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# Controls on benthic biomass size spectra in shelf and deep-sea sediments – a modelling study

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8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerreyn et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Abstract

Factors controlling biomass distributions in marine benthic organisms (meio- to macrofauna, 1 µg–32 mg wet weight) were investigated through observations and allometric modelling. Biomass (and abundance) size spectra were measured at three locations: the Faroe-Shetland Channel in the north-east Atlantic (FSC, water depth 1600 m, September 2000); the Fladen Ground in the North Sea (FG, 150 m, September 2000); and the hypoxic Oman Margin (OM, 500 m, September 2002) in the Arabian Sea. Biomass increased with body size through a power law at FG (allometric exponent,  $b = 0.16$ ) and at FSC ( $b = 0.32$ ), but less convincingly at OM ( $b$  was not significantly different from  $-1/4$  or 0). Our results question the assumption that metazoan biomass spectra are bimodal in marine sediments.

The model incorporated 16 metazoan size classes, as derived from the observed spectra, all reliant on a common detrital food pool. All physiological (ingestion, mortality, assimilation and respiration) parameters scaled to body size following optimisation to the data at each site, the resulting values being consistent within expectations from the literature. For all sites, body size related changes in mortality played the greatest role in determining the trend of the biomass size spectra. The body size trend in the respiration rate was most sensitive to allometry in both mortality and ingestion, and the trend in body size spectra of the production: biomass ratio was explained by the allometry in ingestion.

Our results suggest that size-scaling mortality and ingestion are important factors determining the distribution of biomass across the meiofauna to macrofauna size range in marine sedimentary communities, in agreement with the general observation that biomass tends to accumulate in larger rather than smaller size classes in these environments.

**BGD**

8, 8189–8240, 2011

### Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## 1 Introduction

Marine sediments are sites of long term removal, via burial, of organic carbon derived from productivity at the ocean surface and so play a key role in global biogeochemical cycles (Dunne et al., 2007). The amount of organic carbon that is buried is determined by the rate of processing by benthic organisms (e.g. DeMaster et al., 1994) with the majority of the settling carbon (the POC flux) respired by bacteria back to the water column (Pfannkuche et al., 1999). A smaller fraction of the POC flux is incorporated into benthic biomass and the remainder is buried.

A major challenge to understanding benthic ecology and carbon flow, especially in the deep sea, is appropriate characterisation of both community composition and its underlying dynamics. There now exists, however, a large volume of body-sized based work suggesting that it is not necessary to resort to characterizing food web complexity and differences in functional groups in order to determine energy flow in ecological communities (e.g. Dickie et al., 1987). Allometry, the use of body size to study biological processes, therefore provides an attractive approach for meeting this challenge. Firstly, body size can be easily measured and so enables direct comparison of different benthic habitats regardless of taxonomic makeup. Secondly, body size is an attribute of individual organisms that is closely coupled to key biological processes such as metabolism, mortality as well as to biomass and abundance (e.g. Schmidt-Nielsen, 1984; Brown et al., 2007). The advent of the metabolic theory of ecology (MTE, West et al., 1997) has raised much interest and debate in the body-size (allometric) approach among ecologists (e.g. Glazier 2005, Hildrew et al., 2007a) while allometric relations have provided many useful ecological insights in terrestrial and aquatic environments (Schmidt-Nielsen, 1984; Hildrew et al., 2007b). Consequently, the body-size approach may prove useful in studies of benthic communities in both shallow (Blanchard et al., 2009) and deep-sea environments.

The biomass distributions of marine benthic communities were first studied using a size-based approach by Schwinghamer (1981). He constructed benthic biomass

**BGD**

8, 8189–8240, 2011

### Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

---

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



size spectra (BBSS) from six intertidal stations in the north-west Atlantic and found a trimodal size spectrum (with biomass peaks in the size ranges 0.5–1  $\mu\text{m}$ , 64–125  $\mu\text{m}$  and >2 mm corresponding to micro-, meio- and macro-fauna, respectively) which was supported by later works (Schwinghamer, 1983, 1985). In contrast, other studies, primarily in shallow-water locations (Strayer, 1986; Drgas et al., 1987; Duplisea 2000), found biomass increases that were continuous with increasing body size, suggesting that discontinuities in biomass distributions could be a result of sampling artefacts.

The pioneering work in modelling benthic community biomass distributions was undertaken by Peters (1983). Organisms within the community were assigned to one of five size classes that all feed from the same detritus food pool, and which were parameterised according to four body-size-based processes: ingestion, respiration, egestion and mortality. Peters applied his model to pesticide bio-accumulation and showed qualitative similarities with observations reported in the literature (Griesbach et al., 1982). More recently, Rakocinski (2009) applied Peters' model to investigate hypoxia in subtidal macrofauna. We are unaware of any other applications of this model although other biomass size-based approaches have been used to model fisheries impacts on shelf benthic ecosystems (e.g. Duplisea et al., 2002; Blanchard et al., 2009).

Here, we firstly describe the biomass size spectrum of benthic metazoans (1  $\mu\text{g}$  – 32 mg) in three marine locations: the northeast Atlantic (Faroe-Shetland Channel – FSC, 1600 m), the North Sea (Fladen Ground – FG, 150 m) and the Arabian Sea (Oman Margin – OM, 500 m) through measurements. The factors that control the distribution of this biomass are then examined using a model that builds on the allometric approach of Peters (1983) by both using an increased number of size classes and through improvements in the equations and parameterisations. To the best of our knowledge, this work is the first application of a numerical model based on allometry to the study of biomass distributions in varied marine benthic environments, especially the deep sea.

## 2 Methods

### 2.1 Field observations – sample collection and processing

For practical reasons our field study focused on a restricted size range of metazoans. The invertebrates span a range of body lengths from 50  $\mu\text{m}$  (e.g. smallest nematodes) to 50 cm (e.g. large sea cucumbers), some 4 orders of magnitude; their corresponding body weights range 5 ng–5 kg wet weight, 12 orders of magnitude. The largest of the invertebrates (megabenthos) can only effectively be sampled by trawls and similar devices which only provide semi-quantitative data at best and their efficiency of collecting specimens is distinctly body-size-related (Bett et al., 2001). The smallest invertebrates also pose considerable difficulties for quantitative study both in terms of their practical handling and visualisation and in their extraction from sedimentary and detrital particles. We have therefore concentrated on intermediate-sized invertebrates, the meio- and macro-benthos, that can be reliably, quantitatively sampled and readily extracted from sediment samples (Gage and Bett, 2005).

Samples were collected from three contrasting locations in 2000/2002: (i) a temperate shelf sea site in the Fladen Ground (FG), North Sea, (ii) an “arctic” deep-water site in the Faroe-Shetland Channel (FSC), and (iii) a tropical mid-slope oxygen minimum zone site on the Oman Margin (OM), Arabian Sea. Site locations are illustrated in Fig. 1 and basic station data and environmental characteristics for each site are given in Table 1. The sampling site in the FSC lies between the Scottish Continental Shelf and Faroe Plateau. Although the area has been a target for oil exploration (Ferguson, 1997), it is representative of a cold ( $<0^{\circ}\text{C}$ , Turrell, 1999), pristine deep-water habitat at 1600 m depth. The Fladen Ground sampling site lies in the deeper part of the North Sea at the centre of a gyre with bottom water currents which are thought to be slight ( $<0.25\text{ ms}^{-1}$ ; De Wilde et al., 1986). Fladen Ground is thermally stratified during the summer months when the thermocline can be found between 30 and 70 m. The annual variation in the bottom water temperature is small (6–8  $^{\circ}\text{C}$ , McIntyre, 1961; Lee, 1980; Faubel et al., 1983). The Arabian Sea sampling site (OM) is characterised by a

### Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerreyn et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



well-developed oxygen minimum zone (OMZ) that extends from about 100 m to 1000 m water depth. The samples were collected from the core of the OMZ (500 m) where the benthic communities are subjected to hypoxic conditions.

At each location, five replicate samples were collected for large (500  $\mu\text{m}$  sieve mesh) and small (250  $\mu\text{m}$ ) macrobenthos, meiobenthos (45  $\mu\text{m}$ ) and an intermediate-sized “mesobenthos” (180  $\mu\text{m}$ ) using a Bowers and Connelly Megacorer (Gage and Bett, 2005). The Megacorer carries up to twelve 10 cm diameter core tubes: eight cores (628  $\text{cm}^2$ ) were collected for a large macrobenthos sample, four cores (314  $\text{cm}^2$ ) for small macrobenthos, one core (78.5  $\text{cm}^2$ ) for mesobenthos, and a 10  $\text{cm}^2$  subsample from a single core for a meiobenthos sample. Macro- and meso-benthos samples were of the 0–10 cm sediment horizon, the meiobenthos sample was of the 0–5 cm horizon.

The fauna of macro- and mesobenthos samples were extracted by wet sieving; the fauna of meiobenthos samples were extracted by differential floatation in colloidal silica (Ludox, specific gravity 1.15; Higgins and Thiel, 1988). The total metazoan fauna of the macrobenthos and meiobenthos samples was enumerated and identified to major taxon. In the case of the mesobenthos samples, a random subsample of the metazoan fauna was enumerated and identified to major taxon. Subsampling was undertaken with a “Jensen sample splitter” (Jensen, 1982).

Individual body weights were determined as the product of biovolume and a specific gravity of 1.13 (Gerlach et al., 1985). Body volume was estimated by dividing the morphology into a number of geometric shapes (e.g. cones, cylinders, truncated cones, etc.) and making the measurements necessary to calculate the volume of each. For each primary sieve fraction (i.e. 500, 250, 180 and 45  $\mu\text{m}$ ) the body weight of every metazoan was calculated except where more than 150 specimens of a particular taxon were present, in which case a subsample of 100 specimens were selected at random from a gridded petri dish.

