

Predicting abundance–body size relationships in functional and taxonomic subsets of food webs

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Abstract Abundance–body size relationships are widely observed macroecological patterns in complete food webs and in taxonomically or functionally defined subsets of those webs. Observed abundance–body size relationships have frequently been compared with predictions based on the energetic equivalence hypothesis and, more recently, with predictions based on energy availability to different body size classes. Here, we consider the ways in which working with taxonomically or functionally defined subsets of food webs affected the relationship between the predicted and observed scaling of biomass and body mass in sediment dwelling benthic invertebrate communities at three sites in the North Sea. At each site, the energy available to body size classes in the “whole” community (community defined as all animals of 0.03125–32.0 g shell-free wet weight) and in three subsets was predicted from estimates of trophic level based on nitrogen stable isotope analysis. The observed and predicted scalings of biomass and body size were not significantly different for the whole community, and reflected an increase in energy availability with body size. However, the results for subsets showed that energy availability could increase or decrease with body size, and that individuals in the subsets were likely to be competing with individuals outside the subsets for energy. We conclude that the study of abundance–body mass relationships in functionally or taxonomi-

cally defined subsets of food webs is unlikely to provide an adequate test of the energetic equivalence hypothesis or other relationships between energy availability and scaling. To consistently and reliably interpret the results of these tests, it is necessary to know about energy availability as a function of body size both within and outside the subset considered.

Keywords Benthic invertebrates · Energetic equivalence · Size spectra · Stable isotope analysis · Trophic structure

Introduction

Abundance–body size relationships are fundamental macroecological patterns and are typically described as scaling relationships between \log_{10} numerical (N) or biomass (B) abundance and \log_{10} body mass (M) (e.g. Brown and West 2000). The processes that determine the observed relationships between N or M and B are the subject of ongoing debate (e.g. Gaston and Blackburn 2000), and if methods for predicting these relationships were identified they would have applications in theoretical and applied ecology (e.g. Belgrano et al. 2005).

Damuth (1981), based on a study of mammalian herbivore populations, demonstrated that N scaled as $M^{-0.75}$. Since the scaling of metabolic rate can be approximated as $M^{0.75}$, Damuth proposed that energy use was independent of M , and that body size did not provide any population with an energetic advantage. Since Damuth, there have been many attempts to test whether his hypothesis, subsequently termed the “energetic equivalence hypothesis”, applied to other

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groups. Blackburn and Gaston (1997), for example, reviewed many of the published studies for animals and calculated that the mean scaling was $M^{-0.51}$, whereas Belgrano et al. (2002) and Li (2002) demonstrated that energetic equivalence correctly predicted scaling of numerical abundance and body mass in phytoplankton and plant communities.

Based on the observations of Damuth (1981), the expectation that N scales as $M^{-0.75}$ and B as $M^{0.25}$ (since $B=MN$) relies on the assumption that the same amount of energy is available to all individuals. This applies, for example, to plants sharing sunlight (Belgrano et al. 2002). However, in food webs, the same amount of energy will not be available for all individuals and species because the transfer of energy through food chains is inefficient. Thus, when abundance–body mass scaling is investigated for subsets of species in food webs that do not all feed at the same trophic level, $N \propto M^{-0.75}$ and $B \propto M^{0.25}$ would not necessarily apply. In the studies of abundance–body size scaling reviewed by Blackburn and Gaston (1997), for example, the species in some individual studies of birds included seed eaters, invertebrate and vertebrate feeders that would not have been sharing the same source of energy. Moreover, in focusing on a subset of a food web, the effects of other species that might compete for prey were not considered.

In circumstances where there is a linear reduction in energy availability at size, as in strongly size-based aquatic food webs, it is straightforward to estimate energy availability in different size classes of animals from knowledge of trophic level (TL) at size, transfer efficiency (TE) and predator prey body size ratios (Jennings et al. 2002). Brown and Gillooly (2003) proposed that scaling of N and B with M would be $>M^{-0.75}$ and $>M^{0.25}$ in such size-based food webs because energy would decrease with trophic level. Jennings and Mackinson (2003) formalised and tested this hypothesis for all individuals in a series of size classes in a marine food web and the observed scalings of $M^{-1.20}$ (N) and $M^{-0.2}$ (B) were not significantly different from the predicted scalings of $M^{-1.24}$ and $M^{-0.24}$.

The prediction of scaling in subsets of a food web poses challenges that are not apparent when working with all individuals in a given size class. Thus, even if a linear model can be used to describe the observed abundance–body mass relationship, and if the energy available to an individual or species in a subset can be estimated, this is not sufficient to predict patterns of abundance without knowledge of the roles of competing individuals and species. In practice, it is usually impractical to consider all separate groups

that contribute to a food web in the analysis of abundance–body mass relationships. This is because sampling and analysing the food web in such detail requires a wide range of different sampling methods to be used at different scales and because of the difficulties of reliably estimating time-averaged trophic levels.

