FEATURE ARTICLE

Characteristic benthic size spectra: potential sampling artefacts

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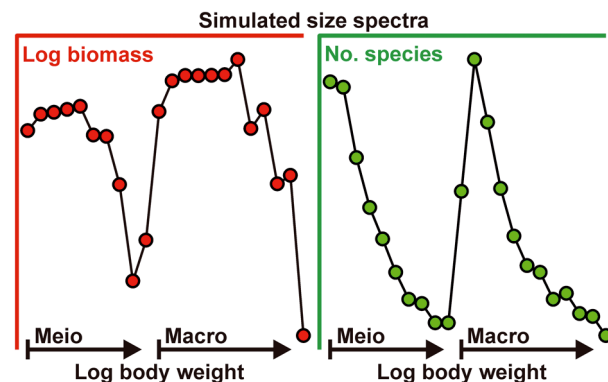
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ABSTRACT: Simple mathematical simulations were carried out to examine the potential influence of sampling protocol on the production of characteristic benthic size spectra (in biomass and species richness). The use of separate samples and sieve meshes for meio- and macrobenthos readily produced a biomass trough at intermediate body sizes where no trough existed in the sampled population (set by simple body size-abundance allometry). The number of specimens sampled per size class was also bimodal across the meio- to macrobenthos size range, providing a simple mechanism by which bimodal species size spectra may result, i.e. a general positive relationship between estimated species richness and the number of specimens examined. These sampling artefacts have the potential to generate characteristic benthic biomass and species size spectra that reflect the sampling protocol rather than the underlying structure of the benthic community. The results suggest the need for caution in regarding the meio- and macrobenthos as coherent entities with distinct ecological attributes. They also raise the prospect of a useful, single mathematical formulation of standing stock and body size for the metazoan benthos as a whole in biogeochemical modelling.

KEY WORDS: Body size relations · Benthic biomass size spectra · Benthic species size spectra · Benthic sampling · Benthic modelling

Simulated size spectra

Benthic size spectra can be sampling artefacts of an underlying continuous distribution defined by a singe body size allometry relationship.

Image: B. J. Bett

INTRODUCTION

During the review process of a manuscript developing a body-size-based model of marine benthic ecosystems (Kelly-Gerreyn et al. 2011), reviewers asked why the field data (Kaariainen 2006) and model output did not reflect a bimodal size distribution across the smaller (meiobenthic) and larger (macrobenthic) metazoan invertebrates. These questions were posed based on an acceptance of the classical work of Schwinghamer (1981, 1983, 1985, 1988, Schwinghamer et al. 1986), who described trimodal benthic biomass spectra with modes corresponding to the conventional body size definitions of micro-, meio-, and macrobenthos. Schwinghamer's work was soon apparently supported by the work of Warwick (1984) and co-authors (Warwick & Clarke 1996, Warwick & Joint 1987, Kendall et al. 1997), who described bimodal species body size spectra for benthic invertebrates with the modes again matching standard definitions of the meio- and macrobenthos. However, Schwinghamer and Warwick size spectra are very different in their ecological character; the former plots total population biomass per size class, while the latter plots the number of species with adult female body weight in a particular size class, i.e. the first deals with standing stock, while the second deals with species richness.

Body size classes offer a simple basis for the mathematical modelling of benthic ecosystems, requiring substantially less complexity than species- or functional group-based approaches (e.g. Andersen & Beyer 2006). Peters (1983) details a very simple size-based benthic model driven by a small number of allometric equations, having previously used the model to assess the distribution of pesticide across size classes of invertebrates (Griesbach et al. 1982). Peters (1983) also examines the allometry of standing stocks, noting the Sheldon spectrum of biomass distribution in pelagic ecosystems (Sheldon et al. 1972). The flat Sheldon spectrum, with near-constant biomass in logarithmic size classes from bacteria to whales, suggests an underlying body size allometry of power –1 with biomass (B) and –2 with abundance (A):

$$A = k \cdot weight^{-2} \text{ and } B = k \cdot weight^{-1}$$

where k is a constant, and

$$A_i = k \cdot weight_i^{-1} \text{ and } B_i = k \cdot weight_i^{0}$$

where $weight_i$ represents logarithmic size class i. Among other things, this allometric relationship has been employed to estimate the density of monsters in Loch Ness (Sheldon & Kerr 1972).

