Bending the rules: exploitation of allochthonous resources by a top-predator modifies size-abundance scaling in stream food webs

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The authors declare no conflict of interest.

Running title: Size-abundance scaling in stream food webs

Article Type: Letter

119 words in the abstract; 4,897 words in the main text (excluding abstract, acknowledgements, references, table and figure legends); 55 references; 4 figures.

Author contributions: GW & ID designed the study; F.E, J.I.J, R.B.L, K.L-D, M.S.A.T, and D.M.P contributed data; D.M.P analysed all data & J.I.J helped analyse the isotope data; D.M.P, wrote the first draft of the manuscript and all authors contributed to the final draft.

Data accessibility: the data supporting the results will be archived in a Dryad public repository and the data DOI will be included at the end of the article.

Key words: allometric scaling, body size, brown trout, energetic subsidies, food webs, metabolic theory, stable isotopes, streams.

ABSTRACT

Body mass – abundance (*M*-*N*) allometries provide a key measure of community structure, and deviations from scaling predictions could reveal how cross-ecosystem subsidies alter food webs. For 31 streams across the UK, we tested the hypothesis that linear log-log *M*-*N* scaling is shallower than that predicted by allometric scaling theory when top predators have access to allochthonous prey. These streams all contained a common and widespread top predator (brown trout) that regularly feeds on terrestrial prey ~~,~~ and, as hypothesized, deviations from predicted scaling increased ~~as hypothesised~~ with its dominance of the fish assemblage. Our study identifies a key beneficiary of cross-ecosystem subsidies at the top of stream food webs and elucidates how these inputs can reshape the size-structure of these ‘open’ systems.

INTRODUCTION

The negative relationship between body mass (*M*) and abundance (*N*) is a prominent pattern in ecology (White *et al.* 2007; Trebilco *et al.* 2013). When individual organisms are grouped into body mass classes, irrespective of species identity, the slope (or scaling exponent) of the resultant frequency distributions on double-log axes (hereafter, *M*-*N* relationship) illustrates how energy flows through the food web, especially in strongly size-structured aquatic ecosystems where gape-limited predation predominates (Kerr & Dickie 2001). Since *M*-*N* relationships provide integrated measures of food-web structure and energy flow (Yvon-Durocher *et al.* 2011) they can be used to gauge community-level responses to environmental stressors (Petchey & Belgrano 2010) such as pH (Mulder & Elser 2009; Layer *et al.* 2011), warming in fresh waters (Dossena *et al.* 2012; O'Gorman *et al.* 2012) and overfishing in marine fisheries (Jennings & Blanchard 2004). However, surprisingly little is known about how external (allochthonous) subsidies might modify *M*-*N* relationships (Trebilco *et al.* 2013).

In closed systems, the inefficient transfer of energy through the food web (Lindeman 1942) means that progressively less energy is available higher in the food web and as body-size increases (Brown & Gillooly 2003; Brown *et al.* 2004). For any given system, the slope of the *M*-*N* relationship describes the rate of biomass depletion, as a proxy for energy flux, and depends on the community-wide mean predator–prey mass ratio (PPMR: the mean size of predators relative to prey), and the trophic transfer efficiency (TE: the proportion of prey production converted to predator production) (Kerr & Dickie 2001). The model of Brown and Gillooly (2003) incorporates general allometric scaling principles to predict the scaling of abundance with body mass as: $N = a \times M^{\lambda} \times M^{\log(\mathrm{TE}) / + \log(\mathrm{PPMR})}$. In this model, the intercept, *a*, represents the carrying capacity at a given size class, and λ is the *M-N* scaling coefficient within trophic levels (typically -¾), the reciprocal of the mass-dependence of metabolic rate for many multicellular taxa (Brown *et al.* 2004). Hence, the *M-N* slope (equal to the individual size distribution exponent + 1; Reuman et al. 2009) is predicted to be -¾ + log(TE) / log(PPMR) for a given food web; this has received some strong empirical support (Brown & Gillooly 2003; Jennings & Mackinson 2003; Dinmore & Jennings 2004; Reuman *et al.* 2008; Blanchard *et al.* 2009).

These principles seem to apply to closed systems, but allochthonous subsidies could lead to deviations from predicted *M-N* scaling in more open systems (Trebilco *et al.* 2013, 2016), especially if this additional energy is not uniformly accessible throughout the food web. Thus allochthonous subsidies could release consumers from energetic constraints that otherwise determine the *M-N* relationship within the food web (e.g. Hocking et al. 2013): for instance, if species high in the food web are subsidised, then *M-N* scaling should be shallower (less negative) than expected because the consumer is more abundant than can be accounted for by authochthonous resources alone (Barneche *et al.* 2016). Such deviations from predicted allometries could help reveal how allochthonous inputs can modify food web size structure.

