

LETTER

Abundance–body mass relationships in size-structured food webs

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Abstract

In communities sharing a common energy source, the energetic equivalence hypothesis predicts that numerical abundance (N) scales with body mass (M) as $M^{-0.75}$. However, in size-structured food webs all individuals do not share a common energy source, and the energy available (E) to larger individuals is constrained by inefficient energy transfer through the food chains that support them. This is expected to lead to steeper scalings of N with M . Here, we formalize and test an existing model for predicting abundance–body mass scaling, where the decline in E with M is calculated from the mean predator–prey body mass ratio (from size-based nitrogen stable isotope analysis) and trophic transfer efficiency. We show that the steep predicted scalings of abundance and body mass (N scales as $M^{-1.2}$, B scales as $M^{-0.2}$) in a marine food web are consistent with empirical estimates and can be attributed to the small predator–prey body mass ratio (106 : 1). As a previous study has shown that environmental stability may favour low predator–prey mass ratios and long food chains, we predict that steeper abundance–body mass relationships will be found in more stable environments.

Keywords

Abundance–body mass relationships, energetic equivalence, food web, marine ecosystem, scaling, size spectra, stable isotope analysis.

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INTRODUCTION

Abundance–body mass relationships are widely studied macroecological patterns (Damuth 1981; Dickie *et al.* 1987; Enquist *et al.* 1998; Brown & West 2000; Gaston & Blackburn 2000; Enquist & Niklas 2001; Kerr & Dickie 2001; Cohen *et al.* 2003). In communities that share a common energy source, numerical abundance (N) often scales with body mass (M) as $M^{-0.75}$. As metabolic rate scales with mass as $M^{0.75}$ (Peters 1983), it has been predicted that the rate of energy use is independent of body size (Damuth 1981, 1987), a prediction known as the energetic equivalence hypothesis (Nee *et al.* 1991). Tests of this hypothesis are difficult, as many ecologists examine abundance–body mass relationships in taxon-based subsets of food webs (Gaston & Blackburn 2000) and may lack accurate information on the energy available to animals of different sizes (Carbone & Gittleman 2002; Brown & Gillooly 2003).

Aquatic food webs are strongly size structured with larger predators eating smaller prey (Sheldon *et al.* 1972; Dickie *et al.* 1987). Many species grow in mass by five orders of

magnitude and cannibalism, cross-predation and transient predator–prey relationships are common (Cushing 1975). While the mean body mass of species is only weakly correlated with their trophic level, trophic level increases continuously with body mass in the whole food web (Fry & Quinones 1994; France *et al.* 1998; Jennings *et al.* 2001, 2002a). These observations provide compelling reasons to adopt size rather than species-based analyses of food web structure and suggest that it is wrong to assign all individuals of a species to a single trophic level.

In size-structured food webs, all individuals do not share a common energy source, and the energy available to larger individuals is constrained by inefficient energy transfer through the food chains that support them (Cyr 2000). The rate at which available energy decreases with increasing mass will depend on the mean predator–prey mass ratio (PPMR) and the trophic transfer efficiency (TE), where TE is the proportion of prey production converted to predator production ($TE = P_c/P_p$ where P_c is predator production and P_p is prey production). One technique, size-based stable isotope analysis (Fry & Quinones 1994; France *et al.* 1998), usefully describes the trophic continuum in many aquatic

food webs (Sheldon *et al.* 1972; Dickie *et al.* 1987), and can be used to estimate mean PPMR (Jennings *et al.* 2002b).

Here, we test a formalization of the model of Brown & Gillooly (2003) for predicting abundance–body mass scaling in a food web, where the decrease in available energy with M is calculated from PPMR and TE. We demonstrate that the steep scaling of abundance and M in a marine food web is consistent with model predictions and attributable to a small PPMR.

METHODS

Biomass abundance (B), N and trophic level (TL) were determined for all animals of 2–2048 g wet mass in a strongly size-structured marine food web in the central North Sea (sampling area 54°00′–55°00′N and 00°30′–02°00′E). Invertebrates and fishes were sampled with a range of appropriate methods (coring, dredging, beam trawling, otter trawling and acoustics, all replicated in space and time) and converted to B and N density (g m⁻² or numbers per m²) as described by Jennings *et al.* (2002b). The TL of invertebrates and fishes was determined using nitrogen stable isotope analysis (Post 2002). We used biomass weighted mean $\delta^{15}N$ of all animals in each body mass class as an index of TL.

