Size-based indicators show depth-dependent change over time in the deep sea

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Size-based indicators are well established as a management tool in shelf seas as they respond to changes in fishing pressure and describe important aspects of community function. In the deep sea, however, vital rates are much slower and body size relationships vary with depth, making it less clear how size-based indicators can be applied and whether they are appropriate for detecting changes through time. The deep-sea fish stocks of the North Atlantic underwent a period of exploitation followed by management and conservation action that relieved this pressure. We used data from a deep-water bottom trawl survey in the Rockall Trough, at depths of 300–2000 m, to test whether size-based indicators changed over a 16-year period, during which fishing pressure decreased. We applied four indicators to these data: mean body length, mean maximum length, large fish indicator (LFI), and the slope of the biomass spectrum. Patterns were analysed within four different depth bands. The LFI and slope of the biomass spectrum 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 LFI were much higher overall than in shelf seas, so the same reference points cannot be applied to all marine ecosystems. These findings imply that size-based indicators can be usefully applied to the deep sea and that they potentially track changes in fishing pressure in the medium term.

Keywords: body size, demersal fish, deep-sea fishing, size structure.

Introduction

The deep sea is the largest ecosystem on the planet (Ramirez-Llodra et al., 2011), but due to its inaccessibility, we have known relatively little about it until recent decades. Exploitation of the deep sea increased dramatically at the end of the 20th century as technologies allowed industrial-scale trawling of the deep sea to progress (Morato et al., 2006). Initial high-yield fisheries for species such as blue ling (Molva dypterygia), orange roughy (Hoplostethus atlanticus), and deep-water sharks including the Portuguese dogfish (Centroscymnus coelolepis) quickly underwent serial depletion and eventual collapse. This mainly reflected the slow vital rates (slow growth, late age at maturity) of deep-sea fish that make them more vulnerable to exploitation and disturbance than their shallow-water counterparts (Drazen and Haedrich, 2012). Consequently, there has been growing concern over the sustainability of human activities in the deep sea and a need to measure how the ecosystem is responding to human exploitation so that we can better manage these pressures.

One way to monitor changes in fish communities is to use size-based indicators. These indicators represent the health of communities by summarizing their size structure. Body size is particularly relevant when examining impacts of fishing for two main reasons. First, 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). Second, 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 *et al.*, 2000), maturity and fecundity (Winemiller and 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 and Dulvy, 2005; Greenstreet *et al.*, 2011) and the Celtic Sea (e.g. Blanchard *et al.*, 2005; Shephard *et al.*, 2013). The responsiveness of size-based indicators to changes in fishing pressure has also been corroborated by modelling studies (Blanchard *et al.*, 2014; Thorpe *et al.*, 2015).

Deep-sea fish communities are harder to access and have been less routinely sampled than those in shelf seas, and size-based indicators have not yet been widely applied to this ecosystem. There is some evidence for a steepening of the size spectrum in the deep sea to the west of the British Isles between 1973 and 2000 due to increasing fishing pressure over this period (Basson *et al.*, 2001). However, these results remained somewhat inconclusive due to the variety of surveys and gears considered, and the lack of data for depths beyond 1400 m. As deep-sea research surveys continue, longer time series of abundance and body size data that have been measured consistently throughout the study period are becoming more available. One such survey has been conducted by Marine Scotland on the continental slope of the Rockall Trough, Northeast Atlantic. Fishing pressure has been decreasing in this area since the early 2000s due to the introduction, and subsequent decline, of Total Allowable Catches, and recently it has been proposed that no bottom trawl fisheries will operate at depths of more than 800 m. Therefore, the Rockall Trough provides a model study site to examine the effect of decreasing fishing pressure in the deep sea (at depths of 300–2067 m) using size-based indicators.

Due to the large environmental differences between sites of different depths (namely water pressure, temperature, and oxygen levels; Lalli and Parsons, 1993; Kaiser *et al.*, 2011), species composition changes across depths (e.g. Gordon and Bergstad, 1992; Carney, 2005; Yeh and Drazen, 2009), as does body size (e.g. Polloni *et al.*, 1979; Macpherson and Duarte, 1991; Collins *et al.*, 2005; Mindel *et al.*, 2016a). Additionally, fishing pressure in the Rockall Trough has only occurred at depths up to 1500 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 and we must account for depth when investigating trends over time.

