Title: Systematic variation in food web body-size structure linked to external subsidies

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Abstract

The relationship between body mass (M) and size class abundance (N) depicts patterns of community structure and energy flow through food webs. While the general assumption is that M and N scale linearly (on log-log scales), non-linearity is regularly observed in natural systems, and is theorised to be driven by non-linear scaling of trophic level (TL) with M resulting in the rapid transfer of energy to consumers in certain size classes. We tested this hypothesis with data from 31 stream food webs. We predicted that allochthonous subsidies higher in the web results in non-linear M-TL relationships and systematic abundance peaks in macroinvertebrate- and fish size classes (latter containing salmonids), that exploit terrestrial plant material and terrestrial invertebrates, respectively. Indeed, both M-N and M-TL significantly deviated from linear relationships and the observed curvature in M-TL scaling was inversely related to that observed in M-N relationships. Systemic peaks in M-N, and troughs in M-TL occurred in size classes dominated by generalist invertebrates, and brown trout. Our study reveals how allochthonous resources entering high in the web systematically shape community size structure and demonstrates the relevance of a generalized metabolic scaling model for understanding patterns of energy transfer in energetically ‘open’ food webs.

1. Introduction

The scaling of organism abundance with body mass is recognised as one of the few 'laws' in ecology [1,2]. When plotted on double logarithmic axes, total abundance (N) typically declines linearly with body mass (M) classes (M-N relationship *henceforth*) and reflects the efficiency of energy transfer from prey (of smaller size) to predators (of larger size) [1]. Consequently, M-N relationships have been used for many decades as an integrated proxy for food web structure [3], particularly in strongly size-structured aquatic ecosystems [4]. According to metabolic scaling theory [5,6], the slope of the M-N relationship can be predicted by the general model: $-\frac{3}{4} + \log(TE) / \log(PPMR)$, where PPMR is the community-wide mean predator–prey mass ratio (the mean size of predators relative to prey) and TE is the trophic transfer efficiency. Thus, metabolic theory predicts a negative, linear M-N slope on log-log axes, and this has been reported widely in the literature [1,2].

However, these patterns are by no means universal and pronounced deviations from a linear M-N slope (and thus power-law relationship) are regularly observed [11]. This is commonly referred to as 'secondary structure' [11] and is characterised by dome-shaped patterns in the log-log M-N space [10–14], signifying that some size classes are over-represented relative to others. Although typically ignored, such deviations might provide an important signal of additional factors structuring natural food webs that can significantly improve predictions of energy flow over 'simpler' metabolic models [5,6].

A generalized metabolic scaling model of Chang et al. [13] proposes that the secondary structure of M-N relationships can arise under equilibrium conditions when the monotonic positive relationship between (log) body mass and trophic level (TL) is violated; that is, the M–TL relationship is nonlinear and PPMR varies with body mass. For example, large omnivorous zooplankton in lakes can occupy a lower trophic level than smaller, more carnivorous zooplankton but can exhibit similar abundances, resulting in points of local minima and maxima clearly visible in the residuals from linear M-N and M-TL fitting [13].

Allochthonous subsidies entering food webs in more 'energetically open' systems could conceivably lead to similar non-linearity in M-N and M-TL, if this additional energy is not uniformly accessible throughout the food web. For instance, energy flow in streams is supported by allochthonous resources received from the catchment [15], with terrestrial plant material and terrestrial invertebrates supporting a significant proportion of the production of detritivorous invertebrates [16] and drift-feeding fish, such as salmonids [17–19], respectively. Large invertebrates and fish that exploit these terrestrial subsidies should (in theory) therefore have especially high abundances and occupy similar or lower trophic levels than other smaller, less abundant, organisms not exploiting the subsidy. Stable isotope analysis is a useful tool to test the latter and estimate the trophic position of consumers [7–9] and can be used to test this idea: nitrogen isotope values (δ^{15}N) increase predictably with trophic level [7–9] and if consumers of terrestrial plant material and terrestrial invertebrates - which exhibit lower δ^{15}N values than autochthonous counterparts (e.g. [20,21]) - manifest lower δ^{15}N than expected based on their body size, it is indicative of more generalist feeding via the exploitation of subsidies from beyond the aquatic food web.

