.

Additionally, I used the morphological traits to calculate two measures of functional diversity: functional richness and functional divergence (Villéger, Mason & Mouillot 2008). Functional richness does not take species abundances into consideration and is a measure of the functional space occupied by the species in an assemblage. Functional divergence does take species abundances as an input and represents how widely and evenly spread the species are around the trait space. The two measures of functional diversity did not produce the same results, with functional richness being highest at 800 m and functional divergence being highest at 300 m and 2000 m. These patterns could also potentially be explained by the relative positioning and exploitation of the DVM community. At the shallower end of the slope, pelagic and benthic feeders can reach the DVM community, which could result in low functional richness, as different feeding guilds are exploiting the same resources, and high functional divergence, because resources must be partitioned among co-existing species. Functional divergence may then decrease at intermediate depths where pelagic feeders experience competitive release and all possess similar traits used for exploiting planktonic invertebrates. Finally, at the deepest parts of the slope studied, the DVM community can no longer be reached by any demersal fish, and feeding habits of these assemblages are less well known. However, these explanations for the patterns seen in functional diversity are only hypotheses at present, and more data are needed on the movement and interaction of assemblages. Functional diversity is therefore helpful in comparing the biodiversity of different areas along the slope, but may not be useful in a practical context because it is not always clear what the results mean in practice. Functional diversity can be calculated in many different ways (Schleuter et al. 2010) and cannot be compared across systems or studies due to variation in methodology and the traits used. Even within one dataset, two measures of functional diversity showed opposite patterns, highlighting the need to fully justify which method is used and how the results are interpreted.

When calculating average trait values and functional diversity, I used species-level trait values that were calculated relative to body size. In using relative traits, I controlled for the large differences in size between fish of different ages, and relative traits have been found to relate to function (Sibbing & Nagelkerke 2001; Reecht et al. 2013). I made the assumption that relative traits are unlikely to change over the course of an individual's life, because although its size will change, its body plan will remain inherently constant. In this case, it is therefore appropriate to use one trait value for all individuals of a species. However, traits could also be examined on an individual basis, in the way that was possible for body size. This would allow us to capture any changes that occur throughout an individual's life, such as the switch made by the abyssal grenadier (*Coryphaenoides armatus*) from feeding on benthic invertebrates to pelagic fish as it ages (Froese & Pauly 2016). Although desirable, this level of data collection was not realistic on the survey used in this work.

6.3. Change over time

Fishing pressure in the Rockall Trough has been decreasing due to the introduction in 2003 and subsequent decline of Total Allowable Catches (STECF 2013). As my first two data chapters showed, it would be naive to disregard depth when examining any effects of fishing. All aspects of the community that were examined changed with depth, as does fishing effort. I therefore used depth bands to separate out potentially different recovery scenarios. Fractional size increased, indicating recovery, in all depth bands. The Large Fish Indicator (LFI) and the slope of the biomass spectrum indicated recovery in the shallowest depth band (up to 750 m), which is where most fishing pressure is targeted. The medium depth band (751–1200 m) also experiences fishing pressure, but without depth-resolved effort data, it is difficult to say whether the lack of change in the indicators is due to a lack of recovery in this depth band, or because there was a lower level of exploitation so it was never visibly impacted by fishing. The signs of recovery in the shallow depth band, and in the medium and deep depth bands for fractional size, are particularly encouraging as it was previously thought that deep-sea communities would be very slow to recover from exploitation (Norse et al. 2012).

There was no change in any depth band of mean body length or mean maximum length over the study period. Mean body length may not change over time as it can be reduced by an influx of small individuals due to higher recruitment success (Shin et al. 2005; Houle et al. 2012), meaning that it does not consistently increase when a community is recovering. It is perhaps more surprising that mean maximum length did not show a response. It may be that the timescale considered was not long enough for this indicator to show a trend, or the system's changes are better captured when the sizes of every individual are considered, as is the case in the LFI, the slope of the biomass spectrum, and fractional size. The latter three indicators all appear to be well-suited to capture changes in deep-sea fish assemblages, however, only fractional size showed change in any depth band other than the most shallow (once the deepest depth band has been disregarded due to issues with sampling effort). This may be because the impacts of fishing can propagate beyond the depth range fished (Bailey et al. 2009), and fractional size may be a more sensitive indicator to these changes than the LFI or the slope of the biomass spectrum. Alternatively, the different patterns may be because the indicators are able to capture slightly different aspects of community structure. For example, an increase in fractional size could be because individuals are reaching larger sizes, which would also manifest itself as an increase in the LFI, or the increase in fractional size could also be due to shifting species composition. A shift to overall smaller species, but with individuals remaining roughly constant in their size, would result in an unchanging LFI and an increasing fractional size, because individuals would be proportionally bigger for which species they are. Both indicators may therefore be beneficial in examining different aspects of community structure.

In this study it was difficult to accurately map changes in size-based indicators onto changes in fishing effort, as effort data are incomplete, and even where they are present, they are not depth-resolved. In this work I attributed the changes seen to a reduction in fishing effort by looking at temperature as an alternative driver, and finding that it did not change over the timescale of the survey. Ideally, this would be taken further by predicting unexploited values for the size-based indicators in the deep sea. With these, it would be possible to establish how impacted the fish community of the Rockall Trough was before fishing pressure started to reduce. Unexploited values could be predicted by models such as those described by Andersen & Pedersen (2010) and Blanchard et al. (2011), but as has been extensively revealed in this work, depth must be included in any such model. The issue of including depth is not a trivial one. Species span different depth ranges and will be of different sizes depending on what depth they occupy (Chapter 2). There is also migration up and down the slope over different timescales (Gordon & Duncan 1985, 1987; Magnússon 2001; Lin et al. 2012; Trueman, Rickaby & Shephard 2013) and it is still not well known how assemblages, such as demersal fish, pelagic fish, and benthic invertebrates, interact in the deep sea. Until we have a greater understanding of these aspects of deep-sea systems, it may be more beneficial to use empirical data for a variety of deep-sea locations, which experience a range of fishing pressures, to establish baseline indicator values for different depths. The baseline values are most likely not comparable to those used in shelf seas, because the shelf has been exploited for hundreds of years (Barrett, Locker & Roberts 2004; Kerby, Cheung & Engelhard 2012). It has been suggested that a Large Fish Indicator value of 0.3 represents a healthy ecosystem in coastal seas (ICES 2007; Greenstreet et al. 2011). If this were to be applied to the deep sea, then in the Rockall Trough we could be fishing much more heavily than we have been since 1998. However, before recommending such a specific value of an indicator, further work is needed to establish how much fishing pressure the system could retain and still be able to function and recover. Alternatively, if it were assumed that the Rockall Trough system is currently healthy, then the recommended values of the LFI could be as high as 0.75 or even 0.9. Despite the difference needed in setting reference points between the shelf and deep water, I have shown that indicators developed for coastal waters can successfully be applied to the deep sea, and the reference directions (Jennings & Dulvy 2005; Shin et al. 2005) are the same.

6.4. Macroecological patterns

Another potential indicator that I have tested in the deep sea is based on the generally positive relationship between local abundance and regional occupancy (Chapter 5; Gaston et al. 2000). The abundance–occupancy relationship (AOR) can be calculated at the interspecific level, where abundance and occupancy are calculated on average for each species and analysed across species, or at the intraspecific level, when abundance and occupancy are calculated yearly and analysed for each species separately. The intraspecific AOR therefore captures some change over time in assemblages, and the form and strength of the interspecific relationship can also be analysed over time in order to investigate responses to exploitation or environmental change (Fisher & Frank 2004; Webb, Noble & Freckleton 2007). These positive relationships are remarkably consistent across ecosystems and taxa (Blackburn, Cassey & Gaston 2006) and can be important for conservation due to the theory of "double jeopardy" (Lawton 1993, 1996; Gaston 1999). This is when any reduction in the range of a species results in a disproportionate loss of that species, due to the accompanying decline in local abundance at remaining occupied sites (Gaston et al. 2000; Freckleton et al. 2005).

I found that the positive interspecific AOR holds true for deep-sea demersal fish and that the intraspecific AOR is also mostly positive, but only significantly so in less than a quarter of species. The form and strength of the interspecific AOR did not change over the course of the study period, which is surprising as fishing pressure has altered enough over the timescale of the study to show changes in other aspects of community structure (Chapter 4). This implies that the AOR is not a good indicator for deep-sea community health in the medium term, and indeed current predictions of the effect of environmental change on the form of the AOR are not consistent (Fisher & Frank 2005; Webb, Noble & Freckleton 2007). In this case, the lack of change in the form of the AOR may be because fishing did not have a large enough impact on species abundances or distribution to show an effect, despite altering the body size structure of the system. This could occur if fishing pressure was not high enough to cause any local extinctions, or if any changes in the abundance of large individuals was balanced out by recruitment of small individuals, hence not impacting the measure of local abundance used in the AOR. An alternative method could be to use average local biomass rather than numerical abundance, as this would capture any changes that occur due to a reduction in the size of individuals. Additionally, AORs can also be calculated using size classes rather than species identity to separate individuals (Webb et al. 2011). It would be interesting to reveal whether the AOR based on sizes shows more change over time than the AOR based on species abundances.

One way in which I propose we incorporate depth further into ecological methods is to use what I term the bathymetric AOR. This is the inter- or intraspecific relationship between local abundance and proportional occupancy of depths. I found that it showed the same positive relationship as the interspecific spatial AOR, and also mostly showed positive intraspecific relationships, though fewer were significant than for the spatial AOR. This analysis has implications for understanding the depth distributions of deep-sea species. Little is known about deep-sea fish physiology due to the problems with studying them in a laboratory environment, and our understanding of physiological impacts on depth ranges is currently limited to differences between slope and abyssal species (Carney 2005; Yancey et al. 2014). The positive interspecific bathymetric AOR could imply that species depth ranges are not determined by physiological or evolutionary adaptations, but rather by average abundance and local effects such as interspecific competition. Intraspecific AORs are also mostly positive when occupancy is based on depth, which could imply that all species have broad potential depth ranges that are constricted in some years due to fluctuating effects of local factors such as fishing pressure, temperature or resource availability. Those species with no bathymetric AOR could be already occupying their full depth range and cannot expand in years that are good for abundance due to their physiology.

Together, all of these results imply that there may be another layer to the "double jeopardy" situation (Lawton 1993, 1996; Gaston 1999) whereby species are triply vulnerable as they occupy a small geographic space and narrow depth range when they have low local abundance. In addition, deeper-living species exhibit more positive AORs, meaning that they are more vulnerable to double, or triple, jeopardy than species that live further up the slope. In other words, a vulnerable species could decrease in abundance, geographical range and depth range in response to an external pressure, hence potentially increasing extinction risk in three ways. This adds a macroecological explanation to the decreased resilience of deep-sea species due to their life histories (Drazen & Haedrich 2012; Norse et al. 2012).

Bathymetric AORs can be used alongside spatial AORs in any study of a marine system where data are taken from different depths in order to account for the fact that distribution varies vertically as well as horizontally in fish. Ideally, future work could incorporate both spatial and bathymetric distribution into one abundance–occupancy analysis so that one relationship can be examined rather than two. Additionally, it would be interesting to calculate the bathymetric AOR based on size classes, as was suggested for the spatial AOR. Understanding how the depth occupancy of different size classes changes would add another layer to our understanding of size-based metrics along a depth gradient.

6.5. Future directions

Our understanding of the deep sea has increased over recent decades and this new knowledge has allowed us to challenge long-held beliefs about the characteristics of the system (Danovaro, Snelgrove & Tyler 2014). We now need to focus on expanding our knowledge of the traits of deep-sea species, particularly those relating to behaviour and ecology. This is a feat that is becoming possible with the use of deep-sea submersibles and remotely operated underwater vehicles (Kaiser et al. 2011). Linkages between the demersal environment and other assemblages, such as pelagic fish and benthic invertebrates, should also not be disregarded. Future work should aim to establish how the whole system interacts, including how species move up and down the slope or between the demersal and pelagic environments. We also must start to link our improved mapping of the sea floor (Danovaro, Snelgrove & Tyler 2014) with the movement of individuals and how these different habitats are utilised.

The following specific research questions are suggested as a continuation of the work presented in this thesis:

- Can we apply fractional size to other taxa such as invertebrates and to illustrate recovery of other fish communities?
- Does body size decrease beyond 2000 m?
- How do assemblage functional traits change with depth when they are analysed at the individual, rather than species, level?
- What are the predicted unexploited values of size-based indicators at different depths?
- How much fishing pressure can be sustained in the deep sea at different depths?
- Do the positive spatial and bathymetric abundance–occupancy relationships hold when individuals are classified in terms of size class rather than species, and does this relationship change over a period of exploitation?

6.6. Concluding remarks

This work has revealed some surprising characteristics of the deep sea. It has high functional and species diversity, it can recover from fishing pressure, and it follows generalised macroecological patterns. Two potentially important ecological advances have been made: the development of a new size-based indicator, fractional size, and the analysis of abundance–occupancy relationships based on depth distributions. Body size remains an all-important factor in the marine environment and is a good descriptor of community recovery and change with depth. Depth impacts every characteristic of assemblages on the continental slope examined here and deep-sea communities cannot be assumed to group together. This thesis sets the stage for further depth-resolved deep-sea ecology.

7. References

Andersen, K.H. & Pedersen, M. (2010) Damped trophic cascades driven by fishing in model marine ecosystems. *Proceedings of the Royal Society B*, 277, 795–802.

Anderson, C.N.K., Hsieh, C-H., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M. & Sugihara, G. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature*, 452, 835–839.

Angel, M.V. (1993) Biodiversity of the pelagic ocean. *Conservation Biology*, 7, 760–772.

Angilletta, M.J., Steury, T.D. & Sears, M.W. (2004) Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, 44, 498–509.

Auguie, B. (2016) gridExtra: miscellaneous functions for “grid” graphics. R package version 2.2.0. https://CRAN.R-project.org/package=gridExtra

Bailey, D.M., Collins, M.A., Gordon, J.D.M., Zuur, A.F. & Priede, I.G. (2009) Long-term changes in deep-water fish populations in the northeast Atlantic: a deeper reaching effect of fisheries? *Proceedings of the Royal Society B*, 276, 1965–1969.

Barrett, J.H., Locker, A.M. & Roberts, C.M. (2004) The origins of intensive marine fishing in medieval Europe: the English evidence. *Proceedings of the Royal Society B*, 271, 2417–2421.

Basson, M., Gordon, J.D.M., Large, P., Lorance, P., Pope, J. & Rackham, B. (2001) *The Effects of Fishing on Deep-water Fish Species to the West of Britain*. Final Report for Joint Nature Conservation Committee.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Paya, I., Sainsbury, K., Sanchez, F. & Zwanenburg, K. (2000) Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science*, 57, 558–571.

Blackburn, T.M., Cassey, P. & Gaston, K.J. (2006) Variations on a theme: sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. *Journal of Animal Ecology*, 75, 1426–1439.

Blackburn, T.M., Gaston, K.J., Greenwood, J.J.D. & Gregory, R.D. (1998) The anatomy of the interspecific abundance-range size relationship for the British avifauna: II. Temporal dynamics. *Ecology Letters*, 1, 47–55.

Blanchard, J.L., Dulvy, N.K., Jennings, S., Ellis, J.R., Pinnegar, J.K., Tidd, A. & Kell, L.T. (2005a) Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES Journal of Marine Science*, 62, 405–411.