Shallow-water benthic invertebrate communities receive energy from phytoplankton and detritus. The majority of sediment-dwelling benthic animals share these resources and are supported by associated food chains. The abundance and body mass of sediment dwelling animals across a range of body size classes and in groups with different feeding characteristics can be estimated with a single sampling method, and the relative trophic level of individuals or groups in the food web can be estimated using nitrogen-stable isotope analysis. Estimates of trophic level allow the relative availability of energy to individuals or groups of individuals to be predicted (Jennings et al. 2002).

Here, we describe overall abundance–body mass relationships in three communities of sediment dwelling benthic animals and compare these with the abundance–body mass relationships in three subsets of the community: predatory polychaetes, filter- and deposit-feeding bivalves, and other species. The energy available to body mass classes in the whole community and in each subset is predicted from estimates of trophic level based on nitrogen stable isotope analysis (Post 2002). We test whether the abundance–body mass relationships in the whole community and subsets are consistent with predictions based on energy availability. Our results show that abundance–body mass relationships in subsets of the community can easily be misinterpreted if the structure of the community in which subsets are embedded is not known.

Materials and methods

Study locations

Abundance–body mass relationships were investigated at three sites in the North Sea during September 2003 and April 2004; the Hills (site 1), the Middle Rough (site 2) and the Indefatigable Banks (site 3). Sites were defined as boxes of one square nautical mile in positions 54°26.0'N to 54°27.0'N and 01°07.0'E to 01°08.7'E (site 1), 55°44.0'N to 55°45.0'N and 03°00.0'E to 03°01.6'E (site 2) and 53°48.0'N to 53°49.0'N and 02°07.0'E to 02°08.7'E (site 3). Depths at the Hills ranged from 47 to 63 m, and the sediment was a sand/gravel mix (mean sediment diameter = 1.38–2.4 mm;

CEFAS, unpublished). Depths at the Middle Rough and Indefatigable varied from 64 to 68 m and 27 to 32 m, respectively, and the sediment at both sites was predominantly sandy (mean particle size diameter = 0.13–0.24 mm; CEFAS, unpublished). All sites were deliberately chosen in areas where trawl fishing disturbance, as recorded by satellite vessel monitoring systems, was known to be negligible, since trawling disturbance can substantially modify the size structure of benthic communities (Duplisea et al. 2002).

Sampling and processing of the benthos

Infaunal invertebrates (defined as those species that live predominantly in the substratum) were sampled with a Hammon Grab deployed from the RV Cefas Endeavour on cruises from 11 to 24 September 2003 (European autumn) and from 7 to 17 April 2004 (spring). On each cruise, ten randomly located replicate deployments were made at five randomly selected locations within each of the three sites. The mean volume of sediment taken per sample was 4.95, 4.5 and 5.8 l at sites 1, 2 and 3, respectively. All samples were sieved through a 1 mm² square mesh with those free-living infaunal species retained on the mesh being removed and frozen for processing.

In the laboratory, all animals were partially defrosted and sorted into four higher taxonomic groups: polychaetes, bivalves, spatangoids, and “other”. For the bivalves and molluscs in the “other” category, each individual was weighed (blotted wet weight) with the shell removed. Tests were removed from spatangoids, but all body tissues were immersed in water before weighing to remove sand and debris, and then reblotted before weighing a second time. For all the remaining groups, *M* was recorded as individual blotted wet weight. A proportion of the animals sampled were inevitably damaged, and for consistency we applied the following rules. First, we tried to assemble “complete” animals from the fragments collected, and where this was done they were recorded as a single individual. Second, if the fragments of an animal weighed less than 30% of the expected total body mass of a whole animal, the fragments were discarded. All individuals collected from replicates within a location were pooled, and the individuals within each of the four taxonomic categories were divided into log₂ body mass classes based on their individual wet weight. The combined weight and the number of individuals in each size class was recorded, and the animals were refrozen and freeze-dried over a period of 48 h before reweighing to determine dry weight.

Stable isotope analysis

Nitrogen stable isotope analysis was used to estimate the relative trophic levels of animals in the different size classes and faunal groups. Relative trophic levels were then used to calculate relative energy availability. This application of isotope analysis was not intended to provide information on diets of different groups. An assumption was made that the total energy available to the community (via any dietary pathway) would decline with relative trophic level. Since the calculations of energy availability rely on the relative change in trophic level with size, relative energy availability can be calculated from the estimated fractionation of $\delta^{15}\text{N}$ without rebasing the trophic level to that of a “source” material.

For the stable isotope analysis, freeze-dried tissue samples were ground to a fine homogeneous powder (particles <60 µm). The ¹⁵N composition of the samples was determined using continuous flow isotope ratio mass spectrometry (CF-IRMS) (Preston and Owens 1983; Preston 1992). Samples were processed with a single inlet dual collector mass spectrometer (Automated Nitrogen Carbon Analysis (ANCA) SL 20-20 system; PDZ Europa, Crewe, UK). This was a continuous flow system, so two samples of reference material (spring samples: (Iso-Analytical Ltd., Sandbach, UK), IA-R014 standard of powdered bovine liver; autumn samples: (PDZ Europa) standard of ammonium sulfate and beet sugar) were analysed after every four to six samples to calibrate the system and compensate for drift with time. Ratios of ¹⁵N:¹⁴N were expressed relative to N₂ in air for nitrogen using standard delta notation ($\delta^{15}\text{N}$). The SD for the repeated $\delta^{15}\text{N}$ measurements made with the reference material was <0.1% for both spring and autumn samples.

