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Reply

Two Processes Regulating Trophic Energy Flow in Pelagic and Terrestrial Ecosystems: Trophic Efficiency and Body Size–Dependent Biomass Production

(A Reply to Giacomini)

Richard McGarvey,[1,*] **Natalie Dowling,**[2] **and Joel E. Cohen**[3]

1. Aquatic Sciences, South Australian Research and Development Institute, PO Box 120, Henley Beach, South Australia 5022, Australia; 2. Commonwealth Scientific and Industrial Research Organisation Oceans and Atmosphere, GPO Box 1538, Hobart, Tasmania 7001, Australia; 3. Laboratory of Populations, Rockefeller and Columbia Universities, New York, New York 10065; Earth Institute and Department of Statistics, Columbia University, New York, New York 10025; and Department of Statistics, University of Chicago, Chicago, Illinois 60637

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abstract: We proposed two hypotheses to explain why food chains are longer in pelagic than terrestrial ecosystems: greater trophic efficiency of pelagic animal taxa at lower trophic levels and a higher pelagic biomass production rate at lower trophic levels because of smaller pelagic body masses. Giacomini favored the former, invoking in support the energetic equivalence hypothesis. We reply that the energetic equivalence hypothesis does not describe populations at differing trophic levels and so does not refute a significant role for body-mass dependence in explaining faster trophic transfer in pelagic ecosystems. Metabolic scaling as body mass to the exponent 1/4, widely accepted, remains important for trophic dynamic models. We suggest a likelihood method to compare the two hypotheses on the basis of models of whole-ecosystem energetics.

Keywords: allometric relationships, animal body size, energetic equivalence hypothesis, food chain length, biomass production rate, trophic efficiency.

Giacomini (2018) asks which of two hypotheses we proposed (McGarvey et al. 2016) is dominant in permitting greater trophic energy flow along pelagic than terrestrial animal food chains. The two hypotheses we found evidence for were (1) trophic efficiency as more efficient conversion of consumed prey to biomass by pelagic metabolic classes (invertebrates and fish) at lower animal trophic levels and (2) the higher biomass production rate, and so also higher trophic transfer rate, of pelagic animals at lower trophic levels owing to their orders-of-magnitude smaller body masses M. Giacomini (2018) argues against the transfer rate hypothesis.

Giacomini's (2018) principal challenge to the transfer rate hypothesis rests on the energetic equivalence hypothesis (EEH). He argues that with each successive trophic level, total biomass (B, as density per unit of area) increases with the same exponent (1/4 in $B \propto M^{1/4}$) that production per unit biomass P/B decreases ($P/B \propto M^{-1/4}$), canceling overall dependence of transfer rate on organism body mass M. Here we first state those aspects of his comment that we endorse. Then we explain why Giacomini's (2018) argument does not negate the need to consider body size and specifically why the EEH does not apply in this case.

We agree with Giacomini (2018) that trophic efficiency is an important factor in the rates of energy flow from primary producers to higher trophic levels in both pelagic and terrestrial food chains. The proportions of trophic energy consumed that are converted into biomass at each trophic level directly affect overall trophic flow. We estimated a rough difference of about 100-fold between pelagic and terrestrial ecosystems from trophic efficiency proportions accumulated across the first four animal trophic levels. Endotherms found at low trophic levels in terrestrial ecosystems are highly inefficient, burning most of what they consume for maintenance. Invertebrates, which dominate as lower animals in pelagic ecosystems, are about 10 times more efficient, allocating about 10 times more of what they consume into producing biomass. Thus, as Giacomini (2018) emphasizes, differences in trophic efficiency between pelagic and terrestrial food webs help to explain the observed longer pelagic food chains.

We also agree with Giacomini (2018) that steady state or time-averaged rates are relevant in quantifying trophic flows

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[*] Corresponding author; e-mail: richard.mcgarvey@sa.gov.au.

ORCIDs: McGarvey, http://orcid.org/0000-0001-8698-8774; Cohen, http://orcid.org/0000-0002-9746-6725.

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for purposes of assessing how many trophic levels a given rate of primary production can support. Giacomini's (2018) equation (1) is analogous to our equation (2) (McGarvey et al. 2016) in modeling biomass production at each animal trophic level, while his equation (2) (Giacomini 2018) is analogous to our equation (6) (McGarvey et al. 2016), describing the effect on trophic energy flow to a fifth trophic level due to only ecosystem differences in the transfer efficiency between trophic levels.

