Biogeosciences Discuss., 9, C9271–C9284, 2013
www.biogeosciences-discuss.net/9/C9271/2013/

Biogeosciences
Discussions

Interactive comment on "Unravelling the environmental drivers of deep-sea nematode biodiversity and its relation with carbon remineralisation along a longitudinal primary productivity gradient" *by* E. Pape et al.

E. Pape et al.

ellen.pape@ugent.be

Received and published: 1 April 2013

We would like to thank the two anonymous referees for the helpful suggestions, which will definitely lead to an improvement of the manuscript. The questions and suggestions of the referees are repeated below. The line numbers mentioned by Referee #1 refer to line numbers in a submitted word documented which is not available on the website.

Line 61: more recent paper produced an estimate of 1 million or less marine species.

See Appeltans et al. 2012 Current Biology 22: 2189

Author's response: The first paragraph of the introduction will be removed, as advised by the second anonymous referee, since the introduction is already lengthy and the subject of the ms is not the high diversity in the deep sea, but rather the environmental drivers and the effect on ecosystem function of deep-sea diversity.

Line 76: end of sentence should read: ".. competition, and predation."

Author's response: This sentence is part of the first paragraph of the introduction. The first paragraph of the introduction will be removed, as advised by the second referee.

Line 78: delete "regional"

Author's response: The first paragraph of the introduction will be removed, as advised by the second referee.

Line 86: the difference between studies is probably due to the different range of productivities sampled. In this respect, it would be useful if the authors commented on where their study sites may lie along the productivity continuum (i.e., are they oligo-, meso-, or eutrophic). This would help predict what kind of relationship might be expected, in particular if we assume that the overall relationship for the full productivity range is unimodal (see Rex and Etter 2010 book).

Author's response: Indeed, the different productivity ranges sampled in the different studies may explain (part of) the differences in documented diversity-productivity trends. The Mediterranean Sea is generally considered to be oligotrophic, which is also mentioned in the book of Rex and Etter (2010) (page 41), having a primary productivity of less than 100 g C m-2 yr-1. This can be added to the modified manuscript, and as such we may expect a positive relation between diversity and productivity for our stations. However, note that we used net primary productivity (NPP) values from the vertically generalized production model for our study areas to estimate seafloor particulate organic carbon (POC) flux. These NPP values ranged between 716.2 g C

m-2 yr-1 and 384.2 g C m-2 yr-1. Hence, according to the classification of Nixon et al. (1995) (which is also used in the book of Rex and Etter), all of our stations should be eutrophic (300 - 500 g C m-2 yr-1) or even hypertrophic (> 500 g C m-2 yr-1). The large discrepancy between our values and those obtained in other studies strongly suggests that our NPP values are huge overestimates. I would thus suggest to regard the Mediterranean as oligotrophic (eastern basin) or mesotrophic (western basin), and the Galicia Bank region in the northeast Atlantic as mesotrophic (assuming NPP is here 220 g C m-2 yr-1; (Joint et al. 2002)). We may add here: "Deep-sea diversity has been documented to vary positively (Glover et al., 2002; Lambshead et al., 2000, 2002), negatively (Gooday et al., 2012) or unimodally (Leduc et al., 2012a; McClain et al., 2012; Tittensor et al., 2011) with productivity for different taxa and geographic regions. These differences in diversity-productivity trends may be related to the differential productivity ranges considered (Rex and Etter 2010). A unimodal curve may only be found when the range of productivity is sufficiently large, whereas a positive and linear relation may be retrieved under a low and high productivity regime, respectively." Then, at the end of the introduction, we may add the following: "Specifically, we explored the form of the diversity-productivity curve by characterizing the relationship between nematode diversity and the magnitude of the POC flux to the seabed. Since most of our stations were located within the oligotrophic Mediterranean Sea, we expected to see a positive relation between diversity and seafloor POC flux."

Line 97: The authors may want to look a little further in the literature, as it appears that some models are more likely than others, the redundancy model in particular. The results of Danovaro et al. for the deep sea are quite exceptional in that the relationship is exponential. The authors may want to discuss which model they think deep-sea nematodes will fit.. for example they are typically very diverse, and in some cases, with high within-genus diversity (eg Acantholaimus) and therefore with high level of functional redundancy?