Sheldon et al. (1972) and Peters (1983) based their ideas on early field observations and experimental data. The approach, however, remains of key interest in the current mathematical modelling of aquatic communities; see e.g. the progression of ideas through Andersen & Beyer (2006) to Hartvig et al. (2011) and Rossberg (2012). The Sheldon spectrum is specifically dealt with in Brown et al.'s (2004) development of a metabolic theory of ecology (MTE). These authors noted that their MTE would predict that within a trophic level, abundance in log size classes should scale with $-\frac{3}{4}$ power, and biomass with $\frac{1}{4}$ power (see Fig. 1a). They considered that the flat Sheldon spectrum (i.e. biomass scaled with 0 power) was a composite of $\frac{1}{4}$ power relationships across trophic levels, e.g. phytoplankton, zooplankton, and planktivorous fish (see Fig. 1b). In deriving their interpretation of the Sheldon spectrum, Brown et al. (2004) assumed a general energy transfer efficiency between trophic levels of 10% and a prey-predator mass ratio of $1:10^4$. The latter ratio is also taken to be the typical body weight range of a single trophic level, equating to approximately 14 X2 geometric body weight classes (Warwick 1984), as illustrated in Fig. 1b.

As a first approximation, the difference between size spectra within and across trophic levels might be equated with decomposer and grazer systems (e.g.

Begon et al. 1990), respectively. The phytoplankton-zooplankton-planktivorous fish grazer chain reflects the pelagic situation (Fig. 1b), and the consumption of phytodetritus by a very broad size range of metazoan invertebrates represents the benthic situation (Fig. 1a). The smallest nematode (8 ng wet wt) to the largest holothurian (8 kg wet wt) may consume the same detrital resource, despite a body weight range ratio of $1:10^{12}$, equivalent to 3 complete typical trophic levels (see above; Brown et al. 2004). Simultaneous use of a common detrital food pool across multiple body size classes is a key feature of Peters' (1983) model.

From Peters (1983) through Brown et al. (2004) to Rossberg (2012), many authors have seen the value and simplicity of allometry in the modelling of aquatic communities. Application of this approach to the marine benthos may be somewhat complicated if Schwinghamer's characteristic benthic size spectra are accepted *a priori*. In the following, I consider whether apparently characteristic spectra could be
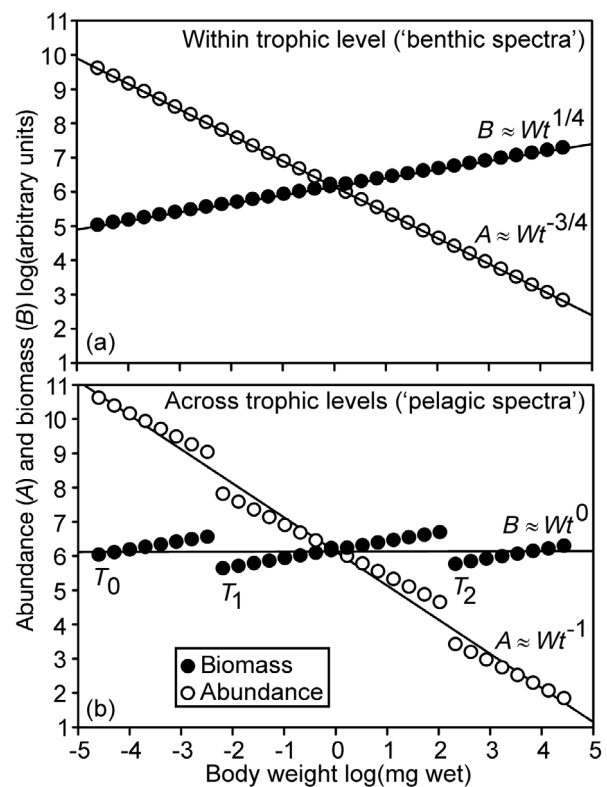