The abundance of benthic invertebrates is expected to decline logarithmically with body size (Peters, 1983), such that the upper end of the body-size range likely to be encountered will depend on the physical size of the sampling unit. As abundance

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



per sampling unit approaches unity, the resultant data will become erratic with a high variance. Consequently we have set an upper body-size limit (39.1 mg wet weight) in the following analyses, above which we believe the data lack sufficient precision. The lower body-size limit is notionally set by the minimum sieve mesh size employed (45  $\mu\text{m}$ ) to extract invertebrates from the sediment samples. The variable body forms, protruding appendages and adherent debris of individual specimens all act, however, to blur this lower boundary. Again, a lower limit was set (0.6  $\mu\text{g}$  wet weight), below which we believe specimens were not efficiently sampled in the present study. In total, this yields 16 size classes (5–20) on the geometric ( $\log_2$ ) scale of Warwick (1984) in which each size class is twice that of the adjacent class below.

## 2.2 Size spectra and regression analysis

### Field data – statistical analyses

In the subsequent analyses, only size classes 5–20 have been included, on the basis that they represent the reliably sampled portion of the total size range encountered (see above). Replicate size spectra data were summarised to geometric mean and 95 % confidence intervals following logarithmic transformation (see e.g. Elliot, 1977). A  $\log(x+1)$  transformation was employed in the case of abundance data and a  $\log(x+wtn)$  in the case of biomass data, where  $wtn$  is the nominal weight of a single individual in size class  $n$ . For nominal weight we follow Blanco et al. (1998):

$$wt_n = wt_l \left( \frac{c^{b+1} - 1}{(c-1)(b-1)} \right)^{\frac{1}{b}} \quad (1)$$

where  $wt_l$  is the lower weight limit of the size class (see Table 2, and Warwick, 1984),  $c$  is the ratio of geometric increase (i.e. 2), and  $b$  is the slope of the abundance-size spectrum (uniformly set to  $-0.7$ , for consistency and repeatability of the method). Geometric mean abundance and biomass data were then log transformed and regressed

on log transformed nominal size class weights (simple least squares regression, implemented using Minitab 15, Minitab Inc.). Regression slopes were compared to standard allometric ratios (e.g. 1/3, 1/4 etc.) using a t-test method (e.g. Sokal and Rohlf, 1995).

## 2.3 Model description

### 2.3.1 Model structure

The model incorporates 16 metazoan size classes feeding on a single food pool that originates from the supply of POC from the water column above (Fig. 2). The number of model size classes is derived directly from our measurements and defined by a logarithmic scale (base 2) with mean body sizes ( $M_i$ ) ranging from  $8.9 \times 10^{-7}$  to  $2.9 \times 10^{-2}$  grams wet weight (Table 2). Each metazoan size class undertakes ingestion, defecation, assimilation of ingested substrates, respiration, growth and mortality. Size classes do not directly interact. In marine sediments, respiration and assimilation of organic carbon is also carried out by bacteria, with bacterial respiration accounting for the major fraction of benthic carbon processing (Pfannkuche et al., 1999). Similarly, Foraminifera can be important in respiration of sedimentary organic matter (e.g. Moodley et al., 2002; Woulds et al., 2009) although direct measurements in a recent study (Geslin et al., 2010) suggest that Forams account for less than 3% of total benthic respiration. Although Foraminifera were present at all three study sites, their biomass was not estimated in this study as it is a highly uncertain computation (Gooday et al., 2009) and, subsequently, inclusion of Foraminifera in biomass size-spectra needs to be treated with caution (Gerlach et al., 1985). An earlier version of the model (not shown), which explicitly accounted for bacteria, indicated that these organisms only influence the total amount of biomass ending up in the metazoans and not the shape of the size spectra. Since the focus here is on controls on the latter, a simpler approach is adopted which implicitly accounts for bacterial (and Foraminiferal) respiration (see below).

A key assumption of the model is that species coexistence occurs in an environment of shared rather than partitioned resources, i.e. the common food pool. We believe this is a reasonable first-order assumption for sublittoral, and deeper, soft-bottom benthic

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



communities. This is supported by a number of lines of evidence. Firstly, the majority of the macro- and meio-fauna at the three sites are deposit feeders. Secondly, feeding by macrofauna on meiofauna is generally negligible even in shelf sediments (Reise, 1979; Kennedy, 1993) such as the FG site. Thirdly, it is well recognized that the deeper sea benthos (e.g. at FSC and OM) form a detritus-based consumer system, entirely dependent on the POC flux for its nutrition (Gooday, 2002). Consequently, all members of benthic communities from the smallest (e.g. bacteria) to the largest (e.g. sea cucumbers) species ultimately feed directly on this limited food pool, helping to explain why deep-sea benthic communities, in particular, are characterised by weak predator prey interactions (Bailey et al., 2006; Drazen et al., 2009). Note that some studies (e.g., Stowasser et al., 2009) have shown a strong link between the diet of deep-sea fish and benthic fauna. We are, however, unaware of any studies that convincingly show predatory behaviour between the size classes considered in this study. Fourthly, stable isotope studies show significant overlap in food sources between meio- and macro-fauna in deep-sea environments (Iken et al., 2001, 2005). In particular, the dominant meiofauna in our study (see Results) were nematodes and the major macro-fauna were polychaetes, two taxa shown to occupy the same trophic level (Iken et al., 2001). While some innovative isotope studies (e.g. Jennings et al., 2002) show the link between trophic level and body size, these are based on organisms of greater size (e.g. megabenthos: starfish, crabs and fish) than used in this study. Finally, Gooday et al. (2009) argue that predation is negligible among benthic metazoans in the oxygen minimum zones of the Arabian Sea, including the Oman Margin. Thus, we assume that predation between the sampled fauna at all sites is negligible limited within the size range considered and it is therefore not explicitly included in the model.

The few available studies suggest that spatial and temporal variability in benthic biomass size spectra appears to be minimal (Schwinghamer, 1981, 1983, 1985; Drgas et al., 1998; Duplisea et al., 2000) and thus in the absence of direct evidence to the contrary, we consider only steady state solutions of the model. At steady state, the sum of the loss terms (total metazoan respiration) equals the POC flux from the water

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

column. Model biomass units are expressed in g wet weight per m<sup>2</sup> (g wwt m<sup>-2</sup>) and fluxes given as yearly values (g wwt m<sup>-2</sup> yr<sup>-1</sup>). A dry to wet weight ratio of 0.25 (Rowe, 1983) is used to convert to units of carbon. The model equations are given below and parameter descriptions and values are in Table 3. We first describe the main model equations before detailing the allometry.

The rate of change of metazoan biomass in each size class,  $B_i$  is:

$$\frac{dB_i}{dt} = \underbrace{\alpha_i I_{\text{ing}_i}}_{\text{assimilation}} - \underbrace{r_i \alpha_i I_{\text{ing}_i}}_{\text{respiration}} - \underbrace{m_i \frac{B_i^2}{K_{m_i} + B_i}}_{\text{mortality}} \quad (2)$$

Net production

where  $I_{\text{ing}_i}$  is the ingestion rate

$$I_{\text{ing}_i} = I_i \frac{R}{R + K_{\text{ing}_i}} \quad (3)$$

$\alpha_i$  is the assimilation efficiency,  $r_i$  is the respiration coefficient expressed as a fraction of assimilation,  $m_i$  is the specific metazoan natural mortality rate,  $K_{\text{ing}}$  and  $K_m$  are the half saturation constants for metazoan ingestion and mortality, respectively,  $I_i$  is the specific ingestion rate and  $i$  denotes size classes 5 to 20 (see Table 2). The subscript  $i$  indicates that a process or parameter can be body-size dependent as described below.

Net metazoan production (= growth) is calculated as the difference between rates of assimilation and respiration (Eq. 1), representing a departure from the Peter's (1983) model which has an explicit body-size dependent growth term. Rates of assimilation (Eq. 1) are parameterised as a function of ingestion based on the product of assimilation efficiency ( $\alpha_i$ ) and food intake (Eq. 2). Respiration rates (Eq. 1) are the product of assimilation rates and a respiration coefficient,  $r_i$ , representing the fraction of assimilation lost to the respiratory pathway (see below). Our approach is closely allied to contemporary pelagic ecosystem models (e.g. Anderson and Pondaven, 2003;

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Kelly-Gerreyn et al., 2004) in which parameters such as assimilation and growth efficiencies are assigned to specify the fate of material ingested by consumers.

The loss terms for each size class are defecation (the fraction of ingestion not assimilated), mortality and respiration. Losses through defecation and mortality are returned to the food pool (Eq. 3), while respiration across the size classes balances the POC flux at steady state.

Monod type limitation functions are used to model both ingestion (Eq. 2) and mortality (Eq. 1), representing a further departure from the Peters (1983) model. These limitation functions mean that ingestion and mortality are regulated by the concentration of the food source and biomass, respectively, yielding a density dependent formulation in the case of mortality, as in, for example, Benoit and Rochet (2004). Use of density dependent terms, through either resource limited growth or mortality, is an established way of preventing competitive exclusion in model systems (Brown, 1989; Chesson 2000) which prevents the 16 size classes within the model from becoming extinct. Although data are currently lacking to provide support for such density-dependence in the benthic realm, density dependent mortality is a recognized mechanism for regulating natural populations of pelagic organisms (Ohman and Hirche, 2001; Minto et al., 2008).

The role of bacteria and Foraminifera is represented in the food pool Eq. (4) through the parameter  $f_{bac}$ , the fraction of the POC flux that is respired by these components of the benthic community (= the fraction not reaching the metazoans).