We assumed that available energy (E) in a size-based food web would scale as M^0 when the animals shared a common food resource and that the exponent would be <0 when larger predators fed on smaller prey. The expected scaling of $\log_{10} E$ with $\log_{10} M$ was calculated as $\log_{10} TE / \log_{10} PPMR$. Predator–prey mass ratios were calculated from the slope of the relationship between $\delta^{15}N(y)$ and \log_{10} body mass (x) [$PPMR = 10^{(3.4/\text{slope})}$], based on the assumption that the mean fractionation of $\delta^{15}N$ was 3.4‰ per trophic level (Post 2002).

Transfer efficiency can be estimated from the relationship between TL and production (P) (Jennings *et al.* 2002b), as $P : B$ scales as $c. M^{-0.25}$ (Banse & Mosher 1980). However, this approach is not appropriate in the present context, as P will be a function of measured B . Accordingly, we predicted the scaling of E and M based on the measured PPMR and assumed values of TE consistent with those reported in marine ecosystems (Pauly & Christensen 1995; Ware 2000). For the calculated scaling of E and M , we then predicted the scaling of N or B and M as $M^{(\log_{10} TE / \log_{10} PPMR)} \times M^{-0.75}$ and $M^{(\log_{10} TE / \log_{10} PPMR)} \times M^{0.25}$, respectively.

The North Sea ecosystem is heavily fished. Up to 40% of the production of many larger species is caught each year and the abundance of fishes in larger body mass classes is significantly reduced (Gislason 1994; ICES 2003). We limited our analyses to those parts of the size spectrum where direct biomass reductions because of fishing have not been observed, in this case animals <256 g (Jennings *et al.* 2002b). As such, this is not an analysis of a complete food

web, but is a comprehensive analysis of those parts of the food web that can be effectively sampled and for which the slope of the abundance–body mass relationship is not dramatically affected by fishing.

RESULTS

The scaling of abundance with M was near linear for animals of 2–256 g. Numerical abundance (N) scaled as $M^{-1.2}$ and B scaled as $M^{-0.2}$ (Fig. 1a). Predator–prey body mass ratios did not appear to vary consistently with M (Fig. 1b) and the mean PPMR was 106 : 1. As B and $\delta^{15}N$ estimates were based on data collected with many gears and sampling designs it was not possible to provide meaningful confidence limits for the mean. However, the confidence limits associated with mean B or $\delta^{15}N$ estimates for each gear and survey design are provided by Jennings *et al.* (2002b).

Based on the model, the predicted scalings of N and B with M in the food web were $M^{-1.24}$ and $M^{-0.24}$

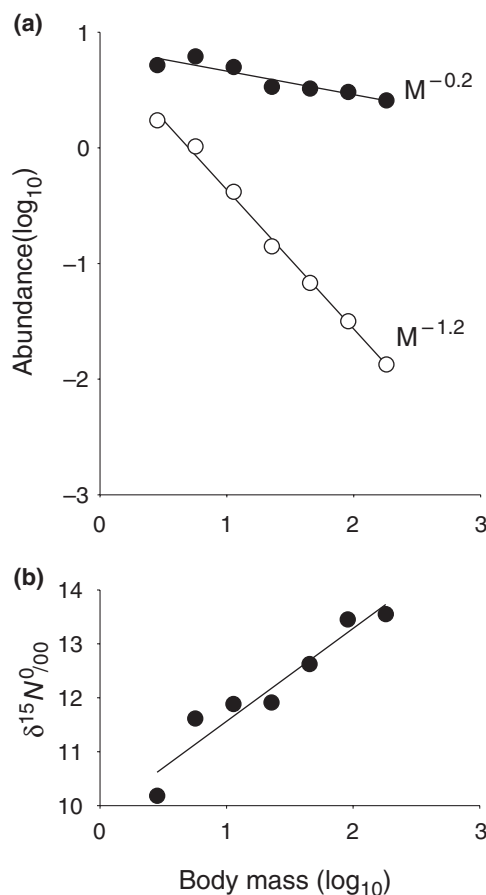


Figure 1 (a) Relationship between biomass abundance (fill circles) or numerical abundance (open circles) and body mass in a marine food web. The fitted scaling relationships for animals of 2–256 g are shown. (b) The relationship between $\delta^{15}N$ and body mass.

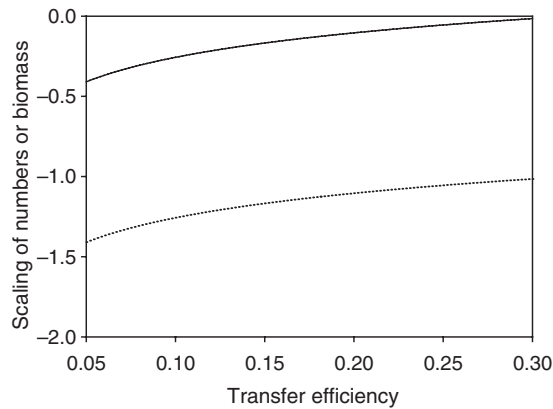


Figure 2 Predicted scaling of numbers (continuous line) and biomass (broken line) as a function of transfer efficiency.

respectively, given a TE of 0.10 and PPMR of 106 : 1. These are not significantly different from the observed values of $M^{-1.20}$ and $M^{-0.20}$ ($P < 0.05$). We tested the sensitivity of predicted scalings to changes in TE (Fig. 2). The scaling of N or B with M is relatively insensitive to changes in TE across the range of TE expected in temperate marine food webs (typically 0.1–0.2; e.g. Ware 2000), but increasingly sensitive to low values of TE (< 0.07).