Fig. 1. Theoretical abundance and biomass size spectra adapted from Brown et al. (2004) Fig. 10. (a) Distribution of abundance and biomass across X2 geometric body size classes (Warwick 1984) within a trophic level following the metabolic theory of ecology (MTE): a possible approximation of benthic size spectra. (b) Distribution of abundance and biomass across trophic levels ($T_{0,1,2}$) as interpreted by the MTE: a possible approximation of pelagic (Sheldon) size spectra

produced as a result of sampling methods (sieve mesh size and sample size) rather than as a reflection of true community structure. I use simple allometry of biomass on body weight, consistent with Brown et al.'s (2004) MTE, and simulate conventional benthic sampling methods, initially considering the flat Sheldon spectrum allometry ($\approx Wt^0$), then adjusting this power to better reflect the slight positive slope of benthic biomass spectra ($\approx Wt^{1/4}$).

MATERIALS AND METHODS

For the analysis and display of body size spectra, the size classes employed were those of Warwick (1984), namely X2 geometric body weight classes where class 0 is 19–37 ng wet wt and class 30 is 20–40 g wet wt. Schwinghamer (1981) originally employed X8 classes (a X2 scale of equivalent spherical diameter), later switching to a X2 scale (Schwinghamer 1988). To simplify the simulation of sampling benthic body size distributions, the following assumptions were employed: (1) there is a continuous distribution of body sizes through classes 0 to 30; (2) all organisms are perfect spheres (increased complexity in body form is considered in Supplement 1 at www.int-res.com/articles/suppl/m487p001_supp.pdf), (3) with a density of 1.0 (volume mm^3 = mg wet wt); and (4) they are sampled with perfect sieves.

The underlying distribution of individuals in body size classes was set by simple allometry; for example, in the case of the Sheldon spectrum, $A = k \cdot Wt^{-2}$, where A is abundance (density), Wt is wet weight, and k is an arbitrary constant. This underlying distribution was sampled using various sieve mesh sizes often used in meiobenthos (45 and 63 µm) and macrobenthos (500 µm) studies. A fixed number of individuals were then randomly drawn from the underlying distribution for the sieve sample, and this process was repeated several times. Biomass per size class was then calculated as the product of the number of individuals per size class and the geometric mean body weight of that size class. For presentation, the biomass values were converted to geometric means with 95% confidence intervals based on log (x + 1) transformations (Sokal & Rohlf 1995).

RESULTS AND DISCUSSION

The first simulation carried out was based on an underlying Sheldon spectrum distribution with a power of −2, sampled using 45 µm (meiobenthos) and

500 µm (macrobenthos) mesh sieves. For each sieve size, 10 random samples of 100 individuals were generated. The resultant biomass spectrum is shown in Fig. 2a. An obvious biomass trough was produced between the metazoan meiobenthos and macrobenthos. The trough resulted primarily from undersampling of the larger meiobenthos. Given the underlying body size abundance distribution and the meiobenthic sample size, there is a very low probability of sampling individuals from the largest meiobenthos size classes. The first size class of both the meiobenthos and macrobenthos was also systematically undersampled because the sieve mesh boundary fell partway through the size class.

The first simulation was then repeated with the power of the underlying body size distribution set to −1.8, i.e. yielding a biomass spectrum with a slight positive slope more representative of observed benthic biomass spectra (e.g. see Schwinghamer 1988). Again, an obvious biomass trough was produced be-
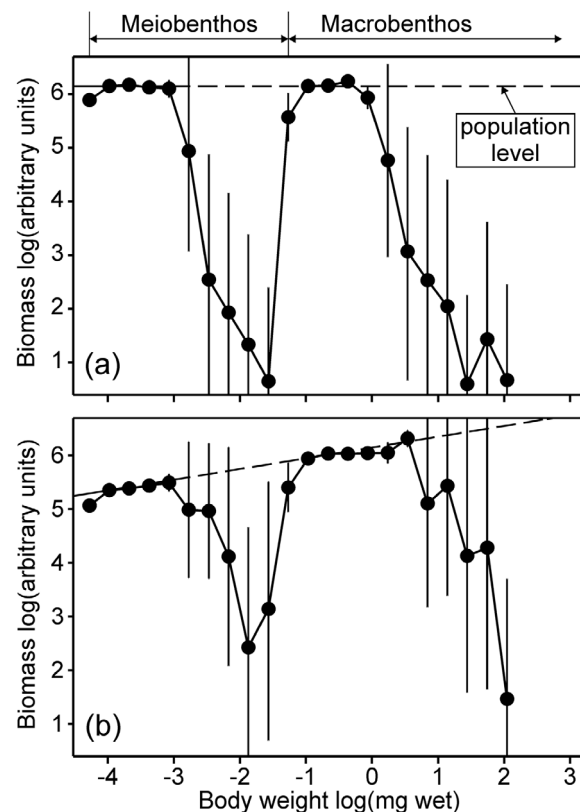