Data analysis

Since some body mass classes in the taxonomic groups were sparsely represented, spatangoids and “other” were combined to form a single faunal group, “other fauna”. Initial sorting of the animals produced 16 log₂ wet weight (*M*) classes ranging from 0.0009765 to 32 g. However, the analyses presented are based only on those categories ≥0.03125 g wet weight, since previous research had shown that a significant percentage of annelids in the smaller size classes (0.0009765–0.03125 g) were able to pass through a 1 mm² sieve and would have been lost during sieving (Cefas, unpublished).

Relationships between B and M were described with a linear model. Linear models were used to describe the relationships because they have been widely adopted in existing studies of abundance–body mass relationships; both for subsets (Gaston and Blackburn 2000) and whole communities (Brown and Gillooly 2003). For whole communities, there is empirical and theoretical evidence to support the expectation that the abundance–body mass relationship approximates linearity across the size classes considered (Schwinghamer 1988; Duplisea 2000; Duplisea et al. 2002). For subsets of the communities, however, linear models may not effectively describe the relationships.

Since the calculated abundance–body mass relationships were based on all individuals binned into M classes, the slopes of these abundance–body mass relationships are identical to the slopes of size spectra widely reported for benthic communities (e.g. Schwinghamer 1988; Duplisea 2000). The slopes will not be the same as the slopes of abundance–body mass relationships that are calculated from mean M and mean B for individual species (e.g. Damuth 1981). Notwithstanding issues surrounding the statistical methods used to calculate slopes (Cohen and Carpenter 2005), new theoretical analyses suggest that slopes calculated for all individuals usually provide a more effective test of the energetic equivalence hypothesis than slopes based on mean M and mean B (Jennings et al., unpublished).

All $\log_2 M$ classes were converted to $\log_{10} M$ for analysis. Preliminary analysis showed that the use of wet weight or dry weight had no significant effect on

the slopes of B and M relationships. The analyses presented were therefore conducted using wet weight as a measure of B and M , since wet weights have usually been reported in other studies. Nitrogen stable isotope ratios were calculated by M class as biomass weighted mean $\delta^{15}\text{N}$. Relationships between B and M as well as mean $\delta^{15}\text{N}$ and M were calculated for each faunal group by season. To compare seasonal differences, two linear regression models were fitted to the data. Model (1) assumed the same slope for each season, but each was given a different intercept; model (2) assumed a different intercept and slope for both seasons. The differences in the slopes by season were tested using analysis of covariance to see if model (2) fitted significantly better than model (1). For B and M relationships, the tests showed that differences between seasons were significant ($P < 0.05$) in only one of nine cases. For $\delta^{15}\text{N}$ and M relationships, the tests showed that differences between seasons were never significant ($P < 0.05$) (Table 1). Based on the results of these analyses, we calculated slopes from data pooled across seasons.

Mean rates of change in trophic level with M are reflected in the slope (b) of the relationship between $\delta^{15}\text{N}$ (y) and $\log_{10} M$ (x). Based on the assumption that the mean fractionation of $\delta^{15}\text{N}$ is 3.4‰ per trophic level (Post 2002), then the rate of change in available energy (E) with M will be $\log_{10} \text{TE}/(3.4/b)$, where TE is transfer efficiency (Jennings and Mackinson 2003). Thus the predicted relationship between B and M was calculated as

Table 1 Comparison of seasonal differences in the slopes of relationships between $\log_{10} B$ and $\log_{10} M$ as well as $\delta^{15}\text{N}$ and $\log_{10} M$ (M and B measured as wet weight)

Model 1 assumed the same slope (b) for each season, but each season was given a different intercept. Model 2 assumed a different intercept and slope for both seasons. The reported P indicates the probability of significant differences in slope by season as tested using analysis of covariance

Site	Group	Model 1	Model 2 (different)		P
		(same) b (pooled)	b (autumn)	b (spring)	
$\log_{10} B$ (y) and $\log_{10} M$ (x)					
1	Polychaetes	0.228	0.194	0.262	0.801
1	Bivalves	0.618	0.534	0.728	0.589
1	Other fauna	0.053	−0.056	0.110	0.666
2	Polychaetes	0.327	0.431	0.224	0.495
2	Bivalves	0.860	0.875	0.841	0.793
2	Other fauna	−0.458	0.026	−0.943	0.056
3	Polychaetes	0.352	0.170	0.546	0.325
3	Bivalves	0.935	0.781	1.155	0.024
3	Other fauna	0.671	0.414	0.978	0.264
$\delta^{15}\text{N}$ (y) and $\log_{10} M$ (x)					
1	Polychaetes	−0.179	0.041	−0.399	0.486
1	Bivalves	0.570	0.909	0.121	0.447
1	Other fauna	−0.454	−0.700	−0.325	0.757
2	Polychaetes	1.126	0.791	1.461	0.253
2	Bivalves	0.685	0.539	0.877	0.490
2	Other fauna	−2.550	−3.138	−1.962	0.409
3	Polychaetes	1.314	1.955	0.630	0.096
3	Bivalves	−0.035	0.062	−0.174	0.370
3	Other fauna	0.309	0.871	−0.363	0.408

$$B \propto M^{\frac{\log_{10} TE}{(3.4/b)}} \times M^{0.25}, \quad (1)$$

where $M^{0.25}$ is the assumed scaling when E is shared equally among individuals (Damuth 1981). Assumed values of TE from 0.10 to 0.15 were considered, following Ware (2000).