Streams and rivers are open systems and energy flow is supported by allochthonous resources received from the catchment, with terrestrial plant material and invertebrates contributing significantly to secondary production (Cummins *et al.* 1973; Baxter *et al.* 2005). Allochthonous prey are available to a range of aquatic consumers (Townsend & Hildrew 1979; Baxter *et al.* 2005), but are primarily exploited by drift-feeding fish, such as salmonids, towards the top of the food web (Nakano *et al.* 1999b; Nakano & Murakami 2001; Dineen *et al.* 2007). These additional resources are a leading explanation for why the production of one of the world’s most common and economically important freshwater predators (Elliott 1989) – the brown trout (*Salmo trutta* L.) - often exceeds values that could be explained by autochthonous prey production alone (Waters 1988; Huryn 1996).

Here, we use trout streams to investigate the impact of allochthonous resources on community size structure, combining published information (Layer *et al.* 2010; Gilljam *et al.* 2011; Thompson *et al.* 2017) and contemporary data from a large-scale project (Durance *et al.* 2016) to give the largest catalogue of standardised stream food webs described to date, where body mass was determined at the individual level. The dominance of the fish assemblage by trout varied among streams. Therefore, we used these data to test the overall hypothesis that, in communities where the trout is particularly numerically dominant, its consumption of allochthonous prey will be associated with shallower *M-N* slopes and greater deviations from allometric scaling predictions than where it is less dominant (see simulations in Supporting Information Fig. S1). When considering the within-stream food web, we expected the effects of allochthonous prey subsidies to be associated with a high apparent biomass flux to trout (e.g. the ratio of trout biomass to authochthonous prey biomass). Stable isotope signatures provide a time- and space-integrated representation of the trophic ecology of organisms (Post 2002) and can be used to assess variation in the dietary niche of consumers across environmental gradients (Layman *et al.* 2007; O’Gorman *et al.* 2016). We expected that the dietary niche of trout would decrease (they would be more specialized) with increasing trout dominance and reduced competition from other consumer taxa. By comparing empirical scaling patterns with allometric scaling predictions, we can gauge the effect of cross-ecosystem energy subsidies on the size-structure of stream food webs.

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METHODS

Methods overview

We assembled information on the body mass, numerical abundance and stable isotopic ratios of invertebrates and fish (10^{-3} to 10^{6} mg dry mass) from 31 streams across the UK (Fig. 1), ranging from small, upland, acidic headwaters to large, lowland and base-rich chalk streams (Table S1). Sampling of biota at each site was conducted once in spring (April to June) in a single year between 2005 and 2012 (Table S1), over 25 - 100 m reaches. We used these data to test the hypotheses and to characterise macroecological patterns in the size structure of food webs. In addition to these snapshots across 31 streams, we assembled body mass - abundance and dietary analysis data from an intensively sampled, 'focal' system (Tadnoll Brook, site 29). Here, detailed seasonal food web data were available (Gilljam *et al.* 2011), so we could assess temporal variability in the reliance of trout on allochthonous prey subsidies and in *M-N* scaling. These different methods are explained in more detail in the following paragraphs.

Empirical surveys: abundance, body mass and stable isotopes

Quantitative depletion electrofishing was undertaken at each site (Seber & Le Cren 1967), and all captured fish were identified to species, measured (fork length) and weighed. Wet body mass was converted to dry mass using published conversion factors (Table S2). Where abundant, bullheads (*Cottus gobio*) were sampled using a bespoke benthic sampler (Table S1; Lauridsen *et al.* 2012). Stream invertebrates were quantified using 8 to 10 replicate Surber samples or, for slow-flowing streams, Hess samples (Table S1). Preserved samples were sorted under a microscope (×10 magnification) and measurements of individual linear dimensions (e.g. head-capsule width or body length) were made with a calibrated ocular micrometer (×200–400 magnification) and individual dry mass was calculated from published regression equations (Table S2). A total of 32,512 individuals (not including the intensive sampling of Tadnoll Brook) of invertebrates and fish were sampled and measured.