Blanchard, J.L., Mills, C., Jennings, S., Fox, C.J., Rackham, B.D., Eastwood, P.D. & O'Brien, C.M. (2005b) Distribution-abundance relationships for North Sea Atlantic cod (*Gadus morhua*): observation versus theory. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 2001–2009.

Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M-J. & Benoit, E. (2009) How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology*, 78, 270–280.

Blanchard, J.L., Law, R., Castle, M.D., Matthew, D. & Jennings, S. (2011) Coupled energy pathways and the resilience of size-structured food webs. *Theoretical Ecology*, 4, 289–300.

de Boer, W.F. & Prins, H.H.T. (2002) The community structure of a tropical intertidal mudflat under human exploitation. *ICES Journal of Marine Science*, 59, 1237–1247.

Boettiger, C., Lang, D.T. & Wainwright, P.C. (2012) rfishbase: R Interface to FishBASE. R package version 0.2-1. https://github.com/ropensci/rfishbase.

Borregaard, M.K. & Rahbek, C. (2010) Causality of the relationship between geographic distribution and species abundance. *The Quarterly Review of Biology*, 85, 3–25.

Botsford, L.W., Castilla, J.C. & Peterson, C.H. (1997) The management of fisheries and marine ecosystems. *Science*, 277, 509–515.

Boubee, J.A.T. & Ward, F.J. (1997) Mouth gape, food size, and diet of the common smelt *Retropinna retropinna* (Richardson) in the Waikato River system, North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 31, 147–154.

Boudreau, P.R. & Dickie, L.M. (1992) Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 1528–1538.

Bremner, J. (2008) Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology*, 366, 37–47.

Bridge, T.C.L., Luiz, O.J., Coleman, R.R., Kane, C.N. & Kosaki, R.K. (2016) Ecological and morphological traits predict depth-generalist fishes on coral reefs. *Proceedings of the Royal Society B*, 283, 20152332.

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, 124, 255–279.

Brown, A. & Thatje, S. (2014) Explaining bathymetric diversity patterns in marine benthic invertebrates and demersal fishes: physiological contributions to adaptation of life at depth. *Biological Reviews*, 89, 406–426.

Bulafu, C.E. (2015) Disturbance-driven variation in abundance-occupancy relationships over time in tropical forest fragments. *African Journal of Ecology*, 53, 502–511.

Campbell, N., Neat, F., Burns, F. & Kunzlik, P. (2010) Species richness, taxonomic diversity, and taxonomic distinctness of the deep-water demersal fish community on the Northeast Atlantic continental slope (ICES Subdivision VIa). *ICES Journal of Marine Science*, 68, 365–376.

Carney, R.S. (2005) Zonation of deep biota on continental margins. *Oceanography and Marine Biology – An Annual Review*, 43, 211–278.

Childress, J.J. (1995) Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trends in Ecology and Evolution*, 10, 30–36.

Clark, M. (2001) Are deepwater fisheries sustainable? The example of the orange roughy (*Hoplostethus atlanticus*) in New Zealand. *Fisheries Research*, 51, 123–135.

Clarke, K.R. & Warwick. R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. Primer-E Ltd, Plymouth.

Clavel. J., Poulet, N., Porcher, E., Blanchet, S., Grenouillet, G., Pavoine, S., Biton, A., Seon-Massin, N., Argillier, C., Daufresne, M., Teillac-Deschamps, P. & Julliard, R. (2013) A new freshwater biodiversity indicator based on fish community assemblages. *PLOS ONE*, 8, e80968.

Cochran, W.G. (1977) *Sampling Techniques*. Wiley, New York.

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldaña, J. (1993) Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, 62, 67–78.

Collins, M.A., Bailey D.M., Ruxton, G.D. & Priede, I.G. (2005) Trends in body size across an environmental gradient: A differential response in scavenging and non-scavenging demersal deep-sea fish. *Proceedings of the Royal Society of London B*, 272, 2051–2057.

Daan, N., Gislason, H., Pope, J.G. & Rice, J. C. (2005) Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES Journal of Marine Science*, 62, 177–188.

Danovaro, R., Snelgrove, P.V.R. & Tyler, P. (2014) Challenging the paradigms of deep-sea ecology. *Trends in Ecology and Evolution*, 29, 465–475.

Devine, J.A, Baker, K.D. & Haedrich, R.L. (2006) Deep-sea fishes qualify as endangered. *Nature*, 439, 29.

Dickie, L.M., Kerr, S.R. & Boudreau, P.R. (1987) Size-dependent processes underlying regularities in ecosystem structure. *Ecological Monographs*, 57, 233–250.

Drazen, J.C. & Haedrich, R.L. (2012) A continuum of life histories in deep-sea demersal fishes. *Deep-Sea Research I*, 61, 34–42.

Ellingsen, K.E. (2002) Soft-sediment benthic biodiversity on the continental shelf in relation to environmental variability. *Marine Ecology Progress Series*, 232, 15–27.

Elton, C.S. (1927) *Animal Ecology*. The MacMillan Company, New York.

Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., Sloat, L.L. & Savage, V.M. (2015) Scaling from traits to ecosystems: developing a general Trait Driver Theory via integrating trait-based and metabolic scaling theories. *Advances in Ecological Research*, 52, 249–318.

Faulks, L., Svanback, R., Ragnarsson-Stabo, H., Eklov, P. & Ostman, O. (2015) Intraspecific niche variation drives abundance-occupancy relationships in freshwater fish communities. *American Naturalist*, 186, 272–283.

Fenton, G.E., Short, S.A. & Ritz, D.A. (1991) Age-determination of orange roughy, *Hoplostethus atlanticus* (Pisces, Trachichthyidae) using Pb-210-Ra-226 disequilibria. *Marine Biology*, 109, 197–202.

Fisher, J.A.D. & Frank, K.T. (2004) Abundance-distribution relationships and conservation of exploited marine fishes. *Marine Ecology Progress Series*, 279, 201–213.

Fisher, J.A.D., Frank, K.T. & Leggett, W.C. (2010) Dynamic macroecology on ecological time-scales. *Global Ecology and Biogeography*, 19, 1–15.

Fisher, R., Leis, J.M., Clark, D.L. & Wilson, S.K. (2005) Critical swimming speeds of late-stage coral reef fish larvae: variation within species, among species and between locations. *Marine Biology*, 147, 1201–1212.

Fort, H. (2014) Quantitative predictions of pollinators' abundance from qualitative data on their interactions with plants and evidences of emergent neutrality. *Oikos*, 123, 1469–1478.

Freckleton, R.P., Gill, J.A., Noble, D. & Watkinson, A.R. (2005) Large-scale population dynamics, abundance-occupancy relationships and the scaling from local to regional population size. *Journal of Animal Ecology*, 74, 353–364.

Frisk, M.G., Duplisea, D.E. & Trenkel, V.M. (2011) Exploring the abundance-occupancy relationships for the Georges Bank finfish and shellfish community from 1963 to 2006. *Ecological Applications*, 21, 227–240.

Froese, R. & Binohlan, C. (2000) Empirical relationships to estimate asymptotic length, length at first maturity, and length at maximum yield per recruit in fishes, with a simple method to evaluate length frequency data. *Journal of Fish Biology*, 56, 758–773.

Froese, R. & Pauly, D. (2014) FishBase. World Wide Web electronic publication. www.fishbase.org.

Froese, R. & Pauly, D. (2016) FishBase. World Wide Web electronic publication. www.fishbase.org.

Frost, M.T., Attrill, M.J., Rowden, A.A. & Foggo, A. (2004) Abundance-occupancy relationships in macrofauna on exposed sandy beaches: patterns and mechanisms. *Ecography*, 27, 643–649.

Fung, T., Farnsworth, K.D., Reid, D.G. & Rossberg, A.G. (2012) Recent data suggest no further recovery in North Sea Large Fish Indicator. *ICES Journal of Marine Science*, 69, 235–239.

Gambi, C., Pusceddu, A., Benedetti-Cecchi, L. & Danovaro, R. (2014) Species richness, species turnover and functional diversity in nematodes of the deep Mediterranean Sea: searching for drivers at different spatial scales. *Global Ecology and Biogeography*, 23, 24–39.

Gaston, K.J. (1999) Implications of interspecific and intraspecific abundance-occupancy relationships. *Oikos*, 86, 195–207.

Gaston, K.J. & Blackburn, T.M. (1996) Range size-body size relationships: evidence of scale dependence. *Oikos*, 75, 479–485.

Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Interspecific abundance-range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, 66, 579–601.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M. & Lawton, J.H. (2000) Abundance-occupancy relationships. *Journal of Applied Ecology*, 37, 39–59.

Gatz, D.F. & Smith, L. (1995) The standard error of a weighted mean concentration – I. Bootstrapping vs other methods. *Atmospheric Environment*, 29, 1185–1193.

Genner, M.J., Sims, D.W., Southward, A.J., Budd, G.C., Masterson, P., Mchugh, M., Rendle, P., Southall, E.J., Wearmouth, V.J. & Hawkins, S.J. (2010) Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology*, 16, 517–527.

Glover, A.G. & Smith, C.R. (2003) The deep-sea floor ecosystem: current status and prospects of anthropogenic change by the year 2025. *Environmental Conservation*, 30, 219–241.

Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M. & Evans-Freke, I. (1998) Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, 281, 2045–2047.

Gordon, J.D.M. (2003) The Rockall Trough, Northeast Atlantic: the cradle of deep-sea biological oceanography that is now being subjected to unsustainable fishing activity. *Journal of Northwest Atlantic Fishery Science*, 31, 57–83.

Gordon, J.D.M. & Bergstad, O.A. (1992) Species composition of demersal fish in the Rockall Trough, north-eastern Atlantic, as determined by different trawls. *Journal of the Marine Biological Association of the United Kingdom*, 72, 213–230.

Gordon, J.D.M. & Duncan, J.A.R. (1985) The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, Northeastern Atlantic. *Progress in Oceanography*, 15, 37–69.

Gordon, J.D.M. & Duncan, J.A.R. (1987) Deep-sea bottom-living fishes at two repeat stations at 2200 and 2900m in the Rockall Trough, northeastern Atlantic Ocean. *Marine Biology*, 96, 309–325.

Greenstreet, S.P.R., Rogers, S.I., Rice, J.C., Piet, G.J., Guirey, E.J., Fraser, H.M. & Fryer, R.J. (2011) Development of the EcoQO for the North Sea fish community. *ICES Journal of Marine Science*, 68, 1–11.

Guedo, D.D. & Lamb, E.G. (2013) Temporal changes in abundance-occupancy relationships within and between communities after disturbance. *Journal of Vegetation Science*, 24, 607–615.

Haedrich, R.L. & Rowe, G.T. (1977) Megafaunal biomass in the deep sea. *Nature*, 269, 41–42.

Hall, S.J., Collie, J.S., Duplisea, D.E., Jennings, S., Bravington, M. & Link, J. (2006) A length-based multi-species model for evaluating community responses to fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 1344–1359.

Hallett, C.S. & Daley, R.K. (2011) Feeding ecology of the southern lanternshark (*Etmopterus baxteri*) and the brown lanternshark (*E. unicolor*) off southeastern Australia. *ICES Journal of Marine Science*, 68, 157–165.

Harfoot, M.B.J., Newbold, T., Tittensor, D.P., Emmott, S., Hutton, J., Lyutsarev, V., Smith, M.J., Scharlemann, J.P.W. & Purves, D.W. (2014) Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. *PLOS Biology*, 12, e1001841.

Hazel, J.R. & Williams, E.E. (1990) The role of alterations in membrane lipid composition in enabling physiological adaptations of organisms to their physical environment. *Progress in Lipid Research*, 29, 167–227.

Head, A.W., Hardin, J.S. & Adolph, S.C. (2012) Methods for estimating peak physiological performance and correlating performance measures. *Environmental and Ecological Statistics*, 19, 127–137.

Heath, M.R., Neat, F.C., Pinnegar, K.J., Reid, D.G., Sims, D.W. & Wright, P.J. (2012) Review of climate change impacts on marine fish and shellfish around the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22, 337–367.

Hilario, A., Cunha, M.R., Genio, L., Marcal, A.R., Ravara, A., Rodrigues, C.F. & Wiklund, H. (2015) First clues on the ecology of whale falls in the deep Atlantic Ocean: results from an experiment using cow carcasses. *Marine Ecology – An Evolutionary Perspective*, 36, 82–90.

Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54, 427–432.

Hixon, M.A., Johnson, D.W. & Sogard, S.M. (2014) BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, 71, 2171–2185.

Holliday, N.P., Cunningham, S.A., Johnson, C., Gary, S.F., Griffiths, C., Read, J.F. & Sherwin, T. (2015) Mutidecadal variability of potential temperature, salinity, and transport in the eastern subpolar North Atlantic. *Journal of Geophysical Research: Oceans*, 120, 5945–5967.

Holt, A.R., Gaston, K.J. & He, F. (2002) Occupancy-abundance relationships and spatial distribution: a review. *Basic and Applied Ecology*, 3, 1–13.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous inference in general parametric models. *Biometric Journal*, 50, 346–363.

Houle, J.E., Farnsworth, K.D., Rossberg, A.G. & Reid, D.G. (2012) Assessing the sensitivity and specificity of fish community indicators to management action. *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 1065–1079.

Hsieh, C-H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M. & Sugihara, G. (2006) Fishing elevates variability in the abundance of exploited species. *Nature*, 443, 859–862.

Hsieh, C-H., Yamauchi, A., Nakazawa, T. & Wang, W-F. (2010) Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, 72, 165–178.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, USA.

Hubbell, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, 19, 166–172.

Hutchings, J.A. & Myers, R.A. (1994) What can be learned from the collapse of a renewable resource – Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 2126–2146.

ICES. (2007) *Report of the Working Group on the Ecosystem Effects of Fishing Activities (WGECO)*. 11-18th April, Copenhagen, Denmark. ICES CM 2007/ACE:04.

ICES. (2008) *Report of the Working Group on the Biology and Assessment of Deep-Sea Fisheries Resources (WGDEEP)*. 3rd-10th March, Copenhagen, Denmark. ICES CM 2008/ACOM 14.

ICES. (2012) *Manual for the International Bottom Trawl Surveys*, Series of ICES Survey Protocols, SISP 1-IBTS VIII, pp. 35-37.

ICES. (2013) *Report of the Working Group on the Ecosystem Effects of Fishing Activities (WGECO)*. 1-8th May, Copenhagen, Denmark. ICES CM 2013/ACOM:25.

Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J.L., Bode, A. & Echevarria, F. (2014) Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Communications*, 5, 3271.

Jackson, J.B.C. 2010. The future of the oceans past. *Philosophical Transactions of the Royal Society B*, 365, 3765–3778.

Jennings, S. & Blanchard, J.L. (2004) Fish abundance with no fishing: predictions based on macroecological theory. *Journal of Animal Ecology*, 73, 632–642.

Jennings, S. & Dulvy, N.K. (2005) Reference points and reference directions for size-based indicators of community structure. *ICES Journal of Marine Science*, 62, 397–404.

Jennings, S., Pinnegar, J.K., Polunin, N.V.C. & Boon, T.W. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70, 934–944.

Jobling, M. (1983) Growth studies with fish – overcoming the problems of size variation. *Journal of Fish Biology*, 22, 153–157.

