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

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Running Headline:

Trait-based metrics in the deep sea

Abstract

1. 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.
2. We 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. We test the implementation of fractional size in demersal fish assemblages along a depth gradient in the deep sea. We use data from an extensive trawl survey at depths of 300-2030m 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.
3. 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.

4. 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.

Key Words

Bathymetry; deepwater fish; FishBase; functional role; L_{max}; ontogeny; Redundancy Analysis; trait-based analysis

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. We 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 inter-specific variation in size; an aspect that is often ignored in ecology (Rudolf & Rasmussen 2013a, b).

Here we 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 we 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. We 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 inter-specific 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.

Materials and Methods

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 2cm. 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 300m to 2030m, 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 same ICES statistical rectangle (of area 1° longitude by 30' latitude) and within 100m 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 (Appendix 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 (Appendix 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 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 (Appendix 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 2013) 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, we 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 S3). To determine whether there were any depth-related biases produced by using this method, we 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 1500m 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 S3). We 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.

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 S3), 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 inter-specific 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). Inter-specific 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 100m 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 10kg. 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.

Results

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 500-1000m, and the suggestion of a decline beyond the range of depths considered here (Fig. 2b).

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 inter-specific variation in size. Some species were very large at all depths (e.g. the black scabbardfish *Aphanopus carbo* [Lowe 1839] and the small-eyed rabbitfish *Hydrolagus affinis* [de Brito Capello 1868]; Fig. 3a) while some were very small at all depths (e.g. the blackbelly rosefish *Helicolenus dactylopterus* [Delaroche 1809] and the hollowsnout grenadier *Coelorinchus caelorhincus* [Risso 1810]; 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* [Johnson 1862]; Fig. 3a); species that are larger in shallower waters were rare (e.g. the rabbitfish *Chimaera monstrosa* [Linnaeus 1758]; Fig. 3a). This conclusion that intra-specific 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 0.008cm/m (SE: $6.9*10^{-6}$). The inter-specific 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).

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 1500m 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 1100m where shallow-living species disappear, such as *H. dactylopterus*, *C. caelorhincus*, and the greater argentine *Argentina silus* [Ascanius 1775] (Fig. 4a). Up to this depth, abundances tended to decrease as depth increased. Deeper than 1100m, species with particularly large depth ranges started to dominate, such as *S. kaupii, A. carbo*, the roundnose grenadier *Coryphaenoides rupestris* [Gunnerus 1765], and Baird's smoothhead

Alepocephalus bairdii [Goode & Bean 1879] (Fig. 4a). These deeper-living species with larger depth ranges showed a variety of patterns in abundance (Fig. 4a).

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 1700m, 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 1200m (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, inter-specific 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 our 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 inter-specific 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 1100m (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 1000m in depth: light is available for vision up to 1000m (Kaiser et al. 2011), and there is rapidly decreasing salinity above 1000m, but constant salinity below 1000m (Lalli & Parsons 1993). The dominance of species with large depth ranges below 1100m, such as the roundnose grenadier *C. rupestris*, and Baird's smoothhead *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 1500m, 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 2000m 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. We 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 1500m. 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.

Acknowledgements

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Figure Legends

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).

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 10kg 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 10kg 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.

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 10kg 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.

Data Accessibility

The data used in this study are available on Figshare at http://dx.doi.org/10.6084/m9.figshare.1403630 (Mindel 2015).

Supporting Information

The following Supporting Information is available for this article online:

Appendix S1: Concatenation of hauls into stations.

Table S1: Description of the reduced dataset, whereby hauls were concatenated into stations if they were repeated across years in the same ICES statistical rectangle and at depths within 100m of each other.

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

Table S2: List of all taxa caught on the survey, the lengths measured, and their conversion factors.

Appendix S3: The robustness of L_{max} allocation.

Fig. S1. The relationship between fractional size and depth using two different methods.

Table S3. Statistical results of the relationship between fractional size and depth using two different methods.

Table S4: List of all taxa caught on the survey, their L_{max} listed on FishBase, and the maximum observed size from the survey.