Tissue samples of large and/or dominant fish and aquatic macroinvertebrate prey were collected at each site for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analyses. Fish tissue was obtained from adipose fin clips (McCarthy & Waldron 2000) for a subset of individuals of each species caught during electrofishing surveys and invertebrates were collected using a kick net (350 μm mesh aperture). All samples were frozen (at -80 °C) in individually labelled tubes. After thawing, macroinvertebrates were identified to the lowest taxonomic level possible (typically to species), measured to estimate individual body mass (as described above), and guts removed before further preparation for stable isotope analysis. Both invertebrate- and fish samples were then dried in an oven at 60°C to constant mass, powdered and weighed into replicates (0.2 – 1.3 mg) and analysed using a ThermoFinnigan DeltaPlus (Thermo Finnigan, Bremen, Germany) or a Sercon Integra2 (Sercon Ltd, Crewe, UK) continuous flow isotope ratio mass spectrometer. Depending on individual mass, the number of individuals required for elemental analysis ranged from 1 to 30; where pooling was required, we used similar sized individuals (after Layer et al. 2010). Isotopic composition is expressed in standard delta notation as: $\delta_x = [(R_{sample} / R_{standard}) - 1] * 1000$, where δ_x is ^{13}C or ^{15}N, denoting the per-mille (‰)

deviation of the sample from the recognised isotope standards (Pee Dee Belemnite for δ^{13}C; atmospheric N_2 for δ^{15}N).

Trout dietary analysis

Since stable isotope analyses of terrestrial prey at each site were generally not available, we used gut content of trout available from ten of the study streams (Table S3) and the intensively sampled Tadnoll Brook to establish a baseline contribution of allochthonous (terrestrial) prey to trout diet. For Tadnoll Brook, gut contents analysis was performed on a total of 549 trout (0+ to 2+ in age) over five occasions from May 2005 to March 2006 (Gilljam *et al.* 2011). Small trout (< 70 mm fork length) were killed and frozen for subsequent dissection of the gut, whilst larger individuals were gut-flushed, and the contents immediately preserved in 4% formalin. In the laboratory, ingested prey items were identified, linear dimensions measured and published length-mass regressions used to calculate the dry mass of individual prey items (Gilljam *et al.* 2011). Prey were classified as autochthonous (aquatic, including aerial-adult, taxa) or allochthonous (terrestrial taxa).

Generalised linear mixed-effects models (GLME) were used to quantify the contribution of allochthonous prey to trout diet in Tadnoll Brook including ontogenetic and seasonal variation. We used a quasibinomial error distribution and logit link function with a response variable comprising a vector of allochthonous prey biomass and autochthonous (including the aerial adults of aquatic insects) prey biomass in each individual gut. ‘Month’ nested within ‘Year-class’ was fitted as a random effect, since we were primarily interested in estimating the fixed effects of ontogeny (year-class) and seasonality (month), but not the interaction between the two. The significance of the fixed effects were estimated using likelihood-ratio tests on nested models compared to a χ^2 distribution (Zuur *et al.* 2009).

To assess variation in trout diet across sites we calculated the isotopic niche area of trout using Bayesian standard ellipse areas (SEA$_{B}$~~$_{c}$~~; Jackson et al. 2011) based on the distribution of individuals in δ^{15}N and δ^{13}C bivariate space using the SIBER package in R. We had sufficient data (isotopic signatures for ≥ 5 individuals) to perform this analysis in only 16 of the 31 streams (Table S4). ~~. A small sample size correction (indicated by the subscript ‘c’; Jackson et al., 2011) was used to avoid the bias that arises when samples are small (5-15 individuals per stream).~~ Markov Chain Monte Carlo simulation with 10^4 iterations for each group was used to calculate SEA$_{B}$, (Jackson et al., 2011), which is a robust measure of isotopic dietary niche when samples sizes are small (Jackson et al., 2011; Table S4). Since ~~SEA$_{c}$~~dietary niche width can be influenced by spatial and temporal differences in isotopic baselines ~~(Jackson et al., 2011)~~, we also calculated SEA$_{B}$~~$_{c}$~~ for each macroinvertebrate community (see Table S4 for sample sizes) and tested for correlation with trout SEA$_{B}$~~$_{c}$~~ and trout dominance. To assess the potential effects of ontogenetic shifts in trout diet on isotopic niche area we tested whe~~a~~ther trout SEA$_{B}$~~$_{c}$~~ was related to the average body size of the trout population sampled for isotopic analysis.

