

Review of Kelly-Gerreyn et al. – Controls on benthic biomass size spectra in shelf and deep-sea sediments

Kelly-Gerreyn et al. describe a model to analyze benthic biomass size spectra (BBSS) at three contrasting soft sediment localities. The paper has two components. First component are the field data. The abundance and biomass of different size classes of benthic organisms has been studied thoroughly. Second component is the model that is strongly influenced by a size-based model developed by Peters et al. Basic assumptions are that the different size classes of benthos share the same food source (i.e. detritus), that predator relations are absent and that physiological processes may change with organism size. Although some of these assumptions are clearly simplifications of reality, it represents an interesting null model to use to investigate how well such a simplified model can describe real BBSS. Moreover, it provides several thought provoking and testable results/predictions regarding the scaling of physiological parameters with organism size.

The paper is reasonably well written, especially given the complexity of the matter presented. I do however have some important issues that need to be addressed.

Major comments

Test for bimodality in abundance and biomass relations

One of the claims of the authors is that “The observed biomass size spectra revealed that biomass increased with body size, although qualitatively some local minima/maxima may be identified in the spectra”. I concur with the authors that the minima in the BBSS are less pronounced than in the figures by Swinghammer (1981). However, a test for bimodality with proper statistics is needed instead of the statement that “qualitatively some local minima/maxima may be identified”. Fig. 3b and 3f look rather bimodal. The authors report significant linear regressions in the BBSS (table 4), but have not tested alternative models that include bimodality.

Inclusion of bacteria in the model

The way that bacteria are included in the model is not realistic. Bacteria directly consume a fraction of the flux before it enters the detritus pool (fig. 2), but on the other hand the authors note that bacteria “mineralise organic material of different reactivities, in both the presence and absence of oxygen”. Degradation of material of lower reactivity and/or in the absence of oxygen are processes that occur deeper in the sediment. Based on this reasoning it is actually the bacteria that can be expected to feed on the detritus stock rather than the detritus flux. Moreover, the authors also state that an earlier model that treated bacteria differently only acted to change the amount of detritus processed by the metazoans. Finally, the authors also state that the “POC flux term, $(1-f_{bac}) POC_{flux}$, in Eq. (3) is not well constrained”. It would therefore be more realistic to simply eliminate the bacteria from the model and only focus on the POC flux that is processed by the metazoans, since the focus of the paper is on the BBSS. The differential equation of the detritus pool (eqs. 4) means that

the authors have also solved for the detritus stock in the sediment on which the fauna are actually feeding. I did not find any output of the detritus pool in the paper, but it would be very interesting to compare this modeled detritus stock with the measured detritus stock in the sediments (e.g. through the POC content in the upper centimeters of the sediment). I also wonder whether R differs between stations.

Mortality as structuring factor

The importance of mortality as a structuring factor is not inferred from a comparison of the importance of different processes. The model is solved in steady-state, which implies that the single “uptake” process of net production and the only “loss” process represented by “mortality” must balance. Hence, the importance as a structuring factor cannot be inferred from the importance of one process over the other. Instead, the authors investigate the structuring role of uptake and loss on the BBSS curve by investigating the sensitivity of its shape to changes in the parameters values. The increase in the BBSS curve, as seen in the data, is particularly sensitive to the settings of the mortality parameters, hence the authors conclude that mortality is an important structuring factor. Although this is a valid approach it would be good if this methodology would already be introduced in the Introduction rather than in the course of the Discussion. It would make it an easier read.

This followed method, however, also implies that the process descriptions should be judged extra carefully, because these determine the sensitivity of the BBSS to the model parameters.

The net production process for a particular size-class (so ignoring subscripts) is described by:

$$(1 - r) \alpha I \frac{R}{R + K_{ing}}$$

These parameters are fitted in the optimization procedure and give fixed parameters per size-class. Hence, net production is **dependent** on food concentration but **independent** of the biomass of the size-class. This seems like a very unrealistic situation and deviates from other applications such as Yodzis and Innes (1992). I considered it may have been a typo, but biomass is consistently missing in eqs 2, 3 and 4 and they state that “ingestion and mortality are regulated by the concentration of the food source and biomass, respectively” (pg 8199 line 8-9).

