Ecological community description using the food web, species abundance, and body size

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Measuring the numerical abundance and average body size of individuals of each species in an ecological community's food web reveals new patterns and illuminates old ones. This approach is illustrated using data from the pelagic community of a small lake: Tuesday Lake, Michigan, United States. Body mass varies almost 12 orders of magnitude. Numerical abundance varies almost 10 orders of magnitude. Biomass abundance (average body mass times numerical abundance) varies only 5 orders of magnitude. A new food web graph, which plots species and trophic links in the plane spanned by body mass and numerical abundance, illustrates the nearly inverse relationship between body mass and numerical abundance, as well as the pattern of energy flow in the community. Species with small average body mass occur low in the food web of Tuesday Lake and are numerically abundant. Larger-bodied species occur higher in the food web and are numerically rarer. Average body size explains more of the variation in numerical abundance than does trophic height. The trivariate description of an ecological community by using the food web, average body sizes, and numerical abundance includes many well studied bivariate and univariate relationships based on subsets of these three variables. We are not aware of any single community for which all of these relationships have been analyzed simultaneously. Our approach demonstrates the connectedness of ecological patterns traditionally treated as independent. Moreover, knowing the food web gives new insight into the disputed form of the allometric relationship between body mass and abundance.

allometry | biomass spectrum | body mass | energetics | pelagic zone

Ecological communities are not purely randomly constituted (1). For example, predators are often larger and rarer than their prey (2, 3), if parasites and herbivorous insects on trees are ignored. To illuminate the structure of an ecological community in finer detail and more comprehensively, we combine its food web, body sizes, and species abundances. A food web (4) is a directed graph or flow diagram. Each node is labeled by a species' name and each arrow (link or directed edge) from one node to another indicates a flow of nutrients from a resource (prey) species to a consumer (predator) species. How trophic relations among the species are related to patterns such as rank-abundance relations, body size distributions, abundance-body size allometry, and biomass spectra has been little studied. Augmenting a traditional food web with information on the average body mass M and numerical abundance N of each species makes it possible to study trivariate patterns that involve the food web, M and N; bivariate patterns that involve any pair of these; and univariate patterns that involve any one (Table 1). The approach is illustrated and tested using data on Tuesday Lake from 1984 (Fig. 1).

This brief report focuses on the trivariate relationships (last line of Table 1). Jonsson *et al.* (5) report trivariate, bivariate, and univariate patterns, evaluate a major experimental manipulation (6, 7) of Tuesday Lake in 1985, review related work, and give complete data for 1984 and 1986.

In the next section, we develop some energetic theory to guide description. The following section presents definitions and the data on Tuesday Lake from 1984. Then the trivariate patterns derived from these data are described. Some major findings regarding bivariate and univariate patterns are summarized. The concluding section reviews the insights gained by our trivariate approach.

Table 1. Ecological community descriptions that combine the food web, body size, and abundance

Food web	Body size	Abundance	Distributions and relationships
Yes			Food web statistics, distributions of trophic links and chain lengths, trophic generality and vulnerability
	Yes		Distribution and rank of body size
		Yes	Distribution and rank of numerical and biomass abundance
Yes	Yes		Predator–prey body size allometry, body size vs. trophic height, trophic generality and vulnerability
	Yes	Yes	Abundance–body size allometry and spectrum, species diversity in relation to body size and abundance
Yes		Yes	Predator–prey abundance allometry, abundance vs. trophic height, generality, and vulnerability
Yes	Yes	Yes	All trophic variables in relation to body size and abundance

Theory

Body Mass Rank and the Distributions of Body Mass, Abundance, and Trophic Height. Cohen (8) hypothesized that the average body mass M of a species in a community could be related to its rank in M, where the biggest species has rank $i = 1$, the next biggest has rank $i = 2$, and so on. If M is allometrically related to rank i in M by $\log M_i = a - b \log i$, where a and b are known constants, then the distribution of M in a community can be predicted from the number of species S. If N is allometrically related to M by $\log N_i = c - d \log M_i$ (9–11), then $\log N_i = (c - da) + (db)\log i$, i.e., N is allometrically related to M-rank i. Then biomass abundance $B = MN$ is also allometrically related to M-rank

Abbreviations: B, biomass abundance; H, trophic height; M, body mass; N, numerical abundance; R, metabolic rate.

See commentary on page 1467.

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