Kaiser, M.J., Attrill, M.J., Jennings, S., Thomas, D.N., Barnes, D.K.A., Brierley, A.S., Hiddink, J.G., Kaartokallio, H., Polunin, N.V.C. & Raffaelli, D.G. (2011) The Deep Sea, in *Marine Ecology: Processes, Systems and Impacts*, 2nd edition. pp. 251–276. Oxford University Press, UK.

Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164.

Kerby, T.K., Cheung, W.L. & Engelhard, G.H. (2012) The United Kingdom's role in North Sea demersal fisheries: a hundred year perspective. *Reviews in Fish Biology and Fisheries*, 22, 612–634.

Koslow, J.A. (1996) Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. *Journal of Fish Biology*, 49 (Supplement A), 54–74.

Koslow, J.A., Boehlert, G.W., Gordon, J.D.M., Haedrich, R.L., Lorance, P. & Parin, N. (2000) Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science*, 57, 548–557.

Laguionie-Marchais, C., Billett, D.S.M., Paterson, G.L.D., Ruhl, H.A., Soto, E.H., Smith Jr., K.L. & Thatje, S. (2013) Inter-annual dynamics of abyssal polychaete communities in the North East Pacific and North East Atlantic – A family level study. *Deep Sea Research I*, 75, 175–186.

Laliberté, E. & Shipley, B. (2011) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-11.

Lalli, C.M. & Parsons, T.R. (1993) Deep Sea Ecology, in *Biological Oceanography: An Introduction*. pp. 238–250. Pergamon, Elsevier Science Ltd, Oxford, UK.

Lampitt, R.S., Salter, I., de Cuevas, B.A., Hartman, S., Larkin, K.E. & Pebody, C.A. (2010) Long-term variability of downward particle flux in the deep northeast Atlantic: causes and trends. *Deep Sea Research II*, 57, 1346–1361.

Larcombe, J. & Begg, G. (2007) Fishery Status Reports 2007. *Status of fish stocks managed by the Australian Government*. Australian Government Bureau of Rural Sciences, Department of Agriculture, Fisheries and Forestry, pp. 249.

Law, R., Plank, M.J. & Kolding, J. (2012) On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES Journal of Marine Science*, 69, 602–614.

Lawton, J.H. (1993) Range, population abundance and conservation. *Trends in Ecology and Evolution*, 8, 409–413.

Lawton, J.H. (1996) Population abundances, geographic ranges and conservation: 1994 Witherby Lecture. *Bird Study*, 43, 3–19.

Leinster, T. & Cobbold, C.A. (2012) Measuring diversity: the importance of species similarity. *Ecology*, 93, 477–489.

Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271–280.

Legendre, P. & Legendre, L. (2012) *Numerical Ecology*. 3rd Edition, Elsevier.

Lin, H-Y., Shiao, J-C., Chen, Y-G. & Iizuka, Y. (2012) Ontogenetic vertical migration of grenadiers revealed by otolith microstructures and stable isotopic composition. *Deep-Sea Research I*, 61, 123–130.

Litchman, E., de Tezanos Pinto, P., Klausmeier, C.A., Thomas, M.K. & Yoshiyama, K. (2010) Linking traits to species diversity and community structure in phytoplankton. *Hydrobiologia*, 653, 5–28.

Lorance, P. & Dupouy, H. (2001) CPUE abundance indices of the main target species of the French deep-water fishery in ICES Sub-areas V-VII. *Fisheries Research*, 51, 137–149.

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, 101, 377–385.

Macpherson, E. (2003) Species range size distributions for some marine taxa in the Atlantic Ocean: effect of latitude and depth. *Biological Journal of the Linnaean Society*, 80, 437–455.

Macpherson, E. & Duarte, C.M. (1991) Bathymetric trends in demersal fish size: is there a general relationship? *Marine Ecology Progress Series*, 71, 103–112.

Magnussen, E. (2002) Demersal fish assemblages of Faroe Bank: species composition, distribution, biomass spectrum and diversity. *Marine Ecology Progress Series*, 238, 211–225.

Magnússon, J.V. (2001) Distribution and some other biological parameters of two morid species *Lepidion eques* (Gunther, 1887) and *Antimora rostrata* (Gunther, 1878) in Icelandic waters. *Fisheries Research*, 51, 267–281.

Marshall, C.T. & Browman H.I. (2007) Disentangling the causes of maturation trends in exploited fish populations. *Marine Ecology Progress Series*, 335, 249–251.

Marshall, C.T. & Frank, K.T. (1995) Density-dependent habitat selection by juvenile haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Sciences*, 52, 1007–1017.

Mauchline, J. & Gordon, J.D.M. (1991) Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology Progress Series*, 74, 109–115.

May, R.M., Beddington, J.R., Clark, C.W., Holt, S.J. & Laws, R.M. (1979) Management of multispecies fisheries. *Science*, 205, 267–277.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21, 178–185.

Michener, R.H. & Schell, D.M. (1994) Stable isotope ratios as tracers in marine and aquatic food webs. In *Stable Isotopes in Ecology and Environmental Science*, pp. 138–157. Eds: Lajtha, K. & Michener, R.H. Blackwell Scientific Publications, Oxford.

Mindel, B.L., Webb, T.J., Neat, F.C. & Blanchard, J.L. (2016) A trait-based metric sheds new light on the nature of the body size-depth relationship in the deep sea. *Journal of Animal Ecology*, 85, 427–436.

Moorad, J.A., Promislow, D.E.L., Flesness, N. & Miller, R.A. (2012) A comparative assessment of univariate longevity measures using zoological animal records. *Aging Cell*, 11, 940–948.

Morato, T., Watson, R., Pitcher, T.J. & Pauly, D. (2006) Fishing down the deep. *Fish and Fisheries*, 7, 24–34.

Mouillot, D., Dumay, O. & Tomasini, J.A. (2007) Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine, Coastal and Shelf Science*, 71, 443–456.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, 28, 167–177.

Møller, A.P. (2013) Biological consequences of global change for birds. *Integrative Zoology*, 8, 136–144.

Myers, R.A., Barrowman, N.J., Hoenig, J.M. & Qu, Z. (1996) The collapse of cod in Eastern Canada: the evidence from tagging data. *ICES Journal of Marine Science*, 53, 629–640.

Nanola, C.L., Alino, P.M. & Carpenter, K.E. (2011) Exploitation-related reef fish species richness depletion in the epicenter of marine biodiversity. *Environmental Biology of Fishes*, 90, 405–420.

Neat, F.C. & Burns, F. (2010) Stable abundance, but changing size structure in grenadier fishes (Macrouridae) over a decade (1998–2008) in which deepwater fisheries became regulated. *Deep-Sea Research I*, 57, 434–440.

Neat, F.C. & Campbell, N. (2013) Proliferation of elongate fishes in the deep sea. *Journal of Fish Biology*, 83, 1576–1591.

Nicholson, M.D. & Jennings, S. (2004) Testing candidate indicators to support ecosystem-based management: the power of monitoring surveys to detect temporal trends in fish community metrics. *ICES Journal of Marine Science*, 61, 35–42.

Noronha, A.C. (1925) *A Fish from Madeira: The Black Scabbardfish or* Aphanopus carbo. Porto, Portugal, pp. 15.

Norse, E.A., Brooke, S., Cheung, W.W.L., Clark, M.R., Ekeland, I., Froese, R., Gjerde, K.M., Haedrich, R.L., Heppell, S.S., Morato, T., Morgan, L.E., Pauly, D., Sumaila, R. & Watson, R. (2012) Sustainability of deep-sea fisheries. *Marine Policy*, 36, 307–320.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) vegan: Community Ecology Package. R package version 2.10-10. http://CRAN.R-project.org/package=vegan.

Pante, E. & Simon-Bouhet, B. (2013) marmap: A package for importing, plotting and analyzing bathymetric and topographic data in R. *PLoS ONE*, 8, e73051.

Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science*, 39, 175–192.

Pauly, D. (1989) A simple index of metabolic level in fishes. *Fishbyte*, 7, 22.

Pauly, D. (2008) Global fisheries: a brief review. *Journal of Biological Research*, 9, 3–9.

Pauly, D. (2009) Beyond duplicity and ignorance in global fisheries. *Scientia Marina*, 73, 215–224.

Pawar, S., Woodward, G. & Dell, A.I. (2015) Trait-based ecology – from structure to function. *Advances in Ecological Research*, 52, 2–367.

Petchey, O.L. & Gaston, K.J. (2002) Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5, 402–411.

Piet, G.J. (1998) Ecomorphology of a size-structured tropical freshwater fish community. *Environmental Biology of Fishes*, 51, 67–86.

Piet, G.J. & Jennings, S. (2005) Response of potential fish community indicators to fishing. *ICES Journal of Marine Science*, 62, 214–225.

Platt, T. & Denman, K. (1977) Organization in pelagic ecosystem. *Helgolander Wissenschaftliche Meeresuntersuchungen*, 30, 575–581.

Polloni, P., Haedrich, R., Rowe, G. & Clifford, C.H. (1979) The size-depth relationship in deep ocean animals. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, 64, 39–46.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A. & Richardson, A.J. (2013) Global imprint of climate change on marine life. *Nature Climate Change*, 3, 919–925.

Pope, J.G., Rice, J.C., Daan, N., Jennings, S. & Gislason, H. (2006) Modelling an exploited marine fish community with 15 parameters – results from a simple size-based model. *ICES Journal of Marine Science*, 63, 1029–1044.

Powles, H., Bradford, M.J., Bradford, R.G., Doubleday, W.G., Innes, S. & Levings, C.D. (2000) Assessing and protecting endangered marine species. *ICES Journal of Marine Science*, 57, 669–676.

Price, A.R.G., Keeling, M.J. & O'Callaghan, C.J. (1999) Ocean-scale patterns of 'biodiversity' of Atlantic asteroids determined from taxonomic distinctness and other measures. *Biological Journal of the Linnean Society*, 66, 187–203.

Priede, I.G. & Froese, R. (2013) Colonization of the deep sea by fishes. *Journal of Fish Biology*, 83, 1528–1550.

Priede, I.G., Godbold, J.A., King, N.J., Collings, M.A., Bailey, D.M. & Gordon, J.D.M. (2010) Deep-sea demersal fish species richness in the Porcupine Seabight, NE Atlantic Ocean: global and regional patterns. *Marine Ecology*, 31, 247–260.

Priede, I. G., Godbold, J.A., Niedzielski, T., Collins, M.A., Bailey, D.M., Gordon, J.D.M. & Zuur, A.F. (2011) A review of the spatial extent of fishery effects and species vulnerability of the deep-sea demersal fish assemblage of the Porcupine Seabight, Northeast Atlantic Ocean (ICES Subarea VII). *ICES Journal of Marine Science*, 68, 281–289.

le Quesne, W.J.F. & Jennings, S. (2012) Predicting species vulnerability with minimal data to support rapid risk assessment of fishing impacts on biodiversity. *Journal of Applied Ecology*, 49, 20–28.

Quintana, X.D., Arim, M., Badosa, A., Blanco, J.M., Boix, D., Brucet, S., Compte, J., Egozcue, J.J., de Eyto, E., Gaedke, U., Gascon, S., de Sola, L.G., Irvine, K., Jeppesen, E., Laurisden, T.L., Loez-Flores, R., Mehner, T., Romo, S. & Sondergaard, M. (2015) Predation and competition effects on the size diversity of aquatic communities. *Aquatic Sciences*, 77, 45–57.

R Core Team. (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

R Core Team. (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R., Levin, L.A., Arbizu, P.M., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B.E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A. & Vecchione, M. (2010) Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. *Biogeosciences*, 7, 2851–2899.

Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L., Menot, L., Rowden, A.A., Smith, C.R. & Van Dover, C.L. (2011) Man and the last great wilderness: human impact on the deep sea. *PLOS ONE*, 6, e22588.

Reecht, Y., Rochet, M.J., Trenkel, V.M., Jennings, S. & Pinnegar, J.K. (2013) Use of morphological characteristics to define functional groups of predatory fishes in the Celtic Sea. *Journal of Fish Biology*, 83, 355–377.

Reuman, D.C., Mulder, C., Raffaelli, D. & Cohen, J.E. (2008) Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecology Letters*, 11, 1216–1228.

Roark, E.B., Guilderson, T.P., Dunbar, R.B., Fallon, S.J. & Mucciarone, D.A. (2009) Extreme longevity in proteinaceous deep-sea corals. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 5204–5208.

Rudolf, V.H.W. & Rasmussen, N.L. (2013a) Population structure determines functional differences among species and ecosystem processes. *Nature Communications*, 4, 2318.

Rudolf, V.H.W. & Rasmussen, N.L. (2013b) Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology*, 94, 1046–1056.

Rudolf, V.H.W., Rasmussen, N.L., Dibble, C.J. & Van Allen, B.G. (2014) Resolving the roles of body size and species identity in driving functional diversity. *Proceedings of the Royal Society B*, 281, 20133203.

Ruhl, H.A. (2008) Community change in the variable resource habitat of the abyssal northeast Pacific. *Ecology*, 89, 991–1000.

Rutterford, L.A., Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J.L., Schoen, P.J., Sims, D.W., Tinker, J. & Genner, M.J. (2015) Future fish distributions constrained by depth in warming seas. *Nature Climate Change*, 5, 569–574.

Sambilay, V.C. Jr. (1990) Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. *Fishbyte*, 8, 16–20

Scharf, F.S., Juanes, F. & Rountree, R.A. (2000) Predator size – prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*, 208, 229–248.

Scheffer, M. & van Nes, E.H. (2006) Self-organised similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences*, 103, 6230–6235.

Scheffer, M., Vergnon, R., van Nes, E.H., Cuppen, J.G.M., Peeters, E.T.H.M., Leijs, R. & Nilsson, A.N. (2015) The evolution of functionally redundant species; evidence from beetles. *PLOS ONE*, 10, e0137974.

Schleuter, D., Daufresne, M., Massol, F & Argillier, C. (2010) A user's guide to functional diversity indices. *Ecological Monographs*, 80, 469–484.

Schmitz, O.J., Buchkowski, R.W., Burghardt, K.T. & Donihue, C.M. (2015) Functional traits and trait-mediated interactions: connecting community-level interactions with ecosystem functioning. *Advances in Ecological Research*, 52, 319–343.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671–675.

Shannon, C.E. (1948) A mathematical theory of communication. *Bell System Technical Journal*, 27, 379–423.

Sheldon, R.W., Prakash, A. & Sutcliffe, W.H. (1972) The size distribution of particles in the ocean. *Limnology & Oceanography*, 17, 327–340.

Shephard, S., Fung, T., Rossberg, A.G., Farnsworth, K.D., Reid, D.G., Greenstreet, S.P.R. & Warnes, S. (2013) Modelling recovery of Celtic Sea demersal fish community size structure. *Fisheries Research*, 140, 91–95.

Shin, Y-J, Rochet, M-J, Jennings, S., Field, J.G. & Gislason, H. (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science*, 62, 384–396.

Sibbing, F.A. & Nagelkerke, L.A.J. (2001) Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries*, 10, 393–437.

Snelgrove, P.V.R. & Haedrich, R.L. (1985) Structure of the deep demersal fish fauna off Newfoundland. *Marine Ecology Progress Series*, 27, 99–107.