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Empirical M-N scaling

M-N relationships were derived after logarithmic binning of individual body mass, *M*. The range of $\log_{10} M$ values for each site was divided into *n* equal size-bins (on a logarithmic scale), and the $\log_{10}$ of the total number (*N*) of all organisms in each size-bin was regressed against the central value of each bin (White *et al.* 2007). The number of size bins ($n = 6$) was selected to optimize the linearity of the relationship and minimise zero counts (after Dossena et al. 2012). However, to assess the sensitivity of *M*-*N* slopes on the number of size bins, we repeated the procedure using four and twelve size bins. The lower boundary of *M* was set at 0.0026 mg for each site to avoid including size classes likely to be affected by under-sampling close to the limits of the mesh apertures of the Surber or Hess samplers used in the field (Fig. S2). We centred $\log_{10} M$ bins by the mean bin mass in the data set ($\log M - \log \bar{M}$), to reduce correlation between slopes and intercepts (Zuur *et al.* 2009).

To investigate the general form of *M*-*N* relationships, we performed linear mixed effects (LME) analysis using the *lmer* function in 'lme4' package in R v 3.4.0 (R Development Core Team 2013). 'Stream' was fitted as a random effect on the slope and intercept, allowing us to quantify the fixed effects of mean slopes and intercepts accounting for spatial variation (Zuur *et al.* 2009). We then assessed the significance of the fixed effect (body mass), using likelihood-ratio tests and refitted the model using restricted maximum likelihood to determine the average among-stream slope ($\bar{b}$) and 95% confidence intervals.

Predator-prey body mass ratios and trivariate food web analysis

Body mass and abundance data for stream invertebrates and fish were used to construct 'trivariate' food webs in order to estimate community predator-prey body mass ratios (PPMR) and assess variation in the inferred biomass flux to trout. Trivariate food webs depict feeding links overlain on double-log scatterplots of the mean species body mass and numerical abundance (Cohen *et al.* 2009). Here, species identity was retained, as opposed to our size-binning approach, where it was ignored.

Where possible, feeding links were observed directly via dissection of consumer gut contents in 17 of the study streams (Layer *et al.* 2010; Gilljam *et al.*

2011; Thompson *et al.* 2017) but were also inferred from a database of 22, 263 interactions collated from 42 freshwater studies (Gray *et al.* 2015). We used this information and the WebBuilder function in R (Gray et al. 2015) to construct food webs for each stream. This approach assumes that if a trophic interaction has been reported between two species in the literature then it also occurs wherever those two species coexist; an assumption supported through the analysis of three streams studied here (Gray *et al.* 2015). To minimise bias among nodes for which the quantity of directly observed information varies, it was necessary to extend this assumption to coarser taxonomic levels in some instances (e.g. family or order) and we used the same resource and consumer generality levels implemented by Gray et al. (2015). We used the Cheddar R package to construct the trivariate food webs and PPMR was then derived as the mean of the log body mass ratios from all predator-prey links in each web (Reuman *et al.* 2009). We filtered links to remove instances where prey body mass exceeded predator body mass through ontogenetic size reversal (e.g. bullhead, *Cottus gobio*, preying on trout) to avoid underestimating PPMRs for species-based interactions (Woodward & Warren 2007), as individual aquatic predators seldom feed on prey larger than themselves (Gilljam *et al.* 2011). We show through additional analyses of Tadnoll Brook data (Appendix S1) that this approach yields a PPMR estimate consistent with that based upon directly observed individual-based feeding events.

Differences in mean species body mass and numerical abundance among pairwise links, and resultant ‘link angles’ (*sensu* Cohen *et al.* 2009), can be used as a proxy for the biomass flux (and by extension energy flow) to focal nodes (e.g. Thompson *et al.* 2017). In size-structured food webs, trivariate link angles are typically negative, and the shallower (less negative) the average angle, the greater the

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inferred biomass flux to the consumer. We used the link angles between trout and their autochthonous prey to assess if the inferred biomass flux to trout (assuming a closed system) was related to trout dominance and *M-N* slopes. The median of trout link angles was used rather than the mean because of kurtosis in the data.

Testing allometric theory

PPMR estimates were used to predict *M-N* slopes for each stream, b_{pred}, from the reformulation of the Brown and Gillooly (2003) model: $b_{pred} = \lambda + \log(\mathrm{TE}) / \log(\mathrm{PPMR})$, where λ is - ¾ and TE (transfer efficiency) is 10% (e.g. Jennings and Mackinson 2003, Reuman et al. 2008). Ordinary least squares (OLS) regression analysis was used to test for the relationship between the predicted *M-N* slope (b_{pred}: predictor variable) for each stream and the observed *M-N* slope (*b:* response variable). We then re-arranged the allometric scaling model to determine the TE required to explain the observed *M-N* slope, *b*, given the empirical PPMR and constant value of λ: TE = PPMR ^ (*b* + 0.75). If the confidence intervals of *b* contained b_{pred} with TE within a reasonable range (10–30%), the allometric prediction was not rejected (Reuman *et al.* 2008). The value of λ is related to the scaling of body mass and metabolism (Brown *et al.* 2004) which can potentially vary with ontogeny, across many animal groups and with the dimensionality of consumer search space (Glazier 2006; Pawar *et al.* 2012; Barneche & Allen 2018). We assessed the sensitivity of allometric scaling predictions to λ by repeating the analysis using additional λ values of 2/3 and 1 (Glazier 2006; Pawar *et al.* 2012; Barneche & Allen 2018).