The rate of change of the organic matter (the detrital food pool,  $R$ ) is

$$\frac{dR}{dt} = (1 - f_{bac})POC_{flux} + \underbrace{\sum_{i=5}^{i=20} (1 - \alpha_i) I_{ing_i}}_{defecation} + \underbrace{\sum_{i=5}^{i=20} m_i \frac{B_i^2}{k_{m_i} + B_i}}_{mortality} - \underbrace{\sum_{i=5}^{i=20} I_{ing_i}}_{ingestion} \quad (4)$$

where  $POC_{flux}$  is the flux of organic carbon to the seabed. Both  $POC_{flux}$  and  $f_{bac}$  are determined by the optimisation procedure (see below) from a predefined range (Table 3).

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerreyn et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The model equations do not describe a continuous system, i.e. growth giving rise to transfer of individuals in size class  $i$  to size class  $i+1$ . This approach is not unreasonable given both the steady state assumption and the work of Borgmann (1987), which showed biomass size spectra produced with continuous and discrete model approaches were similar.

## Parameterisation

The form of the function for the specific ingestion rate ( $I_i$ ) follows that in Cammen (1980) showing a power relationship between organic carbon ingestion rate and body size of benthic deposit feeders and detritivores:

$$I_i = a_1 M^{-b_1} \quad (5)$$

where the prefactor,  $a_1$ , and the power scaling,  $b_1$ , are subject to parameter optimisation (see Table 3 and *Parameter optimisation*). Natural mortality rates for benthic organisms are difficult to parameterise because of scarcity of relevant experimental data. We adopted a size based approach following studies of mortality in both aquatic (Savage et al., 2004) and non-aquatic (Hendriks, 1999) organisms, as well as for consistency with the power scaling for specific ingestion rates (Eq. 4):

$$m_i = a_2 M^{-b_1} \quad (6)$$

where parameter  $b_1$  is the same as in Eq. (4). 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). Again, the parameter values are determined through optimisation. An alternative parameterisation comes from Brey (1999), who provides a linear relationship between the specific mortality rate and the PB (production : biomass) ratio. This would require two parameters – the slope and intercept of this relationship – together with the model PB ratio. While such a relationship is useful for determining specific mortality rates, we chose to compute the mortality directly from the easier measurement (relative to production) of body size.

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The remaining parameters are formulated according to

$$\rho = x_1 + x_2 M^{b_2} \quad (7)$$

where  $\rho$  represents the individual parameters ( $\alpha_i, k_{\text{ing}_i}, k_{m_i}, r_i$ ) and  $x_1, x_2$  and  $b_2$  are coefficients derived from boundary conditions (the lower and upper bounds of  $\rho$ ) which are chosen by the optimisation procedure (see below) from pre-defined ranges (Table 3). Note that the optimised values for  $x_1, x_2$  and  $b_2$  are different for the individual parameters. This formula (7) allows parameters for which we have some knowledge (e.g.  $\alpha_i, r_i$ ) to be constrained within ranges from the literature (Table 3), while at the same time allowing for allometric scaling. For the parameters ( $k_{\text{ing}_i}, k_{m_i}$ ) which lack observational data, Eq. (6) is used for consistency, with the other parameters defined by this equation. The advantage of Eq. (6) is that model parameters can be either dependent or independent of body size, on account of the boundary conditions having the same range (Table 3) for each individual parameter (e.g., the optimisation routine may choose the same value for the upper and lower bounds of  $\rho$ , yielding a size-invariant parameter). Furthermore, the relationship to body-size can be either increasing or decreasing. The final relationship to body-size emerges from the optimisation procedure.

### 2.3.2 Parameter optimisation

The model was fitted to the full dataset, in which all replicates were used to enable the most robust fit possible in this study. The fitting was achieved using the micro-genetic algorithm found in Ward et al. (2010). A brief summary is presented here. For each parameter, a range of allowed values is chosen based on previous observations wherever possible (Table 3). The range for each parameter is then divided to give 64 ( $=2^6$ ) equally spaced values between the allowed lower and upper limit inclusive. This allows the parameter value to be encoded by a 6 bit binary number. The 6 bit binary representations of each parameter value are then stitched together to give a multi-digit binary number, referred to as a “genotype”. In this study, this gives an 84 digit binary number as there are 14 parameters in the model. This is referred to as the “genotype”

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



corresponding to this parameter set. Initially, the optimiser randomly generates 14 genotypes – the rule of thumb is that the number of genotypes should match the number of parameters. The model is run using the parameter set corresponding to each genotype. A cost function is then calculated for each parameter set, calculated as the simple sum of least squares between log-transformed observation and model output for each size class. As there are 5 observations for each size class, each size class contributes 5 terms to the sum. The genotype corresponding to the lowest cost is automatically passed intact to the next “generation”. To generate the other 13 genotypes necessary for the next generation, pairs of genotypes are combined. Each of the pairs used to make a genotype for the next generation is chosen at random – with probability proportional to the reciprocal of their cost – so those with lowest costs are most likely to be chosen. Once a pair have been chosen, a random integer between 2 and 83 is chosen and the two genotypes are combined at this location e.g. if the combination location is 34, the new genotype has the first 33 elements of the binary genotype of parent 1 and the last 51 elements of parent 2. Once a new set of 14 genotypes has been created the process repeats. The optimiser is run through 5000 generations. Typically there is little change to the optimal solution after 2000 generations. As a further precaution against getting caught in local minima of the cost function, the whole process is repeated 10 times using different sets of initial genotypes. The best fit (i.e. the lowest cost function of the 10 repeats) is presented below for each site. Because of difficulties involved in handling zeroes when log-transforming to calculate the cost function, zero values were removed. As a check, the optimisation was repeated using data with zeroes replaced by mean values for that biomass interval and similar results were obtained.

Two criteria, taken from the literature, were imposed in determining the passing of genotypes to the next generation in the optimisation procedure: (1) that the annual PB ratio decreases with body size (e.g. Banse and Mosher, 1980) with a value falling between  $0.5\text{--}2\text{ yr}^{-1}$  for the largest (macrofaunal) class and a value falling between  $4\text{--}7\text{ yr}^{-1}$  for the smallest (meiofauna) size class (Schwinghamer et al., 1986); and (2) that

## BGD

8, 8189–8240, 2011

### Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



respiration rates increase with body size (e.g. Peters, 1983) . It should be noted that the optimisation procedure was also run without these latter two criteria imposed (a so-called “free” run, not shown). The optimisation did not converge on a solution which satisfied these two criteria, simultaneously, in the free run and thus, it was necessary to impose the conditions. Note that these conditions represent a “reality check” on the model.

### 2.3.3 Sensitivity analysis

The analysis investigated the role of each parameter, separately and in combination with others, in determining the shape of the biomass size spectra and the body-size relationships of respiration and the PB ratio at each site. Each parameter had three possible settings: an increase with body size, independent of body size and a decrease with body size. For clarity, we report here that the optimisation procedure yielded settings for  $K_{ing}$ ,  $K_m$ ,  $r$  and  $\alpha$  which increased with body size (see *Optimised allometry*);  $l$  and  $m$  decreased with body size according to Eqs. (4) and (5), respectively. The reverse of all these functions gave the opposite trends for the settings above. The size independent settings were the median values of the allometric settings. All combinations of the 6 parameters and their 3 settings were run, yielding 729 runs encompassing all  $3^6$  combinations. The sensitivity investigated which parameter settings produced a positive or negative trend in both the biomass size spectra and the respiration and PB size spectra. Note that the outcome of the sensitivity analysis was the same at all sites and so, for clarity, we only show the results from the FSC.

The focus of the sensitivity analysis was on the six physiological parameters of the metazoans. The fraction of the POC flux accounted for by bacterial respiration ( $f_{bac}$ ) together with the POC flux does not affect the shape of the size spectra, only the total amount of biomass that ends up in the metazoans (not shown).

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 2.4 Results

### 2.4.1 Observed size spectra: abundance and biomass

Abundances decreased with size at all sites (Fig. 3). The abundance-body size relationships were all statistically significant with scaling exponents of  $-0.83$ ,  $-0.68$  and  $-0.91$  at FG, FSC and OM, respectively (Table 4). The scaling exponent at FG was not significantly different from  $-3/4$ , in line with metabolic theory (Brown et al., 2003), whereas at FSC the scaling was not significantly different from  $-2/3$ , in line with surface area: volume theory (Schmidt-Nielsen, 1984). OM has the steepest abundance-body size slope which is consistent with other studies of hypoxic environments (Chapelle and Peck, 1999, Quiroga et al., 2005). The latter suggest that the steeper slopes may be due to smaller body sized organisms being more adapted to low oxygen environments, an adaptation found in terrestrial environments (Klok and Harrison, 2009). Whereas we are unable to confirm that the smaller organisms in our size range were better adapted to low oxygen, polychaetes (the macrofauna) from the hypoxic zone of the Oman Margin had enlarged gill structures that are thought to represent an adaptation to the reduced oxygen levels (Lamont and Gage, 2000).

Total abundance (in classes 5–20) was highest at FG ( $5.11 \times 10^5$  ind.  $m^{-2}$ , 95 % CI:  $3.28$ – $7.31 \times 10^5$  ind.  $m^{-2}$ ) and lowest at FSC ( $1.51 \times 10^5$  ind.  $m^{-2}$ , 95 % CI:  $0.96$ – $2.19 \times 10^5$  ind.  $m^{-2}$ ). At all sites, meiofauna contributed most to the total abundance (84–99 %), with mesofauna and macrofauna far less abundant (Table 5). The exception was at FG where mesofauna (molluscs, mostly *Veneroidae* and *Philinidae*) accounted for almost 20 % of the total, most likely representing a recent recruitment event (M. Shearer, personal communication, 2010). Nematodes dominated the meiofaunal size range (>90 %) and polychaetes (mostly *Paraonidae*, *Capitellidae* and *Aricidae* at FSC, *Amphinomidae*, *Capitellidae* and *Nereidae* dominating at FG and almost exclusively *Ampharetidae* at OM) accounted for the majority (>60 %) of individuals in the macrofaunal size range at all sites. Molluscs (mostly *Veneroidae* and *Philinidae*)

### Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



dominated the mesofauna at FG while no one group dominated the mesofaunal size classes at the other sites.