Soto, E.H., Paterson, G.L.J., Billett, D.S.M., Hawkins, L.E., Galeron, J. & Sibuet, M. (2010) Temporal variability in polychaete assemblages of the abyssal NE Atlantic Ocean. *Deep Sea Research II*, 57, 1396–1405.

STECF. (2013) *Scientific, Technical and Economic Committee for Fisheries - Evaluation of fishing effort regimes in European waters - Part 1.* Publications Office of the European Union, Luxembourg, EUR 26901EN, JRC 83567.

Stefanescu, C., Rucabado, R. & Lloris, D. (1992) Depth-size trends in western Mediterranean demersal deep-sea fishes. *Marine Ecology Progress Series*, 81, 205–213.

Stein, D.L., Tissot, B.N., Hixon, M.A. & Barss, W.A. (1992) Fish habitat associations on a deep reef at the edge of the Oregon continental shelf. *Fishery Bulletin*, 90, 540–551.

Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoldi, L., Becerro, M.A., Campbell, S.J., Dawson, T.P., Navarrete, S.A., Soler, G.A., Strain, E.M.A., Willis, T.J. & Edgar, G.J. (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, 501, 539–542.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A. & Wiegand, T. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101, 58–67.

Tamburri, M.N. & Barry, J.P. (1999) Adaptations for scavenging by three diverse bathyal species, *Eptatretus stouti*, *Neptunea amianta* and *Orchomene obtusus*. *Deep Sea Research I*, 46, 2079–2093.

Tilman, D. (2001) Functional diversity. In *Encyclopedia of Biodiversity*, pp. 109–120. Ed: Levin, S.A. Academic Press, San Diego, CA.

Tittensor, D.P., Micheli, F., Nystrom, M. & Worm, B. (2007) Human impacts on the species-area relationship of reef fish assemblages. *Ecology Letters*, 10, 760–772.

Tolimieri, N. & Levin, P.S. (2006) Assemblage structure of eastern pacific groundfishes on the US continental slope in relation to physical and environmental variables. *Transactions of the American Fisheries Society*, 135, 317–332.

Trenkel, V.M., Beecham, J.A., Blanchard, J.L., Edwards, C.T.T. & Lorance, P. (2013) Testing CPUE-derived spatial occupancy as an indicator for stock abundance: application to deep-sea stocks. *Aquatic Living Resources*, 26, 319–332.

Trueman. C.N., Rickaby, R.E.M. & Shephard, S. (2013) Thermal, trophic and metabolic life histories of inaccessible fishes revealed from stable-isotope analyses: a case study using orange roughy *Hoplostethus atlanticus*. *Journal of Fish Biology*, 83, 1613–1636.

Trueman, C.N., Johnston, G., O'Hea, B. & MacKenzie, K.M. (2014) Trophic interactions of fish communities at midwater depths enhance long-term carbon storage and benthic production on continental slopes. *Proceedings of the Royal Society B*, 281, 20140669.

Tyler, E.H.M., Somerfield, P.J., Vanden Berghe, E., Bremner, J., Jackson, E., Langmead, O., Palomares, M.L.D. & Webb, T.J. (2012) Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. *Global Ecology and Biogeography*, 21, 922–934.

Vergnon, R., Dulvy, N.K. & Freckleton, R.P. (2009) Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecology Letters*, 12, 1079–1090.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, 116, 882–892.

Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J. & Kattge, J. (2014) The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13690–13696.

Walker, B.H. (1992) Biodiversity and ecological redundancy. *Conservation Biology*, 6, 18–23.

Webb, T.J. (2012) Marine and terrestrial ecology: unifying concepts, revealing differences. *Trends in Ecology and Evolution*, 27, 535–541.

Webb, T.J., Noble, D. & Freckleton, R.P. (2007) Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. *Journal of Animal Ecology*, 76, 123–134.

Webb, T.J., Tyler, E.H.M. & Somerfield, P.J. (2009) Life history mediates large-scale population ecology in marine benthic taxa. *Marine Ecology Progress Series*, 396, 293–306.

Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I. & LeRoy Poff, N. (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology letters*, 13, 267–83.

Webb, T.J., Dulvy, N.K., Jennings, S. & Polunin, N.V.C. (2011) The birds and the seas: body size reconciles differences in the abundance-occupancy relationship across marine and terrestrial vertebrates. *Oikos*, 120, 537–549.

Weiher, E. & Keddy, P.A. (1995) Rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, 74, 159–164.

Wickham, H. (2009) ggplot2: elegant graphics for data analysis. Springer, New York.

Wilding, T.A. & Nickell, T.D. (2013) Changes in benthos associated with mussel (*Mytilus edulis* L.) farms on the West coast of Scotland. *PLOS ONE*, 8, e68313.

Winemiller, K.O. & Rose, K.A. (1992) Patterns of life-history diversification in North American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2196–2218.

Wood, S.N. (2006) *Generalized Additive Models: An Introduction with R*. Chapman & Hall/CRC, Boca Raton, USA.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, 73, 3–36.

WoRMS Editorial Board. (2013) World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ.

Yancey, P.H. & Siebenaller, J.F. (1999) Trimethylamine oxide stabilizes teleost and mammalian lactate dehydrogenases against inactivation by hydrostatic pressure and trypsinolysis. *Journal of Experimental Biology*, 202, 3597–3603.

Yancey, P.H., Gerringer, M.E., Drazen, J.C., Rowden, A.A. & Jamieson, A. (2014) Marine fish may be biochemically constrained from inhabiting the deepest ocean depths. *Proceedings of the National Academy of Sciences*, 111, 4461–4465.

Ye, L., Chang, C.Y., Garcia-Comas, C., Gong, G.C. & Hsieh, C.H. (2013) Increasing zooplankton size diversity enhances the strength of top-down control on phytoplankton through diet niche partitioning. *Journal of Animal Ecology*, 82, 1052–1060.

Yeh, J. & Drazen, J.C. (2009) Depth zonation and bathymetric trends of deep-sea megafaunal scavengers of the Hawaiian Islands. *Deep Sea Research I*, 56, 251–269.

Zintzen, V., Anderson, M.J., Roberts, C.D. & Diebel, C.E. (2011) Increasing variation in taxonomic distinctness reveals clusters of specialists in the deep sea. *Ecography*, 34, 306–317.

Zuckerberg, B., Porter, W.F. & Corwin, K. (2009) The consistency and stability of abundance-occupancy relationships in large-scale population dynamics. *Journal of Animal Ecology*, 78, 172–181.

8. Supporting Information

Table S1. Concatenation of hauls into stations (survey data 1998–2012). Hauls were grouped into stations if they were repeated across years in the same ICES (International Council for the Exploration of the Sea) rectangle and at depths within 100 m of each other.

Station number	ICES statistical rectangle	Number of years represented	Mean and range of depths represented (m)
1	38D9	6	1500 (1500-1500)
2	38D9	1	1800 (1800-1800)
3	39D9	3	417 (400-430)
4	39D9	4	500 (500-500)
5	39D9	2	615 (600-630)
6	39D9	1	750 (750-750)
7	39D9	1	991 (991-991)
8	39D9	7	1007 (1000-1050)
9	39D9	1	1396 (1396-1396)
10	39D9	2	1500 (1500-1500)
11	39D9	2	1800 (1800-1800)
12	44D9	1	2000 (2000-2000)
13	40E0	4	427 (400-450)
14	40E0	4	728 (700-750)
15	40E0	4	982 (950-1000)
16	41E0	9	503 (500-528)
17	41E0	1*	715 (700-730)
18	41E0	3	868 (850-890)
19	41E0	8	1012 (1000-1050)
20	41E0	1	1070 (1070-1070)
21	41E0	9	1503 (1497-1530)
22	41E0	3	1800 (1750-1850)
23	42E0	9	517 (500-550)
24	42E0	2	607 (592-622)
25	42E0	4	757 (709-800)
26	42E0	1	890 (890-890)
27	42E0	11	1005 (966-1050)
28	42E0	2	1259 (1237-1300)
29	42E0	10	1501 (1500-1508)
30	42E0	7	1800 (1800-1800)
31	43E0	3	417 (409-425)
32	43E0	6	513 (500-525)
33	43E0	2	561 (552-570)
34	43E0	1	696 (696-696)
35	43E0	2	760 (750-770)
36	43E0	2	825 (800-850)
37	43E0	8	999 (990-1005)
38	43E0	8	1500 (1500-1500)
39	43E0	1	2030 (2030-2030)
40	44E0	3	303 (300-310)

Table S1. Continued.

Station number	**ICES statistical rectangle**	**Number of years represented**	**Mean and range of depths represented (m)**
41	44E0	1	400 (400-400)
42	44E0	6	513 (500-540)
43	44E0	8	612 (580-650)
44	44E0	2	700 (700-700)
45	44E0	5	812 (760-850)
46	44E0	2	900 (900-900)
47	44E0	9	1004 (994-1050)
48	44E0	2	1250 (1250-1250)
49	44E0	10	1503 (1500-1540)
50	44E0	3	1650 (1650-1650)
51	44E0	3	1800 (1800-1800)
52	45E0	2	348 (345-350)
53	45E0	3	527 (500-550)
54	45E0	8	612 (570-650)
55	45E0	1	852 (852-852)
56	45E0	9	1001 (1000-1015)
57	45E0	1	1134 (1134-1134)
58	45E0	9	1503 (1500-1529)
59	45E0	2	1700 (1650-1750)
60	45E0	2	1800 (1800-1800)
61	46E1	1	300 (300-300)
62	46E1	2	510 (500-550)
63	46E1	4	603 (597-613)
64	46E1	7	1003 (1000-1034)
65	46E1	6	1501 (1500-1504)
66	47E1	2	1500 (1500-1500)
67	46E2	5	518 (500-550)
68	46E2	1	660 (660-660)
69	46E2	4	1000 (1000-1000)
70	46E2	2	1059 (1058-1060)
71	47E2	3	1033 (1000-1050)
72	47E2	1	1086 (1086-1086)

*Station where a haul of similar depth and location was repeated in the same year, resulting in an average being taken across hauls, but only one year being represented. All other stations listed as representing only one year consisted of a single haul.

Table S2. Conversion of lengths measured on the survey to total length. The body plan of many deep-sea species is such that their tails break off easily when caught by a trawl (ICES 2012). Without its tail, an individual's total length (TL; tip of snout to end of tail) cannot be measured, so standard length (SL; tip of snout to start of tail), pre-anal fin length (PAFL; tip of snout to first ray of anal fin), or pre-supra caudal fin length (PSCFL; tip of snout to start of supra caudal fin) is measured, depending on what species it is (ICES 2012). These values were then multiplied by a conversion factor calculated from a subset of survey data in order to predict the total length including the tail. If it was not known what measurement was taken, the conversion factor of a species of the same genus was used. If there was more than one related species' conversion factor then an average was used.

Taxon	Measured length	Conversion factor
Aldrovandia affinis	TL	1
Aldrovandia phalacra	TL	1
Alepocephalus spp.	SL	1.121333333
Alepocephalus agassizii	SL	1.139
Alepocephalus australis	SL	1.148
Alepocephalus bairdii	SL	1.089
Alepocephalus productus	SL	1.121333333
Alepocephalus rostratus	SL	1.127
Amblyraja jensenii	TL	1
Anarhichas denticulatus	TL	1
Anoplogaster cornuta	TL	1
Antimora rostrata	TL	1
Aphanopus carbo	TL	1
Apristurus aphyodes	TL	1
Apristurus laurussonii	TL	1
Apristurus madaerensis	TL	1
Apristurus manis	TL	1
Apristurus melanoasper	TL	1
Apristurus microps	TL	1
Apristurus spp.	TL	1
Arctozenus risso	TL	1
Argentina silus	TL	1
Argentina sphyraena	TL	1
Bajacalifornia megalops	SL	1.068
Barbantus curvifrons	SL	1.152
Bathygadus melanobranchus	TL	1
Bathylagus euryops	TL	1
Bathypterois dubius	TL	1

Table S2. Continued.

Taxon	**Measured length**	**Conversion factor**
Bathyraja richardsoni	TL	1
Bathyraja spp.	TL	1
Bathysaurus ferox	TL	1
Bathytroctes microlepis	SL	1.139
Benthodesmus simonyi	TL	1
Beryx decadactylus	TL	1
Brama brama	TL	1
Brosme brosme	TL	1
Callionymus lyra	TL	1
Callionymus maculatus	TL	1
Capros aper	TL	1
Cataetyx laticeps	TL	1
Cataetyx spp.	TL	1
Centrolophus niger	TL	1
Centrophorus granulosus	TL	1
Centrophorus squamosus	TL	1
Centroscyllium fabricii	TL	1
Centroscymnus coelolepis	TL	1
Centroselachus crepidater	TL	1
Chaunax pictus	TL	1
Chimaera monstrosa	PSCFL	1.31
Chimaera opalescens	PSCFL	1.31
Chimaeriformes spp.	TL	1
Coelorinchus caelorhincus	PAFL	2.82
Coelorinchus labiatus	PAFL	2.5
Conger conger	TL	1
Conocara macropterum	SL	1.118
Conocara murrayi	SL	1.118
Coryphaenoides carapinus	PAFL	3.79
Coryphaenoides guentheri	PAFL	3.25
Coryphaenoides mediterraneus	PAFL	4.5
Coryphaenoides rupestris	PAFL	4.33
Cottunculus thomsonii	TL	1
Dalatias licha	TL	1
Deania calcea	TL	1
Deania profundorum	TL	1
Dipturus batis	TL	1
Dipturus intermedia	TL	1
Diretmus argenteus	TL	1
Echiodon drummondii	TL	1
Enchelyopus cimbrius	TL	1
Epigonus telescopus	TL	1

Table S2. Continued.

Taxon	**Measured length**	**Conversion factor**
Etmopterus princeps	TL	1
Etmopterus spinax	TL	1
Eutrigla gurnardus	TL	1
Gadiculus argenteus	TL	1
Gadomus longifilis	PAFL	3.2
Gadus morhua	TL	1
Gaidropsarus argentatus	TL	1
Gaidropsarus macrophthalmus	TL	1
Gaidropsarus vulgaris	TL	1
Galeus melastomus	TL	1
Galeus murinus	TL	1
Glyptocephalus cynoglossus	TL	1
Guttigadus latifrons	TL	1
Halargyreus johnsonii	TL	1
Halosauropsis macrochir	TL	1
Harriotta haeckeli	TL	1
Harriotta raleighana	PSCFL	1.29
Helicolenus dactylopterus	TL	1
Hexanchus griseus	TL	1
Hippoglossoides platessoides	TL	1
Hippoglossus hippoglossus	TL	1
Histiobranchus bathybius	TL	1
Holtbyrnia anomala	SL	1.206
Holtbyrnia macrops	SL	1.206
Hoplostethus atlanticus	TL	1
Hoplostethus mediterraneus	TL	1
Hydrolagus affinis	PSCFL	1.07
Hydrolagus mirabilis	PSCFL	1.28
Hydrolagus pallidus	PSCFL	1.08
Hymenocephalus italicus	TL	1
Ilyophis blachei	TL	1
Ilyophis brunneus	TL	1
Lepidion eques	TL	1
Lepidorhombus boscii	TL	1
Lepidorhombus whiffiagonis	TL	1
Leucoraja circularis	TL	1
Leucoraja fullonica	TL	1
Leucoraja naevus	TL	1
Limanda limanda	TL	1
Lophius budegassa	TL	1
Lophius piscatorius	TL	1
Lycenchelys sarsii	TL	1

Table S2. Continued.