We also agree that to compute overall trophic flow to higher trophic levels, the free energy proportions transmitted along each step of trophic energy transfer should be multiplied. This simple mathematical function (our eq. [6], his eq. [2]) follows because along each trophic pathway, the trophic energy transmitted upward at each link is directly proportional to the energy received as input, with some losses, at each stage. This process is like survival of a cohort over successive life-history stages, in that only losses are possible at each stage.

Giacomini's (2018) preference for the trophic efficiency hypothesis over the transfer rate hypothesis rests on the assumption that $B \propto M^{1/4}$ across trophic levels. $B \propto M^{1/4}$ follows from the lower metabolic rate (Damuth 1981, 1987) of larger organisms, which require less food to sustain their metabolisms per unit of biomass. We respond with four observations: (1) The literature often fails to support the EEH relationship between individual body mass and population biomass $B \propto M^{1/4}$. (2) Even in theory, the EEH applies only to species or populations sharing a common food resource, and in all the studies that have detected it, evidence supported the EEH only among species at the same trophic level, but its use here in quantifying trophic energy flow requires applying it to differing trophic levels. (3) In studies where EEH has been confirmed, the variation in population biomass given body mass about the fitted log-log regression has been orders of magnitude wide, which is too imprecise for application in the current problem. (4) The EEH implications for how biomass should vary among trophic levels is not observed in real food webs. In conclusion, we shall propose a more rigorous likelihood method to test these two hypotheses statistically, using data now becoming available for whole-ecosystem food webs.

Observation 1

The EEH has been tested many times in the literature, including many metadata studies, and these have often failed to find support for the EEH. Giacomini (2018) acknowledges that a simple $B \propto M^{1/4}$ relationship of biomass to body size is far from universal. Numerous tests of $B \propto M^{1/4}$ rejected a 1/4 exponent, which is equivalent to an exponent of $-3/4$ in the number density versus mass allometric relationship (Cotgreave and Harvey 1992; Currie and Fritz 1993; Marquet et al. 1995; Blackburn and Gaston 1997; Russo et al. 2003; Glazier 2005; McGill 2008; Hayward et al. 2009; Isaac et al. 2011; Ehnes et al. 2014). Moreover, Isaac et al. (2011) found no systematic correlation of exponents of population energy use with density, as the mass-canceling model simplification of Giacomini (2018) supposes. Mohr (1940), Peters and Raelson (1984), and others have found an exponent of 0 (or −1 in density by numbers vs. body mass), implying no dependence of biomass on body size. Overall, a wide range of EEH exponents has been observed. Further, there is no evidence for the EEH along trophic pathways within webs (Reuman et al. 2009).

Observation 2

As Giacomini (2018) acknowledges, the EEH, as postulated, applies to populations sharing a common energy source. Proponents of the EEH state that it applies separately at different trophic levels. Damuth (1987, p. 196) states that these EEH regressions would ideally be done with only those mammals that have identical diets. Brown and Gillooly (2003, p. 1468) indicate that energy invariance theoretically applies when all species use a common source of energy. The EEH applies to populations with the same food supply because, in addition to the metabolism dependence on body mass that underlies the EEH, prey food supply and how much of it is consumed must also strongly affect biomass density. The lower metabolism rates of larger organisms will yield $B \propto M^{1/4}$ in real populations only if all other factors, other than metabolism, that affect biomass are the same. That this uniformity of food supply would rarely occur explains the huge variability observed about this relationship (reviewed below) and the frequent inability (shown above) to confirm $B \propto M^{1/4}$.

Most of the published animal studies (which were in the minority) that did find evidence for $B \propto M^{1/4}$ did so for species within a given trophic level. Such studies include Damuth (1981; terrestrial mammalian herbivores), Damuth (1987; mammals and invertebrates, tropical and nontropical, multiple categories), Brown et al. (2004, their fig. 6; terrestrial mammals, herbivores, and carnivores), and Nee et al. (1991; British and Swedish birds). Peters and Wassenberg (1983, their table 1) found agreement with the EEH (with an exponent near 0.75) for mammals and vertebrate poikilotherms but not for birds and less reliably for invertebrates, and more importantly, they observed quite different biomass versus body mass relationships for different taxonomic categories. All these studies presented results separately by trophic level and by taxonomic grouping.