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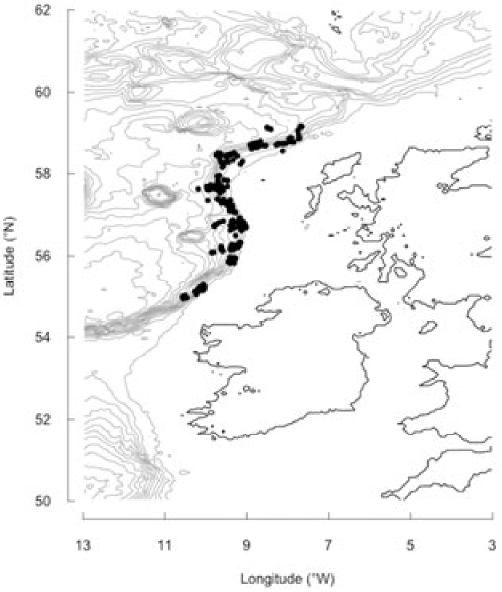
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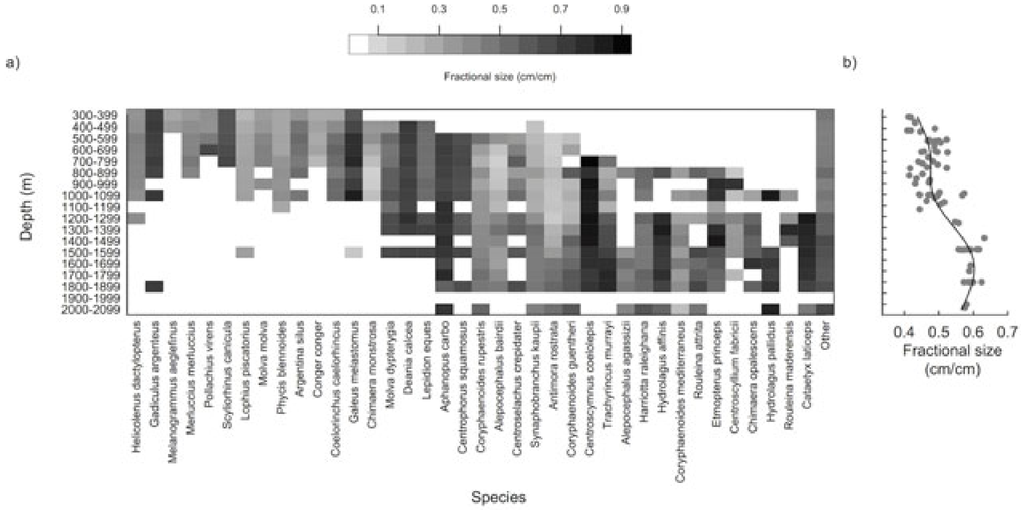
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0.3
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0.7
0.9
Fractional size (cm/cm)
a)
b)
Depth (m)
300-399
400-499
500-599
600-699
700-799
800-899
900-999
1000-1099
1100-1199
1200-1299
1300-1399
1400-1499
1500-1599
1600-1699
1700-1799
1800-1899
1900-1999
2000-2099
Helicolenus dactylopterus
Gadiculus argenteus
Melanogrammus aeglefinus
Merluccius merluccius
Pollachius virens
Scyliorhinus canicula
Lophius piscatorius
Molva molva
Phycis blennoides
Argentina silus
Conger conger
Coelorinchus caelorhincus
Galeus melastomus
Chimaera monstrosa
Molva dypterygia
Deania calcea
Lepidion eques
Aphanopus carbo
Centrophorus squamosus
Coryphaenoides rupestris
Alepocephalus bairdii
Centroselachus crepidater
Synaphobranchus kaupii
Antimora rostrata
Coryphaenoides guentheri
Centroscymnus coelolepis
Trachyrincus murrayi
Alepocephalus agassizii
Harriotta raleighana
Hydrolagus affinis
Coryphaenoides mediterraneus
Rouleina attrita
Etmopterus princeps
Centroscyllium fabricii
Chimaera opalescens
Hydrolagus pallidus
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Cataetyx laticeps
Other
Species
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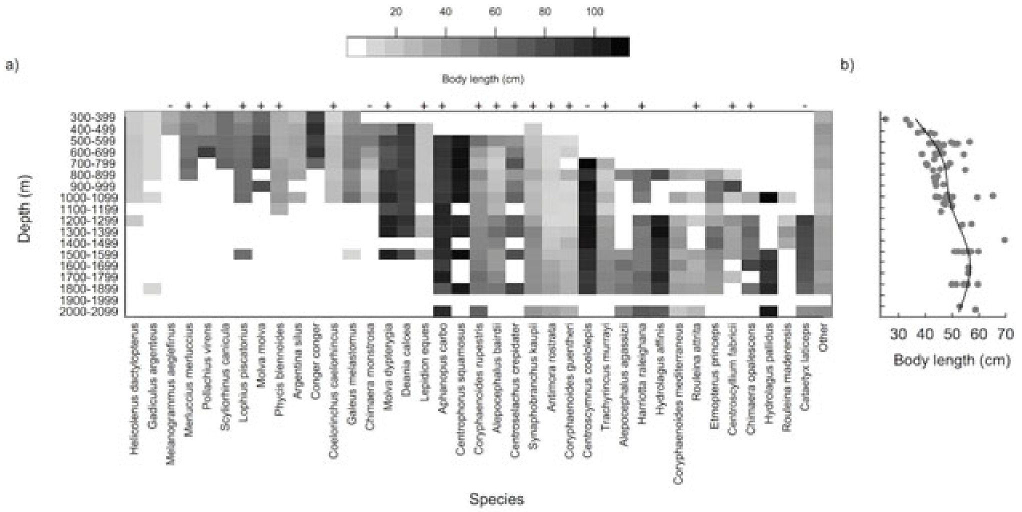
0.5
0.6
0.7
Fractional size
(cm/cm)