Here, we build upon an extensive analysis of M-N scaling in 31 streams across the UK [19] by constructing M-TL relationships from size-based δ^{15}N analysis to test these ideas about size structure and energy flow in these energetically open ecosystems. Specifically, we hypothesised that (i) stream food webs show nonlinear M-N and M-δ^{15}N relationships; (ii) the extent of non-linearity in M-δ^{15}N relationships can be predicted from M-N scaling (and *vice versa* [17]) and (iii) non-linearity of M-N and M-δ^{15}N relationships is linked to greater allochthonous resource use by certain consumer size classes.

2. Methods

(a) Data acquisition

We analysed data from Perkins et al. [19] comprising the body mass, numerical abundance and stable isotopic ratios of invertebrates and fish (10^{-3} to 10^{6} mg dry mass) from 31 streams, spanning a broad environmental gradient (Table S1). Quantitative depletion electrofishing and invertebrate benthic sampling was performed over 25 - 100 m reaches at each stream, once in spring between 2005-2012 [19], to derive body mass and abundance per unit area data. Linear dimensions (e.g. head capsule width or body length) of each individual were measured to estimate body mass and individuals were identified to a high taxonomic level (usually species).

Fish fin clips and whole invertebrates (as well as basal and terrestrial resources) were analysed for carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes, selecting a range of different sized individuals for each taxon (see Appendix S1 for detailed methods). Taxa sampled for isotope analysis represented the majority of macroinvertebrate and fish biomass (on average 64 % and 94 %, respectively; Table S2).

(b) Body mass-abundance and body mass-trophic level scaling

M-N relationships were constructed with these data in Perkins et al. [19] using the logarithmic binning method, with individuals from a food web assigned to six ($\log_{10}$) body mass bins, determined based upon the body mass range of each web [22]. Here we use the same binning approach and bin positions to estimate M-TL relationships using the isotope dataset [23]. We constructed M-δ^{15}N relationships [7–9], where δ^{15}N represents the relative trophic level of consumers. We did this rather than converting δ^{15}N to TL using a known baseline [13,24] because allochthonous (e.g. terrestrial detritus) and autochthonous (e.g. biofilm) basal resources in stream food webs can have very different δ^{15}N values [20,21] but effectively have the same trophic level (TL = 1). Therefore changes in nitrogen isotope values of consumers do not necessarily reflect changes in trophic level. Instead, M-δ^{15}N relationships allow us to identify the 'apparent' trophic level of each consumer size class and their primary resource (i.e. allochthonous or autochthonous). We account for potential variation in δ^{15}N baselines between streams using cluster analysis and our statistical modeling approach (described below). δ^{15}N values were biomass-weighted to reflect the proportional biomass of each taxon within each size bin [8,9], by calculating the contribution to total bin biomass for each taxon (Appendix S1).

(c) Statistical analysis

We followed the approach of Chang et al. [13] and grouped communities (streams) together using *K*-means cluster analysis (Fig. S1) because this yields a more robust estimate of the M-δ^{15}N relationship compared to doing this for individual food webs when sample sizes are small (Table S2). This was performed on the basis of similarity in mean δ^{15}N and δ^{13}C of invertebrates and fish (trophic structure), and the taxonomic richness (node diversity) of these groups (six variables × 31 streams matrix). *K*-means clustering was performed in R v 3.4.0 [25] and the optimal number of clusters was determined from the lowest AIC score [12]. Two distinct clusters emerged with 8 (lowland, eutrophic) streams in cluster k_1 and 23 (upland, oligotrophic) streams in cluster k_2 (Fig. S1).