Observation 3

The minority of studies that reproduced Damuth's exponent of $-3/4$ show large variation about the fitted line from at least two (Brown et al. 2004, their fig. 6) up to five (Nee et al. 1991) orders of magnitude in population density at given body mass. Both Peters and Raelson (1984, their fig. 1) and Damuth's

(1981) comparable figure show that a range in density of almost three orders of magnitude may be expected at given body size. Unlike organism-specific metabolic and energetic relationships, which show consistent and relatively tight adherence to allometric or exponential relationships (e.g., Brown et al. 2004, their fig. 2), the much wider variation in observed population biomass versus body mass and the wide range of exponents estimated for B versus M support the hypothesis that population biomass varies in response to numerous and variable influences. As Peters and Raelson (1984) indicate, the EEH does not provide an effective tool for predicting the abundance of individual populations. Two to five orders of magnitude of error is too wide to serve reliably in the role suggested by Giacomini (2018).

Observation 4

The prediction of the EEH for biomass versus trophic level is not observed in most real food webs. Given that predators are usually larger in mass than their prey, $B \propto M^{1/4}$ applied across successive trophic levels implies that the standing biomass of predators will be greater than their prey. But rather than a slow increase, pelagic ecosystems show a generally slow decrease (Kerr and Dickie 2001) of biomass density with increasing trophic level. Terrestrial mammalian carnivores show a large decrease in biomass density of typically two orders of magnitude relative to that of their herbivorous mammalian prey (Mohr 1947; Peters 1983, his fig. 10.1; Carbone and Gittleman 2002; Brown et al. 2004, their fig. 6). Slow or large decreases in biomass with increasing trophic level (the food web pyramid) are not consistent with the increase predicted by $B \propto M^{1/4}$.

Testing Hypotheses of Whole-Ecosystem Energetics

A formal statistical test based on measurements from whole ecosystems could establish which hypothesis has stronger support. Data such as those for Tuesday Lake (Cohen et al. 2003)—which included body size, trophic level, and population density for each trophic species in a food web—could support statistical comparisons of the trophic efficiency and transfer rate hypotheses, based on a food web energetics model. If a food web energetics model were fitted by maximum likelihood to relatively complete food web data, like those from Tuesday Lake, likelihood ratios could be used to compare the trophic efficiency and transfer rate hypotheses. This full energetics model should, to the extent feasible, account for major trophic processes, including body size–dependent and metabolic class–dependent processes. To quantify the relative improvement in fit to data from including the trophic efficiency hypothesis, the complete fitted food web model should be compared with a simplified version of that full model obtained by setting transfer efficiency equal to a constant (the mean). This simplified submodel will fit the data less well by not assigning each trophic species a trophic efficiency on the basis of its metabolic type. Likewise, the transfer rate hypothesis should be tested by fitting a submodel that has the dependence of production rate (P/B) on body size removed. Each of the two submodels would give a difference of its maximized log likelihood from the maximized log likelihood of the full model. This difference is the log of the likelihood ratio, which quantifies the reduction in fit to whole-ecosystem data of omitting each hypothesis. The hypothesis that shows the greater reduction in fit when its corresponding model feature is turned off is more strongly supported. Likelihood ratios (or Akaike information criteria, when models compared are not nested submodels) could serve to rank multiple proposed ecosystem energetics models. Analogous Bayes factors could be computed and used for hypothesis testing under a Bayesian framework.

Two steps to achieving this more formal and general hypothesis test are (1) to construct a full energetics food web model, which includes at least the features given in our model and Giacomini's (2018), and (2) to fit this model (and each of the two submodels) to Tuesday Lake and other whole-ecosystem data using maximum likelihood or Bayesian integration. Assuming a trophic energetics model by assigning a priori biomasses based on $B \propto M^{1/4}$ and ignoring the metabolic class–dependent coefficients in the various quarter-power scaling relationships would oversimplify the model and make it a much less accurate one.

We support the need for a full trophic model accounting for now well-established energetics relationships that describe individual organisms—such as metabolism, consumption, and production—as functions of body mass, metabolic class, and temperature (as advocated in Brown and Gillooly 2003; see the model of Yodzis and Innes 1992). This will yield predictions more accurate than the simplified model that Giacomini (2018) proposes.

Giacomini (2018) makes a good point that population biomass cannot be assumed to be independent of body mass, as we did in implicitly assuming that all body mass dependence is due to differences in production rate. We accept his criticism that our trophic energetics model is incomplete. A better description of biomass dependence is needed, as Giacomini (2018) suggests.

A more complete trophic energetics model might be able to predict biomass as a function of trophic level, as an outcome of multiple factors acting at each trophic level. In particular, the differing trends of biomass as a function of trophic level in pelagic versus terrestrial environments or, more generally, under different energetic constraints might be deduced from such a model. That would represent progress.