Results

The scaling of relationships between B and M varied among faunal groups (subsets of the whole community) from slightly negative to highly positive (Fig. 1; Table 2). There were pronounced deviations from linearity in the relationships, but these deviations were not consistent among sites. Bivalves exhibited the most positive abundance–body mass scalings at all sites and

“other fauna” the most negative, except at site 3, while polychaete scalings were close to $M^{0.25}$ at all sites and the scalings for “all fauna” varied from $M^{0.13}$ to $M^{0.44}$ (Table 2). The confidence intervals for the slopes were generally wide, especially for the polychaete, bivalve and “other fauna” groups. Trends in mean $\delta^{15}\text{N}$ with M varied among sites for the polychaete, bivalve and “other fauna” groups, but $\delta^{15}\text{N}$ decreased slowly with M for all fauna at all sites (Fig. 2).

The predicted slopes of scaling relationships were generally not strongly dependent on the assumed TE (Table 3), a reflection of the generally weak relationships between mean $\delta^{15}\text{N}$ and M (Fig. 2). The $\delta^{15}\text{N}$ of polychaetes in any M class is typically higher than the $\delta^{15}\text{N}$ of bivalves or “other fauna”, but the $\delta^{15}\text{N}$ of bivalves and other fauna is often comparable within sites in at least a proportion of the M classes considered.

Fig. 1 Relationships between biomass and body mass for faunal groups at the three study sites. Slopes (b) of the fitted linear relationships $\log_{10} B = a + b(\log_{10} M)$ are shown

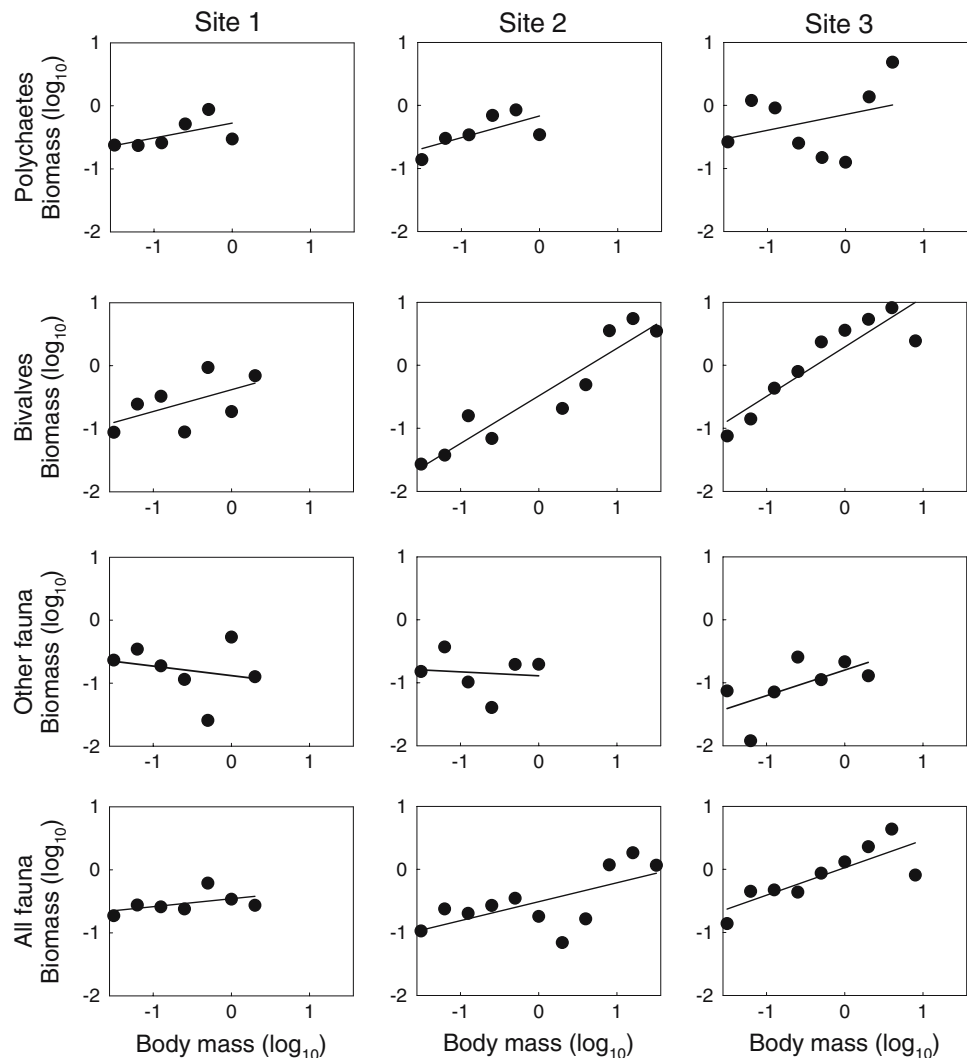


Table 2 Slopes of relationships \log_{10} biomass and \log_{10} body mass by site and faunal group, when body mass is measured as wet weight