In this study we used four indicators that are well established in shallow seas: (i) mean body length, (ii) mean maximum length, (iii) large fish indicator (LFI), and (iv) slope of the normalized biomass spectrum. 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 illustrates changes in species composition and the relative abundance of small and large species; it is also expected to decrease under exploitation because high pressure will favour short-lived species that mature faster (Shin *et al.*, 2005). The LFI 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
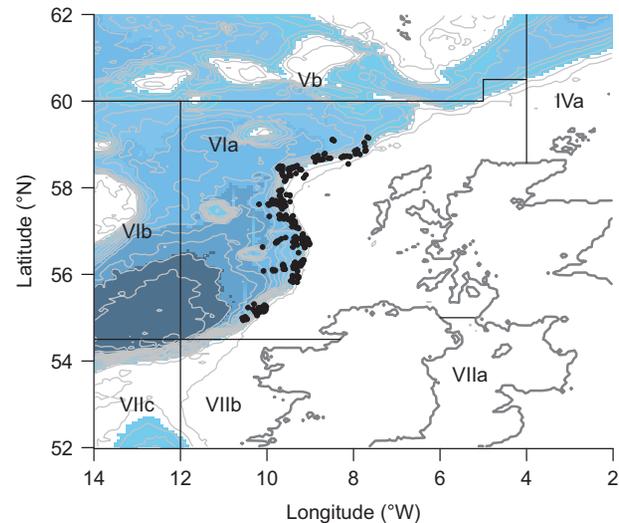

Figure 1. Location of hauls of the Marine Scotland deep-water bottom trawl survey in the Northeast Atlantic from 1998 to 2013. Shading indicates depth, where light represents shallow and dark represents deep. Labelled sections represent ICES areas.

and high values indicate a healthy system. The normalized biomass spectrum is important in the marine environment because it symbolizes how all individuals are arranged along a size axis (Sheldon *et al.*, 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.*, 2005).

The trends in these four indicators were analysed over time from 1998 to 2013 [a time period of a length that has been shown to have sufficient power to detect trends in size-based indicators (Jennings and Dulvy, 2005)] in each of four depth bands. We tested the hypothesis that all four indicators would 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. We predicted that the two shallower depth bands would show the biggest change, as these are the depths at which fishing occurs. We interpreted these patterns alongside data on fishing effort (STECF, 2013) and sea bottom temperature. The latter was examined because increasing temperatures can have a positive effect on size-based indicators (Marshall *et al.*, 2016; Robinson *et al.*, 2017).

Methods
Data
A deep-water bottom trawl survey was conducted by Marine Scotland (Scottish Government) in September 1998, 2000, 2002, 2004–2009, and 2011–2013 along the continental slope of the Rockall Trough in the Northeast Atlantic (Figure 1; ICES area VIa, latitude 55°–59°N, longitude ∼9°W) at depths of 300–2067 m (Neat and Burns, 2010). The gear was designed to sample 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 this analysis. Sea bottom temperature was recorded on the survey at the depth of the haul from 2005 onwards (205 out of a total of 325 hauls).

Table 1. Number of hauls taken in each year of the survey from each depth band.

Year	Shallow ≤ 750 m	Medium 751–1200 m	Deep 1201–1650 m	Very deep > 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**

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 (Supplementary Table S1). 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. Individuals for which length–weight relationships were unknown ($n = 7006$; 0.01% of individuals caught) were excluded from the analysis. This resulted in a final dataset of 686 832 individuals, belonging to 105 species. The full taxonomy of species was determined using the World Register of Marine Species (WoRMS Editorial Board, 2014).

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 = 2067 m). There was a consistent increase over time in the number of hauls taken in the deepest depth band (Table 1) so the results from this depth band were interpreted with caution.

The Scientific, Technical and Economic Committee for Fisheries (STECF, 2013) reported on fishing effort in the deep sea of ICES (International Council for the Exploration of the Sea) area VI by ICES member states. As these data are not depth-resolved, we use them for illustrative purposes only, rather than to quantify the impact of fishing. Here we present bottom trawl effort data, in order to focus on demersal fish, from the EU waters of ICES area VI, which equates to area VIa (Figure 1). We exclude 2002 as recommended in the report due to the unreliability of that year's data (STECF, 2013).

Indicators

Due to the unreliability of catching very small individuals on the survey, all individuals of ≤ 32 g were excluded from the calculation of indicators. This value was suggested by Jennings and 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:

$$\bar{L} = \sum_{N} L/N$$

where L is body length and N is numerical abundance.