We tested for curvature in M-N and M-δ^{15}N relationships (hypothesis i) for each cluster using a two-step fitting procedure (after [13]). First, linear mixed effects analysis was performed using the lme4 package in R to determine M-N or M-δ^{15}N relationships for each cluster separately, with stream fitted as a random effect on the intercept [13] (Table S3). Second, the within-group residuals of the models were extracted and tested for polynomial relationships with body mass [13]. We fitted cubic, quadratic and linear models and assessed model fit through AIC scores, and performed backwards model selection on these nested models using *F*-tests [26]..

To test the generalized metabolic scaling model (hypothesis ii) we used the polynomial M-N relationship for each cluster to derive the predicted polynomial coefficients of the M-δ^{15}N relationships (after [13]). We adopted this approach rather than *vice versa*, since we expect the M-N dataset to be sampled with less error than the M-TL dataset where not all representatives within a size class were sampled (Table S2). To evaluate the model performance, a prediction on the second- or third-order coefficient was considered statistically consistent with the empirical observation if its 95% confidence interval overlaps with that of the observed coefficients [13].

Finally, to test whether non-linearity of M-N and M-TL relationships is linked to greater allochthonous resource use by certain consumer size classes (hypothesis iii), we inspected the taxonomic composition and allochthonous feeding by taxa within the size classes that overlapped with points of local minima and maxima of M-N and M-δ^{15}N relationships. We further assessed whether allochthonous food resources for invertebrates and salmonids had distinct isotopic signatures compared to their autochthonous counterparts. Traditionally δ^{13}C is used to distinguish between such sources ([24]), but in our data differences between autochthonous and allochthonous sources were weak (Fig. S2), compared to differences in δ^{15}N [20,21]. Therefore, analysis of variance (ANOVA) was used to test for differences in δ^{15}N between allochthonous detritus and biofilm, two ubiquitous resources for primary consumers [16]. In addition, we used detailed data from Tadnoll Brook where both terrestrial and stream invertebrates had been sampled more intensively [19], and compared using ANOVA δ^{15}N values of these resources, as key components of salmonid diet [17–19].

3. Results

Both M-N and M-δ^{15}N were reasonably approximated by linear relationships for both stream clusters (Fig. 1a,c). As hypothesized, however, significant curvature in M-N and M-δ^{15}N residuals were evident for each cluster (Fig. 1b,d) and within individual sites (Fig. S3). AIC scores and backwards model selection revealed that these non-linear patterns were best characterised by 3rd order (cubic) polynomial models (Table 1), thus consistent with our prediction of two distinct entry points for energy from allochthonous resources along the body mass continuum. Indeed, the cubic model provided a significantly better fit than the simpler quadratic or linear model (Table 1 & Table S3), with one marginal exception (Table 1). Estimates of N and δ^{15}N from linear models deviated considerably from those estimated from polynomial relationships for large invertebrate and fish size classes, indicated by large residual values (> 1; Fig. 1b,d & Fig. 2).

As hypothesized, the generalized metabolic scaling model [13] successfully predicted the link between the non-linear M-N and M-δ^{15}N relationships. Model predictions based upon polynomial fit to M-N residuals were statistically consistent with the observed residuals of M-δ^{15}N relationships in three of the four cases (Table 2).

Two clear local maxima were evident in residuals of M-N relationships (Fig. 1b), occurring at approximately zero and five on the log10 body mass scale (c. 1 mg and 100g dry weight, respectively), the same size classes where local minima in M-δ^{15}N residuals occurred (Fig. 1d; Fig. 2a). In line with our expectations, the relatively lower δ^{15}N of these invertebrate and fish size classes (Fig. 2b,c) matched the consistently more depleted δ^{15}N of allochthonous resources than their autochthonous counterparts: detritus had significantly lower δ^{15}N compared to biofilms (k_1 ANOVA: $F_{1,14} = 7.36$, $P = 0.0169$ & k_2 ANOVA: $F_{1,44} = 8.79$, $P = 0.0049$; Fig. 2d) and δ^{15}N of terrestrial prey taxa was significantly lower than comparable stream invertebrates (ANOVA: $F_{1,46} = 41.21$, $P < 0.0001$; Fig. 2e). Thus, non-linearity in M-N and M-δ^{15}N scaling (Fig. 2a) was associated with more depleted δ^{15}N (and relatively higher abundances) of large invertebrate and fish size classes (Fig. 2b,c), matching the lower δ^{15}N values of allochthonous resources (Fig. 2d,e).