Fig. 2. Simulated sampling of biomass spectra. (a) Sheldon spectrum (power −2): 10 samples of 100 individuals on both 45 µm (meiobenthos) and 500 µm (macrobenthos) sieve meshes. (b) Benthic spectrum (power −1.8): 10 samples of 100 individuals on 45 µm (meiobenthos) and 500 µm (macrobenthos) sieves. Results summarised as geometric mean and 95% confidence interval. Population biomass level indicated by dashed line

tween the meiobenthos and macrobenthos (Fig. 2b). The trough was less deep, because of the increased probability of sampling individuals from the largest meiobenthos size class produced by the higher power of the underlying distribution, but nonetheless distinct.

The first 2 simulations suggested that the apparent biomass trough between meiobenthos and macrobenthos can result from an undersampling of the larger meiobenthos at the sample sizes employed (i.e. 100 individuals). A third simulation was then run to make a direct comparison with experimental data published in Schwinghamer (1988). These data derive from the Intergovernmental Oceanographic Commission's Group of Experts on the Effects of Pollutants Practical Workshop on Biological Effects of Pollutants, as detailed in Marine Ecology Progress Series special volume 46 (Bayne et al. 1988). Specifically, they are the combined data from a series of mesocosm experiments (see Fig. 3 in Schwinghamer 1988). Note that no significant differences in biomass spectra were detected among the control and treatments in these experiments (analysis of similarities pairwise tests p > 0.05; Schwinghamer 1988).

To simulate these experimental data, the power of the underlying body size distribution was set to −1.77 to approximately match the general slight positive slope of the published biomass spectrum. Meiobenthos were sampled with a 63 µm sieve and 16 samples of 100 individuals generated to match Schwinghamer's (1988) methodology. Similarly, macrobenthos were sampled with a 500 µm sieve and 16 samples of 1000 individuals generated. Macrobenthos sample size was set at a representative value of the total number of specimens recovered from each of the mesocosm experiments (see Appendix 3, Tables 3 & 4, in Mar Ecol Prog Ser 46:263−276).

The biomass spectra of experimental and simulated data are compared in Fig. 3. The biomass trough between meiobenthos and macrobenthos produced by simulation is very closely located with that of the experimental data. The depth of the simulated trough, however, is substantially greater than that of the experimental data. The simulation includes only perfect spheres as model organisms; in the 'real world', the variety of invertebrate morphologies and the variability in the probability that they will be retained on a particular sieve mesh will likely act to blur the boundaries of the trough (see also Supplement 1). Nonetheless, parsimony would suggest that a sampling artefact is a more likely cause of the biomass trough rather than a complex underlying body size distribution. Occam's razor proposes that among competing hypotheses, the hypothesis with the fewest

assumptions should be selected. In the present case, I suggest that a simply described allometric relationship common to the meio- and macrobenthos should be selected over more complex modal descriptions.