DISCUSSION

Abundance–body mass scaling in the North Sea food web was accurately predicted by our formalization of the Brown & Gillooly (2003) model. This analysis was possible because mean PPMR can now be measured in size-based food webs (Jennings *et al.* 2002b) and further shows how new types of empirical data can underpin the testing of ecological theory (Brown & Gillooly 2003; Cohen *et al.* 2003). The relatively steep scaling of the abundance–body mass relationship we describe can be attributed to the small predator–prey body mass ratio in the food web. As a previous study has shown that environmental stability may favour low predator–prey mass ratios and long food chains (Jennings & Warr 2003), the results suggest that steeper abundance–body mass relationships may be characteristic of more stable environments.

Analyses of complex open sea food webs are inevitably ambitious and the sampling biases and problems associated with compiling a ‘complete’ food web were discussed by Jennings *et al.* (2002b). Marine ecosystems are all impacted by fisheries exploitation (Pauly *et al.* 1998; Myers & Worm 2003), and the results of any macroecological study will be influenced by the ongoing removal of a substantial proportion of the biomass of larger animals (> 256 g in the present context). We tried to minimize the effects of fishing on our results by excluding large animals from the analysis. However, we cannot account for the effects of

fishing on competition and predation, and the extent to which they influence both slope and intercept of the abundance–body mass relationship for small animals (Duplisa & Kerr 1995; Rice & Gislason 1996). We have to accept this shortcoming if research on macroecological patterns in real marine ecosystems is to progress.

In our analyses, we assumed that (1) the fractionation of $\delta^{15}\text{N}$ with trophic level was 3.4‰, (2) TE was 0.10 and (3) PPMR does not depend on M . The assumed fractionation of $\delta^{15}\text{N}$ (1) is consistent with available empirical evidence, and while it may not apply to all individual predator–prey relationships it is an appropriate assumption in a complex community (Post 2002). Transfer efficiency (2) is unlikely to be precisely 0.10, and for this reason we ran sensitivity analyses. These showed that changes in TE from 0.05 to 0.30 would alter the predicted scaling exponents of N and B with M by ± 0.2 and that the conclusions of our analysis could be questioned if TE was found to be very low or very high in this food web. However, for typical values of TE (0.1–0.2; Ware 2000) the conclusions are robust. In relation to (3), our results demonstrated that the PPMR was relatively independent of body mass for animals of 2–256 g. However, it is unlikely that PPMR is size invariant throughout the food web, as the largest animals in marine ecosystems typically feed down the food chain on smaller size classes of animals with greater total productivity.

In a previous analysis, we estimated TE from the relationship between TL and production. Production (P) was estimated from B assuming that $P : B$ scaled as $M^{-0.25}$ (Jennings *et al.* 2002b). This yielded TE = 0.27, rather higher than the 0.1 we assumed here. The method we used in the previous paper depends on whether the scaling of $P : B$ with M has the same intercept for both fish and invertebrates. Previously we assumed that the $P : B$ for fish was 4× the $P : B$ of invertebrates at a given M (Banse & Mosher 1980). However, if we assume that the intercepts for fish and invertebrates do not differ, then the corresponding TE is 0.07 rather than 0.27. Unfortunately, the compilations of $P : B$ and M that we have access to do not provide sufficient resolution to firmly differentiate intercepts for fish and invertebrates. Given these uncertainties we prefer to use the mean TE (0.1) from Ware’s (2000) review of TE in a range of temperate marine ecosystems.

Numerical abundance and B have been reported to scale as M^{-1} and M^0 respectively in aquatic food webs (Sheldon *et al.* 1972). These scalings would be consistent with the predictions of the Brown & Gillooly (2003) model when PPMR was large (Brown & Gillooly 2003). The relatively small PPMR at our sites in the central North Sea appears to account for the steep negative scalings of N (scales as $M^{-1.2}$) and B ($M^{-0.2}$) that we observed. Improved understanding of the factors influencing PPMR and TE and any relationship between

them will be critical to understanding variation in the scaling of abundance–body mass relationships in size-based food webs and for testing our prediction that abundance scales more negatively with M in more stable environments.

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