

COMMENT

North Atlantic latitudinal diversity patterns in deep-sea marine nematode data: a reply to Rex et al.**P. John D. Lamshead^{1,*}, John Tietjen², Clive B. Moncrieff¹, Timothy J. Ferrero¹**¹Department of Zoology, The Natural History Museum, London SW7 5BD, United Kingdom²Division of Invertebrate Zoology, American Museum of Natural History, New York, New York 10024, USA

Lamshead et al. (2000) analysed the most coherent deep-sea nematode data available for evidence of bio-diversity gradients over latitudinal distances. But, as these authors pointed out, there are considerable problems with extant deep-sea data, including the nematode data, when analysed for this purpose. However, we still feel that 'new data will only be acquired slowly and are likely to possess many of the inadequacies of the old data for much the same reasons' so it seems 'worthwhile to test for latitudinal gradients with the data we have while bearing in mind their problems' (Lamshead et al. 2000). Nevertheless, analysis of large-scale deep-sea patterns is an important new area of enquiry; we published the data to facilitate reanalysis and discussion and it is encouraging to see such a thoughtful response (Rex et al. 2001, this volume).

The main comment in Rex et al. 2001 concerns the omission of depth from the multiple regression of species richness (on sample size and latitude), and they rightly point out that if depth is included, the significance of latitude is lost. Unfortunately, latitude and depth are confounded amongst our station locations with a negative correlation between latitude and depth—higher latitude stations tend to be shallower, partly due to the geography of the North Atlantic.

The question is whether depth should be incorporated into the analysis. We will address this by (1) considering what is known about the relationship between nematode diversity and depth, (2) re-analysing the data to test for whether depth or latitude is more powerful as an explanation of the results, and (3) exploring whether the pattern produced by Lamshead et al. (2000) fits within what is known about deep-sea nematode biodiversity.

(1) Nematode depth-diversity relationships: The relationship between depth and nematode ecological

diversity was analysed by Boucher & Lamshead (1995) using a large, by nematode standards, data-set (that included the data analysed in Lamshead et al. 2000). These authors reported that there was no difference between bathyal and abyssal nematode diversity but that the hadal Puerto Rico Trench samples had significantly lower diversity; so, a case could be made for removing the hadal stations from the analysis.

Rex et al. (2001) suggest that a diversity-depth relationship in the nematode data-set over abyssal-bathyal depth ranges might be present but hidden because the nematode data have been collected from a number of locations. Diversity-depth relationships for nematodes at a single location have not been investigated to the same extent as for macrofauna. Such relationships were analysed for nematode and polychaete assemblages in the Rockall Trough (Lamshead et al. 1994, Paterson & Lamshead 1995), although it must be admitted that the nematode data were sparse (3 depth stations only, data given in Lamshead et al. 2000). The polychaetes show a depth-diversity pattern but there is little evidence that nematodes are similarly affected. The explanation for a different response for the 2 taxa may be that the polychaete pattern appears to be a response to water current disturbance. Deep-sea polychaetes are sensitive to physical disturbance (e.g. Glover et al. 2001) whereas both shallow water and deep-sea nematodes are robust to such disturbance (Warwick et al. 1990, Lamshead et al. 2001, respectively).

A more comprehensive study of nematode depth-diversity relationships at a single location was carried out by Soetaert et al. (1991). This work investigated the diversity at 6 depth stations, but unfortunately only from 160 to 1220 m, in the western Mediterranean. These authors showed no evidence for an association between nematode diversity, or species richness, and depth. The nematode pattern is quite different from

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the relationship reported for macrofauna by many authors (see Paterson et al. 1995).

(2) Reanalysis of the data in Lamshead et al. (2000):

The regression analysis in the original paper showed that latitude was significant as an explanation of species richness even when the effect for sample size is accounted for. Rex et al. 2001 point out that the inclusion of depth into the multiple regression removes the significance of latitude, although latitude is just insignificant at our chosen 5% level ($p = 5.1\%$), when depth and depth squared (to correct for curvilinearity) are added.

Employing the rarefaction analytical method of Rex et al. (1993, 1997, 2000; which investigates ecological diversity rather than species richness as such) on the nematode data to control for depth gives a regression analysis of the residuals of diversity, ES(51), versus depth against the residuals of latitude versus depth of $y = 0.000 - 0.0498x$, $r^2 = 5.3\%$, $p = 0.38$ (excluding the Norwegian Sea, $y = 0.000 - 0.0175x$, $r^2 = 0.7\%$, $p = 0.76$). Controlling for depth using this method does not change the conclusions in Lamshead et al. (2000). Nematode diversity, as measured by ES(51), is independent of latitude; it shows neither a negative nor a positive latitudinal gradient. This is probably because rarefaction is greatly influenced by the local ecology of the North Atlantic basins, because it incorporates a measure of evenness (Gage & May 1993).

Here we have reanalysed nematode species richness to explore the role of depth and of latitude in greater detail. We have transformed the counts of species, sample size and depth logarithmically. The analysis investigates the effects of depth (log transformed), with both linear and quadratic components, and of latitude (untransformed). In all analyses, the effect of sample size is allowed for by inclusion (log transformed) as an initial term in the regression. The Norwegian Sea site was excluded as before because it is an outlier and because it has had a different history from the other North Atlantic basins (Lamshead et al. 2000). The analyses were conducted with the 3 deep-trench sites both included and excluded.