In deriving predictions for *M-N* scaling, allometric theory assumes demographic and resource steady state (Brown *et al.* 2004). However, the point sampling of food webs conducted (in spring) for each stream provides only a snapshot of community structure, which may deviate from steady-state depending on the local disturbance history. We used the *M*-*N* data available for Tadnoll Brook, where sampling was repeated (every two months) over the course of a year, to assess if snapshots of *M*-*N* scaling held for communities averaged over a full annual cycle.

Trout dominance effects

The proportional abundance of trout within the fish assemblage in each stream was used as an index of its dominance. The rationale for using this index was that calculating the proportional abundance (or biomass) of trout in the whole food web would not necessarily be independent of *M*-*N* slopes in trout-only streams (where a high index value must result in shallow slopes). Because trout were present in all 31 streams, a value of 1 denotes complete numerical dominance of trout within fish assemblages (i.e. food webs with trout as the only fish species present) and, therefore, values < 1 represent the extent of the dilution of trout amongst other fish species.

OLS regression analysis was used to test for the effects of trout dominance on site-level responses: (1) *M*-*N* slopes; (2) deviations from predicted *M*-*N* slopes (observed slope minus predicted slope), (3) median trout link angles and (4) trout isotopic niche area. Furthermore, to investigate the underlying drivers of trout link angles, trout biomass and total invertebrate biomass were $\log_{10}$-transformed and regressed against trout dominance independently. We tested whether polynomial relationships provided a better fit to the data on the basis of *F* tests on nested models (Crawley 2012).

RESULTS

Across all 31 streams, abundance decreased significantly with body mass (LME: χ^2 = 101.38, d.f. = 1, $P < 0.001$; Fig. 2a). The mean *M-N* slope ($\bar{b}$) was -0.79 (95% confidence interval of -0.~~72~~ 85 to -0.~~85~~72, Fig. 2b) and was generally robust to the number of size bins used in the size spectra analysis (Table S5). The mean predator-to-prey mass ratio ($\overline{\mathrm{PPMR}}$), derived from feeding link analysis (Fig. 2c,), was 141:1 (95% confidence interval of 92:1 to 216:1; Fig. 2d). Adding $\overline{\mathrm{PPMR}}$ (and 95% confidence intervals around this estimate) into the allometric scaling model yielded a predicted mean *M-N* slope ($\overline{b_{pred}}$) of -1.2 (range -1.26 to -1.18), considerably more negative than $\bar{b}$~~: $\overline{b_{pred}} = -1.2 = \lambda + \log(0.1) / \log(\overline{\mathrm{PPMR}})$.~~ (-0.79). In fact, a~~A~~chieving $\bar{b}$ using this model would require an unrealistic TE (TE > 50% for λ of 0.66 to 1; Table S6), suggesting that large consumers are more abundant than can be accounted for by autochthonous resources alone.

Variation in *M-N* slopes among streams (Fig. 2b & Fig. S3) was not related to predicted *M-N* slopes (Linear regression: $F_{1,29} = 0.53$, $P = 0.474$) and allometric predictions were rejected in 28 of the 31 streams (Table S7). The number of streams where allometric scaling predictions were rejected was reduced when a λ value of 0.66 was used (Table S6). The observed *M-N* scaling derived from the point sampling of Tadnoll Brook (in spring 2015: y = 2.49 + -0.93x) was indistinguishable to the annual-average *M-N* scaling (averaged across bi-monthly sampling events: y = 2.49 + -0.93x) (Fig. S4), supporting our assumption that the snapshots in the extensive spatial survey were broadly representative of the average annual relationship.