Mean maximum length of the community was calculated by assigning each individual an $L_{\max}$ based on its species and averaging this across all individuals in a haul:

$$\overline{L_{\max}} = \sum_{i} N_i L_{\max_i}/N$$

where i is a species index. $L_{\max}$ illustrates the potential maximum size of a species and was set as the maximum length listed on FishBase for that species (Froese and Pauly, 2016), or the maximum length recorded on the deep-water trawl survey, whichever was the greater (Supplementary Table S1). This approach was chosen so that $L_{\max}$ consistently equates to the largest known length for that species (Mindel *et al.*, 2016a).

The LFI was calculated as the proportion by weight of individuals >40 cm in length per haul (ICES, 2013):

$$\text{LFI} = W_{>40 \text{ cm}}/W$$

where W is biomass and $W_{>40 \text{ cm}}$ is biomass of individuals greater than 40 cm in length.

The slope of the size spectrum was calculated using a normalized biomass spectrum (Platt and 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 and Denman, 1977). The slope of the normalized size spectrum was then derived from the relationship between $\log_{10}$ of the mid-point of the weight class versus $\log_{10}$ of the normalized 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.*, 2005), which was judged to start from the weight class 2^5–2^6 g.

Analysis

General linear models (LMs) 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, and LFI, 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 *et al.*, 2008). The relationship between sea bottom temperature and year was analysed for each depth band using general LMs. 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 and Simon-Bouhet, 2013).

Results

For mean body length in the community, there was no interaction between year and depth band ($F = 1.3$, $p = 0.29$) so the model was fitted without the interaction, and this model had high explanatory power (LM: F = 73.8, df = 4, 320, $R^2 = 0.47$). There was no significant change in mean body length over time, but the trend was increasing (Figure 2a; LM: $b = 0.13$, s.e. = 0.10, $p = 0.17$). 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 (Figure 2a; Table 2).

For mean maximum length in the community, there was no interaction between year and depth band ($F = 2.4$, $p = 0.07$) so the model was fitted without the interaction, and this model had high explanatory power (LM: F = 91.4, df = 4, 320, $R^2 = 0.53$). There was no significant change in mean maximum length over time (Figure 2b; LM: $b = -0.05$, s.e. = 0.17, $p = 0.79$). Overall mean maximum length differed significantly between all depth bands apart from M and Very deep (V) (Figure 2b; Table 2).

For the LFI, there was a significant effect of year ($F = 33.8$, $p < 0.001$), depth band ($F = 110.5$, $p < 0.001$), and their interaction ($F = 4.3$, $p = 0.005$), and the model had high explanatory power (LM: F = 54.0, df = 7, 317, $R^2 = 0.53$). The LFI increased over time in depth band S (Figure 2c; LM: $b = 0.011$, s.e. = 0.0027, $p < 0.001$), but did not change over time in any of the other depth bands (Figure 2c; LM: M: $b = -0.0011$, s.e. = 0.0038; D: $b = -0.0010$, 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 ($F = 2.7$, $p = 0.058$), 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: $F = 12.2$, df = 7, 37, $R^2 = 0.64$). There was a significant effect of year (F = 28.5, $p < 0.001$) and depth band ($F = 16.3$, $p < 0.001$) 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 bands S and V, but did not change over time in depth bands

Table 2. Statistical results of *post hoc* multiple comparison Tukey tests for indicators not found to have a significant interaction.

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	15.1	1.8	<0.001
	S-D	37.2	2.0	<0.001
	S-V	18.4	2.8	<0.001
	M-D	22.1	2.0	<0.001
	M-V	3.3	2.8	0.63
	D-V	−18.8	2.9	<0.001