Biomass increased with size class at all locations (Fig. 3). This trend was statistically significant ( $p \leq 0.001$ ) at FSC and FG with scaling exponents of 0.32 and 0.16, respectively (Table 4). In contrast, an increase in biomass with size was less convincing at OM (the scaling exponent was not significantly different from zero or  $-1/4$ ), which is unsurprising given the greater variability of these data (Fig. 3). The scaling at FSC was not significantly different from  $1/3$  power scaling, consistent with the scaling for abundance at this site (Table 4).

Total mean biomass at FG ( $12.1 \text{ g wet wt m}^{-2}$ , 95 % CI:  $6.8\text{--}21 \text{ wet wt m}^{-2}$ ) was approximately twice the value at the FSC site ( $6.6 \text{ g wet wt m}^{-2}$ , 95 % CI:  $3.5\text{--}11.7 \text{ wet wt m}^{-2}$ ) and more than three times higher than at OM ( $3.4 \text{ g wet wt m}^{-2}$ , 95 % CI:  $1.6\text{--}6.3 \text{ wet wt m}^{-2}$ ). Tukey simultaneous tests indicated that only the difference between FG and OM was statistically significant ( $p < 0.05$ ). Hence, it is not possible to conclude from our data that the lower biomass at OM is simply a result of low oxygen conditions (e.g. Rakocinski, 2009).

Macrofauna (*sensu stricto*: i.e.  $>500 \mu\text{m}$  excluding taxa typically regarded as meiofaunal; Hessler and Jumars, 1974) accounted for most of the total biomass at all locations (92 % ,69 % and 68 % at FG, FSC and OM respectively), with polychaetes dominating this group. Mesofaunal biomass ( $<500 \mu\text{m}$ ,  $>180 \mu\text{m}$ , excluding meiofaunal taxa) contributed less than 4 % at the FSC and OM but 26 % at FG. Polychaetes dominated the mesofaunal biomass at FG and OM, with no overall dominant group at FSC. The meiofauna ( $>45 \mu\text{m}$ , excluding macrofaunal taxa), dominated by nematodes, accounted for less than 7 % of the total biomass at FG and FSC. At OM, the proportion of meiofaunal biomass was more than four times greater (28 %) than at the other two sites, potentially reflecting the tolerance of nematodes to hypoxic conditions (e.g. Heip et al., 1985).

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## 2.4.2 Modelled biomass size spectra: standard runs

The standard runs produced by the parameter optimisations at each site are shown in Fig. 4 and the associated parameter values are shown in Table 3. Model biomass increases with body size at all sites. The best fit (using the least squares criterion) among the sites is for the FSC, followed by the FG and then the OM. The total biomass modelled at FSC (6.6 g wet wt m<sup>-2</sup>), FG (14.7 g wet wt m<sup>-2</sup>) and OM (6.6 g wet wt m<sup>-2</sup>) is similar to measured values (Table 5).

## 2.4.3 The optimised allometry in model parameters

The allometric exponents (b1) for mortality (Eq. 5, Fig. 5a) and ingestion (Eq. 4, Fig. 5e) were close to the 1/4 power law (0.24, 0.20, 0.27 for FSC, FG and OM respectively, Table 3), consistent with empirical studies (e.g. Cammen, 1980; Savage et al., 2004).

The physiological parameters ( $\alpha$ ,  $r$ ,  $K_{ing}$ ,  $K_m$ ), emerge from the optimisation procedure as parameters which increase with size at all sites (Fig. 5).

The few studies on benthic assimilation and body size suggest that larger organisms have higher assimilation efficiency because of increased gut passage time which is thought to permit a relatively more complete digestion of food material (Jumars et al., 1990; Gage and Tyler, 1991). While more extensive reviews across the animal kingdom suggest that assimilation efficiencies do not scale with body size (see Hendriks, 1999), the only published size-based benthic assimilation efficiencies for deposit feeders (Ahrens et al., 2001) suggest otherwise. The assimilation efficiencies derived by the optimisation procedure increase with body size (Fig. 5c), ranging between 0.27 and 0.73 across the sites, falling within the range of the majority of assimilation efficiencies found in the literature (e.g., Calow, 1977; Hendriks, 1999).

The fraction of assimilation lost to respiration, parameter  $r$ , increases with body size at all sites (Fig. 5d). The model suggests that the maximum percentage of assimilated ingestion respired by any one size class is 60%, a value consistent with studies from elsewhere (e.g. Hargrave, 1979).

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



this parameter is to control the total biomass that ends up in the fauna (not shown).

Comparisons of the model POC fluxes with other data are not straightforward, given that POC flux estimates are highly dependent on the methods used (Lampitt et al., 2001). However, the values derived from the model presented here compare well with those from other studies. Cadee (1986) measured POC fluxes of 3–16 g C m<sup>-2</sup> yr<sup>-1</sup> from sediment trap data (40–75 m) in the Fladen Ground in spring. In the FSC, Sauter et al. (2001) used a diagenetic model to estimate a POC flux of 10.6 g C m<sup>-2</sup> yr<sup>-1</sup>, while an annual production estimate of 200–300 g C m<sup>-2</sup> yr<sup>-1</sup> in the FSC region<sup>1</sup> applied to the Suess formula (1980) yields a POC flux to the sea floor of 5.2–7.8 g C m<sup>-2</sup> yr<sup>-1</sup>. Lee et al. (1998) estimated POC fluxes to be 3.9–8.3 g C m<sup>-2</sup> yr<sup>-1</sup> at 500 m depth in the Arabian Sea OMZ from sediment trap data. Given the problems associated with both the sediment trap data (Lampitt et al., 2001) and the satellite data (e.g. approximately 30 % for chlorophyll estimates, Gregg and Casey, 2004) used to estimate POC fluxes, the model derived estimates are not unreasonable.

#### 2.4.4 The role of allometry on biomass, respiration and PB: sensitivity analysis

The three parameter settings used in the sensitivity analysis are shown in Fig. 6. The corresponding results of the sensitivity analysis first focus on the simplest method (Fig. 7), in which each of the six parameters is changed one at a time (OAT) from its optimised setting to its opposite and size-independent setting.

The importance of the mortality parameters in determining the trend (positive or negative) in the BBSS is shown in Fig. 7a, b. When either  $K_m$  or  $m$  is not at its optimised setting (Fig. 6a, b), biomass does not increase with size class (Fig. 7a, b). In contrast, changes to the other parameters do not alter the trend in biomass with size (Fig. 7c–e). Quantitative analysis also shows that model biomass is most sensitive to mortality (Fig. 8a).

<sup>1</sup> (<http://marine.rutgers.edu/opp/swf/Production/results/all2.swf.html> – using the formula of Behrenfield and Falkowski, 1997)

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The optimised settings for the mortality parameters and the coefficients for assimilation ( $\alpha$ ) and respiration ( $r$ ) (Fig. 6) are needed to yield an increase in the model respiration rate with size class (Fig. 9a–d). Quantitative analysis shows that the respiration rate is most sensitive to the mortality parameters followed by the ingestion parameters ( $K_{\text{ing}}$  and  $I$ ) (Fig. 8b).

The trend in PB with body size is most sensitive to the ingestion parameters (Fig. 8c); in particular, the PB ratio reverses the trend (Fig. 10e) when  $I$  increases with body size (Fig. 6e).

Overall, from the OAT analysis, the model is more sensitive to parameter settings which are opposite to the optimised values than the size-independent settings (Fig. 8a–c).

The 729 sensitivity runs are now analysed to investigate the role of interactions of parameters on the model output. Of the 729 runs, 276 combinations of parameters produced an upward trend in the BBSS. The common feature among these 276 runs is that none of them had optimised values, simultaneously set, for both of the mortality parameters ( $K_m$  and  $m$ ). Specifically, as long as mortality was either size-independent or at its optimised setting, biomass increased with body size in line with the observations (Figs. 3, 4).

Of the 276 runs, only 20 produced output satisfying both the respiration and PB criteria (*Parameter optimisation*). These 20 runs were characterized by the respiration coefficient,  $r$ , not decreasing with body size and the specific ingestion rate,  $I$ , not increasing with body size. That is, as long as the respiration or ingestion parameters were size-independent or at their optimised settings, the respiration rate increased with body size and PB decreased with body size, consistent with the literature. None of the remaining runs (i.e. the 709 runs) satisfied these two criteria.

The biomass size spectra had a negative trend (277 runs) for all settings of the mortality parameters, but never with both parameters ( $K_m$  and  $m$ ) simultaneously set to be opposite to their optimised settings.

## BGD

8, 8189–8240, 2011

### Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

The remaining 176 runs produced a variety of biomass size spectra including unimodality and other wave like patterns with body size. Double peaks in the BBSS were not simulated. In addition, none of these runs satisfied the reality check criteria for respiration and the PB ratio.

In summary, the model indicates that the manner in which mortality changes with size is the key control on the trend of the BBSS, the respiration rate is most sensitive to mortality and ingestion, while ingestion is the dominant control on the PB ratio.