Taxon	**Measured length**	**Conversion factor**
Lycodes pallidus	TL	1
Lycodes spp.	TL	1
Lycodes terraenovae	TL	1
Lycodonus flagellicauda	TL	1
Lyconus brachycolus	TL	1
Macrouridae spp.	TL	1
Macrourus berglax	TL	1
Malacocephalus laevis	PAFL	4.57
Malacoraja kreffti	TL	1
Maulisia mauli	TL	1
Maulisia microlepis	TL	1
Melanogrammus aeglefinus	TL	1
Melanolagus bericoides	TL	1
Merluccius merluccius	TL	1
Microstomus kitt	TL	1
Molva dypterygia	TL	1
Molva molva	TL	1
Mora moro	TL	1
Myxine ios	TL	1
Neocyttus helgae	TL	1
Neoraja caerulea	TL	1
Nesiarchus nasutus	TL	1
Nessorhamphus ingolfianus	TL	1
Nezumia aequalis	PAFL	3.78
Nezumia sclerorhynchus	PAFL	3.98
Normichthys operosus	SL	1.138
Notacanthus bonaparte	TL	1
Notacanthus chemnitzii	TL	1
Pachycara bulbiceps	TL	1
Pachycara crassiceps	TL	1
Paraliparis spp.	TL	1
Paraliparis bathybius	TL	1
Phycidae	TL	1
Phycis blennoides	TL	1
Platyberyx opalescens	TL	1
Platytroctes apus	SL	1.17
Platytroctidae spp.	TL	1
Pleuronectes platessa	TL	1
Pollachius virens	TL	1
Polyacanthonotus rissoanus	TL	1
Pseudotriakis microdon	TL	1
Raja clavata	TL	1

Table S2. Continued.

Taxon	**Measured length**	**Conversion factor**
Raja montagui	TL	1
Rajella bathyphila	TL	1
Rajella bigelowi	TL	1
Rajella fyllae	TL	1
Rajella kukujevi	TL	1
Rajella ravidula	TL	1
Rajidae spp.	TL	1
Reinhardtius hippoglossoides	TL	1
Rhinochimaera atlantica	PSCFL	1.39
Rouleina attrita	SL	1.103
Rouleina maderensis	SL	1.181
Sagamichthys schnakenbecki	SL	1.17
Schedophilus medusophagus	TL	1
Scopelogadus beanii	TL	1
Scyliorhinus canicula	TL	1
Scymnodon ringens	TL	1
Searsia koefoedi	SL	1.17
Sebastes marinus	TL	1
Sebastes viviparus	TL	1
Serrivomer beanii	TL	1
Serrivomer brevidentatus	TL	1
Simenchelys parasitica	TL	1
Somniosus rostratus	TL	1
Spectrunculus grandis	TL	1
Squalus acanthias	TL	1
Synaphobranchus kaupii	TL	1
Trachipterus arcticus	TL	1
Trachyrincus murrayi	PAFL	3.1
Trachyscorpia cristulata	TL	1
Trisopterus esmarkii	TL	1
Venefica proboscidea	TL	1
Xenodermichthys copei	SL	1.155
Zoarcidae spp.	TL	1

References

ICES. (2012) *Manual for the International Bottom Trawl Surveys*. Series of ICES Survey Protocols. SISP 1-IBTS VIII.

Appendix 1. The robustness of L_{max} allocation.

As explained in the main body of the thesis, where observed size exceeded L_{max} from FishBase (Froese & Pauly 2014), L_{max} was said to be the maximum observed size from the survey. Although it is not ideal to have to use a combination of sources in this way, I would like to justify this approach as follows. Firstly, as the deep sea is not well known, even comprehensive databases such as FishBase (Froese & Pauly 2014) do not always contain accurate information about deep-sea species. In these instances, a comprehensive trawl survey, such as the one conducted by Marine Scotland and analysed in this thesis, represents more accurate and up-to-date knowledge of deep-sea species.

Given this, it may be suggested that it is better to use survey-derived maximums throughout the study, and not incorporate FishBase values at all. I argue that this is not the case because by using a smaller value of observed maximum, when I know from FishBase that they are capable of reaching larger sizes, then I am actively ignoring information that I have. Also, by using only observed maxima, I would be restricting the relevance of this study to my study site, and this time period, only. By using a global maximum, where possible, I allow for changes in L_{max} over space and time. For example, fractional size can capture changes in body size that have occurred due to fishing pressure with respect to a historical maximum size, and can capture if some populations consist only of young individuals that then move elsewhere to breed. Additionally, by suggesting the method of using FishBase-derived as well as survey-derived values, I encourage readers who wish to use my approach in other study areas to use a globally applicable value if they are lucky enough to have such data for their study species.

I further assure the reader of the robustness of my chosen approach by presenting the results of changes in fractional size with depth (see *Chapter 2: A trait-based metric sheds new light on the nature of the body size–depth relationship in the deep sea*) when all species are included as laid out in the main manuscript, compared with the results when species with maximum sizes greater than those listed on FishBase are excluded from the analysis (Fig. S1). In other words, I present the results from what would be an 'ideal' scenario, with L_{max} being accurately listed on FishBase for all species studied. I show that the patterns are virtually identical when all species are included and when only species for which L_{max} on FishBase is greater than observed L_{max} are included (Fig. S1). This fact is supported by the statistical results in Table S3, which were produced using the methods described in the main manuscript.

Finally, all values of L_{max} from FishBase and from the survey are listed in Table S4.

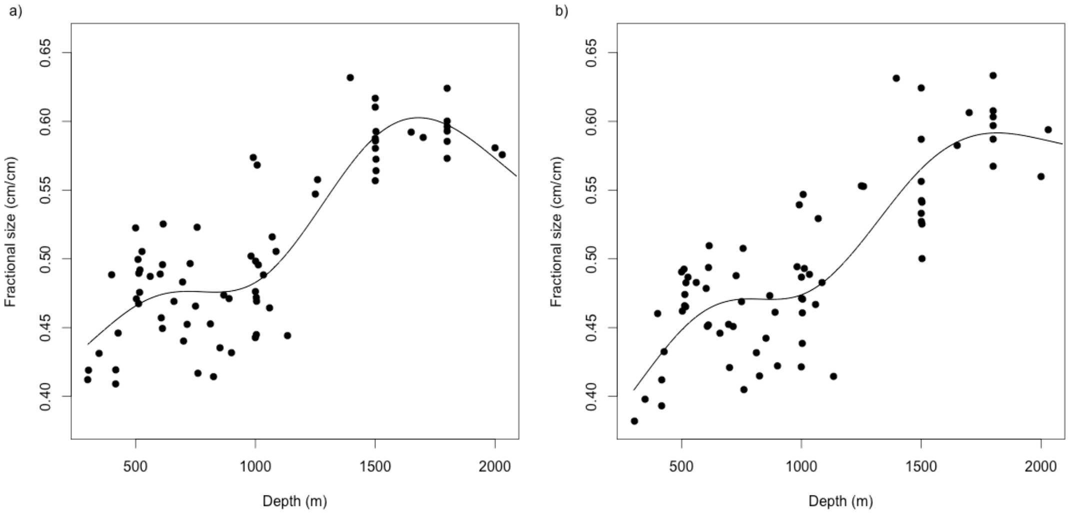

Fig. S1. The relationship between fractional size and depth using two methods: a) all species are included b) only those species for which FishBase L_{max} exceeded observed maximum size. The line represents the fitted GAM (Table S3).

Table S3. Results of Redundancy Analysis and Generalised Additive Models using two methods: all species included, and only species for which FishBase L_{max} exceeded observed maximum size included.

Statistical method	**Test statistic extracted**	**Results for all species**	**Results for species for which FishBase L_{max} exceeded observed maximum size**
RDA	Pseudo-F	25	23
	d.f.	1,70	1,70
	R^2	0.26	0.24
	p	0.001	0.001
GAM	F	50	42
	e.d.f.	3.9	3.8
	R^2	0.74	0.70
	p	<0.001	<0.001

Table S4. FishBase and survey-derived maximum lengths for all taxa caught on the survey between 1998–2012. Taxa for which observed size exceeded L_{max}, resulting in maximum observed size being treated as the new L_{max}, are highlighted.

Taxon	L_{max} from FishBase (cm; May 2014)	Maximum size from survey (cm)
Aldrovandia affinis	55	21
Aldrovandia phalacra	50	44
Alepocephalus spp.	100	49.3
Alepocephalus agassizii	79	123
Alepocephalus australis	60	50.5
Alepocephalus bairdii	100	127.4
Alepocephalus productus	41	38.1
Alepocephalus rostratus	50	58.6
Amblyraja jensenii	85	105
Anarhichas denticulatus	180	106
Anoplogaster cornuta	18	29
Antimora rostrata	75	69
Aphanopus carbo	110	129
Apristurus aphyodes	85	69
Apristurus laurussonii	68	74
Apristurus madaerensis	68	64
Apristurus manis	85	96
Apristurus melanoasper	76.1	78
Apristurus microps	61	85
Apristurus spp.	85	75
Arctozenus risso	30	16
Argentina silus	70	51
Argentina sphyraena	35	27
Bajacalifornia megalops	40	61.9
Barbantus curvifrons	13.1	16.1
Bathygadus melanobranchus	50	8
Bathylagus euryops	13	22
Bathypterois dubius	20.5	29
Bathyraja richardsoni	175	123
Bathyraja spp.	175	125
Bathysaurus ferox	64	65
Bathytroctes microlepis	32.3	30.8
Benthodesmus simonyi	130	85
Beryx decadactylus	100	52
Brama brama	100	53
Brosme brosme	120	86
Callionymus lyra	30	22
Callionymus maculatus	16	12
Capros aper	30	14
Cataetyx laticeps	65	101
Cataetyx spp.	65	14
Centrolophus niger	150	67
Centrophorus granulosus	160	86
Centrophorus squamosus	164	138
Centroscyllium fabricii	107	89
Centroscymnus coelolepis	120	122
Centroselachus crepidater	130	91
Chaunax pictus	40	7

Table S4. Continued.

Taxon	**L_{max} from FishBase (cm; May 2014)**	**Maximum size from survey (cm)**
Chimaera monstrosa	150	108.7
Chimaera opalescens	109.8	99.6
Chimaeriformes spp.	150	70
Coelorinchus caelorhincus	48	42.3
Coelorinchus labiatus	50	42.5
Conger conger	300	158
Conocara macropterum	34	42.5
Conocara murrayi	34	50.3
Coryphaenoides carapinus	45	208.5
Coryphaenoides guentheri	50	52
Coryphaenoides mediterraneus	73	103.5
Coryphaenoides rupestris	110	125.6
Cottunculus thomsonii	35	45
Dalatias licha	182	147
Deania calcea	122	112
Deania profundorum	79	91
Dipturus batis	285	121
Dipturus intermedia	285	107
Diretmus argenteus	27.6	10
Echiodon drummondii	30	29
Enchelyopus cimbrius	41	12
Epigonus telescopus	75	57
Etmopterus princeps	75	80
Etmopterus spinax	60	60
Eutrigla gurnardus	60	28
Gadiculus argenteus	15	17
Gadomus longifilis	30	19.2
Gadus morhua	200	86
Gaidropsarus argentatus	35	15
Gaidropsarus macrophthalmus	25	20
Gaidropsarus vulgaris	60	42
Galeus melastomus	75	75
Galeus murinus	63	46
Glyptocephalus cynoglossus	60	50
Guttigadus latifrons	18.2	10
Halargyreus johnsonii	56	52
Halosauropsis macrochir	90	75
Harriotta haeckeli	65	48
Harriotta raleighana	120	104.5
Helicolenus dactylopterus	47	38
Hexanchus griseus	482	150
Hippoglossoides platessoides	82.6	25
Hippoglossus hippoglossus	470	70
Histiobranchus bathybius	137	79
Holtbyrnia anomala	25	33.8
Holtbyrnia macrops	20	33.8
Hoplostethus atlanticus	75	68
Hoplostethus mediterraneus	42	18
Hydrolagus affinis	130	126.3
Hydrolagus mirabilis	38	84.5

Table S4. Continued.

Taxon	**L_{max} from FishBase (cm; May 2014)**	**Maximum size from survey (cm)**
Hydrolagus pallidus	130	122
Hymenocephalus italicus	25	4
Ilyophis blachei	79.2	84
Ilyophis brunneus	58	53
Lepidion eques	44	41
Lepidorhombus boscii	40	47
Lepidorhombus whiffiagonis	60	56
Leucoraja circularis	120	72
Leucoraja fullonica	120	101
Leucoraja naevus	71	64
Limanda limanda	40	14
Lophius budegassa	100	51
Lophius piscatorius	200	147
Lycenchelys sarsii	20	14
Lycodes pallidus	26	45
Lycodes spp.	26	40
Lycodes terraenovae	45.2	66
Lycodonus flagellicauda	19.9	23
Lyconus brachycolus	52.5	19
Macrouridae spp.	110	155
Macrourus berglax	110	3
Malacocephalus laevis	60	54.8
Malacoraja kreffti	70	56
Maulisia mauli	20	17
Maulisia microlepis	25.5	25
Melanogrammus aeglefinus	112	76
Melanolagus bericoides	20	16
Merluccius merluccius	140	105
Microstomus kitt	65	31
Molva dypterygia	155	143
Molva molva	200	131
Mora moro	80	64
Myxine ios	57	58
Neocyttus helgae	30.5	31
Neoraja caerulea	30	36
Nesiarchus nasutus	130	88
Nessorhamphus ingolfianus	59.8	69
Nezumia aequalis	36	37.8
Nezumia sclerorhynchus	36	31.8
Normichthys operosus	16.4	27.3
Notacanthus bonaparte	26	65
Notacanthus chemnitzii	120	117
Pachycara bulbiceps	51.5	50
Pachycara crassiceps	54	56
Paraliparis spp.	25.3	21
Paraliparis bathybius	25.3	20
Phycidae	110	31
Phycis blennoides	110	74
Platyberyx opalescens	18.5	24
Platytroctes apus	18	21.1

Table S4. Continued.

Taxon	**L_{max} from FishBase (cm; May 2014)**	**Maximum size from survey (cm)**
Platytroctidae spp.	27	8
Pleuronectes platessa	100	28
Pollachius virens	130	86
Polyacanthonotus rissoanus	9.5	56
Pseudotriakis microdon	269	183
Raja clavata	105	83
Raja montagui	80	51
Rajella bathyphila	90	93
Rajella bigelowi	55	53
Rajella fyllae	60	55
Rajella kukujevi	90	83
Rajella ravidula	70	52
Rajidae spp.	285	22
Reinhardtius hippoglossoides	80	97
Rhinochimaera atlantica	140	139
Rouleina attrita	48	57.4
Rouleina maderensis	32	55.5
Sagamichthys schnakenbecki	27	23.4
Schedophilus medusophagus	51	61
Scopelogadus beanii	12.2	32
Scyliorhinus canicula	100	75
Scymnodon ringens	110	111
Searsia koefoedi	15	16.4
Sebastes marinus mentella	58	50
Sebastes viviparus	35	38
Serrivomer beanii	78	100
Serrivomer brevidentatus	60	50
Simenchelys parasitica	61	30
Somniosus rostratus	143	126
Spectrunculus grandis	127	59
Squalus acanthias	160	78
Synaphobranchus kaupii	100	81
Trachipterus arcticus	300	174
Trachyrincus murrayi	37	65.1
Trachyscorpia cristulata	50	4
Trisopterus esmarkii	35	26
Venefica proboscidea	100	164
Xenodermichthys copei	31	26.6
Zoarcidae spp.	54	52

References

Froese, R. & Pauly, D. (2014) FishBase. World Wide Web electronic publication. www.fishbase.org.