Estimates represent the differences in intercept between depth bands. Models were implemented using the R package *multcomp* (Hothorn *et al.* 2008). S = shallow, up to 750 m; M = medium, 751–1200 m; D = deep, 1201–1650 m; V = very deep, over 1650 m.
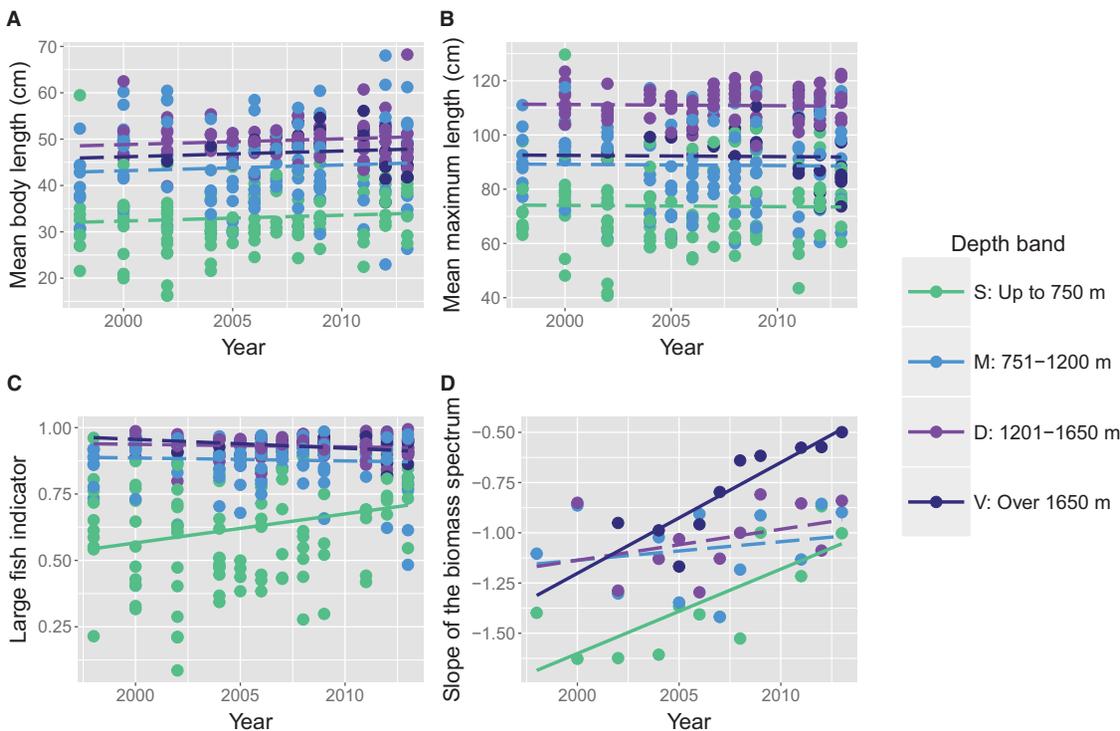

Figure 2. Change over time in the indicators (a) mean body length, (b) mean maximum length, (c) LFI, and (d) slope of the normalized biomass spectrum, in each of four depth bands. Lines represent the fitted general LM; significant changes over time are depicted as solid lines, non-significant relationships are dashed lines.
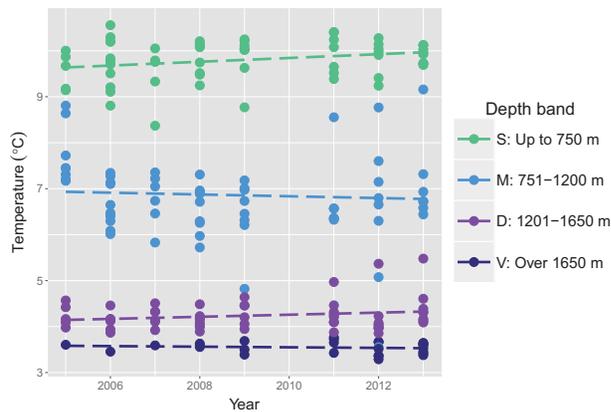
Figure 3. Temperature of hauls from the period 2005–2013 in each of the four depth bands. None of the relationships over time were significant.

Figure 4. Bottom trawl effort in the deep sea of ICES area VIa by ICES member states from 2000 to 2012, as reported by STECF (2013).

M and D (Figure 2d; 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. $= 0.020$). The individual size spectra for each combination of year and depth band, and the associated statistical results, are presented in Supplementary Appendix S1 (Supplementary Figures S1–S4; Supplementary Table S2).

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 (Figure 3; 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. $= 0.010$, $p = 0.54$).

Bottom trawling effort according to STECF (2013) has decreased over the study period (Figure 4) but there is no information as to whether this has been equal across depth bands.