Author's response: Indeed, a saturating relationship between diversity and ecosystem

functioning (i.e. the so-called redundancy model) is the most often hypothesized relation (Hooper et al. 2005). If you assume that species belonging to the same genus have rather similar functions, then there might be a considerable degree of functional redundancy in deep-sea nematode assemblages given the high within-genus diversity as mentioned by the referee. However, as Danovaro et al. (2008) found an exponential relation between nematode species diversity and ecosystem functioning, we may expect to see an exponential curve for nematode genera as well, if we assume that greater relatedness results in higher functional similarity. We may thus add the following to our introduction: "Here, we investigated the variation in nematode taxon (genus) and functional diversity along longitudinal (reaching from the Galicia Bank in the northeast Atlantic to the eastern Mediterranean basin) and bathymetric (1200 – 1900 – 3000m) gradients within deep-sea sediments." . . .and. . . "Danovaro et al. (2008) observed an exponential relationship between nematode species diversity and ecosystem functioning, and so we may expect this type of relation for nematode genus diversity as well if we presume that higher relatedness results in higher functional similarity".

Line 134: It would be worthwhile to include something in the Introduction about how nematode diversity may affect ecosystem function. It is still a black box, but some likely processes should be mentioned.

Author's response: we will add a few lines on how nematode diversity may affect ecosystem functioning (before "Here, we investigated the variation in nematode taxon..." on line 138). "Nematodes may influence an important ecosystem function like the bacterial breakdown of organic matter through bioturbation and –irrigation (Pike et al. 2001), thereby enhancing nutrient and/or oxygen fluxes (Alkemade et al. 1992, Aller and Aller 1992), bacterivory (De Mesel et al. 2003) or the provision of optimal growth conditions for bacteria in their mucus trails (Riemann and Helmke 2002, Moens et al. 2005). Line 152: So function is based on a proxy of proxy. A little indirect. Perhaps the authors could simply consider respiration rates only. Respiration is of course strongly correlated with biomass, which itself largely reflects POC input. Instead of accounting

for the effect of biomass in analyses of the diversity-function relationship, I would instead run the regression for POC flux (to control for the likely impact of this factor on respiration) followed by diversity. I think the authors will agree that POC input cannot be ignored as a driver of ecosystem function in the deep sea, and that its effect needs to be controlled for. And I would not use biomass in this analysis. Author's response: We did consider only nematode respiration rates in this study, but we wanted to acknowledge that these indicate how much organic carbon is mineralized by the nematodes. We understand the point of the referee, but we believe that nematode biomass may serve as a better indicator of food availability than our estimates of seafloor POC flux, since the latter may have been biased. Potential decoupling between overhead productivity and deposition at the seabed may have come from lateral advection, varying contributions of non-algal material to the POC rain, disregard of the plankton community and food web structure, and so on. This was also discussed in a soon to be published paper in Plos One with Ellen Pape as first author ("Benthic-pelagic coupling: effects on nematode communities along southern European continental margins"; available from April 2nd onwards at http://dx.plos.org/10.1371/journal.pone.0059954). Another point that can be made, which was also brought up by Leduc et al. (2012), is that a higher POC deposition does not necessarily translate into a higher food availability to the nematodes.

Line 164: Please provide details of core surface areas. Surface area may affect nematode diversity estimates, i.e., larger core will include a larger number of species aggregations and therefore tend to yield larger diversity estimates than smaller cores. Eg Warwick and Clarke 1996 JEMBE

Author's response: These data were already included in Table 1. We will refer to this table in the text, since this was not done.

Line 180: replace "data on" with "estimates of"

Author's response: We assume (since the line number mentioned here does not ex-

ist) you are referring to the following section "Data on the particulate organic carbon (POC) flux to the seafloor. . ."? (page 19025, line 17)? "Data on" will be replaced with "estimates of" in the new version of the manuscript.

Line 189: did the diversity estimates for the top 10cm take into account the difference in nematode abundance between layers or are they simply averages of all the layers (the latter would be incorrect)?

Author's response: The diversity data in the discussion paper were calculated by pooling nematode genus counts of the different sediment layers. However, we did not take into account differences in total nematode abundance between sediment layers. This has now all been corrected for, leading to different results for the regressions (i.e. no more longitudinal trend for EG(20), H', MI and TD, but longitudinal trends for Δ^* and $1/\Lambda+$; no more decline of EG(20) with SVI; positive relation between average taxonomic distinctness ($\Delta+$ and Δ^*) and SED; negative relation between $\Delta+$ and POC, and between Δ^* and SVI).

Line 190: the rarefied genus richness is based on rather low abundance (18). One core had 18 nematodes only? What was the size of that core?