Table S5. Concatenation of hauls into stations (survey data 1998–2013). Hauls were grouped into stations if they were repeated across years in the same ICES (International Council for the Exploration of the Sea) rectangle and at depths within 100 m of each other

Station number	**ICES statistical rectangle**	**Number of years represented**	**Mean and range of depths represented (m)**
1	38D9	6	1500 (1500-1500)
2	38D9	1	1800 (1800-1800)
3	39D9	3	417 (400-430)
4	39D9	5	501 (500-506)
5	39D9	3	615 (600-630)
6	39D9	2	757 (750-764)
7	39D9	9	1000 (955-1050)
8	39D9	1	1264 (1264-1264)
9	39D9	1	1396 (1396-1396)
10	39D9	3	1506 (1500-1518)
11	39D9	3	1828 (1800-1884)
12	39D9	1	2067 (2067-2067)
13	40E0	4	427 (400-450)
14	40E0	4	728 (700-750)
15	40E0	4	982 (950-1000)
16	41D9	1	2027 (2027-2027)
17	41E0	10	502 (487-528)
18	41E0	1*	715 (700-730)
19	41E0	4	853 (809-890)
20	41E0	10	1011 (966-1050)
21	41E0	1	1070 (1070-1070)
22	41E0	10	1506 (1497-1530)
23	41E0	1	1750 (1750-1750)
24	41E0	3	1827 (1800-1850)
25	42D9	1	2017 (2017-2017)
26	42E0	10	517 (500-550)
27	42E0	2	607 (592-622)
28	42E0	4	757 (709-800)
29	42E0	1	890 (890-890)
30	42E0	11	1016 (1000-1093)
31	42E0	2	1259 (1237-1300)
32	42E0	11	1501 (1500-1508)
33	42E0	7	1800 (1800-1800)
34	43E0	3	417 (409-425)
35	43E0	7	510 (496-525)
36	43E0	2	561 (552-570)
37	43E0	1	696 (696-696)
38	43E0	2	760 (750-770)
39	43E0	2	825 (800-850)
40	43E0	8	999 (990-1005)
41	43E0	1	1075 (1075-1075)
42	43E0	8	1500 (1500-1500)
43	43E0	1	1570 (1570-1570)
44	43E0	1	1804 (1804-1804)
45	43E0	1	2030 (2030-2030)
46	44D9	1	2000 (2000-2000)

Table S5. Continued.

Station number	ICES statistical rectangle	Number of years represented	Mean and range of depths represented (m)
47	44E0	3	303 (300-310)
48	44E0	1	400 (400-400)
49	44E0	6	507 (500-540)
50	44E0	8	612 (580-650)
51	44E0	2	700 (700-700)
52	44E0	4	825 (800-850)
53	44E0	2	900 (900-900)
54	44E0	9	1005 (994-1050)
55	44E0	1	1081 (1081-1081)
56	44E0	2	1250 (1250-1250)
57	44E0	11	1506 (1500-1540)
58	44E0	2	1650 (1650-1650)
59	44E0	3	1810 (1800-1830)
60	45E0	2	348 (345-350)
61	45E0	4	523 (500-550)
62	45E0	8	612 (570-650)
63	45E0	1	852 (852-852)
64	45E0	10	1001 (1000-1015)
65	45E0	1	1134 (1134-1134)
66	45E0	10	1506 (1500-1529)
67	45E0	2	1717 (1700-1750)
68	45E0	3	1802 (1800-1805)
69	46E1	1	300 (300-300)
70	46E1	2	525 (500-550)
71	46E1	4	603 (597-613)
72	46E1	1	660 (660-660)
73	46E1	7	1005 (1000-1034)
74	46E1	6	1501 (1500-1504)
75	46E2	4	510 (500-540)
76	46E2	4	1000 (1000-1000)
77	46E2	2	1059 (1058-1060)
78	47E1	3	1496 (1489-1500)
79	47E2	2	1025 (1000-1050)
80	47E2	1	1086 (1086-1086)

*Station where a haul of similar depth and location was repeated in the same year, resulting in an average being taken across hauls, but only one year being represented. All other stations listed as representing only one year consisted of a single haul.

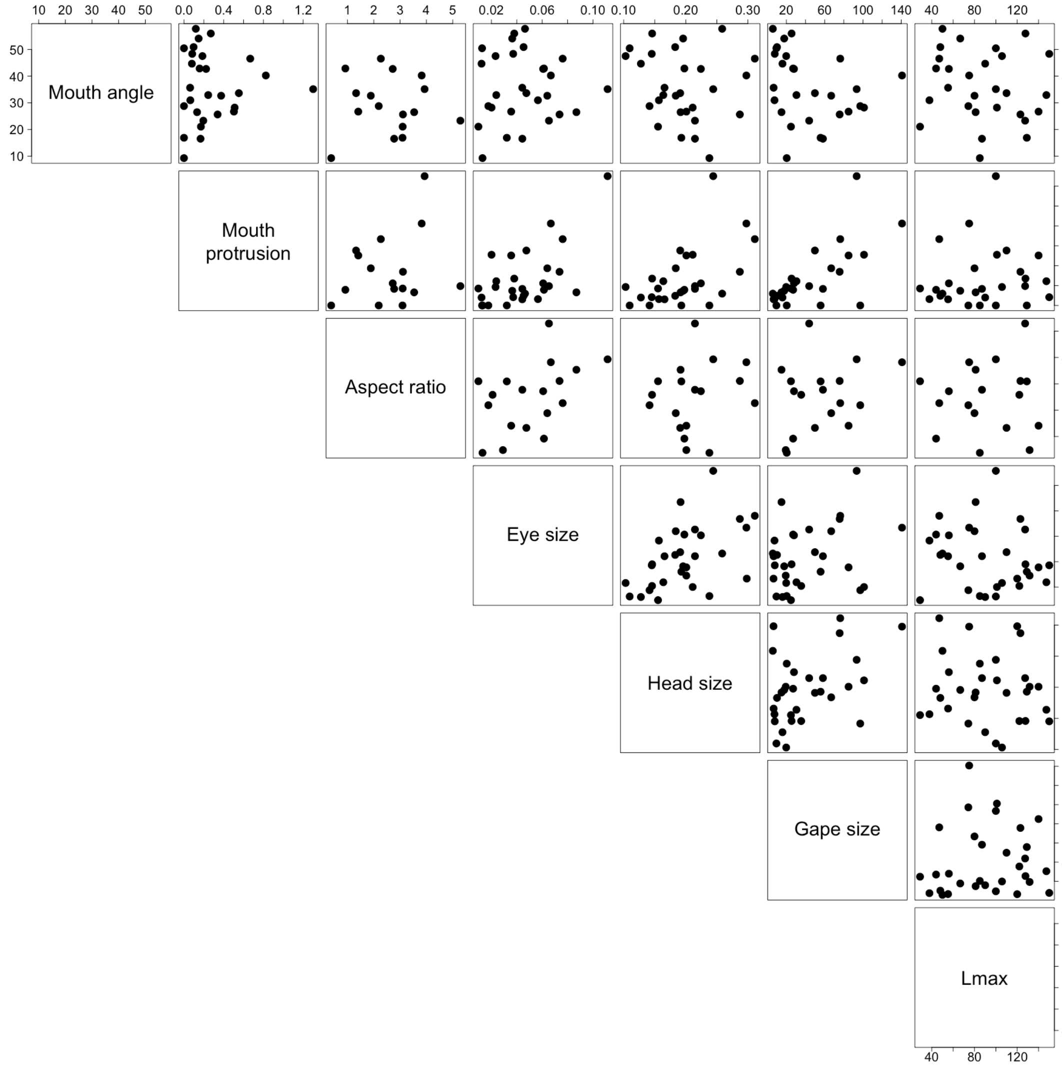

Fig. S2. The relationships between each of the continuous trait variables included in the calculation of functional diversity. Angle of mouth in relation to lateral line (°); relative surface area of mouth protrusion (cm^2/cm); caudal fin aspect ratio (cm^2/cm^2/cm); relative eye size (cm/cm); relative head size (cm/cm); relative gape size (mm^2/cm); L$_{max}$ (cm). Please refer to *Chapter 3: Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea* for definitions and calculations of traits. The statistical correlations between variables were all less than 0.7, and 15/21 correlations were less than 0.5.

Table S6 (on next page). The species caught on the survey, their conversion factors and maximum lengths.

The tails of many deep-sea species break off in the net when caught, so other standard measures of length are used rather than total length (ICES 2012). Conversion factors are then used to predict the total length of the individual including the tail. The types of lengths measured are: TL = total length, tip of snout to end of tail; SL = standard length, tip of snout to start of tail; PAFL = pre-anal fin length, tip of snout to first ray of anal fin; PSCFL = pre-supra caudal fin length, tip of snout to start of supra caudal fin. Conversion factors were mostly calculated from a subset of survey data for which total lengths were available. Species without conversion factors were assigned the average conversion factor across other species in that genus caught on the survey. FishBase (Froese & Pauly 2016) sometimes listed maximum standard lengths rather than maximum total lengths. These were converted to total lengths using the conversion factors calculated from survey data where possible. If there was no survey-derived conversion factor (because the survey recorded total length and FishBase stated standard length) then the conversion factor listed on FishBase was used. If neither conversion factor was available, an average conversion factor (1.16) calculated across all species caught on the survey for which there was a standard length conversion available was used. Conversion factors from FishBase are highlighted in yellow; average conversion factors are highlighted in orange.

'FishBase length' refers to the maximum length listed on FishBase (Froese & Pauly 2016) for that species. This is then converted to 'FishBase total maximum length' using the conversion factors and aforementioned methods. The 'survey maximum total length' is the length of the largest individual of that species caught throughout all years, depths and locations of the Marine Scotland deep-water trawl survey.

The species for which morphometric data were available, hence constituted the majority of analyses in *Chapter 3: Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea*, are highlighted in green.

References

ICES. 2012. *Manual for the International Bottom Trawl Surveys*. Series of ICES Survey Protocols. SISP 1-IBTS VIII.

Froese, R. & Pauly, D. (2016) FishBase. World Wide Web electronic publication. www.fishbase.org.

Table S6. Continued.

Marine Scotland code	**Species name**	**Length type - survey**	**Length type - FishBase**	**FishBase length (cm)**	**Conversion factor**	**FishBase maximum total length (cm)**	**Survey maximum total length (cm)**
AAF	Aldrovandia affinis	TL	TL	55	1	55	21
ALD	Aldrovandia phalacra	TL	TL	50	1	50	44
SMU	Alepocephalus spp.	SL	SL	100	1.121	112.1	49.533
AAG	Alepocephalus agassizii	SL	SL	79	1.139	89.981	123.012
AAU	Alepocephalus australis	SL	SL	60	1.148	68.88	50.512
SMO	Alepocephalus bairdii	SL	SL	100	1.089	108.9	127.413
ALP	Alepocephalus productus	SL	SL	41	1.121	45.961	38.2755
LSM	Alepocephalus rostratus	SL	SL	50	1.127	56.35	58.604
RJE	Amblyraja jensenii	TL	TL	85	1	85	105
JCA	Anarhichas denticulatus	TL	TL	180	1	180	106
EEU	Anguilliformes spp.	TL	TL	300	1	300	21
ACO	Anoplogaster cornuta	TL	TL	18	1	18	29
ARO	Antimora rostrata	TL	SL	75	1.16	87	69
BSC	Aphanopus carbo	TL	SL	110	1.056	116.16	129
AAP	Apristurus aphyodes	TL	TL	85	1	85	69
ALA	Apristurus laurussonii	TL	TL	76	1	76	74
AMA	Apristurus madaerensis	TL	TL	76	1	76	64
AMN	Apristurus manis	TL	TL	85	1	85	96
AME	Apristurus melanoasper	TL	TL	76.1	1	76.1	78
AMI	Apristurus microps	TL	TL	61	1	61	85
APU	Apristurus spp.	TL	TL	85	1	85	75
LBA	Arctozenus risso	TL	SL	30	1.065	31.95	23

Table S6. Continued.

Marine Scotland code	Species name	Length type - survey	Length type - FishBase	FishBase length (cm)	Conversion factor	FishBase maximum total length (cm)	Survey maximum total length (cm)
GAR	Argentina silus	TL	SL	70	1.158	81.06	52
LAR	Argentina sphyraena	TL	SL	35	1.16	40.6	29
BAM	Bajacalifornia megalops	SL	SL	40	1.068	42.72	61.944
BCU	Barbantus curvifrons	SL	SL	13.1	1.152	15.0912	16.128
BML	Bathygadus melanobranchus	TL	TL	50	1	50	30.6255
BAE	Bathylagus euryops	TL	TL	13	1	13	23
BDU	Bathypterois dubius	TL	SL	20.5	1.16	23.78	29
RRA	Bathyraja richardsoni	TL	TL	175	1	175	131
RBU	Bathyraja spp.	TL	TL	175	1	175	125
BFE	Bathysaurus ferox	TL	SL	64	1.16	74.24	65
BMI	Bathytroctes microlepis	SL	SL	32.3	1.139	36.7897	36.448
FRO	Benthodesmus simonyi	TL	SL	130	1.16	150.8	88
BDE	Beryx decadactylus	TL	TL	100	1	100	55
RBE	Brama brama	TL	TL	100	1	100	53
TOR	Brosme brosme	TL	TL	120	1	120	87
DRA	Callionymus lyra	TL	TL	30	1	30	22
SDR	Callionymus maculatus	TL	TL	16	1	16	12
BFI	Capros aper	TL	TL	30	1	30	14
CLA	Cataetyx laticeps	TL	TL	65	1	65	101
CAU	Cataetyx spp.	TL	TL	65	1	65	14
BLF	Centrolophus niger	TL	SL	150	1.166	174.9	67
CGR	Centrophorus granulosus	TL	TL	170	1	170	86

Table S6. Continued.

Marine Scotland code	Species name	Length type - survey	Length type - FishBase	FishBase length (cm)	Conversion factor	FishBase maximum total length (cm)	Survey maximum total length (cm)
LSQ	Centrophorus squamosus	TL	TL	164	1	164	138
CFA	Centroscyllium fabricii	TL	TL	107	1	107	91
PSH	Centroscymnus coelolepis	TL	TL	120	1	120	122
CCR	Centroselachus crepidater	TL	TL	130	1	130	91
CPI	Chaunax pictus	TL	TL	40	1	40	7
CHI	Chimaera monstrosa	PSCFL	TL	150	1.31	150	108.73
COP	Chimaera opalescens	PSCFL	TL	109.8	1.31	109.8	100.87
RAU	Chimaeriformes spp.	TL	TL	150	1	150	86.56666667
COC	Coelorinchus caelorhincus	PAFL	TL	48	2.82	48	47.94
SSG	Coelorinchus labiatus	PAFL	TL	50	2.5	50	43.75
CEE	Conger conger	TL	TL	300	1	300	158
LSH	Conocara macropterum	SL	SL	34	1.118	38.012	42.484
MUC	Conocara murrayi	SL	SL	34	1.118	38.012	50.31
CAG	Coryphaenoides carapinus	PAFL	TL	45	3.79	45	221.4666667
GGR	Coryphaenoides guentheri	PAFL	TL	50	3.25	50	55.25
MGR	Coryphaenoides mediterraneus	PAFL	TL	73	4.5	73	105.75
RNG	Coryphaenoides rupestris	PAFL	TL	110	4.33	110	127.735
PAS	Cottunculus thomsonii	TL	TL	43	1	43	45
DCH	Dalatias licha	TL	TL	182	1	182	147
SHS	Deania calcea	TL	TL	122	1	122	112
DPR	Deania profundorum	TL	TL	79	1	79	91
SKA	Dipturus batis	TL	TL	285	1	285	121

Table S6. Continued.