### 3 Discussion

#### 3.1 The biomass size spectra

Our datasets add to a rare collection of observed biomass size spectra in marine benthic communities, especially in the deep sea. Such scarcity of data makes it difficult to assess how conservative biomass distributions are in time and space. The few available studies suggest that spatial and temporal variability appears to be minimal (Schwinghamer, 1981, 1983, 1985; Drgas et al., 1998; Duplisea et al., 2000). Consequently, we have chosen to adopt the Occam's Razor simplicity approach by assuming a steady state system in our modelling study.

Schwinghamer (1981, 1983, 1985) constructed benthic biomass size spectra in different marine settings including the abyssal Atlantic Ocean and concluded that the spectra were conservative and characterised by peaks corresponding to micro-, meio- and macro-benthos. These peaks were a few orders of magnitude greater than the troughs between them. Other studies of benthic species body-size spectra (see Warwick, 2007) appear to support the multi-modal features found by Schwinghamer (1981, 1983, 1985), suggesting that these are conservative characteristics of benthic biomass. Hence, initially, it may seem surprising that our data show little evidence of troughs and peaks (of the magnitude observed by Schwinghamer).

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Drgas et al., 1998; Duplisea 2000) appear to show that biomass generally increases with body size, even in the presence of multi-modality. Global data analysis suggests that this general pattern may be depth dependent with macrofauna dominating biomass on the shelf and upper continental slope (<2000 m) while bacteria and meiofauna dominate in deeper waters (Rex et al., 2006). It appears that the tendency for biomass to concentrate in larger benthic size classes is a common feature of non-abyssal marine sedimentary environments.

## 3.2 Controls on the biomass size spectra

### 3.2.1 Mortality

The model suggests that mortality is the main factor in determining the positive trend in biomass with body size (Fig. 7a, b). This control by mortality is achieved through the model derived allometry in  $K_{m_i}$  and  $m_i$  (Fig. 5d, e) which gives larger size classes lower specific mortality rates compared to the smaller size classes, enabling biomass to accumulate more in the larger organisms. Schwinghamer (1983) suggested that biomass concentrates in larger species of benthic organisms on account of their greater longevity, providing support for size-based mortality. In addition, our results contrast with the predictions of the metabolic theory of ecology (Brown et al., 2007) suggesting that mortality rather than respiration (metabolic rate) may be the more important factor in determining biomass size spectra in the deep sea. This does not negate the MTE which appears to hold over large spatial scales and for a much broader range in body sizes than in our study, but rather that biomass distributions within specified faunal size ranges (meio- to macro-fauna) may be more influenced by mortality at local scales in marine sediments. Rex et al. (2006) compiled a global data set which showed that biomass was greater in larger benthic organisms (macrofauna and megafauna) at depths <2000 m, whereas bacterial and meiofaunal biomass dominated in deeper sediments. The cause of the shift in the dominance of biomass from the larger to the smaller organisms at approximately 2000 m remains unclear. However, we should note that the comparative rarity of larger organisms in the deep sea may lead to substantial

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



under-estimates of the biomass in larger size classes. In the model, biomass decreases with body size only when mortality is not size dependent (Fig. 7a, b). However, this produces unrealistic allometry in both the respiration and PB ratios.

The sensitivity of size-specific mortality in the Peters (1983) model has recently been acknowledged in an application investigating the influence of hypoxia on subtidal macrofauna (Rakocinski, 2009). However, that study did not carry out a sensitivity analysis and used a time-dependent version of the Peters model in which the mortality was not density dependent, leading to competitive exclusion and hence to the survival of only one size class at equilibrium. Rakocinski (2009) showed that the effects of oxygen limitation favoured a less even distribution of biomass among size classes with more biomass accumulating in the larger size classes. We chose not to adopt a similar approach at the OM because of the high variability in our data which does not lend itself to testing the validity of different parameterisations.

The idea that mortality is a size dependent process contrasts with the view that external factors such as predation control mortality in many ecological systems (Carpenter and Kitchell, 1984; Kerr and Dickie, 2001). However, production must offset the rate of mortality for a population to persist and so the body-size scaling may not be so surprising (Brown et al., 2007). Support for the allometric scaling of mortality comes from studies in both terrestrial (Marba et al., 2007) and pelagic systems (Peterson and Wroblewski, 1984, McGurk, 1986, Savage et al., 2004), most of which have suggested quarter power scaling similar to the power scaling derived in the present study (b1, Table 3).

In the model, the density dependent mortality term (Eq. 2) enables coexistence on a single food source. Although an accepted approach (Brown, 1989; Chesson, 2000), it does not address the reasons for species coexistence in benthic systems (see Etter and Mullineux, 2001). Currently, there is no evidence for density dependent mortality in benthic communities. Density dependent mortality may arise from factors such as pathogens, starvation and predation. Nevertheless, this modelling approach enables an investigation of controls on biomass size spectra without the need for increased

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



degrees of freedom (and thus uncertainty) that would result from the addition of poorly known parameters and terms to account for niche specialization. One may speculate that the single dimensional niche model developed by Williams and Martinez (1999), and used extensively in food web studies, may lead to the density dependencies in mortality used in the current model. However, the lack of predation (see Sect. 2.3.1) within the size range considered in this study makes the application of such a model not so appropriate. As an aside, Williams et al. (2010) found that, when tested, body size alone does not explain the structure of the one-dimensional niche.

### 3.2.2 Ingestion

Ingestion has been shown to scale with body size in the benthos (Cammen, 1980). Production and respiration (metabolism) are also known to scale with body size (e.g. Brown et al., 2003; Banse and Mosher, 1980). In addition, there is evidence that food selection is size dependent (Ritchie and Olf, 1999) whereby small animals can select small patches with high quality food, and larger animals can rely on larger patches of food that are of overall lower quality. The approach of Ritchie and Olf (1999), and formally Ritchie (1998), relies on assuming a fractal geometry of the environment from knowledge of the habitat being studied. While the orders of magnitude that span the size range of the fauna considered in the present study (Table 2) may lend themselves to such an approach, data on the relevant fractal dimensions of both the habitat and resources are generally lacking from benthic datasets. In addition, Warwick et al. (2005) suggest that the role of the fractal dimensions of a habitat may not be as important as factors relating body size to biological characteristics in marine benthic assemblages. Furthermore, the role of food selection in determining the biomass size spectra would require supporting information on the particular food preferences of the fauna in the present study's size range. To our knowledge, there are no studies of resource preferences at greater resolution than can be presently provided by isotope tracer techniques within the size range addressed in this study, although studies involving larger benthic organisms exist in both the deep sea and shallow intertidal sediments (Wigham et al.,

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2003; Woulds et al., 2010). Hence, the modelling approach presented here neglects food selection and assumes that all the size classes share a common food source. However, if food selectivity is size dependent at the three sites, this may impact on the degree of allometry in the assimilation efficiencies across the size classes, particularly as lower quality food tends to favour lower assimilation efficiencies (Ahrens et al., 2001). However, the model has a low sensitivity to allometric changes in the assimilation efficiency (Fig. 8a–c) and so we speculate that food selectivity may not be so important in determining biomass size spectra at these three sites.

### 3.2.3 Predation

Our approach has assumed the negligible role of targeted predation in determining the BBSS. However, it should be noted that passive (non-targeted) predation almost certainly happens, although the extent and the impact on biomass size spectra is unknown. Where targeted pelagic predation on detrital communities is modelled, the impact on the benthic system is non-negligible (Rowe, 1996, Blanchard et al., 2009). The latter have shown that there is a steep decline in the abundance size spectrum for detritivores >1 g in size when top-down pelagic predation is included. This threshold size for the impact of predation is more than 30 times greater than the largest size class (32 mg) considered in this study and may reflect that smaller sized benthic organisms (as in our samples, 0.001–32 mg wwt) are not generally considered the target prey size of most pelagic predators, although passive ingestion may occur. If passive predation is important, one can speculate that such predation will be size dependent, i.e. larger deposit feeders eat smaller individuals. The current approach to modelling marine (pelagic) biomass size spectra in which targeted predation occurs is to use predator-prey ratios (Kerr and Dickie, 2001). However, it is not at all clear how this might be implemented into the present model given that the larger detritivores in our sample range (Table 2) may be passively grazing on benthic organisms one to three orders of magnitude smaller than themselves. This introduces a range of possible predator-prey ratios and thus additional degrees of freedom, adding uncertainty in the model.

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



### 3.2.4 PB ratio

The PB ratio is the quotient of net production (assimilation minus respiration) and biomass. Both assimilation and respiration are functions of ingestion in the model (see Eq. 1, and consistent with the findings of Lu et al., 2004), explaining the sensitivity of the PB ratio to ingestion (Fig. 10e). Hence, the model suggests that allometric ingestion rates of the type identified by Cammen (1980, see also Eq. 4) yield the size dependencies in PB ratios found in the literature (e.g. Banse and Mosher, 1980). The latter authors could find no correlations between the PB ratio and other physiological measures and found no adequate explanation for the size dependency. However, Banse and Mosher (1980) speculated that the PB ratio should be a proxy for specific mortality rates, in that annual production rates should equal annual mortality rates at equilibrium. In support of this idea, Brey (1999) derived a significant linear regression between specific annual growth rates (i.e. PB ratios) and specific annual mortality rates from the application of various growth models. Such a linear relationship is supported by the model presented here which shows a strong correlation between the specific mortality rate and the PB ratio for all sites in the model (e.g.  $m_i = 7.8 \times PB + 0.00092$ ,  $r^2 = 0.99$  at the FSC site), which when used in the model produces similar results to the standard runs (not shown). The linear relationship and the subsequent results it produces in the model are unsurprising given the steady-state assumptions adopted in this study. However, this relationship does not address the question of why the PB ratio is size dependent. The importance of ingestion (and its size dependency) to the sensitivity of the PB ratio in the model may provide a way to answer this question.