Author's response: In the discussion paper, two identifications had been forgotten and the index should actually be EG(20) (which is not that much higher, though). Indeed, one core only counted 20 individuals. This core was collected in the Ionian Sea (eastern Mediterranean) at around 3000 m water depth with a corer with a surface area 10.18 cm^2 see also Table 1).

Line 231: or body size diversity? Seems more directly relevant

Author's response: We presume you mean that it would be more relevant to calculate the diversity in lengths (size) of nematodes? If yes, we do not agree with this suggestion since the variation in individual biomass or body weight is more relevant to respiration because biomass is needed to calculate respiration rates.

Line 258: here I would use POC flux instead of biomass. See previous comment.

Author's response: We do not agree with this suggestion; see one of the previous answers.

Line 273: Please explain. I do not understand why the quadratic term was added.

Author's response: this must indeed not have been very clear. We would like to add this sentence to the section describing the data analysis: "When a unimodal pattern was evident for an independent variable, the quadratic term of this variable was added."

Line 309: is there a relationship between longitude and POC (linear or otherwise)? The authors need to check for collinearity between predictor variables before running the regression. Some variables may be strongly correlated.

Author's response: Firstly, we looked for geographic (longitudinal and bathymetric) trends in nematode diversity, and subsequently we evaluated correlations between diversity and environmental variables (POC flux, SVI and SED). Longitude or water depth are not causes of diversity trends, they merely represent gradients in environmental characteristics. Longitude and POC were never used together as predictors in the regression analyses, and consequently we did not check for collinearity between these two variables. We did check for collinearity amongst the predictor variables that were used together by calculating variance inflation factors (which was also stated in the section on the data analysis). We did not use all environmental variables and geographic variables as predictors in the regression analysis because we had only a limited amount of data (n=31), and models with too many predictors lead to overfitting and generate spurious results.

Line 319: Could the authors confirm that all the relationships they are mentioning here are for partial regressions, and not marginal regressions? Need to make this clearer throughout text. Please provide a table of results for these results from your regressions. Same for previous paragraph.

Author's response: this was indeed not very clear. We will add tables with the results of the regression analyses, and clearly indicate in the legend of the figures whether marginal or partial regression data are displayed.

Line 346: which assumption?

Author's response: this particular sentence will be removed. With the correct data no significant regression was found for Pielou's evenness (J') against respiration.

Line 347: I am really not sure that the factor region is random. I doubt these areas were in fact chosen at random from a wider selection of potential sampling sites. I believe this should be changed in the analyses (i.e., fixed). Again a table of results should accompany this paragraph (regression results).

Author's response: Well, the different Mediterranean sub-basins were random, since we wanted to sample in the western and Eastern Med at different water depths, and so we happened to collect samples from these sub-basins. Furthermore, we modelled the factor region as a random effect since we were interested in estimating variances, not in estimating the mean effect of region on diversity or respiration. The modelling of the random effect region allowed us to control for correlated data from samples within regions. Tables with regression results will be added to the results section.

Discussion:

Line 358: there are still some fairly major issues with using EG(18), especially since it is based on a small number of individuals in this ms. This index can be strongly dependent on dominance and aggregation (the latter will, in turn, be affected by the size of your cores!), especially at small sample sizes (see Gray 2000 JEMBE p.11-12). So it is difficult to say which index is more representative, or less biased, and one cannot be chosen as more meaningful in this context. Perhaps the authors could include N in their regression analyses, so that the effect of abundance on diversity indices can be controlled for? In any case, it would be good to see if there is a relationship between N

and diversity indices. Quantifying diversity is always a problem so it makes sense to at least acknowledge potential biases.

Author's response: we want to refrain from using more predictor variables (such as nematode abundance or N) because of the limited amount of data here and the associated problem of overfitting. Indeed, in general, dominance (lower evenness J') is more outspoken in smaller samples, which may lead to an overestimation of expected genus richness. However, we saw highest evenness in cores with lowest surface area and lowest number of individuals. In fact, J' was the only diversity index that related significantly (negatively) with N (Spearman Rank, r =-0.87, P <0.001). We can add these results to the section describing the link between taxon and functional diversity indices. With the correct diversity data we no longer observe a longitudinal trend for H' and EG(20) (but we do detect a longitudinal rise for J'). Both indices do show a linear decline with increasing water depth. So, now, we observe comparable patterns for H' and EG(20).

Line 376: include reference(s) to back up statement.

Author's response: these lines will be removed, since with the correct diversity data no longitudinal trend is observed for either MI or TD.