The mortality term instead is given by:

$$m B \frac{B}{B + K_m}$$

Hence the mortality term is dependent on the biomass of a size class. It is confusing to see that the parameters I and m have the same units in Table 3, though one process is biomass-dependent while the other isn't. Moreover, I do not see how the unit of I is compatible with the other components in the differential equation of the detritus pool (eqs. 4).

Apart from the inconsistency in parameter units, the answer to the sensitivity of the BBSS curve to mortality may be found in the fact that the loss process “mortality” is considered biomass-dependent, whereas the uptake process “net production” is not. Apart from ingestion that in most

model is biomass dependent, several other processes that are biomass-dependent such as maintenance respiration or interference competition are not included in the model. Moreover, there are several different formulations to implement mortality (Steele and Henderson, 1992) that depend more or less on biomass. The authors acknowledge that “data are currently lacking to provide support for such density-dependence” in mortality, but decide to use this formulation because it is a “recognized mechanism for regulating natural populations of pelagic organisms”. Although this may be true, it is still really important to know how sensitive the model results are when different formulations are tested. It may be that mortality is a structuring factor of the BBSS **only** if mortality proves to be density-dependent.

I do understand that it would go too far to include or analyze every alternative model formulation, but the selectivity with which the authors have chosen to include biomass-dependence only in the loss process may have biased the results greatly and warrants testing of alternative formulations.

Carbon processing by the size-classes

An output from the model that would be of great interest to the readers is the partitioning of net production and respiration among the size classes. I would definitely like to see those figures being included in the paper.

Minor comments

- The first paragraph of the introduction can be deleted because it bears limited relevance to the paper.
- It would be good to delineate the method of how the structuring factors on the BBSS were identified already in the introduction
- Pg. 8192 line 18, give units of ug.
- In the first paragraph of 2.1, the authors state that the full wwt range of benthic metazoans is 5 ng – 5 kg. Due to clearly outlined methodological issues, they decide to work with a more limited size range. It would be good to state this explicitly at the end of this paragraph and refer to Table 1 for details. Moreover, I think it is awkward to repeatedly talk about the “reliable part of size spectrum”. The other part not unreliable in itself, we are just lacking the methods to measure them reliably. So I would define the size range here and remove “reliable” from the rest of the paper and probably also start counting size classes at 1 rather than 5.
- Pg. 8193 line 24, “which are thought to be slight”, finish sentence.
- Pg. 8194 line 26. Add to table 1 a summary with how many organisms were measured for each stations for each size-class. I find it difficult to judge on how many measurements the figures are based.
- Pg 8196 line 1-3. Regression coefficients were compared to standard allometric ratios. It would be good to add to the introduction the rationale for the comparison.
- Pg. 8198 line 2-3. “A dry to wet weight ratio of 0.25 (Rowe, 1983) is used to convert to units of carbon.” I don’t get this, what was the conversion?
- Check references to equation numbers throughout manuscript. I think several references, but not all, go wrong after page 8198 – line 16.

- Pg. 8200. I don't understand why the authors chose that the exponent b_1 should be the same for ingestion and mortality (eqs. 5 and 6). The authors state that "This Eq. (6) essentially yields a mortality term which scales with ingestion rates, an approach commonly adopted in biomass size spectra modelling (e.g. Borgmann, 1987)." I understand the scaling part, but what is the rationale behind it?
- Give details on numerical methods that were used to solve the model.
- Pg. 8206 line 20. The Ahrens et al. paper is only on *Nereis succinea*, whereas the other comparisons are made across taxa. So this is not a fair comparison.
- Pg. 8207 line 9. "Optimisation of the POC flux term, $(1-f_{bac}) POC_{flux}$, in Eq. (3) is not well constrained." Where is it shown in the paper how well the parameters are constrained? It is unclear on which results this statement is based.
- Fig. 7d. How can it be that two different model scenarios for the respiration coefficient give exactly the same output, since red and blue lines overlap completely?

References

- Steele, J.H., Henderson, E.W., 1992. The Role of Predation in Plankton Models. *Journal of Plankton Research* 14 (1), 157-172.
- Yodzis, P., Innes, S., 1992. BODY SIZE AND CONSUMER-RESOURCE DYNAMICS. *American Naturalist* 139 (6), 1151-1175.