Site	Group	Wet weight		
		<i>b</i>	95% lower	95% upper
1	Polychaetes	0.24	-0.227	0.702
1	Bivalves	0.35	-0.241	0.932
1	Other fauna	-0.15	-0.883	0.580
1	All fauna	0.13	-0.122	0.373
2	Polychaetes	0.35	-0.159	0.850
2	Bivalves	0.76	0.520	0.990
2	Other fauna	-0.06	-0.859	0.734
2	All fauna	0.30	0.040	0.562
3	Polychaetes	0.25	-0.461	0.961
3	Bivalves	0.78	0.461	1.109
3	Other fauna	0.41	-0.218	1.029
3	All fauna	0.44	0.158	0.715

Comparison of the observed (regression-based) and predicted (theoretical) slopes of *B* and *M* relationships when $TE=0.125$ (Table 3) showed that observed slopes were not consistent with predictions for bivalves and “other fauna” at two of the three sites (when $P=0.05$). Observed and predicted slopes for polychaetes and “all fauna” were not significantly different at any site. Based on the lower and upper 95% confidence limits for observed slopes (Table 2), a predicted scaling of $M^{0.25}$ (as expected on the basis of the energetic equivalence hypothesis) was also consistent with the observed slopes for “all fauna” at all sites, although in two of three cases, the prediction that allowed for the change in *E* with *M* would have provided a better prediction of the mean observed slope.

Since fractionation of $\delta^{15}N$ was assumed to be 3.4‰, we conducted sensitivity analyses to assess how changes in assumed fractionation ($\Delta\delta^{15}N$) would influence

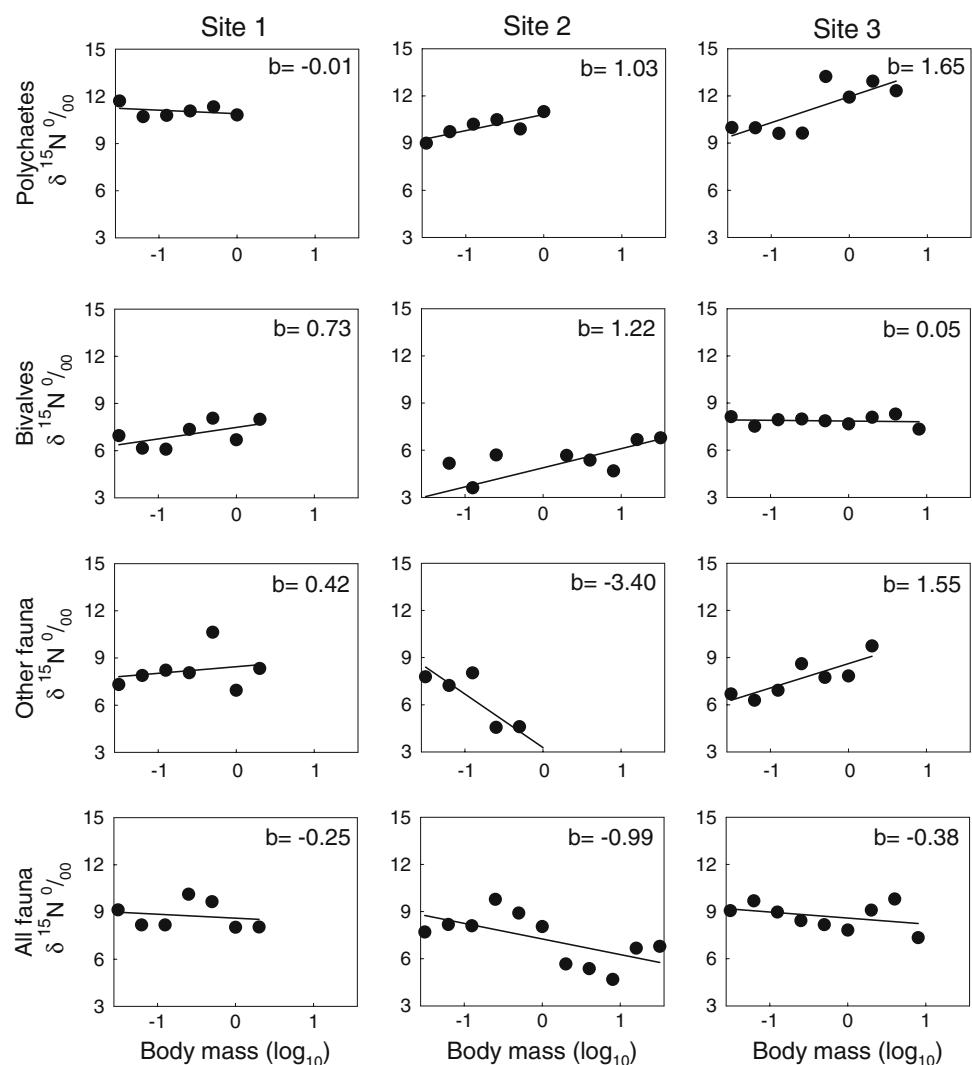
Fig. 2 Relationships between the relative abundance of the heavier isotope of nitrogen ($\delta^{15}N$) and body mass for faunal groups at the three study sites. Slopes (*b*) of the fitted linear relationships $\delta^{15}N=a+b(\log_{10} M)$ are shown