In line with our hypotheses and simulations (Fig. S1), *M-N* slopes became shallower (i.e. less negative) as trout dominance increased (Fig. 3a) and deviations from the predicted *M-N* slopes increased with trout dominance (Fig. 3b): there was a close match between empirical and predicted values when relative trout abundance was low (Fig. 3b). Variation in *M-N* slopes, and deviations from the predicted *M-N* slopes, were best-described by a 4th-order polynomial relationship with trout dominance (Linear regression: $F_{4,26} = 3.97$, $P = 0.012$ and $F_{4,29} = 12.86$, $P < 0.001$, respectively) indicating that trout effects were non-monotonic across the dominance gradient. Total invertebrate biomass declined (Linear regression: $F_{1,29} = 8.9$, $P = 0.006$) whilst trout biomass was statistically invariant (Linear regression: $F_{1,29} = 2.59$, $P = 0.118$) with trout dominance. Consequently, the biomass flux to trout, as inferred through trivariate link angles, increased with trout dominance (Linear regression: $F_{1,29} = 6.55$, $P = 0.016$; Fig. 3c) corroborating the influence of trout on the observed variation in *M-N* slopes. As predicted, trout dietary niche decreased with trout dominance (Linear regression: $F_{1,14}$ = ~~6~~5.~~07~~42, P = 0.~~027~~035; Fig. 3d) signifying more selective feeding by trout in streams where they dominate the fish assemblage numerically. This change in dietary niche occurred even though there was no significant change in the niche width of their macroinvertebrate prey over the trout dominance gradient (Linear regression: $F_{1,14}$ = ~~0~~1.54, P = 0.~~473~~225; Table S4; Fig. S5). There was no significant relationship between the average body size of trout and their dietary niche (Linear regression: $F_{1,14}$ = 0.~~19~~45, P = 0.~~673~~514).

Trout fed on allochthonous prey in 8 of the 10 streams where gut content analysis was performed (Table S3) and the proportion of allochthonous prey items consumed by Tadnoll Brook trout fell in the middle of the range observed across streams. Highly resolved dietary analyses of Tadnoll Brook trout revealed that allochthonous prey contributed substantially to trout diet (Fig. 4) and, unlike *M-N* scaling in Tadnoll Brook, these terrestrial subsides varied significantly over the year (GLME: $\chi^2 = 15.59$, d.f. = 4, $P = 0.004$) ranging from 5% of prey biomass in March (spring) to 89% in October (autumn) (Fig. 4a): note that this change corresponded largely with changes in diet with age within young of the year. On average, the contribution of allochthonous subsidies to trout was c. 50% and did not differ with year class (GLME: $\chi^2 = 1.01$, d.f. = 2, $P = 0.604$; Fig. 4b), corroborating our finding that trout isotopic niche area was invariant with respect to average trout size.

Allochthonous prey were c.10 times larger than autochthonous prey (0.13 mg ± SE 0.10 and 1.22 mg ± SE 0.04, respectively; Fig. 4c-d). However, extending the Tadnoll Brook food web to incorporate allochthonous prey species consumed by trout had little effect on the community-wide PPMR estimate and by extension the observed deviation from the predicted *M-N* slope for this site (Fig 3b). Across sites, trout dominance was a reliable predictor of deviations from expected *M-N* scaling (Fig. 3).

DISCUSSION

We demonstrate that the scaling of body mass and abundance in stream food webs is inconsistent with allometric scaling predictions (assuming a closed system) when a common and globally widespread top predator, brown trout, dominates consumer assemblages. The ability of trout to exploit allochthonous (terrestrial) prey, can increase their populations' carrying capacity, bending the general rules that govern food web size structure within closed ecosystems (Kerr & Dickie 2001; Brown & Gillooly 2003).

Allometric predictions for *M-N* scaling were supported in only 10% of trout streams, and these were streams where the proportional abundance of trout within the fish assemblage was low. In these streams, *M-N* scaling was approximately negatively isometric ($N \sim M^{-1}$), so total biomass per unit area is invariant with body mass, as is often reported for aquatic food webs (Kerr & Dickie 2001). In line with our hypotheses, *M-N* slopes became shallower and diverged increasingly from allometric scaling predictions with increasing trout dominance; in many cases *M-N* slopes were ≥ - ¾, suggesting that larger consumers (i.e. fish) acquired the same or more energy than populations of smaller individuals (i.e. invertebrates) feeding lower in the food web.