Marine Scotland code	Species name	Length type - survey	Length type - FishBase	FishBase length (cm)	Conversion factor	FishBase maximum total length (cm)	Survey maximum total length (cm)
SKF	Dipturus intermedia	TL	TL	285	1	285	144
DAR	Diretmus argenteus	TL	TL	27.6	1	27.6	10
PEF	Echiodon drummondii	TL	TL	30	1	30	29
BUL	Epigonus telescopus	TL	TL	75	1	75	59
EPR	Etmopterus princeps	TL	TL	75	1	75	84
VBE	Etmopterus spinax	TL	TL	60	1	60	65
GGU	Eutrigla gurnardus	TL	TL	60	1	60	31
SPO	Gadiculus argenteus	TL	TL	15	1	15	18
GLO	Gadomus longifilis	PAFL	TL	30	3.2	30	20.8
COD	Gadus morhua	TL	TL	200	1	200	86
SRO	Gaidropsarus argentatus	TL	SL	35	1.16	40.6	15
BER	Gaidropsarus macrophthalmus	TL	TL	25	1	25	20
TBR	Gaidropsarus vulgaris	TL	TL	60	1	60	42
BMD	Galeus melastomus	TL	TL	90	1	90	79
GMU	Galeus murinus	TL	TL	63	1	63	64
WIT	Glyptocephalus cynoglossus	TL	SL	60	1.18	70.8	50
LLA	Guttigadus latifrons	TL	SL	18.2	1.16	21.112	13
HAF	Halargyreus johnsonii	TL	TL	56	1	56	52
HAM	Halosauropsis macrochir	TL	TL	90	1	90	75
HRH	Harriotta haeckeli	TL	TL	65	1	65	67.08
HRA	Harriotta raleighana	PSCFL	TL	120	1.29	120	104.49
BLM	Helicolenus dactylopterus	TL	TL	47	1	47	38

Table S6. Continued.

Marine Scotland code	Species name	Length type - survey	Length type - FishBase	FishBase length (cm)	Conversion factor	FishBase maximum total length (cm)	Survey maximum total length (cm)
SGS	Hexanchus griseus	TL	TL	482	1	482	154
LRD	Hippoglossoides platessoides	TL	TL	82.6	1	82.6	36
HAL	Hippoglossus hippoglossus	TL	TL	470	1	470	125
DAE	Histiobranchus bathybius	TL	TL	137	1	137	79
HAN	Holtbyrnia anomala	SL	SL	25	1.206	30.15	33.768
HOM	Holtbyrnia macrops	SL	SL	20	1.206	24.12	33.768
ORO	Hoplostethus atlanticus	TL	TL	75	1	75	68
HME	Hoplostethus mediterraneus	TL	SL	42	1.328	55.776	30
HYA	Hydrolagus affinis	PSCFL	TL	130	1.07	130	131.61
HMI	Hydrolagus mirabilis	PSCFL	SL	41	1.28	52.48	84.48
HPA	Hydrolagus pallidus	PSCFL	SL	41	1.08	44.28	122.04
IGR	Hymenocephalus italicus	TL	TL	25	1	25	30.6255
IBL	Ilyophis blachei	TL	TL	79.2	1	79.2	84
IBR	Ilyophis brunneus	TL	TL	58	1	58	53
LEQ	Lepidion eques	TL	TL	44	1	44	43
FME	Lepidorhombus boscii	TL	SL	40	1.18	47.2	47
MEG	Lepidorhombus whiffiagonis	TL	TL	60	1	60	59
SAR	Leucoraja circularis	TL	TL	120	1	120	104
SRA	Leucoraja fullonica	TL	TL	120	1	120	101
CRA	Leucoraja naevus	TL	TL	71	1	71	64
CDA	Limanda limanda	TL	SL	40	1.19	47.6	14
BAN	Lophius budegassa	TL	SL	100	1.22	122	66

Table S6. Continued.

Marine Scotland code	Species name	Length type - survey	Length type - FishBase	FishBase length (cm)	Conversion factor	FishBase maximum total length (cm)	Survey maximum total length (cm)
ANG	Lophius piscatorius	TL	SL	200	1.2	240	147
LSA	Lycenchelys sarsii	TL	TL	20	1	20	15
LPA	Lycodes pallidus	TL	TL	26	1	26	45
LYU	Lycodes spp.	TL	TL	45.2	1	45.2	40
LAT	Lycodes terraenovae	TL	TL	45.2	1	45.2	66
LFA	Lycodonus flagellicauda	TL	SL	19.9	1.16	23.084	23
LYB	Lyconus brachycolus	TL	SL	52.5	1.16	60.9	19
RTU	Macrouridae spp.	TL	TL	110	1	110	558.465
MBE	Macrourus berglax	TL	TL	110	1	110	10.809
MLA	Malacocephalus laevis	PAFL	TL	60	4.57	60	61.695
KRA	Malacoraja kreffti	TL	TL	70	1	70	57
MAU	Maulisia mauli	TL	SL	20	1.16	23.2	19.94342857
HAD	Melanogrammus aeglefinus	TL	TL	112	1	112	76
BAB	Melanolagus bericoides	TL	SL	20	1.16	23.2	16
HAK	Merluccius merluccius	TL	TL	140	1	140	105
LSO	Microstomus kitt	TL	TL	65	1	65	31
BLI	Molva dypterygia	TL	TL	155	1	155	143
LIN	Molva molva	TL	TL	200	1	200	131
MOR	Mora moro	TL	TL	80	1	80	75
WHH	Myxine ios	TL	TL	57	1	57	58
BSA	Narcetes stomias	TL	SL	57.5	1.152	66.24	68.68045455
FBF	Neocyttus helgae	TL	TL	30.5	1	30.5	31

Table S6. Continued.

Marine Scotland code	Species name	Length type - survey	Length type - FishBase	FishBase length (cm)	Conversion factor	FishBase maximum total length (cm)	Survey maximum total length (cm)
BCA	Neoraja caerulea	TL	TL	30	1	30	36
JSC	Nesiarchus nasutus	TL	SL	130	1.119	145.47	88
DOE	Nessorhamphus ingolfianus	TL	TL	59.8	1	59.8	82
NAE	Nezumia aequalis	PAFL	TL	36	3.78	36	37.8
RTG	Nezumia sclerorhynchus	PAFL	TL	36	3.98	36	33.83
MSE	Normichthys operosus	SL	TL	16.4	1.138	16.4	27.312
BSE	Notacanthus bonaparte	TL	TL	26	1	26	65
CSE	Notacanthus chemnitzii	TL	TL	120	1	120	117
POB	Pachycara bulbiceps	TL	TL	51.5	1	51.5	50
LCR	Pachycara crassiceps	TL	TL	54	1	54	56
PLU	Paraliparis spp.	TL	SL	25.3	1.09	27.577	24
PBA	Paraliparis bathybius	TL	SL	25.3	1.09	27.577	20
RUN	Phycidae spp.	TL	TL	110	1	110	31
GFO	Phycis blennoides	TL	TL	110	1	110	80
POP	Platyberyx opalescens	TL	SL	11.5	1.16	13.34	24
PAP	Platytroctes apus	SL	SL	18	1.17	21.06	21.06
SSU	Platytroctidae spp.	TL	SL	27	1.16	31.32	10.55828571
PLA	Pleuronectes platessa	TL	SL	100	1.264	126.4	28
SAI	Pollachius virens	TL	TL	130	1	130	99
RSE	Polyacanthonotus rissoanus	TL	TL	9.5	1	9.5	56
WRE	Polyprion americanus	TL	TL	210	1	210	50
PAL	Pseudoscopelus altipinnis	TL	SL	20	1.155	23.1	17

Table S6. Continued.

Marine Scotland code	Species name	Length type - survey	Length type - FishBase	FishBase length (cm)	Conversion factor	FishBase maximum total length (cm)	Survey maximum total length (cm)
FCA	Pseudotriakis microdon	TL	TL	269	1	269	183
TRA	Raja clavata	TL	TL	139	1	139	83
SPY	Raja montagui	TL	TL	80	1	80	51
RBA	Rajella bathyphila	TL	TL	90	1	90	93
RBI	Rajella bigelowi	TL	TL	55	1	55	53
FRA	Rajella fyllae	TL	TL	60	1	60	55
RAK	Rajella kukujevi	TL	TL	90	1	90	83
RAR	Rajella ravidula	TL	TL	70	1	70	52
SKU	Rajidae spp.	TL	TL	285	1	285	22
GHA	Reinhardtius hippoglossoides	TL	TL	130	1	130	97
RAT	Rhinochimaera atlantica	PSCFL	TL	140	1.39	140	143.17
RAA	Rouleina attrita	SL	SL	48	1.103	52.944	57.356
MSH	Rouleina maderensis	SL	SL	32	1.181	37.792	55.507
SSI	Sagamichthys schnakenbecki	SL	SL	27	1.17	31.59	28.08
CBL	Schedophilus medusophagus	TL	TL	51	1	51	61
SUD	Scopeloberyx spp.	TL	SL	12.2	1.17	14.274	16
SBI	Scopelogadus beanii	TL	SL	12.2	1.133	13.8226	32
LSD	Scyliorhinus canicula	TL	TL	100	1	100	75
SRI	Scymnodon ringens	TL	TL	110	1	110	111
KSE	Searsia koefoedi	SL	SL	15	1.17	17.55	17.55
SMM	Sebastes marinus	TL	TL	58	1	58	51
NHA	Sebastes viviparus	TL	TL	35	1	35	38

Table S6. Continued.

Marine Scotland code	Species name	Length type - survey	Length type - FishBase	FishBase length (cm)	Conversion factor	FishBase maximum total length (cm)	Survey maximum total length (cm)
SBE	Serrivomer beanii	TL	TL	78	1	78	100
SBD	Serrivomer brevidentatus	TL	TL	65	1	65	50
SNE	Simenchelys parasitica	TL	TL	61	1	61	32
LSS	Somniosus rostratus	TL	TL	143	1	143	126
SGR	Spectrunculus grandis	TL	SL	127	1.16	147.32	59
SPU	Squalus acanthias	TL	TL	160	1	160	105
SYK	Synaphobranchus kaupii	TL	TL	100	1	100	81
DEA	Trachipterus arcticus	TL	TL	300	1	300	174
TMU	Trachyrincus murrayi	PAFL	TL	37	3.1	37	66.65
TCR	Trachyscorpia cristulata	TL	SL	50	1.16	58	45
NPO	Trisopterus esmarkii	TL	TL	35	1	35	26
VPR	Venefica proboscidea	TL	TL	100	1	100	164
XCI	Xenodermichthys copei	SL	TL	31	1.155	31	26.565
EPU	Zoarcidae spp.	TL	TL	54	1	54	52

Table S7. The Pearson's product-moment correlation coefficient between each measure of diversity, mean trait values, and standard deviation of trait values. Trait definitions and units and those defined in *Chapter 3: Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea*. FRic = functional richness, FDiv = functional divergence, SDiv = size diversity, SRic = species richness, SD(h) = standard deviation of relative head size, SD(as) = standard deviation of caudal fin aspect ratio, SD(e) = standard deviation of relative eye size, SD(an) = standard deviation of angle of mouth in relation to lateral line, SD(p) = standard deviation of relative mouth protrusion, SD(g) = standard deviation of relative gape size, SD(l) = standard deviation of L_{max}, M(h) = mean relative head size, M(as) = mean caudal fin aspect ratio, M(e) = mean relative eye size, M(an) = mean angle of mouth in relation to lateral line, M(p) = mean relative mouth protrusion, M(g) = mean relative gape size, M(l) = mean L_{max}, Size = mean body size.

	FRic	FDiv	SDiv	SRic	SD(h)	SD(as)	SD(e)	SD(an)	SD(p)	SD(g)	SD(l)	M(h)	M(as)	M(e)	M(an)	M(p)	M(g)	M(l)	Size
FRic	1.00	-0.38	0.42	0.40	-0.50	0.54	-0.23	0.57	-0.42	-0.41	0.32	-0.47	0.31	-0.37	-0.24	-0.58	-0.24	0.43	0.20
FDiv	-0.38	1.00	0.05	-0.56	0.45	-0.39	0.07	-0.66	0.54	0.51	0.32	0.28	-0.80	-0.16	0.40	0.53	0.40	-0.27	-0.57
SDiv	0.42	0.05	1.00	0.29	-0.35	0.56	-0.43	0.42	-0.43	-0.43	0.54	-0.64	0.16	-0.73	0.31	-0.46	-0.26	0.52	0.05
SRic	0.40	-0.56	0.29	1.00	-0.47	0.46	-0.42	0.55	-0.69	-0.66	-0.15	-0.41	0.70	-0.38	0.12	-0.35	-0.23	0.47	0.56
SD(h)	-0.50	0.45	-0.35	-0.47	1.00	-0.72	0.63	-0.61	0.84	0.86	-0.13	0.48	-0.52	0.34	0.15	0.54	0.22	-0.35	-0.18
SD(as)	0.54	-0.39	0.56	0.46	-0.72	1.00	-0.43	0.80	-0.74	-0.67	0.48	-0.60	0.59	-0.52	-0.07	-0.67	-0.30	0.61	0.29
SD(e)	-0.23	0.07	-0.43	-0.42	0.63	-0.43	1.00	-0.25	0.68	0.74	0.01	0.27	-0.39	0.48	-0.42	0.05	-0.06	-0.24	-0.10
SD(an)	0.57	-0.66	0.42	0.55	-0.61	0.80	-0.25	1.00	-0.73	-0.63	0.16	-0.53	0.76	-0.44	-0.17	-0.65	-0.27	0.67	0.60
SD(p)	-0.42	0.54	-0.43	-0.69	0.84	-0.74	0.68	-0.73	1.00	0.97	-0.04	0.53	-0.74	0.50	-0.10	0.54	0.26	-0.55	-0.46
SD(g)	-0.41	0.51	-0.43	-0.66	0.86	-0.67	0.74	-0.63	0.97	1.00	0.01	0.55	-0.70	0.47	-0.17	0.51	0.32	-0.47	-0.42
SD(l)	0.32	0.32	0.54	-0.15	-0.13	0.48	0.01	0.16	-0.04	0.01	1.00	-0.47	-0.16	-0.50	0.03	-0.44	-0.23	0.46	-0.23
M(h)	-0.47	0.28	-0.64	-0.41	0.48	-0.60	0.27	-0.53	0.53	0.55	-0.47	1.00	-0.40	0.63	-0.29	0.76	0.78	-0.72	-0.40
M(as)	0.31	-0.80	0.16	0.70	-0.52	0.59	-0.39	0.76	-0.74	-0.70	-0.16	-0.40	1.00	-0.24	0.00	-0.45	-0.28	0.58	0.74
M(e)	-0.37	-0.16	-0.73	-0.38	0.34	-0.52	0.48	-0.44	0.50	0.47	-0.50	0.63	-0.24	1.00	-0.49	0.31	0.08	-0.79	-0.33
M(an)	-0.24	0.40	0.31	0.12	0.15	-0.07	-0.42	-0.17	-0.10	-0.17	0.03	-0.29	0.00	-0.49	1.00	0.29	-0.11	0.22	0.15
M(p)	-0.58	0.53	-0.46	-0.35	0.54	-0.67	0.05	-0.65	0.54	0.51	-0.44	0.76	-0.45	0.31	0.29	1.00	0.74	-0.55	-0.29
M(g)	-0.24	0.40	-0.26	-0.23	0.22	-0.30	-0.06	-0.27	0.26	0.32	-0.23	0.78	-0.28	0.08	-0.11	0.74	1.00	-0.32	-0.28
M(l)	0.43	-0.27	0.52	0.47	-0.35	0.61	-0.24	0.67	-0.55	-0.47	0.46	-0.72	0.58	-0.79	0.22	-0.55	-0.32	1.00	0.67
Size	0.20	-0.57	0.05	0.56	-0.18	0.29	-0.10	0.60	-0.46	-0.42	-0.23	-0.40	0.74	-0.33	0.15	-0.29	-0.28	0.67	1.00