Table 3 Predicted slopes of \log_{10} biomass versus \log_{10} body mass relationships based on assumed transfer efficiencies (TE) of 0.10, 0.125 and 0.15 and the results of the test indicating whether the predicted slope when TE=0.125 is significantly or not significantly different from the observed slope ($P=0.05$)

Site	Group	0.10	0.125	0.15	Significance
1	Polychaetes	0.25	0.25	0.25	NS
1	Bivalves	0.03	0.06	0.07	NS
1	Other fauna	0.13	0.14	0.15	NS
1	All fauna	0.32	0.32	0.31	NS
2	Polychaetes	-0.05	-0.02	0.00	NS
2	Bivalves	-0.11	-0.07	-0.05	S
2	Other fauna	1.25	1.15	1.07	S
2	All fauna	0.54	0.51	0.49	NS
3	Polychaetes	-0.24	-0.19	-0.15	NS
3	Bivalves	0.26	0.26	0.26	S
3	Other fauna	-0.21	-0.16	-0.13	S
3	All fauna	0.36	0.35	0.34	NS

the predicted slopes of the abundance–body mass relationships (Fig. 3). For values of $\Delta\delta^{15}\text{N}$ from 2.4 to 3.4‰, a range that encompasses all values of $\Delta\delta^{15}\text{N}$ within 1 SD of the mean fractionation reported in the review of Post (2002), the variations in predicted slope within sites were relatively small in relation to confidence limits around observed slopes (Table 2) at all realistic transfer efficiencies.

Discussion

The benthic infaunal food webs at the three sites all exhibited structural properties and abundance–body size relationships that were fundamentally different from those observed in predation-based food webs that account for much of the flux of energy in marine ecosystems (e.g. Greenstreet et al. 1997). Thus, the results of the nitrogen stable isotope analyses show that trophic level tends to fall with increasing body size, resulting in potentially greater energy availability for individuals of larger body size. When we account for the scaling of E and M to predict scaling relationships between B and M , the expectation is that slopes will be more positive than $M^{0.25}$, as observed at two of the three sites and in a previous study of scaling in benthic infaunal communities (Dinmore and Jennings 2004). Moreover, the predicted slopes of the B and M relationship for the benthic infaunal food web are much more positive than those that have been reported in food webs where energy is passed by predation from smaller prey to larger predators. For example, Jennings and Mackinson (2003) reported that $B \propto M^{-0.2}$ in such a food web in the central North Sea, a relationship that is not consistent within confidence limits for the observed