Line 382: in my mind these analyses of depth-diversity relationships are getting old. We all know that it is difficult to compare between studies for a wide variety of reasons. What is interesting is to understand the underlying mechanisms. So yes, whatever results one gets will always contrasts with at least some studies. Rex and Etter summarised what we know quite well and I don't think there is a need to make elaborate comparisons.

Author's response: In the following paragraph, we attribute the different results between our and previous studies to the different taxon levels and sediment depth intervals considered. That is why we first need to present the differences between our and previous research.

Line 412: see comment about collinearity.

Author's response: see one of the previous answers.

Line 433: Nice discussion. Line 442: such as?

Author's response: With the correct diversity data, we do not observe a significant negative relation between Shannon-Wiener diversity (H') and SED (instead, no significant relation was found). However, we still see a significant negative association between TD and SED. Any factor that may lead to a decrease in TD but that is associated with an increase in SED may lie at the base of this significant regression, though we can only speculate on which factor is important in this study. One example that comes to mind is higher standing stock of mega- or macrofauna generating higher sediment heterogeneity but lower nematode trophic diversity. We may write: "It should be stressed that the trends described here do not imply causal relationships, and that the decrease in nematode trophic diversity with increasing SED may be driven by a confounding, unmeasured environmental factor (e.g. standing stock of mega- or macrofauna)."

Line 452: replace "strongly" with "may". But one would expect such a positive relationship anyway, no? especially when considering only genera, which are more likely to differ than species. I think the authors are taking it a little bit too far when jumping from diversity of life history strategies to resilience and function.

Author's response: this section was indeed formulated too strongly and will be more nuanced in the modified version of the manuscript. We suggest the following adjustment: "Our results showed that nematode communities with higher taxon diversity were characterized by a greater variety of life history strategies (higher c-p diversity). If higher c-p diversity governs enhanced resistance against environmental fluctuations or resilience following disturbance, this may point to a positive long-term effect of taxon diversity on ecosystem functioning (Loreau 2000)."

Line 472: so how much overall variability was there in genus richness per core? Could

the authors try to explain perhaps how many additional genera might lead to, say, a 50% increase in respiration (or whatever) according to their analyses (even though of course causation cannot be implied)? This would help to put things in context a bit.

Author's response: We are not entirely sure if we understand this question correctly. If you have a positive linear relationship between variables Y and X, then taking the double of X will lead to a doubling of Y. Index EG(20) was on average 13.22, so adding another 13.22 genera (whilst keeping total biomass constant, so not exactly adding genera though) will lead to a two-fold higher respiration. Is this what was meant here?

Line 490: but the environmental variables were not controlled for in these analyses, were they? I thought only biomass was controlled for. See previous comments.

Author's response: Indeed, we only regressed diversity and biomass against respiration, without considering environmental factors. As mentioned before, this was done to avoid overfitting.

Line 501: or there might just not be a relationship between functional diversity and function. This should be acknowledged.

Author's response: Indeed, a significant regression does not imply a causal relation. It is also possible that there is an environmental variable influencing both diversity and respiration, thereby generating a significant regression. This will be acknowledged in the discussion: "We assumed that respiration is dependent on diversity in nematode communities. However, significant regressions do not necessarily imply causation. If both diversity and respiration are influenced by the same environmental factor(s), this would also result in a significant relationship. Temperature promotes respiration rates and, at least for ophiuroids (O'Hara and Tittensor 2010) and mollusks (Tittensor et al. 2011), also biodiversity. Along our transect, higher POC deposition (food availability) resulted in higher standing stock and thus higher respiration rates (Pape et al. in press), but also allowed for more taxa to attain viable population sizes. However, the fact that communities with equal biomass (suggesting equal food availability) with differing di-

versity showed differing respiration rates indicates that food availability is not the sole factor governing the significant diversity-function relation. Experimental studies, employing in situ respiration as an ecosystem function, are needed to verify and elucidate the mechanism(s) behind the observed diversity-function relation."

Line 507: also species vs. genus, sediment depth: : :

Author's response: Here, you are referring to the following lines "The different form of the biodiversity-function curve in the present study (linear) and that of Danovaro et al. (2008a) (exponential) is in all probability related to the different measures that were used to define ecosystem functioning (nematode respiration rates vs. prokaryote biomass and production, bacterial organic matter decomposition and total faunal biomass, respectively)." (page 19038, line 1-5) We totally agree; the fact that different taxon levels (species vs. genus) and sediment depths (0-1 cm vs. 0-10 cm) were considered may have contributed to the differential outcome of these studies. We thus need to rephrase this sentence → "The different form of the biodiversity-function curve in the present study (linear) and that of Danovaro et al. (2008a) (exponential) may be related to the differences in measures of ecosystem function (nematode respiration rates vs. prokaryote biomass and production, bacterial organic matter decomposition and total faunal biomass, respectively), the taxonomic level considered (genus vs. species, respectively) and the sediment depth interval investigated (0-10 cm vs. 0-1 cm, respectively)."