### 3.3 Model simulations of alternative BBSS

The pioneering work of Schwinghamer and Warwick supports the existence of a bimodal BBSS. We have argued that such BBSS may not be real (see *The biomass size spectra*). Nevertheless, we attempted to investigate the controls on bimodal spectra by optimising the model against artificial data in which the observed biomass in size

**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



classes 12–14 was reduced by one to two orders of magnitude – in line with the work of Schwinghamer and Warwick – yielding bi-modal data. The optimisation could not find adequate solutions. However, the sensitivity analysis revealed that the model can produce BBSS which do not show monotonic behavior but, in these cases, realistic size spectra for both respiration and PB ratios could not be simultaneously simulated.

## 4 Conclusions

The purpose of this work was to identify and examine the controls on benthic biomass distributions in marine benthic assemblages (meio- to macro-fauna, 1 µg–32 mg). Our study adds to a sparse collection of observed biomass size spectra in benthic communities, particularly in the deep sea, and involves a rare application of simple allometric modelling to these environments.

At all three sites studied, the metazoan fauna was dominated by deposit feeding meiofauna (nematodes) and macrofauna (polychaetes). The observed biomass size spectra revealed that biomass increased with body size, although qualitatively some local minima/maxima may be identified in the spectra. Our data supports findings from studies post-Schwinghamer, which together question the assumption that a multi-modal biomass size spectrum is characteristic of marine sedimentary communities.

The model suggests that mortality is a key factor controlling benthic biomass distributions at our three study sites. We speculate that this is a more widely applicable conclusion for marine sediments given the overall trends in published data showing that biomass tends to accumulate in larger rather than smaller size classes.

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**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

our considerable thanks, we are also especially grateful to the Masters and crews of the vessel. Finally, we thank Paul Tyler and Henry Ruhl for their comments on the manuscript.

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**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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---

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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**BGD**

8, 8189–8240, 2011

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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---

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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**BGD**

8, 8189–8240, 2011

---

**Controls on benthic biomass size spectra in shelf and deep-sea sediments**

B. A. Kelly-Gerrey et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table 2.** The range and mean weight of geometric ( $\log_2$ ) size classes from the reliable part of the used biomass size spectra.

Size class class (i)	Size range (g wwt)	Mean weight (g wwt)	Approximate mass (wwt)
5	$5.9 \times 10^{-7} - 1.2 \times 10^{-6}$	$8.9 \times 10^{-7}$	1 $\mu\text{g}$
6	$1.2 \times 10^{-6} - 2.4 \times 10^{-6}$	$1.8 \times 10^{-6}$	2 $\mu\text{g}$
7	$2.4 \times 10^{-6} - 4.8 \times 10^{-6}$	$3.6 \times 10^{-6}$	4 $\mu\text{g}$
8	$4.8 \times 10^{-6} - 9.5 \times 10^{-6}$	$7.1 \times 10^{-6}$	8 $\mu\text{g}$
9	$9.5 \times 10^{-6} - 1.9 \times 10^{-5}$	$1.4 \times 10^{-5}$	16 $\mu\text{g}$
10	$1.9 \times 10^{-5} - 3.8 \times 10^{-5}$	$2.9 \times 10^{-5}$	32 $\mu\text{g}$
11	$3.8 \times 10^{-5} - 7.6 \times 10^{-5}$	$5.7 \times 10^{-5}$	64 $\mu\text{g}$
12	$7.6 \times 10^{-5} - 1.5 \times 10^{-4}$	$1.1 \times 10^{-4}$	128 $\mu\text{g}$
13	$1.5 \times 10^{-4} - 3.0 \times 10^{-4}$	$2.3 \times 10^{-4}$	256 $\mu\text{g}$
14	$3.0 \times 10^{-4} - 6.1 \times 10^{-4}$	$4.6 \times 10^{-4}$	512 $\mu\text{g}$
15	$6.1 \times 10^{-4} - 1.2 \times 10^{-3}$	$9.1 \times 10^{-4}$	1 mg
16	$1.2 \times 10^{-3} - 2.4 \times 10^{-3}$	$1.8 \times 10^{-3}$	2 mg
17	$2.4 \times 10^{-3} - 4.9 \times 10^{-3}$	$3.6 \times 10^{-3}$	4 mg
18	$4.9 \times 10^{-3} - 9.7 \times 10^{-3}$	$7.3 \times 10^{-3}$	8 mg
19	$9.7 \times 10^{-3} - 1.9 \times 10^{-2}$	$1.5 \times 10^{-2}$	16 mg
20	$1.9 \times 10^{-2} - 3.9 \times 10^{-2}$	$2.9 \times 10^{-2}$	32 mg

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table 3.** Model parameters, ranges and optimised values. (Ranges used for the parameter optimisation are in square parenthesis; optimised values are in round parenthesis – first value is for size class 5, last value is for size class 20. Parameters  $a_1$ ,  $a_2$ ,  $b_1$  are from Eqs. (3) and (4),  $x_1$ ,  $x_2$ ,  $b_2$  are from Eq. (5). For reasons of presentation, some of the values shown have been rounded.) See also Fig. 5.

Parameter	Units	Site	$a_1$ [0.01 – 0.2] <sup>1</sup>	$a_2$ [0.0001 – 0.1] <sup>2</sup>	$b_1$ [0.1 – 0.5] <sup>3</sup>	$x_1$	$x_2$	$b_2$ [0.1 – 2] <sup>4</sup>	value
$I$	d <sup>-1</sup>	FSC (5.64, 0.47)	0.20		0.24				
Specific ingestion rate		FG (3.22, 0.40)	0.19		0.20				
		OM (7.67, 0.49)	0.19		0.27				
$m$	d <sup>-1</sup>	FSC (0.05, 0.004)		0.0018	0.24				
Specific mortality rate		FG (0.036, 0.004)		0.0021	0.20				
		OM (0.07, 0.005)		0.0018	0.27				
$K_{ing}$ [0.1–1000] <sup>5</sup>	g wet wt m <sup>-2</sup>	FSC(254, 905)				253	5111	0.58	
Half-sat for ingestion		FG (381, 1000)				363	2129	0.34	
		OM (603, 937)				602	2355	0.55	
$K_m$ [0.1–1000] <sup>5</sup>	g wet wt m <sup>-2</sup>	FSC (0.1, 15.97)				0.0627	0.1246	0.58	
Half-sat. for mortality		FG (0.1, 15.97)				-0.37	54.58	0.34	
		OM (0.1, 15.97)				0.049	112.14	0.55	
$r$ [0.01 – 0.6] <sup>6</sup>		FSC (0.16, 0.45)				0.1592	2.28	0.58	
Fraction of assimila- tion respired		FG (0.02, 0.30)				0.6075	0.4203	0.34	
		OM (0.08, 0.6)				0.4442	0.6281	0.55	
$\alpha$ [0.1 – 0.9] <sup>7</sup>		FSC (0.27, 0.42)				0.2663	1.2216	0.58	
Fraction of ingestion assimilated		FG (0.61, 0.73)				0.0110	0.9662	0.34	
		OM (0.44, 0.53)				0.0833	3.6393	0.55	
$f_{bac}$ [0.5 – 0.99] <sup>8</sup>		FSC							0.95
Fraction of POC flux respired by bacteria		FG							0.96
		OM							0.92
POC flux [0.0003 – 0.27] <sup>9</sup>	g wet wt m <sup>-2</sup> d <sup>-1</sup>	FSC							0.053
		FG							0.071
		OM							0.036

<sup>1</sup> Derived from data in Cammen (1980) showing a power relationship between organic carbon ingestion rates and body size of benthic deposit feeders and detritivores. These data were converted to express both body size as grams wet weight (Rowe, 1983) and ingestion as a specific rate (d<sup>-1</sup>) by dividing the measured ingestion rate for a size class by its corresponding body size. This yielded  $I_i = 0.023M_i^{-0.26}$  ( $n = 19$ ;  $r^2 = 0.69$ ;  $p < 0.001$ ). So  $a_1$  and  $b_1$  have ranges which encompass the correspondonding coefficients in this derived equation.

<sup>2</sup> Chosen so as to capture the range of values in  $m_I$  presented in Brey (1999). Note that much higher specific mortality rates may also result.

<sup>3</sup> Cammen (1980), Brown et al. (2004), Hendriks (1999), Savage et al. (2004)

<sup>4</sup> Estimated range which is wide enough to encompass scaling found in size spectra studies (e.g. Glazier 2005)

<sup>5</sup> Large nominal range chosen in the absence of data.

<sup>6</sup> Cammen (1989), Hargrave (1979)

<sup>7</sup> This range encompasses both the fresh and bulk sediment values in Ahrens et al. (2001) and the range across the animal kingdom in Hendriks (1999).

<sup>8</sup> Pfannkuche et al. (1999), Woulds et al. (2009)

<sup>9</sup> Range in POC fluxes expected in shelf and open ocean waters.

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

**Table 4.** Summary of regression analyses for abundance and biomass relationships with nominal body weight for three study locations (FG, Fladen Ground; FSC, Faroe-Shetland Channel; OM, Oman Margin). Regression equations, associated ANOVA probability (p), goodness-of-fit ( $R^2$ ) are given together with the calculated slope (b) and its t-test comparisons probabilities (p) with standard allometric ratios.