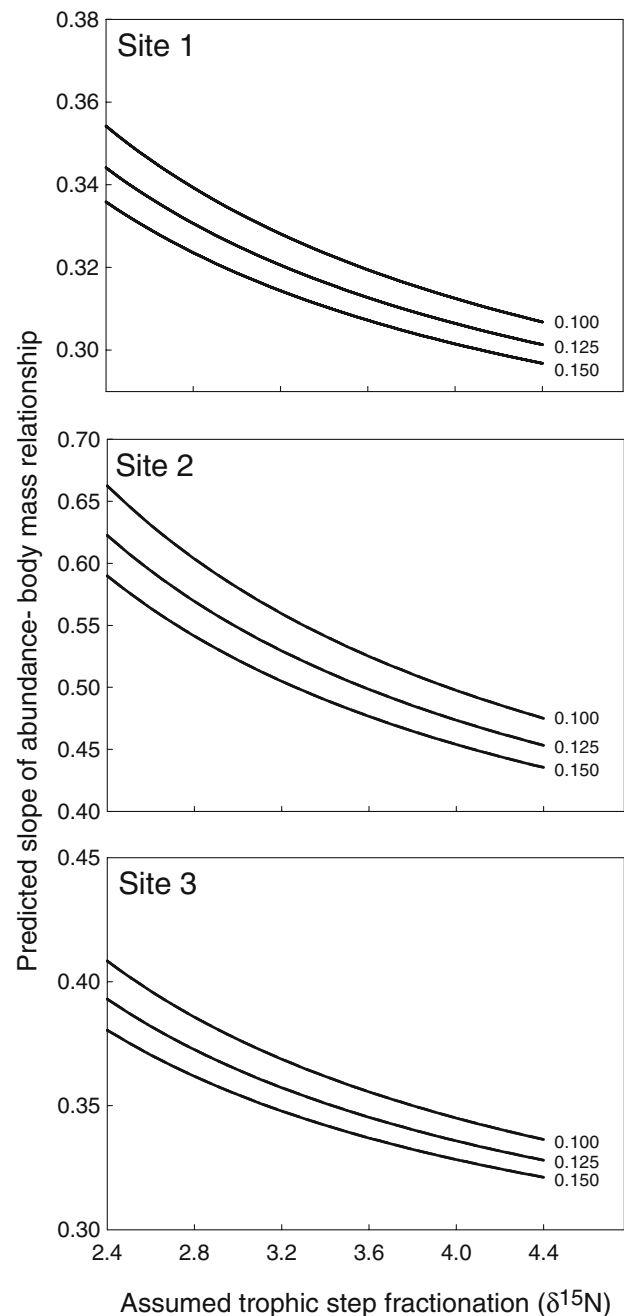


Fig. 3 Sensitivity of the predicted slope of the abundance ($\log_{10} B$)–body mass ($\log_{10} M$) relationship to assumed trophic step fractionation in $\delta^{15}\text{N}$ at the three sites and for three values of transfer efficiency (0.100, 0.125, 0.150)

slopes nor consistent with predictions when E scales positively rather than negatively with M . Consistent with the proposal of Brown and Gillooly (2003), therefore, we conclude that the scaling of B and M can only be predicted from the energetic equivalence hypothesis if E scales as M^0 . If this is not the case, as in many of the existing published studies of abundance–body size relationships (e.g. Blackburn and Gaston

1997), then it is necessary to account for the scaling of E and M when predicting the scaling of B and M and $B \propto M^{0.25}$ would not be expected. Nitrogen stable isotope analysis provides one method of measuring trophic level and hence predicting the scaling of E and M (Jennings et al. 2002).

While the slopes of relationships between $\log_{10} B$ and $\log_{10} M$ for all individuals in a food web are typically characterised by narrow confidence intervals (Boudreau and Dickie 1992), the present results show that the relationships in subsets of the food web and faunal groups can be weaker and more variable. Despite intensive sampling, confidence intervals of observed slopes for the polychaete, bivalve and “other fauna” groups were wide, and thus there was relatively low power to test for differences between observed and predicted B and M scaling. This may reflect the inappropriateness of a linear model for describing abundance–body mass relationships in subsets and/or that the time-averaged sampling was not adequate to account for variations in the abundance of species due to variations in recruitment or mortality. Notwithstanding, the analysis of the relationships between estimated trophic level and M within these faunal groups suggests that different groups can share energy at the same trophic level and that their E and M and B and M relationships cannot be tested independently. For example, at all three sites, the $\delta^{15}\text{N}$ of bivalves and “other fauna” was often comparable in at least a proportion of the M classes considered, implying that these groups were competing for energy. This interaction would not be identified if a single group had been considered in isolation. For polychaetes, $\delta^{15}\text{N}$ in any M class was typically higher than the $\delta^{15}\text{N}$ of bivalves or “other fauna”, suggesting that they fed at higher trophic levels and did not compete for energy with these groups. This is consistent with the expectation that polychaetes are predators on other benthic infauna (Schubert and Reise 1986; Beukema 1987). The higher trophic level of polychaetes may explain why, when this group was considered in isolation, the observed and predicted scalings of B and M were not significantly different.

Our analyses relied on two principal assumptions. First, that $\delta^{15}\text{N}$ at size provides an index of trophic level at size and hence energy availability. Second, that TE can be reliably estimated. The method we adopted avoids the need to assign absolute TL, but does require that $\delta^{15}\text{N}$ is linearly related to TL and that fractionation is known. We assumed a mean fractionation of $\delta^{15}\text{N}$ per trophic level, following Minagawa and Wada (1984) and Post (2002). This assumption does not take account of significant variation in fractionation among

studies, species and species groups. However, our sensitivity analyses demonstrated that varying $\Delta\delta^{15}\text{N}$ from 2.4 to 3.4‰, a range that encompassed all values of $\Delta\delta^{15}\text{N}$ within 1 SD of the mean fractionation reported in Post (2002), had a relatively small effect on predicted abundance–body mass scaling, at least in relation to the confidence limits around observed slopes and the large differences in slopes describing communities with and without size-based predation. In the absence of fractionation estimates for the specific communities we have studied, and given the logistical difficulties associated with time-integrated dietary analysis for many benthic fauna, we conclude that nitrogen stable isotope analysis is the best of the available methods for assessing the time integrated relationship between M and relative TL.

Transfer efficiency was estimated rather than measured, and the values considered spanned a range of values measured in other ecosystems (Ware 2000). Given the relatively shallow slopes of the relationships between TL and M , the results in Table 3 showed that the effects of changing TE on predicted B and M scaling were relatively small in relation to the variability in observed and predicted B within and among faunal groups.