Discussion

The fish community of the deep Northeast Atlantic is functionally and taxonomically diverse and primarily structured by depth (Mindel *et al.*, 2016a,b). Previous studies of this ecosystem have shown that species diversity has remained stable over time (Campbell *et al.*, 2011), but that for some commercial species, such as the roundnose grenadier (*Coryphaenoides rupestris*), there is evidence for recent changes in size composition (Neat and Burns, 2010). Here we show that out of the four size-based indicators examined, two (the LFI and the slope of the normalized biomass spectrum) show change over time in the demersal fish community of the Rockall Trough. The statistically significant trends were positive, which is consistent with recovering fish stocks from coastal areas. Depth had a strong influence on the values of size-based indicators and the positive changes seen in the two significant indicators varied with depth.

The indicator that showed the most striking pattern was the LFI. There was a significant increase over time in the LFI in the Shallow depth band (≤ 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 the Shallow depth band the fish increased in size, which may reflect the relaxed fishing pressure in recent years. In contrast, in the
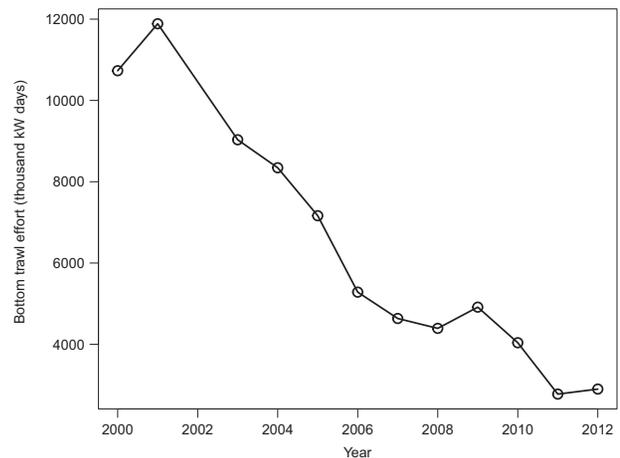
deeper zones the assemblages appear not to have changed significantly, potentially reflecting the lower level of fishing pressure in deeper areas.

Similarly, the slope of the biomass spectrum increased (i.e. the slope became less steep) in the Shallow depth band, but not in the Medium (751–1200 m) or Deep (1201–1650 m) depth bands. In the Very deep depth band (>1650 m) there was 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 are consistent with an effect of 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 and Jennings, 2004; Blanchard *et al.*, 2005, 2009; Piet and Jennings, 2005). As fishing pressure extends as deep as 1500 m in the area, the lack of response in the Medium depth band is likely to be because assemblages therein are slower to recover from fishing pressure than in the Shallow depth band. 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 due to vertical migration or daily movement of fish (Bailey *et al.*, 2009).

Mean body length, on the other hand, did not change over time in any depth band. This may be 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 did not show change over time, implying that species composition has not shifted in favour of larger species during the period of declining fishing pressure. For this indicator, it may be that exploitation was never severe enough to cause an initial shift in species composition to those with smaller maximum sizes.

The positive change in size-based indicators in the Rockall Trough can be qualitatively related to the decreasing fishing pressure 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 issue with the fishing effort data is that they are not depth-resolved. Thus, the different patterns of indicator variation 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, we cannot know the precise effort at the Rockall Trough only. We must also use the report's definition of deep-sea species and are limited to fishing fleets that have provided data for that report (STECF, 2013).

Despite the limitations of the fishing effort data, we can infer that the change in size-based indicators over time is likely to be due to the reduction in fishing pressure. Environmental factors could also potentially affect community size structure, but Blanchard *et al.* (2005) illustrated that the impact of fishing is likely to outweigh these effects. It has been shown that oxygen concentration has a minimal impact on fish community size structure and that net primary production is only the most important determinant when the size structure is stable over time (Marshall *et al.*, 2016). One environmental factor that has been found to affect values of size-based indicators is temperature (Marshall *et al.*, 2016; Robinson *et al.*, 2017); however, we are able to rule out this potential effect in this study, as there was no change in temperature over time for any of the depth bands. Nevertheless, 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 recognize that long-term environmental changes could be impacting overall indicator values, because temperature affects body size (e.g. Angilletta *et al.*, 2004) and climate change can alter the depth distribution of species (Dulvy *et al.*, 2008).