Parameter	Location	Equation	ANOVA (p)	$R^2$ (%)	b	Slope comparisons (t-test, p)				
						1/3	1/4	0	-2/3	-3/4
Abundance	FG	0.401–0.829x	< 0.001	96.7	-0.82928	< 0.00001	< 0.00001	< 0.00001	< 0.002	ns
	FSC	0.548–0.682x	< 0.001	97.5	-0.68206	< 0.00001	< 0.00001	< 0.00001	ns	< 0.05
	OM	-0.646–0.918x	< 0.001	91.9	-0.91802	< 0.00001	< 0.00001	< 0.00001	< 0.005	< 0.05
Biomass	FG	0.359 + 0.162x	=0.001	51.5	0.16206	< 0.001	< 0.05	< 0.005	< 0.00001	< 0.00001
	FSC	0.530 + 0.315x	< 0.001	88.6	0.31491	ns	< 0.05	< 0.00001	< 0.00001	< 0.00001
	OM	-0.539 + 0.123x	ns	8.4	0.12333	< 0.05	ns	ns	< 0.00001	< 0.00001

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

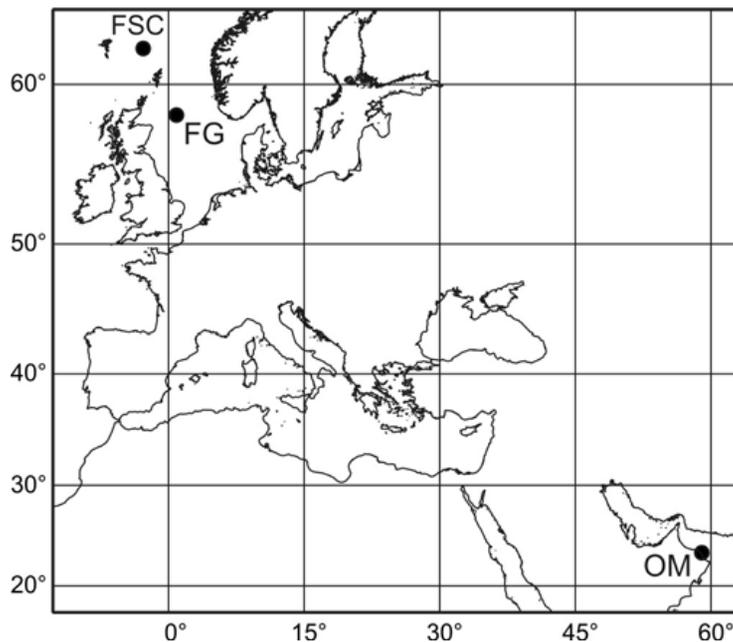
Printer-friendly Version

Interactive Discussion



## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.



**Fig. 1.** Chart showing the locations of the three study sites: Fladen Ground (FG), Faroe-Shetland Channel (FSC), and Oman Margin (OM).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

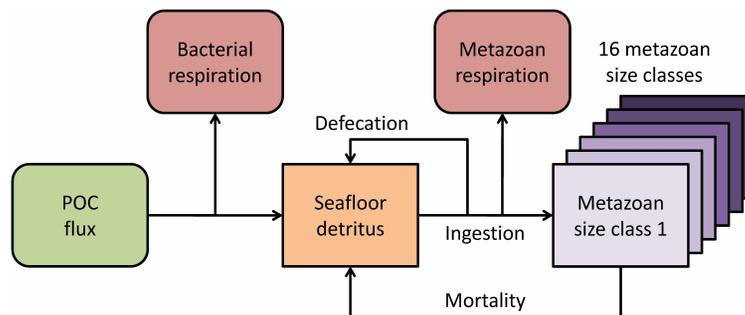
Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.



**Fig. 2.** Flow diagram of model processes. The dotted boxes represent the processes carried out by each size class in the model. The shaded boxes represent the loss terms.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

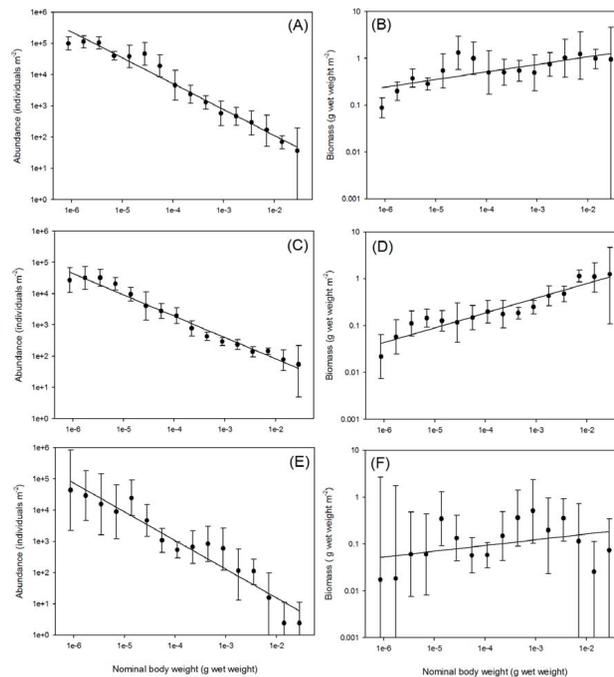
Interactive Discussion

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## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

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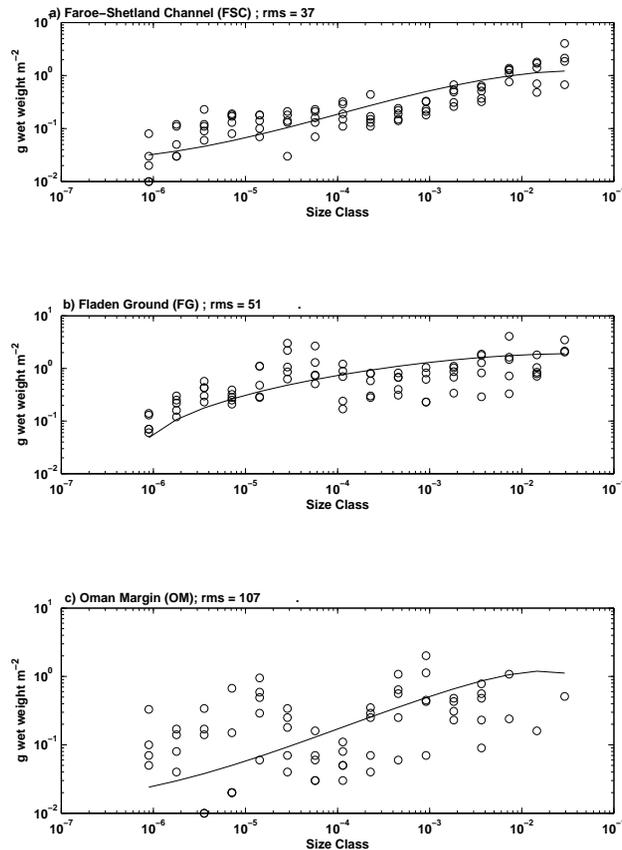


**Fig. 3.** Abundance and biomass spectra for Fladen Ground (**a, b**), Faroe-Shetland Channel (**c, d**) and Oman Margin (**e, f**). Geometric mean (points) and 95% confidence intervals (bars) based on five replicate samples are shown together with regression lines for the geometric mean data.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

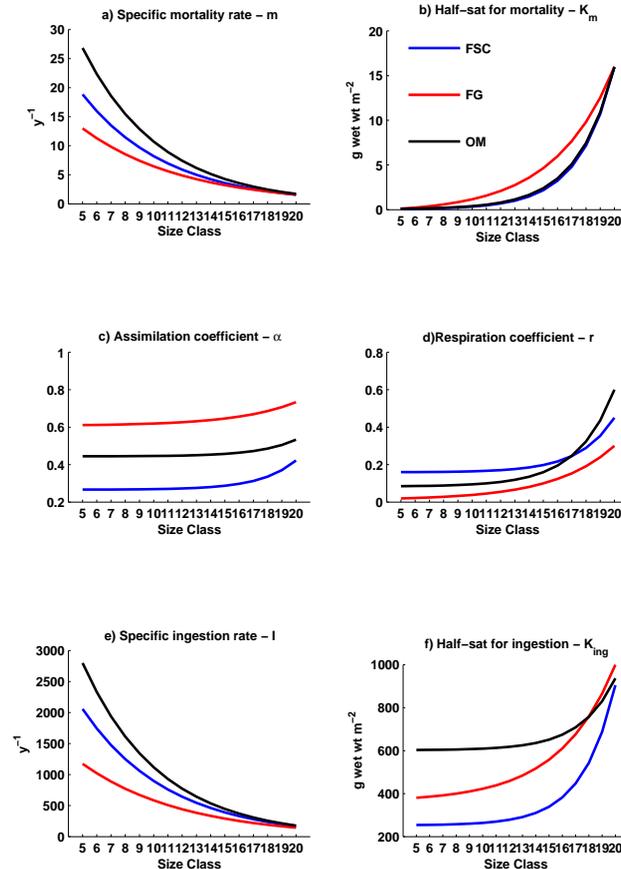


**Fig. 4.** Optimised model biomass size spectra at each site (lines). The observations contain five replicates per size class (open circles). (rms, root mean square of model fit to field data).

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.