Figure 5: what about a graph showing relationship between POC flux and respiration?

Author's response: See previous comment regarding the usage of POC flux instead of biomass in the regressions.

References (for answers to Referee #1 and #2)

Alkemade R, Wielemaker A, De Jong S, Sandee AJJ (1992) Experimental evidence for the role of bioturbation by the marine nematode Diplolaimella dievengatensis in

stimulating the mineralization of Spartina anglica detritus. Marine Ecology Progress Series 90:149–155 Aller RC, Aller JY (1992) Meiofauna and solute transport in marine muds. Limnology and Oceanography 37:1018–1033 Cadotte MW, Cardinale BJ, Oakley TH (2008) Evolutionary history and the effect of biodiversity on plant productivity. PNAS 105:17012–17017 Corliss BH, Brown CW, Sun X, Showers WJ (2009) Deep-sea benthic diversity linked to seasonality of pelagic productivity. Deep-Sea Research I 56:835–841 Danovaro R, Gambi C, Dell'Anno A, Corinaldesi C, Fraschetti S, Vanreusel A, Vincx M, Gooday AJ (2008) Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. Current Biology 18:1–8 De Bovee F, Labat J (1993) A simulation model of a deep meiobenthic compartment: a preliminary approach. PSZNI: Marine ecology 14:159–173 De Mesel I, Derycke S, Swings J, Vincx M, Moens T (2003) Influence of bacterivorous nematodes on the decomposition of cordgrass. Journal of Experimental Marine Biology and Ecology 296:227–242 Godbold JA, Solan M (2009) Relative importance of biodiversity and the abiotic environment in mediating an ecosystem process. Marine Ecology Progress Series 396:273–282 Gooday A, Bett B, Jones DOB, Kitazato H (2012) The influence of productivity on abyssal foraminiferal biodiversity. Marine Biodiversity:1–17 Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35 Hooper DU, Vitousek PM (1997) The Effects of Plant Composition and Diversity on Ecosystem Processes. Science 277:1302–1305 Joint I, Groom SB, Wollast R, Chou L, Tilstone GH, Figueiras FG, Loijens M, Smyth TJ (2002) The response of phytoplankton production to periodic upwelling and relaxation events at the Iberian shelf break: estimates by the C-14 method and by satellite remote sensing. Journal of Marine Systems 32:219–238 Leduc D, Rowden AA, Bowden DA, Probert PK, Pilditch CA, Nodder SD (2012) Unimodal relationship between biomass and species richness of deep-sea nematodes: implications for the link between productivity and diversity. Marine Ecology Progress Series 454:53–64 Moens T, Dos Santos GAP, Thompson F,

Swings J, Fonsêca-Genevois V, Vincx M, De Mesel I (2005) Do nematode mucus secretions affect bacterial growth? Aquatic Microbial Ecology 40:77–83 Nixon SW (1995) Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41:199–219 Paterson D, Defew E, Jabour J (2012) Ecosystem function and coevolution of terminology in marine science and management. In: Solan M, Aspden R, Paterson D (eds.) Marine Biodiversity and Ecosystem Functioning: Frameworks, methodologies, and integration. pp. 24–33. Pike J, Bernhard JM, Moreton SG, Butler IB (2001) Microbioirrigation of marine sediments in dysoxic environments: Implications for early sediment fabric formation and diagenetic processes. Geology 29:923–926 Rex MA, Etter RJ (2010) Deep-Sea Biodiversity: Pattern and Scale. Harvard University Press. Riemann F, Helmke E (2002) Symbiotic relations of sediment-agglutinating nematodes and bacteria in detrital habitats: The enzyme-sharing concept. Marine Ecology 23:93–113 Soetaert K, Vanaverbeke J, Heip C, Herman PMJ, Middelburg JJ, Sandee A, Duineveld G (1997) Nematode distribution in ocean margin sediments of the Goban Spur (northeast Atlantic) in relation to sediment geochemistry. Deep-Sea Research I 44:1671–1683 Solan M, Batty P, Bulling M, Godbold J (2008) How biodiversity affects ecosystem processes: implications for ecological revolutions and benthic ecosystem function. Aquatic Biology 2:289–301

Interactive comment on Biogeosciences Discuss., 9, 19019, 2012.