Shallow *M-N* relationships, and deviations from energetic equivalence, have also been reported in donor-controlled terrestrial (Reuman *et al.* 2008, 2009) and marine systems (Dinmore & Jennings 2004; Blanchard *et al.* 2009; Barneche *et al.* 2016; Trebilco *et al.* 2016). Running waters are also not closed systems (Cummins *et al.* 1973; Baxter *et al.* 2005) and the disparity between our empirical results and allometric scaling theory is consistent with allochthonous prey subsidizing trout near the top of food webs (Waters 1988; Huryn 1996). Highly resolved dietary analyses from our focal site found that, across year classes and seasons, approximately 50% of prey biomass consumed by trout was terrestrial in origin. Terrestrial prey falling upon the surface of streams are recognised as high-quality (i.e. low C:N ratio) food resources (Mason & MacDonald 1982) that represent a valuable subsidy to trout (Waters 1988; Huryn 1996). In particular, the availability of allochthonous invertebrates is high during summer and autumn (e.g. Fig. 4a) coinciding with a decline in the biomass of autochthonous prey with a terrestrial adult phase (Frost & Varley 1967; Nakano & Murakami 2001; Layer *et al.* 2011). Trout fed on allochthonous prey in at least eight out of the ten streams where gut content analysis was performed, ~~suggesting allochthonous prey subsidies were the driver of the~~

~~shallow M-N slopes and deviations from allometric scaling predictions.~~ confirming ~~highlighting~~ the widespread use of allochthonous prey ~~resources~~ by brown ~~differen~~t ~~t~~rout (e.g. Elliott 1994) ~~populations~~. However, there was considerable ontogenetic and temporal variation in trout diets and more extensive dietary analyses (i.e. larger and more frequent samples) across sites would be required to link quantitatively ~~*the reliance of*~~ *M-N* slopes to reliance on allochthonous prey ~~and M-N slopes, especially given the ontogenetic and temporal variation in the consumption of allochthonous prey by trout~~ (Fig. 4). W~~W~~e predict that if the scale of observation was expanded to encompass the source of allochthonous prey, i.e. the riparian zone, the -system -would no longer be subsidized and allometric scaling theory predictions for the size-structure of the whole system would probably hold.

It is interesting to note that *M-N* slopes and deviation from predicted *M-N* slopes were described by polynomial relationships with trout dominance (Fig 3a & b). This suggests that the link between trout and allochthonous resources is not a simple linear function of trout dominance, although this could be due to the under-representation of streams with intermediate values of trout dominance (Fig. 3). Further research is required to investigate additional variables that might interact with trout dominance and influence the size-structure of stream food webs.

Salmonids, including brown trout, are often the first fish taxon to (re)colonise new water bodies as glaciers retreat (Milner 1987), or as acidity ameliorates (Layer *et al.* 2011) and as very cold streams warm (O'Gorman *et al.* 2012). Our results suggest that the dominance of trout in systems with low autochthonous prey abundance (upland streams of fairly low pH in this study) is aided by their ability to exploit allochthonous prey. Trout biomass was statistically invariant with trout dominance, even though autochthonous invertebrate biomass (i.e. potential prey) decreased over

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Formatted: Font: Not Bold, Not Italic four orders of magnitude across this gradient. Thus the apparent biomass flux to trout (inferred through trivariate food web link angles), increased as the dominance of trout increased. As early colonists, it seems likely that trout often have the monopoly of both autochthonous and allochthonous prey, in the absence of other competitors; however, this ‘first to the table’ advantage diminishes with the arrival of other more specialist fish that feed more exclusively on stream prey, so its extreme generalism and plasticity ultimately may come at a cost as other species encroach on its niche space. This notion is supported by our analysis of trout isotopic niche, which declined with trout dominance, signifying a more selective diet when trout dominate fish assemblages numerically. Flexible niche partitioning has been suggested as an important mechanism for coexistence among stream fishes (Nakano *et al.* 1999a; Dineen *et al.* 2007); our study suggests this enables trout to persist in similar numbers across a broad environmental gradient, which might help understand the widespread distribution of this species (Elliott 1994). Further research would be instructive for understanding how biotic (e.g. competition) vs abiotic (e.g. suitable habitat) factors modulate cross-system flows of energy through trout, and drift-feeding fish in general.

Our study highlights how a globally distributed top predator can fundamentally alter *M*-*N* scaling across stream food webs via an external subsidy that it can exploit, but which is seemingly less available to its potential competitors. Through coupling body mass – abundance relationships and allometric scaling theory, our approach provides a powerful method to identify the wider significance of allochthonous resources, especially in regards to population abundance of focal taxa. This framework could be applied to other settings where large consumers exploit external prey, including other salmonids (Nakano *et al.* 1999b; Nakano & Murakami

2001) marine fishes (Trueman *et al.* 2014; Trebilco *et al.* 2016) and stream invertebrate predators (Townsend & Hildrew 1979). Doing so could provide further insights into the contexts under which allochthonous resources shape the size structure of natural systems.