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Literature Cited

Blackburn, T. M., and K. J. Gaston. 1997. A critical assessment of the form of the interspecific relationship between abundance and body size in animals. Journal of Animal Ecology 66:233–249.

Brown, J. H., and J. F. Gillooly. 2003. Ecological food webs: high-quality data facilitate theoretical unification. Proceedings of the National Academy of Sciences of the USA 100:1467–1468.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. Science 295:2273–2276.

Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. Proceedings of the National Academy of Sciences of the USA 100: 1781–1786.

Cotgreave, P., and P. H. Harvey. 1992. Relationships between body size, abundance and phylogeny in bird communities. Functional Ecology 6:248–256.

Currie, D. J., and J. T. Fritz. 1993. Global patterns of animal abundance and species energy use. Oikos 67:56–68.

Damuth, J. 1981. Population density and body size in mammals. Nature 290:699–700.

———. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. Biological Journal of the Linnean Society 31:193–246.

Ehnes, R. B., M. M. Pollierer, G. Erdmann, B. Klarner, B. Eitzinger, C. Digel, D. Ott, M. Maraun, S. Scheu, and U. Brose. 2014. Lack of energetic equivalence in forest soil invertebrates. Ecology 95:527–537.

Giacomini, H. C. 2018. Body size and the energetics of food chain length (a comment on McGarvey et al., "Longer food chains in pelagic ecosystems: trophic energetics of animal body size and metabolic efficiency"). American Naturalist 191:359–363.

Glazier, D. S. 2005. Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. Biological Reviews 80:611–662.

Hayward, A., M. Khalid, and J. Kolasa. 2009. Population energy use scales positively with body size in natural aquatic microcosms. Global Ecology and Biogeography 18:553–562.

Isaac, N. J. B., D. Storch, and C. Carbone. 2011. Taxonomic variation in size-density relationships challenges the notion of energy equivalence. Biology Letters 7:615–618.

Kerr, S. R., and L. M. Dickie. 2001. The biomass spectrum. Columbia University Press, New York.

Marquet, P. A., S. A. Navarrete, and J. C. Castilla. 1995. Body size, population density, and the energetic equivalence rule. Journal of Animal Ecology 64:325–332.

McGarvey, R., N. Dowling, and J. E. Cohen. 2016. Longer food chains in pelagic ecosystems: trophic energetics of animal body size and metabolic efficiency. American Naturalist 188:76–86.

McGill, B. J. 2008. Exploring predictions of abundance from body mass using hierarchical comparative approaches. American Naturalist 172: 88–101.

Mohr, C. O. 1940. Comparative populations of game, fur and other mammals. American Midland Naturalist 24:581–584.

———. 1947. Table of equivalent populations of North American populations of small mammals. American Midland Naturalist 37:223–249.

Nee, S., A. F. Read, J. J. D. Greenwood, and P. H. Harvey. 1991. The relationship between abundance and body size in British birds. Nature 351:312–313.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge.

Peters, R. H., and J. V. Raelson. 1984. Relations between individual size and mammalian population density. American Naturalist 124:498–517.

Peters, R. H., and K. Wassenberg. 1983. The effect of body size on animal abundance. Oecologia (Berlin) 60:89–96.

Reuman, D. C., C. Mulder, C. Banašek-Richter, M. F. C. Blandenier, A. M. Breure, H. Den Hollander, J. M. Kneitel, D. Raffaelli, G. Woodward, and J. E. Cohen. 2009. Allometry of body size and abundance in 166 food webs. Advances in Ecological Research 41:1–44.

Russo, S. E., S. K. Robinson, and J. Terborgh. 2003. Size-abundance relationships in an Amazonian bird community: implications for the energetic equivalence rule. American Naturalist 161:267–283.

Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. American Naturalist 139:1151–1175.

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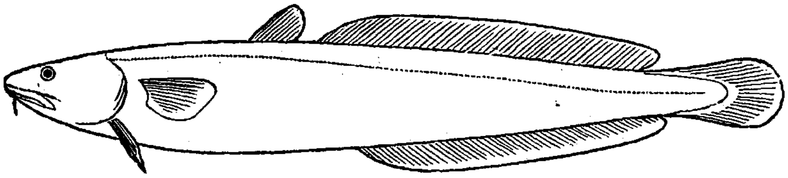

"The *Lota compressa* probably visits the salt water, as it is taken in ascending the Connecticut or its tributaries in the spring of the year, in company with fish from the salt water ascending to spawn." From "The Compressed Burbot or Eel-Pout" by William Wood (*The American Naturalist*, 1869, 3:17–21).