a)
b)
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40
60
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100
Body length (cm)
Depth (m)
300-399
400-499
500-599
600-699
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800-899
900-999
1000-1099
1100-1199
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Helicolenus dactylopterus
Gadiculus argenteus
Melanogrammus aeglefinus
Merluccius merluccius
Pollachius virens
Scyliorhinus canicula
Lophius piscatorius
Molva molva
Phycis blennoides
Argentina silus
Conger conger
Coelorinchus caelorhincus
Galeus melastomus
Chimaera monstrosa
Molva dypterygia
Deania calcea
Lepidion eques
Aphanopus carbo
Centrophorus squamosus
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Alepocephalus bairdii
Centroselachus crepidater
Synaphobranchus kaupii
Antimora rostrata
Coryphaenoides guentheri
Centroscymnus coelolepis
Trachyrincus murrayi
Alepocephalus agassizii
Harriotta raleighana
Hydrolagus affinis
Coryphaenoides mediterraneus
Rouleina attrita
Etmopterus princeps
Centroscyllium fabricii
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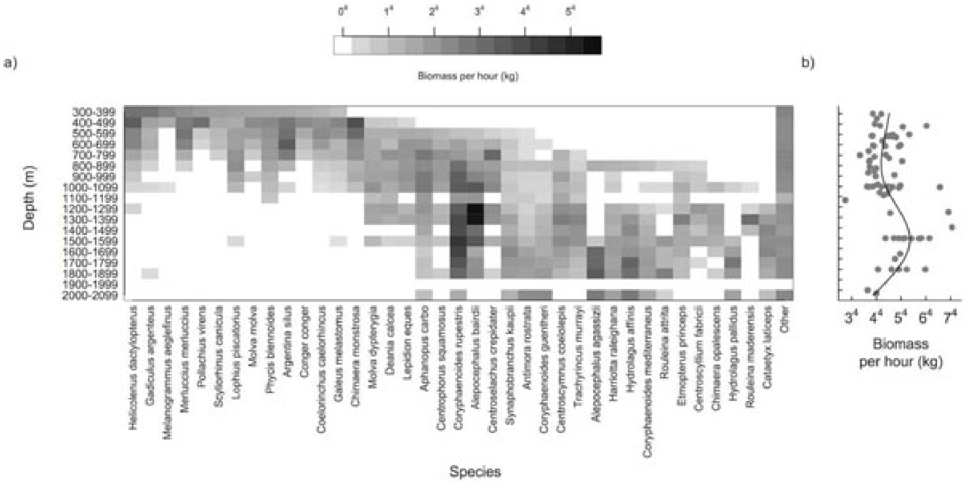
Hydrolagus pallidus
Rouleina maderensis
Cataetyx laticeps
Other
Species
30 40 50 60 70
Body length (cm)


a)
b)
0⁴
1⁴
2⁴
3⁴
4⁴
5⁴
Biomass per hour (kg)
Depth (m)
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400-499
500-599
600-699
700-799
800-899
900-999
1000-1099
1100-1199
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1300-1399
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Helicolenus dactylopterus
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Merluccius merluccius
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Scyliorhinus canicula
Lophius piscatorius
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Conger conger
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Galeus melastomus
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Coryphaenoides rupestris
Alepocephalus bairdii
Centroselachus crepidater
Synaphobranchus kaupii
Antimora rostrata
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Trachyrincus murrayi
Alepocephalus agassizii
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Coryphaenoides mediterraneus
Rouleina attrita
Etmopterus princeps
Centroscyllium fabricii
Chimaera opalescens
Hydrolagus pallidus
Rouleina maderensis
Cataetyx laticeps
Other
Species
3⁴ 4⁴ 5⁴ 6⁴ 7⁴
Biomass
per hour (kg)