ACKNOWLEDGEMENTS

This study is a contribution from Natural Environment Research Council funded DURESS consortium project: 'Diversity in Upland Rivers for Ecosystem Service Sustainability' (Grant reference: NE/J015288/1) which supported D.M.P, K.L-D, J.G, GW and ID. A British Ecological Society Research Grant awarded to D.M.P made additional sample processing possible. A contribution was also made from the Natural Environmental Research Council funded studies at Tadnoll Brook (Grant reference: NE/C511905/1), which supported F.K.E., R.B.L., A.G.H. and J.I.J. We thank the John Spedan Lewis Foundation for supporting M.S.A.T. We also thank Julia Reiss, Samraat Pawar and Eoin O'Gorman for constructive discussions on earlier drafts.

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FIGURE LEGENDS

Figure 1 Location of the 31 UK streams in this study. Numbering refers to individual streams (the corresponding stream names are given in Supporting Information Table S1) and the shading of the points reflects the proportional abundance of brown trout within fish assemblages at each stream location.

Figure 2 Macroecological patterns in the food web size structure of 31 streams**.** (a) Abundance declines with increasing body mass and the average among-stream relationship (regression line) reveals a mean that is shallower than the benchmark ($N \sim M^{-1}$) typically observed in aquatic systems. (b) The distribution of body mass – abundance (*M*-*N*) slopes varies considerably among streams. (c) The trivariate relationship between mean taxon body mass, population abundance and feeding links, aggregated across streams (square and diamond symbols correspond to invertebrate and fish taxa, respectively). The fish node highlighted in black is brown trout: an intermediate sized yet superabundant fish species. (d) Predator-prey mass ratios, calculated from food webs constructed for each stream, reveal that on average predators are c.141 times larger than their prey (represented by dashed line).

Figure 3 Effects of trout dominance on body mass –abundance (*M*-*N*) scaling, energy flow and trout dietary niche. *M*-*N* slopes become shallower (a) and diverge increasing from allometric scaling predictions (b) as trout dominance (the proportional abundance of trout within fish assemblages) increases. The crossed data point in (b) is the deviation from predicted *M*-*N* slopes for Tadnoll Brook when the consumption of terrestrial prey was included (see Fig. 4), which is indistinguishable from when these resources were excluded (adjacent data point). (c) The inferred biomass flux to trout, represented by trout trivariate link angles, increases with trout dominance. (d) Trout dietary niche area (SEA$_{B}$~~$_{c}$~~) decreases with increasing trout dominance signifying a narrowing in diet in streams dominated by trout (triangle symbols denoted streams where gut contents analysis of trout was performed and allochthonous prey were found; Table S3). Our focal site, Tadnoll Brook, where highly resolved stomach analysis was performed is highlighted. The shading of data points (a-d) indicates the number of taxa other than trout present in fish assemblages.

Figure 4 Contribution of allochthonous prey to trout diet in Tadnoll Brook (2005 to 2006). The proportional representation (by biomass) of allochthonous (terrestrial) prey is higher in summer/autumn (a) and is statistically invariant with year class (b). Panels c-e show that older trout consume proportionally more allochthonous prey items (grey bars) than younger trout, but allochthonous prey are generally larger than autochthonous prey (black bars) for younger trout, and overall the reliance on terrestrial subsidies is approximately equal (b).

SUPPORTING INFORMATION

Table S1 Stream environmental variables and details of sampling methodology.

Table S2 Regression parameters for calculation of individual body masses from measured body dimensions or wet mass.

Table S3 Contribution of allochthonous prey to trout diet across streams.

Table S4 Sample sizes for estimating dietary niche width of trout and invertebrates.

Table S5 Assessing the sensitivity of *M*-*N* scaling to the number of size bins used in size spectra analyses.

Table S6 Assessing the sensitivity of *M*-*N* scaling predictions to the value of λ used in the allometric scaling model.

Table S7 Summary output from the size-structure analysis.

Figure S1 Simulations illustrating the potential effects of allochthonous resources on body mass – abundance (*M*-*N*) scaling.

Figure S2 Determining the lower bounds of body mass - abundance relationships.

Figure S3 Body mass - abundance scaling relationships constructed for each stream.

Figure S4 Annual-average body mass - abundance scaling for Tadnoll Brook.

Figure S5 Isotopic dietary niche of trout and primary consumers across streams

Appendix S1 Predator-prey body mass ratio estimates for Tadnoll Brook.