For all of the analyses presented here, only individuals above a predicted weight of 32 g were included. This is to exclude small individuals that are considered to be poorly sampled by the survey gear, and the specific threshold value was chosen based on recommendations by Jennings and Dulvy (2005). When the analysis was repeated with the inclusion of all individuals caught on the survey, the results were unaffected (Supplementary Figure S5). However, the choice of threshold could generate discrepancies 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 ecosystem assessment (Jennings and 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). However, difficulty with using reference directions arises when implementing management action, because reference points are still required to establish when management objectives have been achieved so that the focus can shift to maintaining, rather than improving, the current state of the ecosystem (Modica *et al.*, 2014). Ecosystem assessments may

therefore require a combination of approaches, depending on the data available, the timescale being examined, and the management goals (Samhouri *et al.*, 2011).

The issue of establishing target reference points that are applicable across a range of marine areas is illustrated here, as the values of the LFI seen in the deep sea, even before fishing pressure started to decline, 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 *et al.*, 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), when shelf 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. In order to produce LFI values in the deep-sea assemblages studied here that are similar to the shelf sea reference point of 0.3, the calculation would need to be changed to the proportion of fish at least over 60 cm in length (Supplementary Figure S6). 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 (Supplementary Figure S6).

Although we present higher values of the LFI here than have been recorded in shelf seas, recovery of the LFI in shallow waters can be particularly rapid. The LFI increased from ∼ 0.05 in 2001 to 0.22 in 2008 in the North Sea (Greenstreet *et al.*, 2011) and from 0.17 in 1996 to 0.42 in 2008 in the Bay of Biscay (Modica *et al.*, 2014). However, the extreme to which the LFI has been affected in shallow seas may mean that initial improvement in the indicator can appear to be quick, but that full recovery to baseline levels may take much longer. Shephard *et al.* (2013) predicted that even if fishing pressure were to be removed entirely from the Celtic Sea, recovery of the LFI to the values seen in 1986 would still take ∼30 years. The power to detect meaningful rates of recovery in various size-based indicators can vary from 10 years (Jennings and Dulvy, 2005) to 75 years (Nicholson and Jennings, 2004) of data. Thus, the improvement in the LFI and the slope of the biomass spectrum presented here appears to be occurring on a reasonable timescale, despite the high vulnerability of deep-sea species (Koslow *et al.*, 2000; Morato *et al.*, 2006; Drazen and Haedrich, 2012; Norse *et al.*, 2012).

The slope of the size spectrum also highlights the difficulty of predicting indicator values across different areas of the oceans. The three shallowest depth bands show normalized biomass spectrum slopes of around −1 in the most recent years of the survey, which is in the range of what is expected for unexploited or weakly exploited demersal fish communities in shelf seas using the same method [e.g. in the Mediterranean Sea (Macpherson *et al.* 2002), the Celtic Sea (Blanchard *et al.*, 2005) and the North Sea (Blanchard *et al.* 2014)]. However, in the deepest depth band (over 1650 m), during the most recent years when data collection for these depths was at its highest, the slope approaches values of −0.5. The biomass spectrum for these depths is therefore substantially shallower than at other depths in the deep sea and in shelf seas. This shallow slope may be due to the absence of fishing pressure at those depths, or alternatively the depth bands could naturally differ in the shapes of their size spectra. Indeed, it has

been shown that functional differences within communities result in different values for the slope of the spectrum (Haedrich and Merrett, 1992; Blanchard *et al.*, 2009). Additionally, "subsidized" communities can exhibit inverted biomass pyramids, which may even lead to positive size spectrum slopes (Trebilco *et al.*, 2016). Such external resource subsidies could be said to occur in the deep sea, e.g. through whale falls (Hilario *et al.*, 2015).

Our 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 LFI and the slope of the normalized biomass spectrum, and that the positive change is most apparent at the shallowest depths. Mean body length and mean maximum length did not vary over time, perhaps because the former is unduly influenced by recruitment events that keep body size values low, while the latter may take longer to either be affected or to show signs of reversal. We suggest that size-based indicators can be applied to the deep sea with the same success that they have achieved in shelf seas, but that the same reference points cannot be used for these different ecosystems. It is encouraging that even in the medium-term, deep-sea fish assemblages show signs of recovery, implying that they may be more resilient than previously thought (Koslow *et al.*, 2000), which is just one of many paradigms that are now being questioned in the deep sea (Drazen and Haedrich, 2012; Danovaro *et al.*, 2014). 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.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Data accessibility

The data used in this study are archived on Figshare at doi 10.6084/m9.figshare.5082064.

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