Such a sampling artefact could readily be avoided by directly targeting the larger meiobenthos/smaller macrobenthos with an additional sieve mesh size. For example, Fig. 4 compares simulation results for 2-sieve and 4-sieve sampling schemes. In the 2-sieve scheme, meshes of 63 and 500 µm were employed, and 10 samples of 200 individuals were generated for each. In the 4-sieve scheme, meshes of 63, 180, 500, and 1400 µm were employed (a natural series of 1.5 phi unit intervals), and 10 samples of 100 individuals were generated for each (i.e. in both schemes the total number of individuals assessed was constant). It is apparent that the 4-sieve scheme produced a more extensive and more reliable biomass spectrum than the 2-sieve scheme at a comparable analytical cost. It seems likely that the use of an additional sieve(s) would be much more cost efficient than the very substantial increase in the number of specimens weighed (measured) per sample that would otherwise be required to achieve the same result (see Supplement 2 at www.int-res.com/articles/suppl/m487p001_supp.pdf).
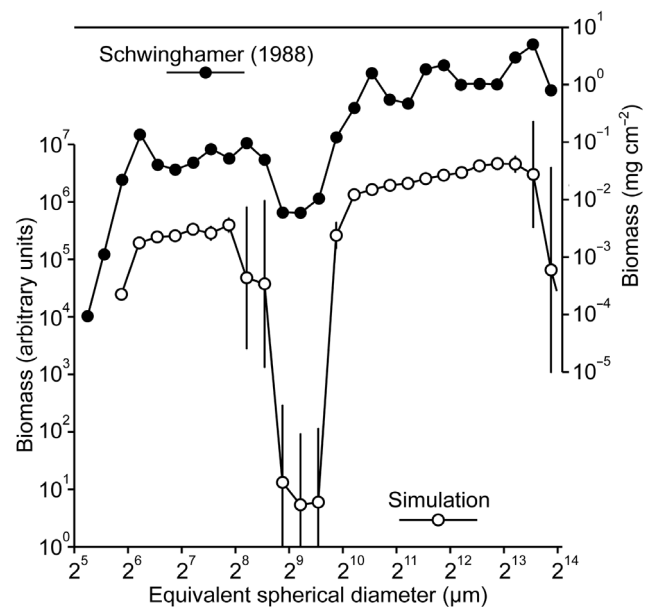

Fig. 3. Simulation of the Intergovernmental Oceanographic Commission's Group of Experts on the Effects of Pollutants mesocosm biomass spectra. Simulated spectrum (power −1.77): 16 samples of 100 individuals on a 63 µm sieve and 16 samples of 1000 individuals on a 500 µm sieve. Results summarised as geometric mean and 95 % confidence interval. Shown with original experimental data of Schwinghamer (1988)
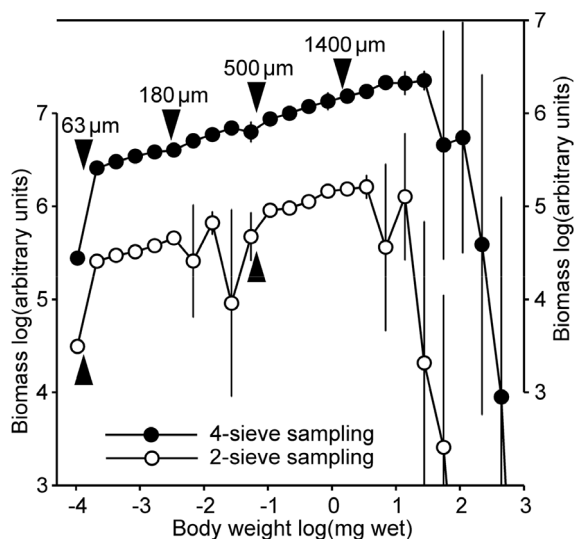
Fig. 4. Simulated sampling of benthic biomass spectra (power −1.8). Two-sieve scheme: 10 samples of 200 individuals on 63 µm sieve and 10 samples of 200 individuals on 500 µm sieve. Four-sieve scheme: 10 samples of 100 individuals on 63, 180, 500, and 1400 µm sieves. Results summarised as geometric mean and 95% confidence interval. Arrowheads indicate minimum body weight retained by each sieve