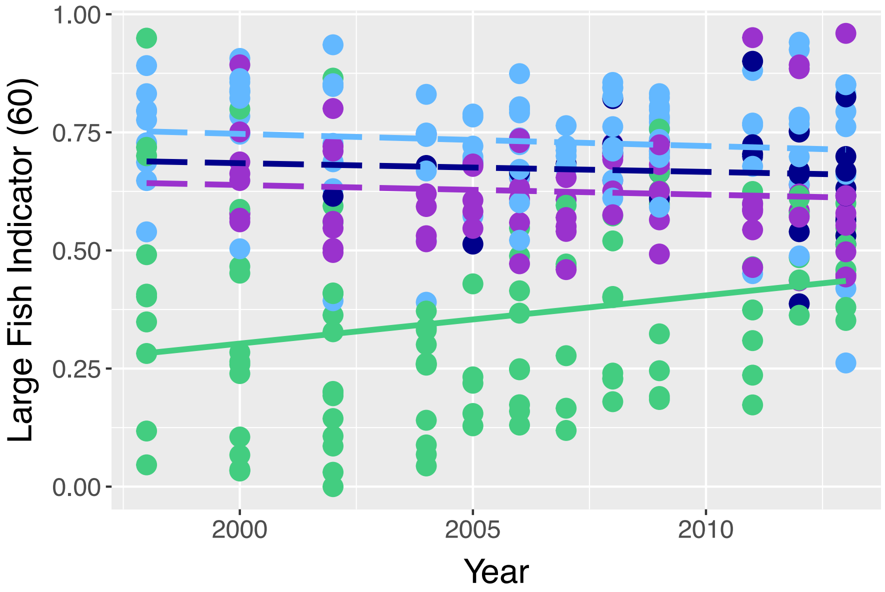

Fig. S3. Large Fish Indicator calculated as the proportion of fish over 60 cm in length (LFI60) in the four depth bands used throughout *Chapter 4: Size-based indicators show depth-dependent recovery from fishing pressure in the deep sea*: S (green) ≤ 750 m; M (light blue) 751–1200 m; D (purple) 1201–1650 m; V (dark blue) > 1650 m. There was a significant effect of year (ANOVA: F = 15, $p < 0.001$), depth band (ANOVA: F = 114, $p < 0.001$), and their interaction (ANOVA: F = 3.2, p = 0.02) on the LFI60, and the model had high explanatory power (LM: F = 52, d.f. = 7, 317, $R^2 = 0.53$). The LFI60 increased over time in depth band S (LM: b = 0.01, S.E. = 0.003, p = 0.002), but did not change over time in any of the other depth bands (LM: M: b = -0.003, S.E. = 0.005; D: b = -0.002, S.E. = 0.005; V: b = -0.002, S.E. = 0.01).

Table S8. The statistical output from intraspecific abundance–occupancy relationships for 93 taxa that occurred in more than six years of the survey. Binomial Generalised Linear Models were fitted of the form: annual occupancy[species$_i$] ~ log(annual abundance[species$_i$]), where model weights were the number of units sampled each year (spatial squares or depth bands).

Species	**Number of observations**	**Spatial AOR**				**Bathymetric AOR**			
		Slope	**Standard error**	**Degrees of freedom**	**p value**	**Slope**	**Standard error**	**Degrees of freedom**	**p value**
Aldrovandia phalacra	7	1.28	0.68	5	0.06	0.57	0.72	5	0.43
Alepocephalus agassizii	9	0.74	0.23	7	0.001	0.52	0.25	7	0.03
Alepocephalus bairdii	13	-0.17	0.49	11	0.73	-0.27	0.35	11	0.44
Alepocephalus rostratus	10	0.08	0.53	8	0.88	0.23	0.41	8	0.57
Amblyraja jensenii	7	1.47	1.08	5	0.17	1.94	1.20	5	0.11
Anoplogaster cornuta	11	0.20	0.55	9	0.72	-0.29	0.60	9	0.64
Antimora rostrata	12	0.65	0.52	10	0.21	0.17	0.52	10	0.74
Aphanopus carbo	13	-0.43	0.31	11	0.17	0.01	0.30	11	0.98
Apristurus aphyodes	11	0.10	0.42	9	0.81	0.13	0.44	9	0.77
Apristurus manis	7	0.19	0.47	5	0.69	0.05	0.53	5	0.93
Apristurus microps	10	1.46	0.39	8	< 0.001	0.43	0.40	8	0.29
Apristurus spp.	11	-0.08	0.20	9	0.70	0.06	0.26	9	0.82
Argentina silus	12	0.66	0.34	10	0.05	0.61	0.34	10	0.07

Table S8. Continued.

Species	Number of observations	Spatial AOR				Bathymetric AOR			
		Slope	Standard error	Degrees of freedom	p value	Slope	Standard error	Degrees of freedom	p value
Bathylagus euryops	11	0.67	0.17	9	< 0.001	0.32	0.15	9	0.03
Bathypterois dubius	12	0.63	0.31	10	0.05	0.68	0.35	10	0.05
Bathysaurus ferox	10	0.11	0.42	8	0.80	0.53	0.45	8	0.24
Brosme brosme	13	-0.14	0.50	11	0.78	-0.54	0.51	11	0.29
Cataetyx laticeps	11	0.45	0.82	9	0.58	-0.99	0.95	9	0.30
Centrolophus niger	10	0.37	0.23	8	0.11	0.27	0.25	8	0.29
Centrophorus squamosus	12	0.33	0.42	10	0.43	0.91	0.45	10	0.05
Centroscyllium fabricii	11	0.55	0.57	9	0.33	0.28	0.58	9	0.64
Centroscymnus coelolepis	12	-0.22	0.31	10	0.47	-0.08	0.29	10	0.79
Centroselachus crepidater	13	-0.38	0.41	11	0.35	-0.10	0.36	11	0.78
Chimaera monstrosa	12	0.20	0.32	10	0.53	0.47	0.33	10	0.15
Chimaera opalescens	10	1.21	0.55	8	0.03	0.22	0.70	8	0.76
Coelorinchus caelorhincus	12	-0.24	0.21	10	0.27	-0.26	0.24	10	0.28

Table S8. Continued.

Species	Number of observations	Spatial AOR				Bathymetric AOR			
		Slope	Standard error	Degrees of freedom	p value	Slope	Standard error	Degrees of freedom	p value
Coelorinchus labiatus	12	0.41	0.34	10	0.23	0.12	0.28	10	0.66
Conger conger	12	0.31	0.36	10	0.39	-0.03	0.40	10	0.94
Conocara murrayi	9	0.24	0.19	7	0.21	0.00	0.21	7	0.99
Coryphaenoides guentheri	12	0.41	0.21	10	0.05	0.21	0.17	10	0.21
Coryphaenoides mediterraneus	11	0.70	0.40	9	0.08	1.27	0.48	9	0.01
Coryphaenoides rupestris	13	-1.66	1.15	11	0.15	-0.88	0.54	11	0.10
Cottunculus thomsonii	13	0.43	0.38	11	0.25	-0.40	0.38	11	0.29
Dalatias licha	10	-0.61	0.54	8	0.26	-0.26	0.56	8	0.65
Deania calcea	13	-0.50	0.32	11	0.12	-0.01	0.31	11	0.97
Dipturus batis	9	0.40	0.77	7	0.60	0.36	0.74	7	0.63
Epigonus telescopus	13	-0.24	0.24	11	0.32	-0.22	0.24	11	0.36
Etmopterus princeps	12	0.18	0.43	10	0.68	-0.48	0.54	10	0.38
Etmopterus spinax	12	-0.53	0.38	10	0.17	-0.51	0.39	10	0.19

Table S8. Continued.

Species	Number of observations	Spatial AOR				Bathymetric AOR			
		Slope	Standard error	Degrees of freedom	p value	Slope	Standard error	Degrees of freedom	p value
Gadiculus argenteus	13	0.18	0.15	11	0.24	0.18	0.15	11	0.24
Galeus melastomus	12	-0.32	0.30	10	0.29	-0.52	0.30	10	0.08
Galeus murinus	12	0.06	0.34	10	0.86	0.02	0.39	10	0.97
Glyptocephalus cynoglossus	13	0.67	0.28	11	0.02	1.01	0.33	11	0.002
Halargyreus johnsonii	13	-0.10	0.20	11	0.61	-0.04	0.20	11	0.83
Halosauropsis macrochir	11	0.91	0.31	9	0.003	0.76	0.34	9	0.03
Harriotta raleighana	11	0.41	0.44	9	0.34	0.74	0.48	9	0.13
Helicolenus dactylopterus	12	0.45	0.17	10	0.01	0.43	0.17	10	0.01
Hexanchus griseus	9	0.13	0.46	7	0.78	0.20	0.56	7	0.72
Holtbyrnia anomala	10	0.84	0.28	8	0.003	0.45	0.30	8	0.13
Holtbyrnia macrops	8	1.22	0.67	6	0.07	0.27	0.66	6	0.68
Hoplostethus atlanticus	11	1.05	0.27	9	< 0.001	0.64	0.27	9	0.02
Hydrolagus affinis	11	0.83	0.29	9	0.004	0.76	0.33	9	0.02

Table S8. Continued.

Species	Number of observations	Spatial AOR				Bathymetric AOR			
		Slope	Standard error	Degrees of freedom	p value	Slope	Standard error	Degrees of freedom	p value
Hydrolagus mirabilis	13	-0.25	0.24	11	0.29	-0.11	0.25	11	0.66
Hydrolagus pallidus	9	0.04	0.40	7	0.93	-0.11	0.38	7	0.78
Ilyophis blachei	10	0.45	0.54	8	0.40	0.72	0.57	8	0.20
Lepidion eques	13	0.89	0.37	11	0.02	0.66	0.38	11	0.08
Lepidorhombus boscii	12	0.04	0.21	10	0.86	-0.08	0.24	10	0.74
Lepidorhombus whiffiagonis	13	0.72	0.23	11	0.002	0.50	0.24	11	0.04
Lophius piscatorius	13	-0.36	0.41	11	0.39	-0.13	0.41	11	0.76
Lycodes terraenovae	11	0.50	0.41	9	0.23	0.08	0.47	9	0.87
Lycodonus flagellicauda	10	-0.45	0.49	8	0.36	0.11	0.55	8	0.84
Macrouridae spp.	9	-0.14	0.38	7	0.71	-0.20	0.40	7	0.62
Malacocephalus laevis	13	0.43	0.18	11	0.02	0.12	0.18	11	0.49
Merluccius merluccius	12	-0.33	0.43	10	0.44	-0.60	0.44	10	0.17
Molva dypterygia	13	-0.13	0.31	11	0.67	-0.31	0.34	11	0.36

Table S8. Continued.

Species	**Number of observations**	**Spatial AOR**				**Bathymetric AOR**			
		Slope	**Standard error**	**Degrees of freedom**	**p value**	**Slope**	**Standard error**	**Degrees of freedom**	**p value**
Molva molva	12	-0.14	0.31	10	0.64	-0.46	0.35	10	0.19
Mora moro	13	0.30	0.18	11	0.10	0.24	0.18	11	0.20
Myxine ios	10	0.34	0.46	8	0.46	0.38	0.52	8	0.46
Nesiarchus nasutus	10	-0.42	0.42	8	0.32	-0.66	0.46	8	0.15
Nessorhamphus ingolfianus	10	-0.40	0.50	8	0.42	-0.10	0.64	8	0.87
Nezumia aequalis	13	0.07	0.43	11	0.87	-0.04	0.41	11	0.93
Normichthys operosus	11	0.17	0.28	9	0.56	0.16	0.31	9	0.60
Notacanthus bonaparte	12	0.51	0.65	10	0.43	0.14	0.64	10	0.83
Notacanthus chemnitzii	12	0.34	0.39	10	0.38	0.57	0.40	10	0.15
Paraliparis spp.	10	0.67	0.41	8	0.10	0.79	0.39	8	0.04
Phycidae spp.	10	-0.71	0.51	8	0.17	-0.63	0.47	8	0.18
Phycis blennoides	13	-0.40	0.34	11	0.25	-0.16	0.32	11	0.61
Pollachius virens	8	0.36	0.15	6	0.02	0.26	0.15	6	0.07

Table S8. Continued.

Species	Number of observations	Spatial AOR				Bathymetric AOR			
		Slope	Standard error	Degrees of freedom	p value	Slope	Standard error	Degrees of freedom	p value
Polyacanthonotus rissoanus	12	0.39	0.26	10	0.13	-0.02	0.23	10	0.92
Rajella bigelowi	9	0.30	0.52	7	0.56	-0.08	0.53	7	0.88
Rajella fyllae	11	-0.44	0.50	9	0.37	-0.78	0.58	9	0.18
Rhinochimaera atlantica	11	0.04	0.37	9	0.92	0.41	0.45	9	0.36
Rouleina attrita	11	0.28	0.12	9	0.02	0.40	0.14	9	0.01
Scopelogadus beanii	11	0.60	0.16	9	< 0.001	0.66	0.17	9	< 0.001
Scyliorhinus canicula	12	-0.12	0.22	10	0.59	-0.33	0.25	10	0.18
Sebastes marinus	9	0.75	0.47	7	0.11	0.52	0.49	7	0.29
Serrivomer beanii	12	1.31	0.33	10	< 0.001	0.89	0.29	10	0.002
Spectrunculus grandis	10	0.91	0.35	8	0.01	0.65	0.40	8	0.11
Synaphobranchus kaupii	13	0.80	0.35	11	0.02	0.61	0.32	11	0.06
Trachipterus arcticus	7	0.05	0.64	5	0.94	0.20	0.74	5	0.79
Trachyrincus murrayi	13	-0.54	0.43	11	0.20	-0.12	0.31	11	0.70
Venefica proboscidea	9	0.35	0.86	7	0.69	0.75	1.34	7	0.58
Xenodermichthys copei	13	0.19	0.18	11	0.28	0.04	0.19	11	0.83