All individuals were binned into size classes to produce our abundance–body mass relationships. Thus the underlying theoretical assumption in our tests of the energetic equivalence hypothesis is that the metabolism of all individuals scales as $M^{0.75}$. Conversely, when cross-species abundance–body mass relationships are calculated from mean M and mean B , the underlying theoretical assumption is that cross-species estimates of metabolism scale as $M^{0.75}$ (e.g. Damuth 1981). These two tests of energetic equivalence are only directly comparable, therefore, when intraspecific and interspecific relationships between metabolism and M are the same. Whether this may or may not be the case is the subject of ongoing debate (van der Meer 2006). However, given the other sources of error and variation in our analysis, it is unlikely that differences in the intraspecific and interspecific scaling of metabolism and M within the expected range (from $M^{2/3}$ to M^1) would have an influence on our conclusions.

We conclude that the study of abundance–body mass relationships in functionally or taxonomically defined subsets of food webs is unlikely to provide an adequate test of the relationships between energy availability and scaling. This is because individuals in the subsets may be competing with individuals outside the subsets for energy and/or because the energy available to individuals in different body size classes is

not known. Moreover, there is no clear expectation that the slopes of relationships in subsets will always be linear, since energy availability at size depends on energy use at size in other subsets. We suggest that many existing tests of the energy equivalence hypothesis and the probability of $N \propto M^{-0.75}$ and $B \propto M^{0.25}$ scaling may not have been reliable, because individuals were not sharing energy, and/or only a proportion of individuals sharing energy were considered. It is notable that when the hypothesis was tested over a wide range of M classes, and when the individuals or populations are clearly competing for energy, then scaling has been consistent with the hypothesis (Belgrano et al. 2002).

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References

- Belgrano A, Allen AP, Enquist BJ, Gillooly JF (2002) Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. *Ecol Lett* 5:611–613
- Belgrano A, Scharler UM, Dunne J, Ulanowicz RE (2005) Aquatic food webs: an ecosystem approach. Oxford University Press, Oxford
- Beukema JJ (1987) Influence of the predatory polychaete *Nephtys hombergii* on the abundance of other polychaetes. *Mar Ecol Prog Ser* 40:95–101
- Blackburn TK, Gaston KJ (1997) A critical assessment of the form of the inter-specific relationship between abundance and body size in animals. *J Anim Ecol* 66:233–249
- Boudreau PR, Dickie LM (1992) Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Can J Fish Aquat Sci* 49:1528–1538
- Brown JH, Gillooly JF (2003) Ecological food webs: high-quality data facilitate theoretical unification. *Proc Natl Acad Sci USA* 100:1467–1468
- Brown JH, West GB (eds) (2000) Scaling in biology. Oxford University Press, Oxford
- Cohen JE, Carpenter SR (2005) Species' average body mass and numerical abundance in a community food web: statistical questions in estimating the relationship. In: de Ruiter P, Wolters V, Moore JC (eds) Dynamic food webs: multispecies assemblages, ecosystem development, and environmental change. Elsevier, Amsterdam, pp 137–156
- Damuth J (1981) Population density and body size in mammals. *Nature* 290:699–700
- Dinmore TA, Jennings S (2004) Predicting abundance–body mass relationships in benthic infaunal communities. *Mar Ecol Prog Ser* 276:289–292
- Duplisa DE (2000) Benthic organism biomass size-spectra in the Baltic Sea in relation to the sedimentary environment. *Limnol Oceanogr* 45:558–568
- Duplisa DE, Jennings S, Warr KJ, Dinmore T (2002) A size-based model of the impacts of bottom trawling on benthic community structure. *Can J Fish Aquat Sci* 59:1785–1795
- Gaston KJ, Blackburn TM (2000) Pattern and process in macroecology. Blackwell, Oxford
- Greenstreet SPR, Bryant AD, Broekhuizen N, Hall SJ, Heath MR (1997) Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *ICES J Mar Sci* 54:243–266
- Jennings S, Mackinson S (2003) Abundance–body mass relationships in size-structured food webs. *Ecol Lett* 6:971–974
- Jennings S, Warr KJ, Mackinson S (2002) Use of size-based production and stable isotope analysis to predict trophic transfer efficiencies and predator–prey body mass ratios in food webs. *Mar Ecol Prog Ser* 240:11–20
- Li WKW (2002) Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean. *Nature* 419:154–157
- van der Meer J (2006) Metabolic theories in ecology. *Trends Ecol Evol* 21:136–140
- Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* 83:703–718
- Preston T (1992) The measurement of stable isotope natural abundance variations. *Plant Cell Environ* 15:1091–1097
- Preston T, Owens NJP (1983) Interfacing an automatic elemental analyser with an isotope ratio mass spectrometer: the potential for fully automated total nitrogen and nitrogen-15 analysis. *Analyst* 108:971–977
- Schubert A, Reise K (1986) Predatory effects of *Nephtys hombergii* on other polychaetes in tidal sediments. *Mar Ecol Prog Ser* 34:117–124
- Schwinghamer P (1988) Influence of pollution along a natural gradient and in a mesocosm experiment on biomass size-spectra of benthic communities. *Mar Ecol Prog Ser* 46:199–206
- Ware DM (2000) Aquatic ecosystems: properties and models. In: Harrison PJ, Parsons TR (eds) Fisheries oceanography: an integrative approach to fisheries ecology and management. Blackwell, Oxford, pp 161–194