Change in size of deep-sea demersal fish over depth and time

Beth L. Mindel[1], Francis C. Neat[2], Thomas J. Webb[3] & Julia L. Blanchard[3].
[1]Department of Animal and Plant Sciences, Alfred Denny Building, University of Sheffield, Western Bank, Sheffield S10 2TN; b.l.mindel@sheffield.ac.uk
[2]Marine Scotland – Science
[3]University of Sheffield

Summary
Deep-sea communities along the continental slope experience a vast environmental gradient, because as depth increases, pressure increases, and temperature, salinity and oxygen decrease. This means that when understanding the effects of fishing or climate change in the deep sea, we must first take account of bathymetric changes. Here we present changes in fish body size over depth and time in the Northeast Atlantic, by accounting for observed size as well as potential maximum size, L_{max}. There is an increase in fish size as depth increases, and this effect becomes even more pronounced when we account for the L_{max} of the species, implying that individuals are further along in their growth trajectory in deeper waters than they are in the shallows. This may be because of fishing impacts at the shallow end of their range, or due to ontogenetic shifts in species depth ranges. When L_{max} is taken into consideration, size has increased over time in shallower waters, possibly due to stricter controls on fishing in the area in recent years. Time trends change depending on the depth range examined, so the "deep sea" cannot be treated as one unvarying system.

Introduction
The use of traits, rather than taxonomy, to describe communities is becoming more common in ecology (McGill *et al.* 2006). Trait-based approaches are more widely applicable because traits are common to multiple systems, even if they share none of the same species (Weiher & Keddy 1995). In the marine environment, body size is an especially important trait. It determines interactions between individuals and is a better predictor of trophic level than is species identity (Jennings *et al.* 2001). L_{max}, the potential maximum size of a species, is a species-level size-based trait that is correlated with many important life history characteristics such as longevity and age at maturity (Froese & Binohlan 2000). Data for traits are often only available at the species level, however it has been suggested that population-level variation must be taken into consideration when utilising the trait-based approach (Rudolf & Rasmussen 2013). Here we combine these individual- and species- level trait-based approaches to investigate changes in deep-sea fish communities over depth and time.

It is vital to consider change across the depth gradient in the deep sea because the continental slope spans thousands of metres in depth. This produces an incredibly pronounced vertical gradient in pressure, temperature, light and nutrient availability. Here we investigate changes across this gradient using body size at the individual level, and a metric that we term 'life stage', which combines traits at the individual and species level. It is calculated as observed size divided by the L_{max} of that species, hence signifying how far along an individual is in its personal growth trajectory. We examine how these two traits change over depth and time, and show that depth must be taken into consideration when studying the deep sea.

Materials and Methods
Demersal fish were sampled by the Marine Scotland – Science deep-water trawl survey in the years 1998, 2000, 2002, 2004-2009 and 2011-2013, at depths of 300-2067m, in the Rockall Trough, Northeast Atlantic. Total length of each individual fish was used as the measure of body size. L_{max} was downloaded from Fishbase (Froese & Pauly 2013). The mean body size and the mean life stage (body

size/L_{max}) were calculated for each haul, and this was analysed with respect to the depth of the haul, or year of the haul for three depth bands, using General Linear Models.

Results and Discussion

Body size of fish increases as depth increases in the deep sea of the Rockall Trough, and this effect is more pronounced when life stage is used as the metric of size, which includes the L_{max} of the species. This shows that we can account for more variation across an environmental gradient when both individual- and species-level traits are used. The increase in size with depth may be due to fishing pressure in shallower waters causing size to decline (Bianchi *et al.* 2000), or because elongation of fishes allows for higher swimming efficiency in high water pressure environments (Neat & Campbell 2013). The increase in life stage may be due to individuals moving to deeper waters as they age and grow (Lin et al. 2012), or because the stable environmental conditions and lack of disturbance in the deep result in a higher likelihood of individuals being able to reach their potential maximum size.

Fishing pressure has been decreasing in the area since quotas were introduced in 2003, so if fish communities are recovering, we would expect to see an increase in body size over time (Bianchi *et al.* 2000). Body size and life stage both appear to increase highly significantly over time when all depths are averaged for each year. However, if depth bands are separated, different patterns are seen, whereby body size no longer increases over time, and life stage only increases over time in the two shallower depth bands. This highlights how important it is not to group "the deep sea" into one entity, as true effects can be masked when traits that vary across communities are averaged. The increase in size over time when all depths are combined can be attributed to more hauls in deeper waters being taken on the survey in recent years. However, there were significant increases in life stage over time for the two shallowest depth bands.

These results imply that the relaxed fishing pressure is allowing individuals to continue to grow, reaching further along their growth trajectory. The contrasting results of body size and life stage hint that including more traits may indicate patterns of recovery sooner than using solely average body size. Both body size and life stage vary substantially across a depth gradient, and when depth is taken into consideration, life stage appears to indicate recovery of fished deep-sea stocks.

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