Fig. 5. Simulated sampling of species size spectra (10 random samples of 100 individuals on each of 45 and 500 µm sieve meshes, drawn from an underlying distribution of individuals with power −1.8; as per Fig. 1b). Estimators of species richness are given as (a) N_i, total number of individuals sampled per size class; and (b) S_i, number of species calculated from Siemann et al. (1996, 1999: $S_i = N_i^{0.5}$)

The simulations above suggest that Schwinghamer's 'characteristic size distributions' may be characteristic of a conventional benthic sampling protocol rather than characteristic of benthic communities per se. What of the apparent support for Schwinghamer (1981) offered by Warwick's (1984) work on species size spectra? Species size distributions do not so readily lend themselves to simple simulation. Nevertheless, it may be useful to examine the potential influence of standard sampling methods on the generation of species size spectra.

The simulation used to produce Fig. 2b is taken as an example (10 random samples of 100 individuals on each of 45 and 500 µm sieve meshes, drawn from an underlying distribution of individuals with power −1.8). Fig. 5a plots the total number of individuals sampled per size class (N_i) during that simulation. The distribution is strongly bimodal, with the modes corresponding to the smallest size classes retained by the 2 sieve meshes. As the number of species recorded in any survey is likely to increase with the number of specimens examined (Magurran 2004), a bimodal species size distribution might simply result from a corresponding bimodal distribution of numbers of individuals per size class.

Siemann et al. (1996, 1999) made a very extensive study of abundance, diversity, and body size in terrestrial arthropods. The species recorded ranged 10^5-
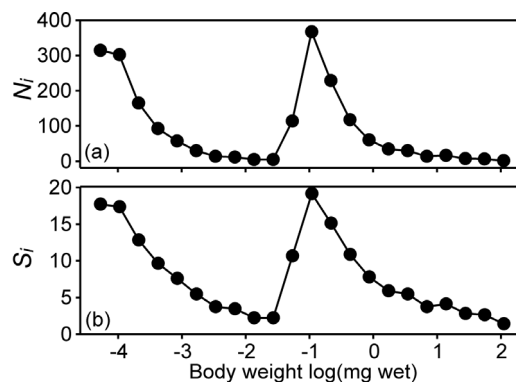
fold in body size, equivalent to a span of ca. 16 X2 geometric body size classes. From these data, they established the relationship $S_i = N_i^{0.5}$, where S_i is the number of species in size class i, and N_i is the number of individuals in that class (X2 geometric size classes). Their work was repeated and broadly confirmed in studies of marine molluscs (littoral Mollusca, Fa & Fa 2002; deep-sea Gastropoda, McClain 2004). Using the N_i of Fig. 5a, the corresponding S_i parameter is plotted as Fig. 5b. The distribution is strongly bimodal, again suggesting that a bimodal species size distribution could result from a conventional benthic sampling protocol rather than an underlying characteristic of the benthic community.

The results presented here are entirely based on very simple mathematical simulations. Nevertheless, they do point to the possibility of generating characteristic benthic size spectra (sensu Schwinghamer and Warwick) that are sampling artefacts rather than true reflections of underlying community structure. They suggest the need for caution in accepting distinct ecological identities and attributes for the metazoan meio- and macrobenthos, when based on the 'self-fulfilling prophecy' of separate meio- and macrobenthos sieve fractions. The integration of all body sizes of benthic metazoans for the purposes of biogeochemical modelling is a potentially useful simplification that has certainly been effective in the pelagic realm, from Sheldon & Parsons (1967) to Rossberg (2012). Further work to additionally incorporate the protozoans and the prokaryote microbenthos in a common modelling framework would be extremely valuable.

CONCLUSIONS

1. Troughs in benthic biomass spectra are readily reproduced by simulated sampling of continuous distributions, suggesting that they could be simple sampling artefacts.

2. A multi-sieve sampling scheme (not one sieve size for meio- and one for macrobenthos) is a simple means of avoiding this problem.

3. Given a general positive relationship between estimated species richness and the number of individuals examined, bimodal metazoan species size spectra could also be simple sampling artefacts.

4. A single mathematical formulation of standing stock and body size for the metazoan benthos as a whole, i.e. not disjunct between meio- and macrobenthos, is an attractive prospect for biogeochemical modelling.

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