The depth data and the latitudinal data are heavily confounded with each other and so impossible to disentangle. In all these analyses, the quadratic component for depth added nothing of statistical significance after due allowance for the principal linear effect, so it would appear that any curvilinear effect of depth is adequately accounted for in the logarithmic transformation. Including the deep-trench sites, the effect of depth, ignoring latitude, showed a significant negative effect whether treated as a linear term ($-0.214\text{Log}(\text{depth})$, $\text{SE} = 0.052$, $t = -4.1$, $\text{df} = 13$, $p = 0.1\%$) or as a Trench versus Non-trench contrast (-0.426 for deep trenches, $\text{SE} = 0.100$, $t = -4.2$, $\text{df} =$

13, $p < 0.1\%$). After adjusting for the contrast between trench and other sites, there appears to be only a small (insignificant) 'linear' effect of depth ($t = -2.06$, $\text{df} = 12$, $p = 6.2\%$). Ignoring depth, the effect of latitude shows a significant positive relationship (0.009 per degree latitude, $\text{SE} = 0.003$, $t = 3.07$, $\text{df} = 13$, $p = 0.9\%$), which corresponds with the previous finding (on unlogged data). The difference between trench and the other sites confirms the analysis of Boucher & Lamshead (1995), and so the effects of depth and latitude should be considered in the absence of the effect of trench sites.

An analysis of the 13 bathyal-abyssal sites showed that depth and latitude considered jointly had an effect that was just insignificant at the 5% level ($F = 4.03$, $\text{df} = 2, 9$, $p = 5.6\%$). Examined separately and sequentially, the effects of depth ignoring latitude and of depth adjusting for latitude were both statistically non-significant. Likewise the effect of latitude was non-significant after allowing for depth, but latitude ignoring depth accounted for most of the joint variation and was apparently statistically significant ($F = 8.81$, $\text{df} = 1, 10$, $p = 1.4\%$). Thus, whilst we cannot draw conclusions regarding any indisputable effect of either depth or latitude, we might argue that latitude has greater explanatory power than depth.

This conclusion is contrary to that found analysing all the non-Norwegian data when both depth and latitude (when ignoring the other) appear statistically significant ($p = 0.1\%$ and $p = 0.9\%$ respectively). In these data depth alone accounts for almost all the joint variation; however, this includes the recognised effect of trenches. Again neither depth nor latitude shows any statistically significant effect after adjusting for the other.

(3) The relationship between nematode diversity and productivity:

Rex et al. (2000) make the point that even if one accepts their criticism of the analysis, the SR patterns reported in Lamshead et al. (2000) might be real. So another way to approach this problem is to ask whether the positive species richness gradient associated with a positive surface productivity gradient reported in Lamshead et al. (2000) is consistent with other studies of the relationship between deep-sea nematode diversity and productivity in the same way that the negative gradients reported by Rex et al. (1993, 1997, 2000) are consistent with what is known about global Mollusca diversity patterns (e.g. Clark & Crame 1997, Crame 2000).

The nematode data are limited but suggestive. Tietjen (1984) was the first to report that surface productivity was linked to deep-sea nematode diversity based on a study located in the Venezuela Basin (1984). Attempts to test this in the eastern North Atlantic were confounded by disturbance of the reference sites (see

Lambshead et al. 2001, Lambshead in press). Brown (1998) reported on the deep-sea nematode diversity at 5 stations in the central Pacific, from 0° to 23°N. The 3 southerly of these stations had a phytodetritus input and a significantly higher diversity, as measured by rarefaction and species richness, than the 2 more northerly stations. This is a particularly convincing study because the central Pacific is not confounded by local basin ecology, unlike the North Atlantic, which is probably why Pacific nematode ecological diversity and species richness show the same pattern. The nematode species richness pattern reported by Lambshead et al. (2000) is, therefore, consistent with other work.

Conclusions. Even when the trench stations (which are known to be lower diversity than bathyal-abyssal stations) are excluded it is impossible to disentangle depth from latitude in the data, partly because of North Atlantic topography. However, the analysis suggests that latitude has more explanatory power than depth, such that even when depth is included latitude is only marginally insignificant (one might wish for more stations – i.e. degrees of freedom). Of course, whether it is correct to include depth at all in the analysis depends on how the comparison between macrofauna and nematode depth-diversity evidence is interpreted.

The nematode diversity patterns reported by Lambshead et al. (2000) are consistent with other nematode data; the comparison with the equatorial Pacific is particularly useful. It is doubtful that the classic, generalised, terrestrial latitudinal patterns are found in most marine benthic systems because the processes that are thought to drive such patterns (solar energy, including evapotranspiration, gradients) are unlikely to operate. It therefore seems likely that different marine benthic taxa will exhibit different large-scale biodiversity patterns depending on their history and biology. We know nothing of marine nematode history, but nematode biology suggests that we might expect patterns that are robust to disturbance but strongly influenced by productivity.

One final thought is that we tend to analyse the diversity of each taxon against a null hypothesis of a zero gradient. Given our limited data, maybe it would be productive to analyse the patterns of different taxa against each other to test for differences between taxa.

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