4. Discussion

Our results reveal systematic variation in the scaling of trophic level and abundance with body mass among a large-scale stream food web dataset. Whilst as a first approximation N scales with M as predicted by general metabolic theory [5,6], the significant deviation from linear M-N relationships we observed signifies that some body mass classes are clearly over represented in terms of ‘expected’ abundance in an energetically closed system [10–14]. This was evident within individual sites (Fig. S3) and clusters of sites (Fig. 1). The generalised metabolic model [13] generally predicted the non-linearity in M-δ^{15}N relationships (and hence variation in PPMR) based upon the observed variation in M-N scaling. Our study therefore supports the notion that M-N and M-TL relationships are quantitatively linked [13], and demonstrates that a more nuanced approach for characterising food web size structure can provide significantly better estimates of how abundance and trophic level changes with consumer body mass.

The extent of non-linearity in M-N and M-δ^{15}N relationships was similar for both stream clusters despite marked variation in trophic structure, diversity and composition (Fig. S1). This is somewhat surprising, especially as there was considerable background environmental variation between streams (lowland, eutrophic streams in k_1 and upland, oligotrophic streams in k_2, Table S1) and given that pelagic systems have been shown to have stronger secondary structure when they are eutrophic [14]. The consistent non-linear M-N and M-δ^{15}N scaling we observed therefore suggests that running waters may be controlled by different mechanisms from those found in pelagic communities [14].

We suggest that allochthonous inputs (re)shape the size structure of stream food webs and give rise to the consistent non-linear relationships. Plotting residuals, we show that systemic peaks in M-N, and troughs in M-δ^{15}N, residuals occurred in size classes dominated by large generalist invertebrates [16] such as the crustacean *Gammarus pulex* (Fig. 2b), and the salmonid, *Salmo trutta* (Fig. 2c), which feed extensively on terrestrial prey items [18,19]. The relatively lower δ^{15}N (and higher abundance) of these classes, which had more depleted nitrogen isotope ratios than autochthonous counterparts [20,21], signifies that their utilisation of allochthonous resources subsidises their numerical abundance. Omnivory and complex microbial interactions have been proposed to give rise to non-linear M-TL relationships and secondary structure in aquatic food webs [13]; our results suggest that dominance of generalist consumers fuelled by allochthonous inputs high in stream food webs can result in similar patterns, reinforcing the notion that curvature in these relationships can be used as a measure of trophic complexity [13] or indeed the ‘openness’ of food webs. Further research is now required to understand how widespread this phenomenon might be within and across different ecosystems. The analytical framework used here could provide an instructive approach, especially where external subsidies have distinct δ^{15}N values. For instance, the transportation of marine derived nitrogen via anadromous salmon carcasses is widely recognised to subsidise terrestrial food webs. In this case we might expect peaks (rather than troughs) in M-δ^{15}N relationships for size classes of terrestrial invertebrates that utilise this resource [27], but the extent of non-linearity in the M-δ^{15}N relationships should be quantitatively linked to that observed in M-N relationships [28]. Intriguingly, species such as brown trout and *G. pulex* are often seen as keystone species in many UK rivers and their disproportionately influential roles might in fact be driven by their ability to partially decouple from the stream food web.

Here we show that non-linearity in M-N and M-TL relationships are related and linked to allochthonous inputs entering these food webs, and greater energy flow to large consumers so they appear “superabundant” as a result. Assessing non-linearity in body size structure could therefore provide a general, and yet powerful, approach for defining the complexity and dynamics of ecological communities, potentially paving the way for better assessments of energy flow in natural ecosystems.

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