**Fig. 5.** Optimised biomass size spectra model parameters for all three study sites (Faroe-Shetland Channel, blue; Fladen Ground, red; Oman Margin, black).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

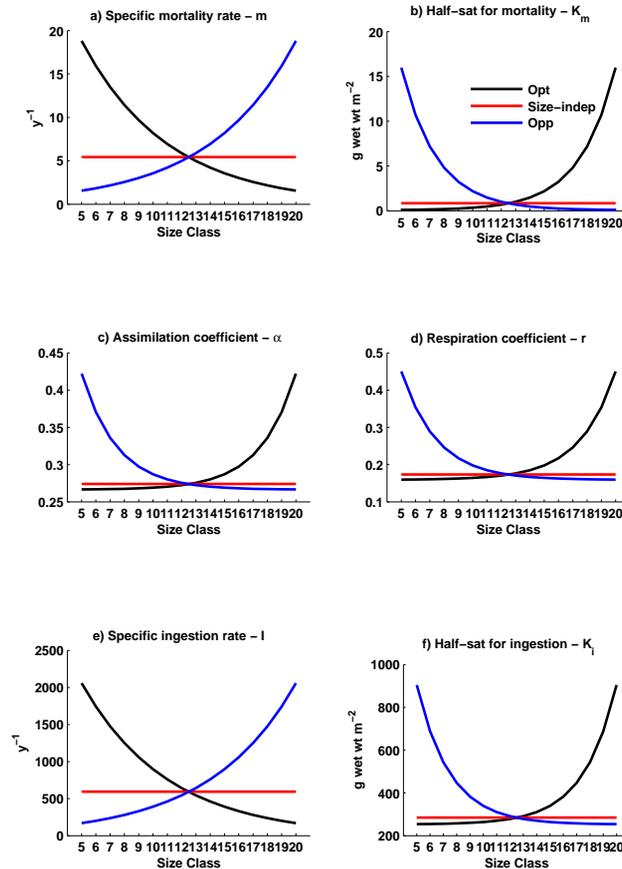
Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Controls on benthic biomass size spectra in shelf and deep-sea sediments**

B. A. Kelly-Gerrey et al.



**Fig. 6.** Biomass size spectra model parameter values used in the sensitivity analysis (optimized, black; size-independent, red; opposite to optimized, blue).

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

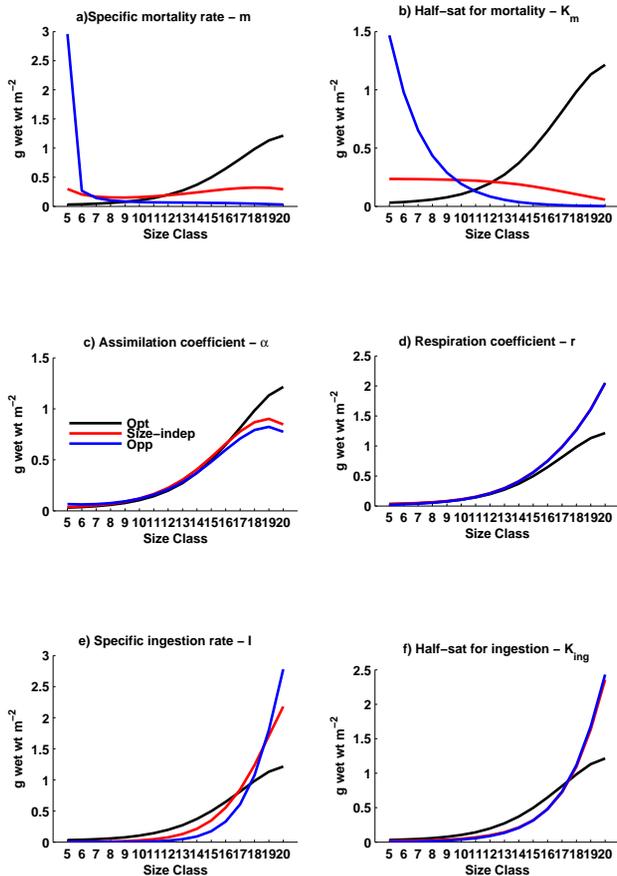
Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





**Fig. 7.** Biomass size spectra model responses to parameter values given in Fig. 6 (optimized, black; size-independent, red; opposite to optimized, blue).

**Controls on benthic biomass size spectra in shelf and deep-sea sediments**

B. A. Kelly-Gerrey et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

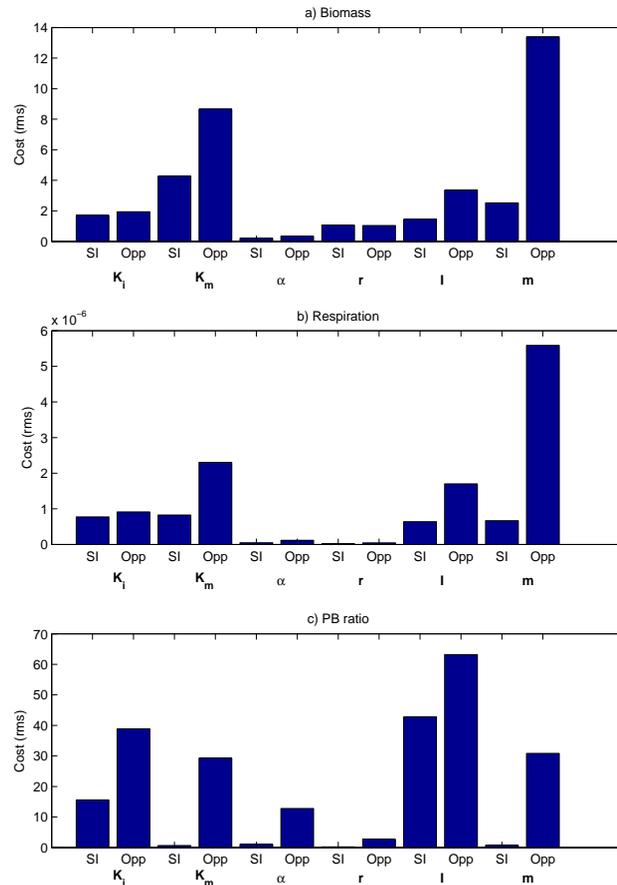
Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

B. A. Kelly-Gerrey et al.

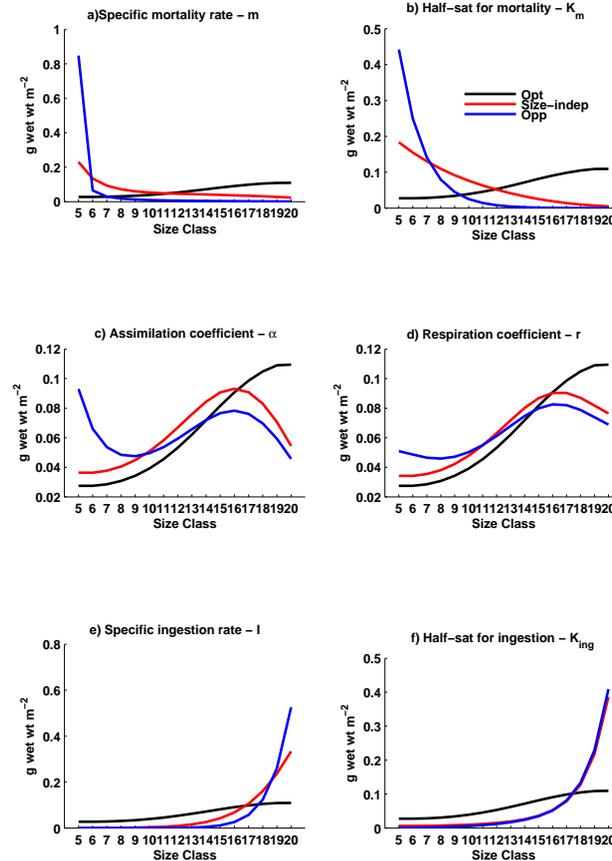


**Fig. 8.** Sensitivity of selected model outputs to parameter settings (SI, size-independent; Opp, Opposite to optimized). The cost is the root mean square difference comparing runs with parameters set to SI or Opp with optimised parameter runs.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[◀](#)
[▶](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

## Controls on benthic biomass size spectra in shelf and deep-sea sediments

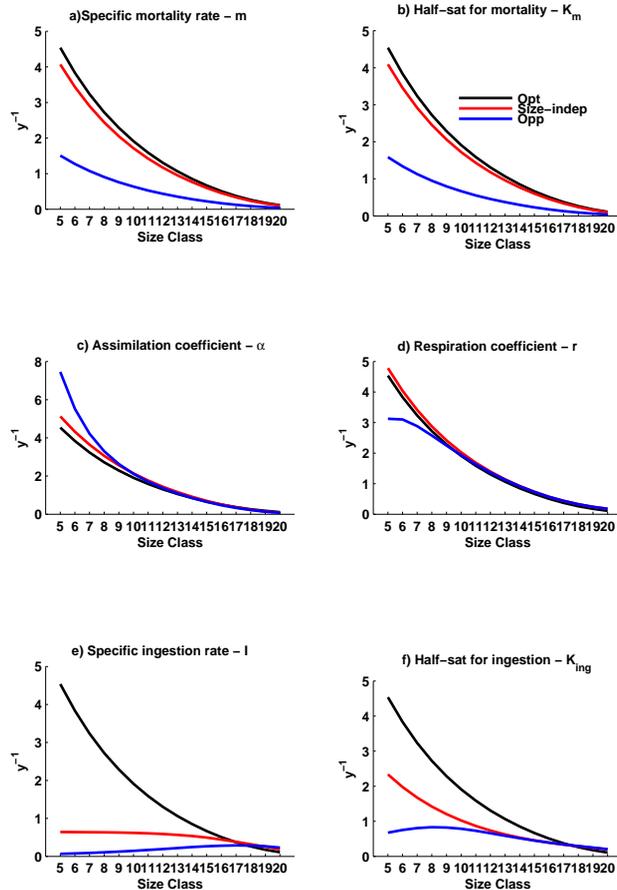
B. A. Kelly-Gerrey et al.



**Fig. 9.** Model respiration rate response to parameter values given in Fig. 6 (optimized, black; size-independent, red; opposite to optimized, blue).

**Controls on benthic biomass size spectra in shelf and deep-sea sediments**

B. A. Kelly-Gerrey et al.



**Fig. 10.** Model PB response to parameter values given in Fig. 6 (optimized, black; size-independent, red; opposite to optimized, blue).

Title Page

Abstract Introduction

Conclusions References

Tables Figures

⏪ ⏩

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion