Food Webs, Body Size, and Species Abundance in Ecological Community Description

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I. SUMMARY

This chapter demonstrates that methods to describe ecological communities can be better understood, and can reveal new patterns, by labeling each species that appears in a community's food web with the numerical abundance and average body size of individuals of that species. We illustrate our new approach, and relate it to previous approaches, by analyzing data from the pelagic community of a small lake, Tuesday Lake, in Michigan. Although many of the relationships we describe have been well studied individually, we are not aware of any single community for which all of these relationships have been analyzed simultaneously. An overview of some of the results of the present study, with further theoretical extensions, has been published elsewhere (Cohen *et al.*, 2003).

Our new approach yields four major results. Though many patterns in the structure of an ecological community have been traditionally treated as independent, they are in fact connected. In at least one real ecosystem, many of these patterns are relatively robust after a major perturbation. Some of these patterns may be predictably consistent from one community to another. Locally, however, some community characteristics need not necessarily coincide with previously reported patterns for guilds or larger geographical scales.

We describe our major findings under these headings: trivariate relationships (that is, relationships combining the food web, body size, and species abundance); bivariate relationships; univariate relationships; and the effects of food web perturbation.

A. Trivariate Relationships

Species with small 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 less numerically abundant. Body size explains more of the variation in numerical abundance than does trophic height. Body mass varies almost 12 orders of magnitude and numerical abundance varies by almost 10 orders of magnitude, but biomass abundance (the product of body mass times numerical abundance) varies by far less, about

5 orders of magnitude. The nearly inverse relationship between body mass and numerical abundance, and the relative constancy of biomass, are illustrated by a new food web graph (Fig. 3), which shows the food web in the plane with axes corresponding to body mass and numerical abundance.

B. Bivariate Relationships

The pelagic community of Tuesday Lake shows a pyramid of numbers but not a pyramid of biomass. The biomass of species increases very slowly with increasing body size, by only 2 orders of magnitude as body mass increases by 12 orders of magnitude. The biomass-body size spectrum is roughly flat, as in other studies at larger spatial scales. Prey body mass is positively correlated to predator body mass. Prey abundance and predator abundance are positively correlated for numerical abundance but not for biomass abundance. Body size and trophic height are positively correlated. Body size and numerical abundance are negatively correlated.

The slope of the linear regression of log numerical abundance as a function of log body size in Tuesday Lake is not significantly different from −3/4 across all species but is significantly greater than −1 at the 5% significance level. This −3/4 slope is similar to that found in studies at larger, regional scales, but different from that sometimes observed at local scales. The slope within the phytoplankton and zooplankton (each group considered separately) is much less steep than −3/4, which is in agreement with an earlier observation that the slope tends to be more negative as the range of body masses of the organisms included in a study increases. A novel combination of the food web with data on body size and numerical abundance, together with an argument based on energetic mechanisms, refines and tightens the relationship between numerical abundance and body size.

The regression of log body mass as a linear function of log numerical abundance across all species has a slope not significantly different from −1, but significantly less than −3/4. The estimated slope is significantly different from the reciprocal of the estimated slope of log numerical abundance as a function of log body mass. Thus, if log body mass is viewed as an independent variable and log numerical abundance is viewed as a dependent variable, the slope of the linear relationship could be −3/4 but could not be −1 at the 5% significance level. Conversely, if log numerical abundance is viewed as an independent variable and log body mass as a dependent variable, the slope of the linear relationship could be −1 but could not be −4/3 (which is the reciprocal of −3/4) at the 5% significance level. While a linear relationship is a good approximation in both cases, Cohen and Carpenter (in press) showed that only the model with log body mass as the independent variable meets the assumptions of linear regression analysis for these data.

C. Univariate Relationships

The food web of Tuesday Lake has a pyramidal trophic structure. The number of trophic links between species in nearby trophic levels is higher than would be expected if trophic links were distributed randomly among the species. Food chains are shorter than would be expected if links were distributed randomly. Species low in the food web tend to have more predators and fewer prey than species high in the web. The distribution of body size is right-log skewed. The rank-numerical abundance relationship is approximately broken-stick within phytoplankton and zooplankton while the rank-biomass abundance relationship is approximately log-normal across all species. The slope of the right tail of the body mass distribution is much less steep than has been suggested for regional scales and not log-uniform as found at local scales for restricted taxonomic groups.

D. Effect of Food Web Perturbation

The data analyzed here were collected in 1984 and 1986. In 1985, three species of planktivorous fishes were removed and one species of piscivorous fish was introduced. The data reveal some differences between 1984 and 1986 in the community's species composition and food web. Most other community characteristics seem insensitive to this major manipulation.

Different fields of ecology have focused on different subsets of the bivariate relationships illustrated here. Integration of the relationships as suggested in this chapter could bring these fields closer. The new descriptive data structure (food web plus numerical abundance and body size of each species) can promote the integration of food web studies with, for example, population biology and biogeochemistry.

II. INTRODUCTION

An *ecological community* is a set of organisms, within a more or less defined boundary, that processes energy and materials. There are many different notions of an ecological community and many approaches to describing and understanding community structure and function (Paine, 1980; May, 1989). Here we integrate some of these approaches.

A *food web* lists the kinds of organisms in a community and describes which kinds of organisms eat which other organisms. The food web approach (e.g. Cohen, 1989; Lawton, 1989) tries to understand the community through a detailed study of the trophic interactions among the species within the community. Sometimes, it focuses on the population dynamic effects of species on each other (e.g. Pimm, 1982).

The pattern catalog approach tries to understand communities through patterns in the distribution of species characteristics in different communities and under different circumstances. For example, rank-abundance relations, body size distributions, abundance-body size allometry, and biomass spectra are all examples of community characteristics that emerge from species characteristics. How the trophic relations among the species affect these patterns and vice versa has largely been ignored.

In this chapter, we integrate these different approaches. We augment a traditional food web with information on two species characteristics, body size, and abundance, without presenting or testing a particular theory of community organization. Instead, we advocate the idea that many previously studied relationships and distributions can be better understood by connecting the food web with species abundance and body size.

This approach will be illustrated and tested by data on the pelagic community of Tuesday Lake, a small lake in Michigan, in 1984 and 1986. In 1985, the lake was subjected to a major perturbation (see Section IV.A): the three incumbent fish species were removed and a new fish species was introduced. The manipulation significantly affected a number of parameters (e.g., primary production, chlorophyll concentration, zooplankton biomass; Carpenter and Kitchell, 1988). Until the present analysis, the effects of the manipulation on community characteristics, such as the distributions of body size and abundance or the relationship between them, were unknown. We analyze how the perturbation affected several community-level patterns.

Cohen (1991) suggested that body size and abundance of the species in a community could be related to a ranking of the body size of the species by simple allometric or exponential functions. If this relation is confirmed by empirical data, it raises the possibility of predicting a large number of community patterns using only a few input variables. For example, the distributions of body size and abundance in a community could then be approximated from a single variable, the number of species, and a small number of coefficients. Using the data of Tuesday Lake, we demonstrate the existence of simple relationships that could be tested in other communities. If these relationships are subsequently found to hold in general, they could then be used to predict the structure of additional ecological communities.

Many studies of relationships among species characteristics have focused on geographical scales other than that of the local ecosystem. For example, the body size-abundance relationship is often studied using data from a large set of communities (e.g. Damuth, 1981). Such studies are hampered by a lack of information on the ecological constraints operating on species within a particular local community because the studies average data over several communities. Other studies have focused on particular taxa or guilds within a community. This focus reduces the number of species, range of body sizes, or range of trophic levels included when compared to a whole community.

The present study combines data on virtually all the nonmicrobial pelagic species of Tuesday Lake. The organisms, from phytoplankton to fish, span approximately 12 orders of magnitude in body mass and up to 10 orders of magnitude in numerical abundance. We compare some community characteristics in the local community of Tuesday Lake with previously reported patterns for specific taxa or larger geographic scales.

This chapter is not primarily about Tuesday Lake. Others have described Tuesday Lake in much more detail (e.g. Carpenter and Kitchell, 1988, 1993a). Rather, we use Tuesday Lake to illustrate how many previously unrelated descriptions of communities can be brought together (Table 1). The main theme of the chapter is that when data on body size and abundance are associated with each species in a food web, then the community-wide distributions of body size, abundance, and feeding relations become

Table 1 Descriptions of an ecological community that combine information on the food web, body size, and abundance (number of individuals or biomass)

Distributions and relationships analyzed	Food web	Body size	Abundance	Section discussed
Food web statistics The distribution of trophic links The distribution of chain lengths Trophic generality and vulnerability	✓			V.C.1
The distribution of body size Rank-body size		✓		V.C.2
The distribution of numerical and biomass abundance Rank-abundance			✓	V.C.3
Predator-prey body size allometry Body size vs. trophic height Trophic generality and vulnerability vs. body size	✓	✓		V.B.1
Abundance-body size allometry Abundance-body size spectrum Diversity, body size and abundance		✓	✓	V.B.2
Predator-prey abundance allometry Abundance vs. trophic height Ecological pyramids Trophic generality and vulnerability vs. abundance	✓		✓	V.B.3
Trophic position, body size and abundance	✓	✓	✓	V.A

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connected, orderly, and intelligible in new ways. Since the relationship among these three attributes affects many other aspects of an ecological community, awareness of these connections contributes to a better overall understanding of community structure and function.

This chapter is organized as follows. Section II.A presents crucial definitions. Section III presents some theoretical predictions for the relationships among the food web and the distributions of body size and abundance. Section IV describes Tuesday Lake, how the data on the food web, body size, and abundance of the species were collected, and the manipulation in 1985. Section V presents and analyzes the data on Tuesday Lake, including the data from 1984 and 1986 but emphasizing the data of 1984. Section VI compares the data of 1984 and 1986 to see the effects on community patterns of the 1985 perturbation. Section VII discusses limitations in the data and the effect of variability. Section VIII summarizes the new insights gained by an integrated trivariate approach.

A. Definitions

Body mass is the average body mass (kg) of an individual of a species. All individuals are included, not only individuals considered adults. *Numerical abundance* means the concentration of individuals (individuals/m^3). *Biomass abundance* is the total amount of biomass per volume (kg/m^3) of a species. Both numerical abundance and biomass abundance depend crucially on the reference volume of water in which average concentration is estimated. Section IV.B describes how these characteristics were measured for different species in Tuesday Lake. Throughout this chapter, the reference volume of water for both estimates of abundance is the epilimnion, which is roughly equivalent to the photic zone, in Tuesday Lake.

A *basal species* is a species recorded as eating no other species. Usually a basal species is autotrophic, but the absence of evidence that a given species consumes any other species may be due to incomplete observation (for example, of endosymbionts). A *top species* is a species recorded as having no other species as predators or consumers. The absence of evidence that a given species is eaten by any other species may be due to incomplete observation (for example, of parasites inside individuals of the species). An *intermediate species* is a species that consumes at least one other species and is consumed by at least one other species in the web. An *isolated species* is a species that has no other species reported as predators or prey.

A *food chain* ($A, B, C, \ldots, X, Y, Z$) is an ordered sequence of at least two species $A, B, C, \ldots, X, Y, Z$, where A is a basal species and Z is a top species such that each species (except the last, here denoted Z) is eaten by the next species in the list. The *trophic position* of a species in a food chain is 1+ the number of species preceding it in the ordered list of species in the chain. For example, in the food chain ($A, B, C, \ldots, X, Y, Z$), species A has trophic position 1, species B has trophic position 2, species C has trophic position 3, and the trophic position of Z is equal to the number of species in the list. *Trophic height* is the average trophic position of a species in all food chains of which it is a part. Probably because of large size (due to coloniality and/or spines), a few phytoplankton species were not eaten by the herbivores in Tuesday Lake. These isolated species are left out of some analyses. A *food web* is a collection of cross-linked food chains and sometimes includes, in addition, isolated species. *Connectance* is calculated as $2 \times L/(S^2 - S)$, where L is the number of noncannibalistic links and S is the number of connected (that is, nonisolated) species in a food web. The *unlumped web* of Tuesday Lake refers to the food web describing the trophic interactions among the species listed in Appendices 1A and 2A. In the *trophic-species webs*, species with identical sets of prey and predators are aggregated into *trophic species. Linkage density* (d) is the number of links per species (i.e., $d = L/S$). The *trophic vulnerability* (V) and the *trophic generality* (G) of a species are the number of predators and the number of prey, respectively, that species has (Schoener, 1989).

For each consumer species j that eats a nonempty set of resource species R_j, we define the available resource biomass B_j and the available resource productivity Π_j as the sum of the available resource biomass or the available resource productivity, respectively, of each of the resource species eaten by consumer j, that is,

$$B_j = \sum_{i \in R_j} \frac{BA_i}{V_i} = \sum_{i \in R_j} \frac{NA_i \times BM_i}{V_i} \tag{1}$$

and

$$\Pi_j = \sum_{i \in R_j} \frac{P_i}{V_i} = \sum_{i \in R_j} \frac{NA_i \times BM_i^{3/4}}{V_i}. \tag{2}$$

The available biomass abundance of a resource species i is calculated as the total biomass abundance BA_i of species i divided by the trophic vulnerability V_i, that is, number of consumer species that the resource species i has (including, of course, consumer species j). The available productivity of a resource species i is calculated as the total productivity P_i of species i divided by V_i. The total productivity (kg $\times$ $\text{year}^{-1}/\text{m}^3$) of a resource species is calculated as the numerical abundance (NA_i) of the resource species times the productivity of an individual, approximated by $BM_i^{3/4}$. The available resource biomass B_j and the available resource productivity Π_j both require trivariate information regarding the food web (the resource species of each consumer, and the consumer species of each of those resource species), body masses, and numerical abundance. In these measures, dividing by the number of consumer species V_i reflects the crude assumption, made for want of better information, that each consumer of a given resource species gets an equal share of the resource's biomass or productivity. This crude assumption could be refined if quantitative data were available on the flows of energy along each trophic link. A random variable, its frequency distribution, or a set of numbers is said to be right-skewed if its third central moment is positive, left-skewed if its third central moment is negative, and symmetric if its third central moment is zero. (The third central moment is the sum of the cubes of the deviations of each number from the mean.) A random variable is said to be right-log skewed if the logarithm of the random variable is right-skewed.

Departure from normality of a distribution is assessed using measures of kurtosis and symmetry (D'Agostino and Pearson, 1973). Characteristics of the observed food web are compared with predictions of a null-model. An appropriate null-model for the trophic-species web is the cascade model (see Section III.A.1). The cascade model's predictions for the mean and expected maximal food chain length, number of basal, intermediate, and top species, and number of links among these species categories were calculated using the formulas in Cohen *et al.* (1986). All logarithms in this chapter are calculated with base 10.

III. THEORY: INTEGRATING THE FOOD WEB AND THE DISTRIBUTIONS OF BODY SIZE AND ABUNDANCE

This section outlines quantitative models and qualitative theoretical arguments to guide the analysis of the data in subsequent sections.

A basic question of community ecology is whether ''the populations at a site consist of all those that happened to arrive there, or of only a special subset, those with properties allowing their coexistence'' (Elton, 1933). Many ecologists probably agree that communities are not purely randomly constituted, apart from stochastic processes (e.g., those related to colonization and extinction, MacArthur and Wilson, 1967). For example, it is well known that large species usually are less numerically abundant and are positioned higher in a food web than small species.

Our goal is to shed additional light on the structure of an ecological community by looking in detail at the univariate, bivariate, and trivariate patterns that involve the food web and the distributions of body size and abundance in a community (Table 1). This theoretical section reviews some simple models of these patterns. The models use only a few input variables. The models will be tested in section V using the data described in Section IV.

A. Predicting Community Patterns

1. The Cascade Model

The cascade model of food web structure tries to predict multiple food web properties from the simplest assumptions possible. A leisurely nontechnical summary of the cascade model and its motivation is given by Cohen (1989). Cohen *et al.* (1990) give a detailed theoretical and empirical exposition. Carpenter and Kitchell (1993a) also use the term "cascade model." Their model describes the dynamics of multiple populations interacting through food webs following major perturbations. As an example of a "trophic cascade" in Carpenter's sense, an increase in the abundance of the top trophic level leads to alternating decrease and increase in the abundance of trophic levels below. In this chapter *cascade* refers only to the following strictly static model of food web structure in the sense of Cohen *et al.* (1990).

Let S denote the number of trophic species in a community. Suppose the trophic species can be ordered from 1 to S (although this ordering is not a priori visible to an observer), and suppose that the ordering specifies a pecking order for feeding, so that any species j in this hierarchy or cascade can feed on any species i only if $i < j$ (which doesn't necessarily mean that j does feed on i, only that j can feed on i). Thus, species j cannot feed on any species with a number k if $k \geq j$. Second, the cascade model assumes that each species eats any species below it according to this numbering with probability d/S, independently of all else in the web. Thus, the probability that species j does not eat species $i < j$ is $1 - d/S$. These assumptions—that the species are ordered and that the probability of feeding is proportional to $1/S$, and that different feeding links are present or absent independently of one another—are all there is to the cascade model.

The cascade model has one parameter, d. To compare the model with an individual food web, the parameter d may be estimated from the observed number of species S and the number of links L as $d = 2L/(S - 1)$. To compare the model with the properties of a collection of food webs, assuming that the parameter d is the same in all of them, the parameter d may be estimated from the total number of species and the total number of links in all webs combined or from the set of pairs (S, L) for each web. All predictions derive solely from the number of species and the number of links. No other parameters are free.

The cascade model makes a surprising variety of predictions about food webs (Cohen, 1989; Cohen *et al.*, 1990, 1991) such as the number of basal, intermediate, and top species; the number of food chains; the mean food chain length; the maximum food chain length; and the numbers of basal-intermediate, basal-top, intermediate-intermediate, and intermediate-top links. These predictions are computed and compared with observations, shown later in Table 3. The cascade model also predicts, for example, how the maximum chain length should change as the area from which a food web is sampled increases (Cohen and Newman, 1991), how the relative frequency of intervality among food webs should change with increasing numbers of trophic species (Cohen and Palka, 1990), and how various proportions of links and species should change with increasing numbers of trophic species. The cascade model predicts that the mean vulnerability of a species should increase linearly as trophic position goes from high (top predators) to low (primary producers) within a community, providing theoretical support for a prediction of Menge and Sutherland (1976). Predictions of the cascade model are not always confirmed. Several elaborations of the cascade model have been proposed (e.g., Cohen, 1990, 1991; Cohen *et al.*, 1993; Solow and Beet, 1998; Williams and Martinez, 2000).

The diversity of predictions from the cascade model and some of its elaborations is important, not because the predictions are always correct (they are not), but because so many different aspects of food webs derive from a few simple assumptions, and are therefore not independent of one another. The important message of the cascade model and of sufficiently analyzed related food web models is that superficially diverse aspects of food webs vary in coordinated ways as a result of simple underlying mechanisms.

It is worthwhile to present and discuss the cascade model even if it sometimes makes predictions that are inconsistent with observations. Caswell (1988) argued persuasively that "models are to theoretical problems as experiments are to empirical problems." In particular, the failure of a model to reproduce some empirical observations or patterns may be a source of insight, stimulating further thought and eventually further theoretical understanding. The cascade model does not claim that real food webs are constructed as described by the cascade model, only that such a simple set of assumptions is capable of integrating in a single perspective a large variety of observable aspects of single food webs and collections of food webs (Caswell, 1988). Kenny and Loehle (1991) make a similar claim for their "random web" model, a model that is biologically even more rudimentary than the cascade model. The cascade model made possible new ways of thinking about the properties of ensembles of food webs, demonstrated the conceptual linkage among these properties, and continues to provide a baseline against which variations in individual food webs can usefully be evaluated, as in this chapter. The deviations between at least some of the food web statistics computed for the Tuesday Lake data and the predictions of the simple cascade model are interesting since they pose the challenge of identifying the biological mechanisms at work that are ignored by the model.

2. Body Mass Rank and the Distributions of Body Mass, Abundance, and Trophic Height

Cohen (1991) hypothesized that, on average, the body masses of the species in a community could be related to their rank in body size. Two simple alternatives are that body mass (*BM*) is related to body size rank *i* starting from the largest species either allometrically

$$BM_i = \alpha i^{\beta}$$

or exponentially

$$BM_i = \alpha\beta^{i}$$

where α and β are two constants (with unknown values for the moment). If either equation is approximately true and if α and β are known, then the distribution of body size in a community can be predicted from the number of species. This relationship could be used to predict the numerical abundance (*NA*) of the species. Assuming that

$$BM_i = \alpha i^{\beta}$$

and that numerical abundance is allometrically related to body mass by

$$NA_i = \gamma(BM_i)^{\delta}$$

as has often been found (Damuth, 1981; Peters and Wassenberg, 1983; Blackburn and Gaston, 1999), then

$$NA_i = \gamma(BM_i)^{\delta} = \gamma(\alpha i^{\beta})^{\delta} = \gamma\alpha^{\delta} i^{\beta\delta} = \varepsilon i^{\varphi}$$

That is, numerical abundance is allometrically related to body size rank *i*. Alternatively, if

$$BM_i = \alpha\,\beta^{i}$$

and

$$NA_i = \gamma(BM_i)^{\delta}$$

then

$$NA_i = \gamma(BM_i)^{\delta} = \gamma(\alpha\beta^{i})^{\delta} = \gamma\,\alpha^{\delta}\beta^{\delta i} = \varepsilon\omega^{i}$$

meaning that numerical abundance is exponentially related to body size rank *i*.

If body mass and numerical abundance are allometrically related to body mass rank, then so is biomass abundance, with an exponent that is determined by the exponents for body mass and numerical abundance. Finally, if larger species on average are found higher up in a food web than small species, the trophic height of species could potentially be related to the rank (or log rank) in body mass. In principle, if the simple models presented here can be validated, the body mass, abundance, and trophic height of the species could be predicted using only the number of species and a few input parameters (the regression coefficients). To be practically useful, however, the regression coefficients of the relationships must be known. As with the cascade model, these simple relationships could provide a baseline against which observations in real communities can be compared, for example, to identify groups of species within a community that deviate from a predicted relationship or communities that behave differently (e.g., because they have been disturbed). If these relationships held in Tuesday Lake prior to the 1985 intervention, as we shall see, then we may hypothesize that body size, abundance, and trophic height in the perturbed community of Tuesday Lake in 1986 will be less predicted by the rank in body size than in 1984.

By treating the number of species as the independent variable to predict the distributions of body size, abundance, and trophic height, we do not mean to suggest that body size is independent of for example trophic organization, or that the number of species in a community is prior to and independent of the distributions of body size, abundance, and trophic organization. We are for the moment interested in analyzing how far this extremely simple approach, free of biological mechanisms, can go.

The relationships described above aim to predict only the expected value (body mass, abundance, or trophic height) of a species and neglect all variation in the dependent variable. Since more and more confounding factors may be included as the rank in body mass is used to predict successively the body mass, numerical abundance, and finally biomass abundance, we predict (not surprisingly) that the distribution of body mass will be best predicted by the rank in body mass, followed by numerical abundance, and then by biomass abundance.

B. The Distribution of Body Sizes

The body size of an organism matters ecologically and evolutionarily, and so does the ensemble of body sizes in an ecological community. Many ecological traits (e.g., generation time, clutch size, ingestion rate, and population density) are significantly correlated with body size (Peters, 1983; Calder, 1984). Harvey and Purvis (1999) point out that some recent mathematical models (Charnov, 1993; Kozlowski and Weiner, 1997) suggest that an organism's body size is an adaptation to its life history characteristics rather than the other way around. Notwithstanding these models, it seems likely that body size and other life history characteristics are jointly determined. Large differences in body size (and thus also in demographic rates) between the species in a community can lead to dynamics on several time scales (e.g., Kerfoot and DeAngelis, 1989; Muratori and Rinaldi, 1992). The ratio of the turnover rates of the primary producers and consumers, as a function of their relative sizes, may affect the stability of the system. Conversely, constraints imposed by requirements for stability could affect the distribution of body size. Body size has also been shown to affect extinction risks of carnivores and primates (Purvis *et al.*, 2000). On an ecological time scale, the feeding interactions of animals are probably constrained by body size, but on an evolutionary time scale, feeding interactions may affect body size.

In community ecology, much attention has been devoted to the shape of body size distributions and how they are affected by sampling biases and spatial scale (see e.g., Brown and Nicoletto, 1991; Blackburn and Gaston, 1994). Histograms of the number of species in logarithmic body size classes are typically right skewed. In global assemblages or for single taxa such as birds, mammals, or fish, the suggested slope of the right tail on log-log scales is $-2/3$ for body mass (May, 1986) but varies considerably among many studies (Loder *et al.*, 1997). Few studies of the body size distribution in entire community assemblages are available. Holling (1992) proposed that a few key biotic and abiotic processes in ecosystems may be responsible for generating spatial and temporal structure, and that the discontinuity in space or time of these processes leads to clumps and gaps in the distribution of body sizes in communities. If Holling's hypothesis holds generally, the distribution of body sizes in Tuesday Lake should show clumps and gaps (Havlicek and Carpenter, 2001).

By definition, the species in a guild or taxonomic group all have similar (but not identical) niches or trophic positions. Assuming that one body size (or body size class) is best adapted to the particular way of living of the guild, this size class can be expected to have more species than other size classes. In a community with many different guilds, the trophic positions and body sizes could be expected to vary much more than within taxonomic groups. Here, other mechanisms such as speciation, immigration, and extinction rates relative to body size may be important in shaping the body size distribution. Thus, for a community, a right-log skewed, perhaps even log-hyperbolic, distribution may be more likely. (The hyperbolic distribution has log-linear tails. The body size distribution is log-hyperbolic if the logarithm of body size is hyperbolically distributed.)

The shape of the size distribution of species may change with the geographical range of the investigation (Blackburn and Gaston, 1994). If the body size and the geographical range of species are positively correlated (as suggested by Brown and Maurer, 1987 and supported by empirical data), then as the geographical range of a study increases, relatively more small-bodied than large-bodied species will be added to the distribution, because a large fraction of the large species will be found at small scales but only a limited fraction of the small species. Local communities would then be expected to have a shallower slope of the right tail of the relationship between body size and number of species than regional assemblages. The slope of regional relations should in turn be shallower than a global relationship. Based on these arguments, we hypothesize that the slope of the right tail of the body size distribution in Tuesday Lake will be less negative than $-2/3$.

C. Rank-Abundance and Food Web Geometry

The rank-abundance relationship has been studied principally in competitive communities, guilds (functional groups), or taxonomical groups, with a focus on organisms thought to compete for some limiting resource(s) in an ecological community. Early work (MacArthur, 1957, 1960; Cohen, 1966) discussed the effect of various resource partitioning mechanisms among organisms on the distribution of abundance.

Here we display the rank-abundance relationship across all the recorded species in Tuesday Lake, including primary producers, primary and secondary consumers, and several guilds and taxonomical groups. Our hypothesis is that the rank-abundance relationship across all species is affected by the shape of the food web. Just as past analyses of the rank-abundance relationship have been carried out to shed light on the resource partitioning mechanism in a particular group of species, the rank-abundance relationship of a community-wide food web reflects and can shed light on the geometric shape of the food web and energy flows through the community.

Assuming (as we will demonstrate later) that body size generally increases and numerical abundance generally decreases from the bottom (primary producers) to the top (top predators) of a food web, a pyramidal web (wide base and narrow top) implies a large number of small and numerically abundant species and fewer large and relatively rare species. In comparison with a pyramidal web, a more rectangular food web would have relatively fewer small and numerically abundant species. If numerical abundance decreases exponentially with every step in a food chain, so that the numerical abundance of a predator on average is a constant small fraction of the numerical abundance of its prey, then the numerical abundances of the species in a simple food chain would follow a geometric series (i.e., a linear decrease in log numerical abundance as a function of abundance rank). Extending this line of reasoning to a whole food web suggests that the shape of the rank-log abundance relationship may reflect the shape of the food web. For example, a pyramidal shape of the food web (plus an exponential decrease in numerical abundance with trophic height) could imply a concave rank-log abundance relationship. We predict that the geometric shape of the food web of Tuesday Lake will be reflected in the rank-log abundance relationship, and conversely that the geometric shape of the food web of Tuesday Lake can be anticipated from the shape of the rank-log abundance relationship.

D. Linking the Food Web to the Relationship Between Body Size and Numerical Abundance

Studies of the relationship between body size and numerical abundance in animals have, with a few exceptions (Marquet *et al.*, 1990; Cyr *et al.*, 1997a), concentrated on "regional" or "global" collections of species (Mohr, 1940; Damuth, 1981; Peters and Wassenberg, 1983; Peters and Raelson, 1984; Brown and Maurer, 1987) or particular taxa or functional groups within local communities (e.g., Morse *et al.*, 1988). Most studies showed that log numerical abundance decreases linearly as log body size increases. The slopes of log numerical abundance as a function of log body size relationship have been more negative at regional than at local scales (Blackburn and Gaston, 1997; Enquist *et al.*, 1998). More restricted taxonomic groups have a less negative slope than broader aggregations (Peters and Wassenberg, 1983; Cyr *et al.*, 1997b). Some investigations, however, claimed that the relationship is polygonal (Brown and Maurer, 1987; Morse *et al.*, 1988) or otherwise nonlinear (Silva and Downing, 1995). Blackburn and Gaston (1997) reviewed different forms of the abundance-body size relationship.

Blackburn and Gaston (1999) also reviewed mechanisms proposed to explain the abundance-body size relationship, including the "energetic constraint mechanism." This hypothesis asserts that the slope of the relationship is a function of the basal metabolic rate of organisms and the amount of energy used by populations. Other explanations for the observed relationship between numerical abundance and body size include sampling from the distributions of abundance and body size (the "concatenation mechanism," Blackburn *et al.*, 1993) or body-size–related extinction risks (the "differential extinction mechanism"). Blackburn and Gaston (1999) concluded that no single mechanism adequately explains the published abundance-body size relationships.

Since metabolic rate scales as BM^{α} with α claimed to be $\frac{3}{4}$ (Kleiber, 1932; Hemmingsen, 1960) or $\frac{2}{3}$ (Heusner, 1982; Dodds *et al.*, 2001), metabolic efficiency should have a significant effect on numerical abundance at least over large ranges in body size, that is, across all species in a community.

Across restricted ranges in body size, other mechanisms such as interspecific interactions could overshadow the effect of metabolic efficiency. Here, the potential effect of the trophic structure of a community on species' resource uses and abundance-body size relationships will be explored.

Assume that the numerical abundance of a consumer population *i* is approximately proportional to the total amount of resources available to the consumer population per unit time (i.e., resource supply rate, ρ_i) divided by the resource use per consumer individual per unit time, and that the resource use per individual per unit time is proportional to the metabolic rate of individuals (MR). The metabolic rate of individuals is allometrically related to body mass as

$$MR \propto BM^{\alpha}$$

where $\alpha < 1$ and α is often claimed to approximate $\frac{3}{4}$ (e.g., Hemmingsen, 1960). Symbolically,

$$NA_i \propto \rho_i / MR_i \propto \rho_i \times BM_i^{-\alpha}$$

(Carbone and Gittleman, 2002). If each consumer species on average has the same amount of net resources available to it (i.e., $\rho_i = c$, a totally arbitrary assumption which we shall challenge in the next paragraph), then

$$NA \propto BM^{-\alpha}$$

so that the slope $-\alpha$ of log numerical abundance as a function of log body mass for consumer species is the negative of the allometric exponent α relating body mass to metabolic rate (see Enquist *et al.*, 1998).

However, the resource supply rate is probably not the same for all consumer species in a community. The structure of the food web, the positions of species within it, and the efficiency with which species extract resources will affect species' resource supply rates. Consequently, the resource supply rate could increase or decrease with increasing consumer body size or trophic height of a consumer species. The larger a species is, the more available prey species there are. On the other hand, prey species are in general shared by other consumers, so the larger a species is, the higher in the food web it may feed, with possibly less energy available due to ecological efficiencies. Unless larger species are more omnivorous than smaller species, the amount of resources available to a larger species could decrease.

If consumer numerical abundance can be divided by an estimate of the resource supply rate to each consumer, theory suggests (Carbone and Gittleman, 2002) that the slope should be closer to $\frac{-3}{4}$ since

$$NA_i \propto \rho_i \times BM_i^{-\alpha} \Longleftrightarrow NA_i / \rho_i \propto BM_i^{-\alpha}$$

We predict that if the slope of log numerical abundance as a function of log body mass in Tuesday Lake deviates from $\frac{-3}{4}$ on log-log scales, then the slope of numerical abundance of consumers divided by an estimate of the resource productivity available to each consumer, versus the body mass of the consumer, will be closer to $\frac{-3}{4}$ on log-log scales. To infer more specifically if resources available to a consumer change with body size or trophic position would require species-specific data on energy flow. In the absence of such data, we analyze these relationships indirectly.

If the resource supply rate is the same for all consumer species and if consumers' metabolic rates are allometrically related to body mass by an exponent of $\frac{3}{4}$, then each consumer species should be found along a line with slope $\frac{-3}{4}$ in the log body mass-log numerical abundance plane, starting from the resource species (i.e., the point [log BM_{prey}, log NA_{prey}]). Deviations from this prediction for individual pairs of consumer and resource species could indicate either that the prey species has more than one predator species, or that the predator species has more than one prey species. The former means that the productivity of a particular prey must be shared with several predator species, leading to lower than expected numerical abundance of the consumer species (thus making the slope steeper than $\frac{-3}{4}$). The second case means that a particular consumer species has more than one prey species to provide resources, leading to a higher than expected numerical abundance of the consumer species (thus making the slope less steep than $\frac{-3}{4}$). Based on these arguments, we predict that in Tuesday Lake, for individual pairs of consumer and resource species, there will be: (1) a positive relationship between the slope of log numerical abundance as a function of log body mass on the one hand, and the consumer's trophic generality on the other; and (2) a negative relationship between the slope of log numerical abundance as a function of log body mass on the one hand, and the prey species' trophic vulnerabilities on the other.

E. Trophic Pyramids and the Relationship Between Consumer and Resource Abundance Across Trophic Levels

In many ecosystems, predators are larger and less numerically abundant than their prey, if parasites are ignored (Darwin and Wallace, 1858). Elton (1927, p. 69) noted that, "... animals at the base of a food chain are relatively abundant, while those at the end are relatively few in numbers ...." A bar plot of numerical abundance in different trophic levels in a community (later illustrated by Fig. 8A, B) often produces the well-known "pyramid of numbers," a monotonic decrease in numerical abundance with increasing trophic level. Alternatively, a bar plot of biomass in different trophic levels may give a "pyramid of biomass" (see Odum, 1983; Wetzel, 1983) or an inverted pyramid (illustrated later by our Fig. 8C, D).

The standing crop of biomass may increase or decrease with increasing trophic height, depending on the balance between the loss of energy along each link in a food chain and the residence time of the energy in the individuals at successive trophic levels or nodes in a food chain. The reciprocal of the residence time is defined as the *turnover rate*. Energy is lost at every trophic transfer in a food chain, but if the resource has a much faster turnover rate than the consumer, a loss in the transfer of energy to the consumer may be compensated for by a longer residence time of energy in the consumer, allowing the standing crop of a consumer to equal or exceed that of its resource (e.g., Harvey, 1950).

Elton (1927) referred to a pyramid of numbers only. Many textbooks use ‘‘trophic’’ or ‘‘ecological’’ pyramids more broadly to refer to the pattern of numerical or biomass abundance, or productivity in successive trophic levels. The very concept of trophic levels has been criticized as an excessive simplification of the trophic structure of communities (e.g., Cousins, 1987). In estimates of the numerical or biomass abundance at different trophic levels in ecosystems, ‘‘trophic levels’’ often are specified as primary producers, primary consumers (herbivores), and secondary consumers (carnivores). Studies with estimates of autotrophic and heterotrophic biomass in freshwater plankton and marine ecosystems are reviewed by Del Giorgio and Gasol (1995) and Gasol *et al.* (1997), respectively. Baird and Ulanowicz (1989) reported energy flows of the Chesapeake Bay food web and of an aggregated food chain with eight trophic levels.

The change in abundance across trophic levels depends in part on the relationship between consumer and resource abundance at the species level. Here we consider a consumer c that feeds on a single resource r. The ratio between consumer and resource numerical abundance in a community may be modeled by using the same energetic assumptions as above (Section III.D) to relate the numerical abundance NA_c of consumer c to its body mass BM_c and to the productivity ρ_r of resource r. We make the assumption, plausible for this situation, that the abundance of the resource depends on its own productivity while the abundance of the consumer depends on the food it can sustainably extract from its resource, which is proportional to the resource productivity. If

$$NA_c \propto \rho_r \times BM_c^{-\alpha} \iff NA_c/\rho_r \propto BM_c^{-\alpha}$$

and

$$\rho_r \propto BM_r^{\alpha} \times NA_r$$

then

$$\frac{NA_c}{NA_r} \propto \left(\frac{BM_r}{BM_c}\right)^{\alpha} \text{ and } \frac{BA_c}{BA_r} \propto \left(\frac{BM_c}{BM_r}\right)^{1-\alpha}$$

The ratio of consumer to resource numerical abundance is predicted to be proportional to the consumer-resource body size ratio raised to the power α. The ratio of consumer to resource biomass abundance is predicted to be proportional to the consumer-resource body size ratio raised to the power $1\text{-}\alpha$. Consequently, the larger in size a predator is relative to its prey, the smaller the ratio between predator and prey numerical abundance is predicted to be, but the larger the ratio between predator and prey biomass abundance is predicted to be. This illustrates the well-known fact that even though predator biomass abundance often tends to be smaller than prey biomass (at least in terrestrial systems), a biomass abundance ratio greater than unity is possible if the difference in turnover rates of the predator and prey is large enough. Because of the allometric relation between turnover rates and body size, a biomass abundance ratio can exceed unity if the consumer is much larger than the resource. We predict that in Tuesday Lake: (1) the ratio of predator to prey numerical abundance will be positively correlated to the prey-predator body mass ratio and (2) the ratio of predator to prey biomass abundance will be positively correlated to the predator-prey body mass ratio. We also predict that the slope of the former relationship should be greater than that of the latter.

These predictions, which apply directly only to a pair of species consisting of one prey and one predator or one resource and one consumer, also have implications for food chains and food webs. If the predator-prey body mass ratio remains constant within a food chain, the ratio of predator to prey biomass abundance is predicted not to change systematically along the food chain. In a food web of cross-linked food chains, the picture could be more complicated. By analogy with the predictions for food chains, we predict that the changes in biomass and numerical abundance across trophic levels in Tuesday Lake will correlate with the average ratios in body mass between the species on different trophic levels. A small change in average trophic level body mass is predicted to be associated with a small change in trophic level numerical abundance between two trophic levels and with a decrease in trophic level biomass abundance. A large change in average trophic level body mass is predicted to be associated with a large change in numerical abundance between two trophic levels and possibly with an increase in biomass abundance from one trophic level to the next.

IV. DATA: TUESDAY LAKE

Tuesday Lake is a small, mildly acidic lake in Michigan (location 89°32′ W, 46°13′ N). Carpenter and Kitchell (1993b) described the physical and chemical characteristics of the lake. Summers are cool and winters are cold. Ice covers the lake from November to late April, on average, and oxygen is depleted during most winters. The fish populations are unexploited and the drainage basin undeveloped. For most of the lake's history, the fish fauna has been typical of winterkill lakes of the region. In 1984, the fish were three (mainly zooplanktivorous) species: 90% northern redbelly dace (*Phoxinus eos*), 5% finescale dace (*Phoxinus neogaeus*) and 5% central mudminnow (*Umbra limi*) (Hodgson *et al.*, 1993). The dace are zooplanktivores capable of altering the size and species composition of a zooplankton community. Since 1984, Tuesday Lake has been part of a series of whole-lake experiments conducted by S. R. Carpenter and colleagues (summarized in Carpenter and Kitchell, 1993a). Data from 1984 and 1986 are analyzed here.

A. The Manipulation

Prior to 1985, Tuesday Lake lacked naturally occurring large piscivores. The first experiment by Carpenter and colleagues consisted of removing 90% of the fish biomass in May and July of 1985 and replacing the planktivorous species with one species of largely piscivorous fish, largemouth bass (*Micropterus salmoides*) from a nearby lake (Table 2). Largemouth bass is a potential keystone predator (Hodgson *et al.*, 1993).

Bass consumed practically all the remaining dace shortly after the introduction. The survival rate of the bass was high and the population recruited successfully in both 1985 and 1986 (Hodgson *et al.*, 1993). However, few members of the cohort of 1985 survived through the winter of 1985–86 (due to a combination of predation by adult bass and size-selective winter mortality), so small juvenile largemouth bass can be considered absent throughout 1986.

The effects of the manipulation were documented by Carpenter and Kitchell (1988, 1993a). Bass introduction in Tuesday Lake caused a dramatic

Table 2 The manipulation of the fishes of Tuesday Lake in 1985

Date	Number of individuals removed	Number of individuals added
May 1985	39,654 redbelly dace (*Phoxinus eos*) 2,692 finescale dace (*Phoxinus neogaeus*) 2,655 mudminnows (*Umbra limi*)	375 largemouth bass (*Micropterus salmoides*, 47.5 kg)
July 1985	None	91 largemouth bass (*Micropterus salmoides*, 10.1 kg)
Total	45,001 individuals (56.4 kg)	466 individuals (57.6 kg)

reduction in vertebrate zooplanktivory. Consequently, the zooplankton assemblage shifted from dominance by small-bodied species (e.g., *Bosmina*, rotifers, and small copepods) to dominance by large-bodied cladocerans (i.e., *Daphnia*), along with a substantial decrease in chlorophyll concentrations and primary production. These changes are examples of "trophic cascades" in the sense of Carpenter (Carpenter *et al.*, 1985; Carpenter and Kitchell, 1993a).

B. The Data

To establish the pelagic food web of Tuesday Lake, intensive diet data were collected for the fish and *Chaoborus*. Stomach content analyses were done on 434 largemouth bass from Tuesday Lake. Minnow and dace diets were based on analyses in 1984 of 40 individuals of each species (Cochran *et al.*, 1988). *Chaoborus* diets were measured by Elser *et al.* (1987a). For predaceous crustaceans, we judged diets on the basis of personal communications with S.I. Dodson and T.M. Frost. For herbivorous zooplankton, grazing experiments conducted in Tuesday Lake or nearby lakes were used whenever possible (Bergquist, 1985; Bergquist *et al.*, 1985; Bergquist and Carpenter, 1986; Elser *et al.*, 1986, 1987b; St. Amand, 1990). Most herbivorous zooplankton are filter-feeders and the filtering apparatus sets limits on the sizes of phytoplankton they can extract. Judgments on the grazer-phytoplankton links considered whether the resource was sufficiently small and vulnerable and co-occurred with the consumer. These decisions may confound the relationships between body size and trophic structure. Diets of some predators change extensively over ontogeny, with consequences for "trophic cascades" (Carpenter *et al.*, 1985). Diets reported here are for the body sizes and life stages present in the lake in either 1984 or 1986. If multiple life stages or a range of body sizes were present, the data represent the aggregate diet for the species during the time period. No information on parasites of the pelagic species of Tuesday Lake is available, and no information on the pelagic microbial community is included. Table 3 summarizes statistics of the food web.

Physical and chemical variables and plankton abundance (not *Chaoborus*) were censused weekly from May to September (Carpenter and Kitchell, 1993b). Night tows and minnow trappings were used every two weeks to census the abundance of *Chaoborus* and planktivorous fish respectively. Largemouth bass were censused twice a year (at the beginning and end of the field season) by angling and electrofishing. The primary data on Tuesday Lake included the average body length (m) of the species, individual volume (m^3) of the phytoplankton, body mass (kg) of the zooplankton (including *Chaoborus*) and fish, and numerical abundance (individuals/m^3). These data were then converted to uniform measures for all species and combined

Table 3 Statistics for the unlumped and trophic species webs of Tuesday Lake

Statistic	Unlumped web, 1984	Trophic web, 1984	Unlumped web, 1986	Trophic web, 1986
Species	56 (50)[a]	27 (21)[a]	57 (51)[a]	26 (20)[a]
Phytoplankton species	31 (14)[b]		35 (18)[b]	
Zooplankton species	22 (6)[b]		21 (5)[b]	
Fish species	3 (3)[b]		1 (1)[b]	
Basal species[a]	25	8 (3.1)[c]	29	6 (3.6)[c]
Intermediate species	24	12 (14.7)[c]	20	12 (12.8)[c]
Top species	1	1 (3.1)[c]	2	2 (3.6)[c]
Food chains	4836	214 (263)[c]	885	59 (115)[c]
Mean food chain length[d]	4.64	3.68 (5.08)[c]	4.21	3.47 (4.30)[c]
Maximum food chain length[d]	7	6 (10)[c,e]	6	5 (8)[c,e]
Links	269 (264)[f]	71 (67)[f]	241 (236)[f]	56 (52)[f]
Basal-intermediate links	166	31 (14.74)[c]	158	20 (12.75)[c]
Basal-top links	0	0 (3.12)[c]	7	2 (3.6)[c]
Intermediate-intermediate links	87	27 (34.39)[c]	68	27 (22.9)[c]
Intermediate-top links	11	9 (14.74)[c]	3	3 (12.75)[c]
Connectance[a,f]	0.2155	0.3190	0.1851	0.2737
Consumers per resource species[a,f]	5.39	3.35	4.82	2.89
Resources per consumer species[a,f]	10.56	5.15	10.73	3.71
Consumers per phytoplankton species[a,f]	5.35		4.71	
Consumers per zooplankton species[a,f]	4.36		3.38	
Resources per zooplankton species[a,f]	10.68		11.10	
Resources per fish species[a,f]	9.67		3	

[a] Isolated species excluded.

[b] Number of unique species in parenthesis (i.e. species that occurred in that year only).

[c] Numbers in parenthesis indicate cascade model predictions.

[d] Number of links.

[e] Longest food chain with an expected frequency greater than one.

[f] Cannibalistic links excluded.

with the trophic data (see above) so that the data analyzed here (Appendices 1 and 2 for 1984 and 1986, respectively) consist of: (1) a list of species; (2) the predators and prey of each species; (3) the trophic height of each species; (4) the average body mass (kg) of the species; (5) numerical abundance (individuals/m^3) of the species; and (6) the biomass abundance (kg/m^3) of the species, which is the product of the body mass times numerical abundance. The data represent seasonal averages during summer stratification.

For the plankton and planktivorous fish, the concentrations of individuals are the average over the weeks in which the taxon was present. For the piscivorous fish, numerical abundance was calculated as the average of the censuses at the beginning and end of the field season. For the phytoplankton and small zooplankton (<0.5 mm), numerical abundance at each census was determined by counting individuals on a lattice (a microscope slide marked with a rectangular grid to minimize confusion while counting) until the standard error of the mean number of individuals per subsample was less than 10%. For small phytoplankton, a minimum of 10 microscope fields at a magnification of 400× were counted (minimum of 100 individuals). For larger phytoplankton, a minimum of 15 fields at a magnification of 200× were counted (minimum of 300 individuals). For larger zooplankton (>0.5 mm diameter), the entire sample was counted.

Body size (length, mass, or volume) was obtained by measuring individuals from Tuesday Lake, in general, until the standard error of the mean was less than 10%. The values are reported as average values. For species with highly variable size, such as colonial species, the range and geometric mean were also reported. For the phytoplankton, the size data are for "algal units:" single cells were measured for solitary species and the size of the colony was measured for colonial species. The only colonial zooplankton in the data is *Conochilus* sp. in 1986, for which colony size is reported. From individual volume (and an assumed density of 1 kg/1), the body mass (kg) of the phytoplankton was estimated. For all species, body mass is kg fresh weight. Fresh weights include a variable proportion of water and cannot be converted to elemental compositions without additional information or assumptions.

The numerical abundance of all species used for all calculations here is the number of individuals per cubic meter in the water volume where the consumers feed (i.e., in the epilimnion), which is roughly equal to the photic zone in Tuesday Lake. Phytoplankton were sampled in the epilimnion. Zooplankton were sampled (using vertical net hauls during day time) over a water mass that is about six times the volume sampled for phytoplankton. Thus, the volume where zooplankton *live* is about six times the epilimnion volume where zooplankton *feed* on phytoplankton. The total sizes of the fish populations in the lake were estimated using mark-recapture and were then divided by the volume of the epilimnion. When zooplankton feed in the epilimnion (typically at night), their concentrations in this zone are considerably higher (Dini *et al.*, 1993) than in the volume where they live.

In Appendices 1A and 2A, in the columns headed *NA* (for "numerical abundance"), the values for phytoplankton and fish were used in statistical analyses without change, but the numerical abundance values for all zooplankton species in Appendices 1A and 2A were multiplied by 6 before use in the statistical analyses reported here. For example, if the stated values in Appendix 1A (for 1984) in the columns headed *BM* and *NA* were used without this adjustment by a factor of 6 for zooplankton numerical abundance, then the coefficients of the linear model

$$\log_{10}(NA) = a + b \times \log_{10}(BM)$$

considered in the first line of Table 6 for all species (“Total”) would be $a = -3.6109$, $b = -0.8877$. However, because all the zooplankton numerical abundances were multiplied by 6 to convert all species to the same reference volume (namely, the epilimnion), the same regression analysis reproduces the values shown in the first line of Table 6 (namely, $a = -2.6863$, $b = -0.8271$). Section VII addresses the effect of multiplying zooplankton numerical abundances by 6.

V. RESULTS: PATTERNS AND RELATIONSHIPS IN THE PELAGIC COMMUNITY OF TUESDAY LAKE

This section can be regarded as an illustrated list (Table 1) of different ways to describe a community, using data on the body size, numerical abundance, and food web in the pelagic community of Tuesday Lake. Many of the relationships presented are previously well studied. To examine the effect of scale, we will compare data from the whole Tuesday Lake pelagic community with previously analyzed data on restricted taxa or data aggregated over several communities.

The three dimensions of our analysis are: the food web, body size, and species abundance. We start by looking at three-dimensional data, then move on to two-dimensional relationships followed by one-dimensional relationships. The three-dimensional perspective is the principal novelty this article offers. It permits ecologists to view Tuesday Lake in a series of new, coherent pictures and provides the baseline against which the two- and one-dimensional relationships will be compared.

A. Trivariate Distributions: Food Web, Body Size, and Abundance

In Tuesday Lake, small-bodied, numerically abundant species occur at low trophic heights, whereas larger-bodied and less abundant species occur at higher trophic heights (Figs. 1A, B, 2A, and B). Biomass abundance does not vary systematically with body mass or trophic height (Figs. 1A, B, 2C, and D).

In Fig. 2, phytoplankton, zooplankton, and fish form three distinct clusters. The data points plotting numerical abundance, body mass, and trophic height lie roughly on a diagonal between the lower left corner and the upper

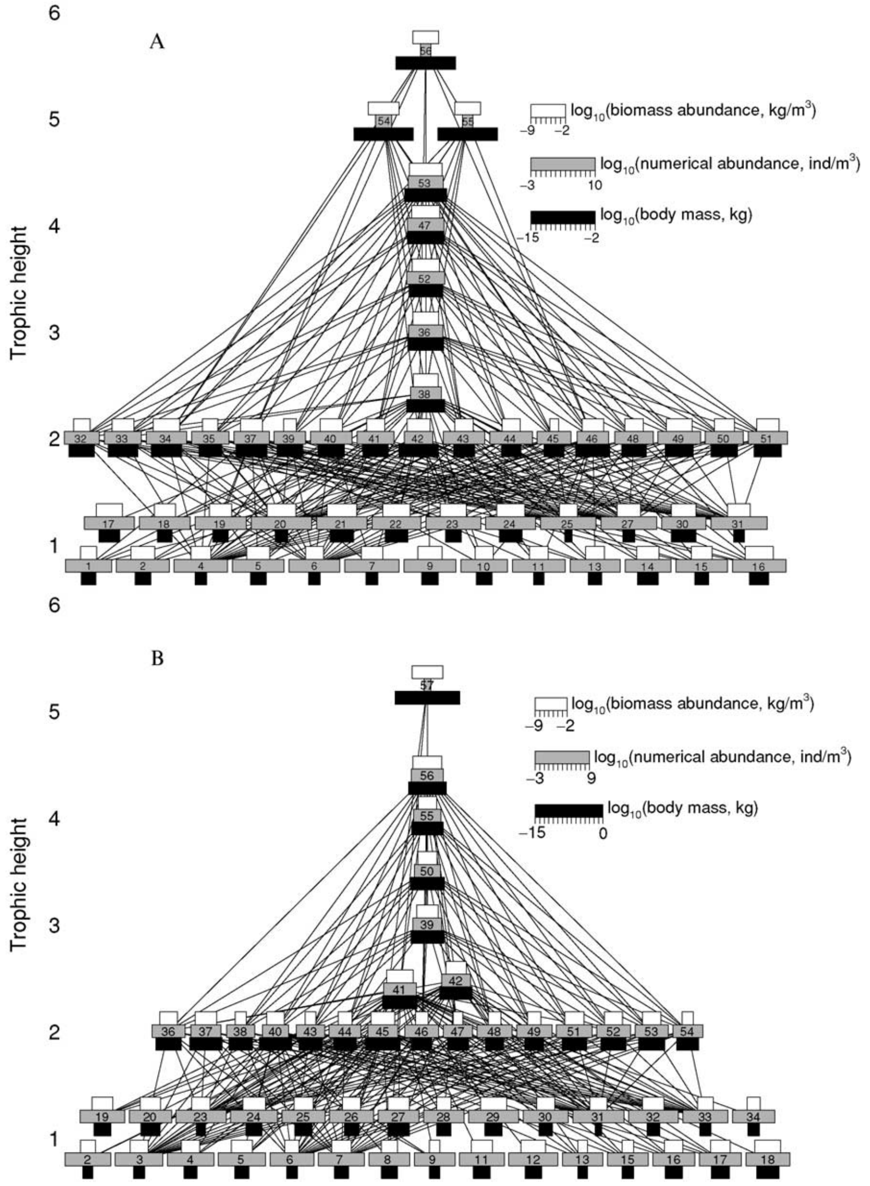

Figure 1 The unlumped food webs of Tuesday Lake in (A) 1984 and (B) 1986. The width of the black, grey and white horizontal bars shows the $\log_{10}$ body mass (kg), numerical abundance (individuals/m^3 in the epilimnion where species eat), and biomass abundance (kg/m^3 in the epilimnion where species eat), respectively, of each species. Species numbers refer to Appendices 1 and 2. The vertical positions of the species show trophic height (see text). Basal species have a trophic height of unity

right corner in Fig. 2A and B. Multiple regression yields trophic height = 0.3421 × log body mass −0.1040 × log numerical abundance +5.8697 (with squared multiple correlation coefficient $r^2 = 0.8404$). An interpretation of the first coefficient in this regression equation is that an increase in mean trophic height by one level is associated with an increase in body mass by a factor of more than 800 (because $1/0.3421 = 2.9231$ and $10^{2.9231} = 837.8$), if all else remains constant. However, in Tuesday Lake, an increase in body mass is usually closely associated with a decrease in numerical abundance. Variation in trophic height due to log body mass and log numerical abundance in combination can be attributed more to log body mass (controlling for log numerical abundance [the partial correlation coefficient of trophic height and log body mass, given log numerical abundance, is 0.5790, $p < 0.01$]) than to log numerical abundance (controlling for log body mass [the partial correlation coefficient of trophic height and log numerical abundance, given log body mass, is −0.2179, $p > 0.05$]).

Among the phytoplankton in 1984, body mass and numerical abundance are negatively correlated, although all phytoplankton have a trophic height of 1 (Table 4). For 17 species of zooplankton with a trophic height of 2, body size and numerical abundance are significantly negatively correlated in 1984 ($r_{84} = -0.5262$, $p < 0.05$). In 1986, the negative correlation, although of similar magnitude, is not significant ($r_{86} = -0.4940$, $p > 0.05$).

Variations in numerical abundance are more closely associated with variations in body mass than with variations in trophic height. Bivariate correlations indicate that log body mass is more closely associated with log numerical abundance ($r^2 = 0.8414$) than trophic height is with log numerical abundance ($r^2 = 0.7628$) in Tuesday Lake in 1984 (Table 4). Multiple correlation analyses of log numerical abundance (dependent variable) on log body mass and trophic height (independent variables) show that trophic height adds little to explaining the variation in numerical abundance.

Figure 3, a new food web graph inspired by the diagrams in Cousins (1996) and Sterner *et al.* (1996), shows the food web of Tuesday Lake in the plane with abscissa log numerical abundance and with ordinate log body mass. Animal ecologists generally put log body mass on the abscissa, while plant ecologists generally put log body mass on the ordinate. Since food webs are conventionally represented with food flowing in an upward

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by definition, but to allow for wider non-overlapping bars, the vertical positions of the basal species have been adjusted around unity. The horizontal position is arbitrary. Isolated species (see Appendices 1 and 2) are omitted. Species with a trophic height of unity are phytoplankton, those with a trophic height greater than 4.5 are fish, and those with intermediate trophic heights are zooplankton. Figure 1A is reprinted from Cohen *et al.* (2003) with permission from the National Academy of Sciences.

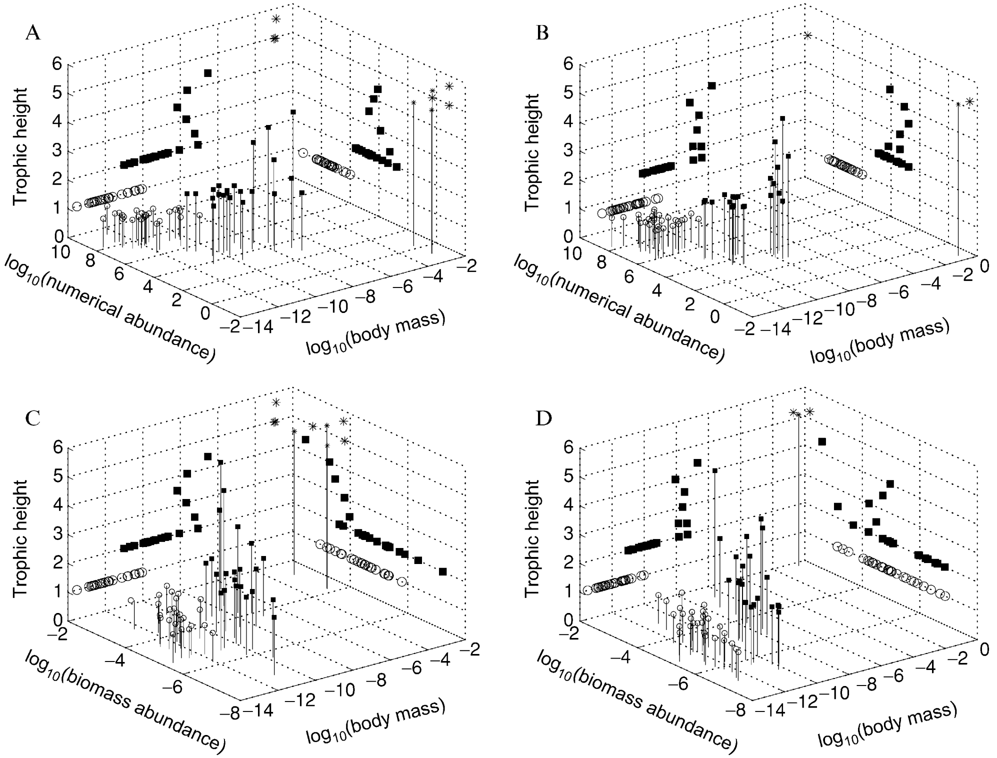

Figure 2 Body mass (kg), trophic height and abundance of the species in Tuesday Lake in 1984 (A & C) and 1986 (B & D). Numerical abundance (individuals/m^3 in the epilimnion where species eat) is shown in (A) and (B), and biomass abundance (kg/m^3 in the epilimnion where species eat) in (C) and (D). Circles = phytoplankton, squares = zooplankton, stars = fish. Small markers on

direction, we prefer the choice of axes customary among plant ecologists so that food usually flows upward (and from right to left) from smaller-bodied, more abundant prey to larger-bodied, rarer predators.

The slope of a trophic link that connects two species, a consumer and resource, in this diagram is defined as (log body mass of consumer – log body mass of resource) divided by (log numerical abundance of consumer-log numerical abundance of resource). The slope indicates the biomass ratio between a predator or consumer species and one of its prey or resource species. A slope of -1 indicates equal biomass abundance of predator and prey. A slope more negative (or less negative) than -1 indicates that the predator has greater (or smaller) biomass abundance, respectively, than the prey. The mean slope of all links that join individual pairs of consumers and resources was -1.1585 in 1984 and -0.8625 in 1986. The mean slope of all links does not equal the slope of the regression of log body mass as a function of log numerical abundance (Section V.B.2.a). Among all noncannibalistic trophic links, 62% in 1984 and 67% in 1986 connect a predator and a prey where the biomass abundance of the prey is smaller than that of its predator.

While the body mass of individual species increases almost 12 orders of magnitude and the numerical abundance of individual species decreases almost 10 orders of magnitude within the food web, biomass abundance increases on average two orders of magnitude from the bottom to the top of the food web (as expected: $12 - 10 = 2$). Biomass abundance varies only five orders of magnitude over all species.

The food web diagram in Fig. 3 carries more information on the pattern of energy flow within a community than a traditional food web graph. We know of no other study that shows the joint variation in body size and numerical abundance, and thus in biomass abundance, of all the species in a community food web.

B. Bivariate Distributions

1. Food Web and Body Size

A data set that includes the food web and the body sizes of the species makes it possible to analyze the predator-prey body size allometry, body size versus trophic height as well as trophic generality and vulnerability versus body size (Table 1).

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stems show the position of each species in the three-dimensional space. The base of the stems on the floor of the box and larger markers on the walls show the bivariate distribution of the species in two-dimensional spaces. Figure 2A and C is reprinted from Cohen *et al.* (2003) with permission from the National Academy of Sciences.

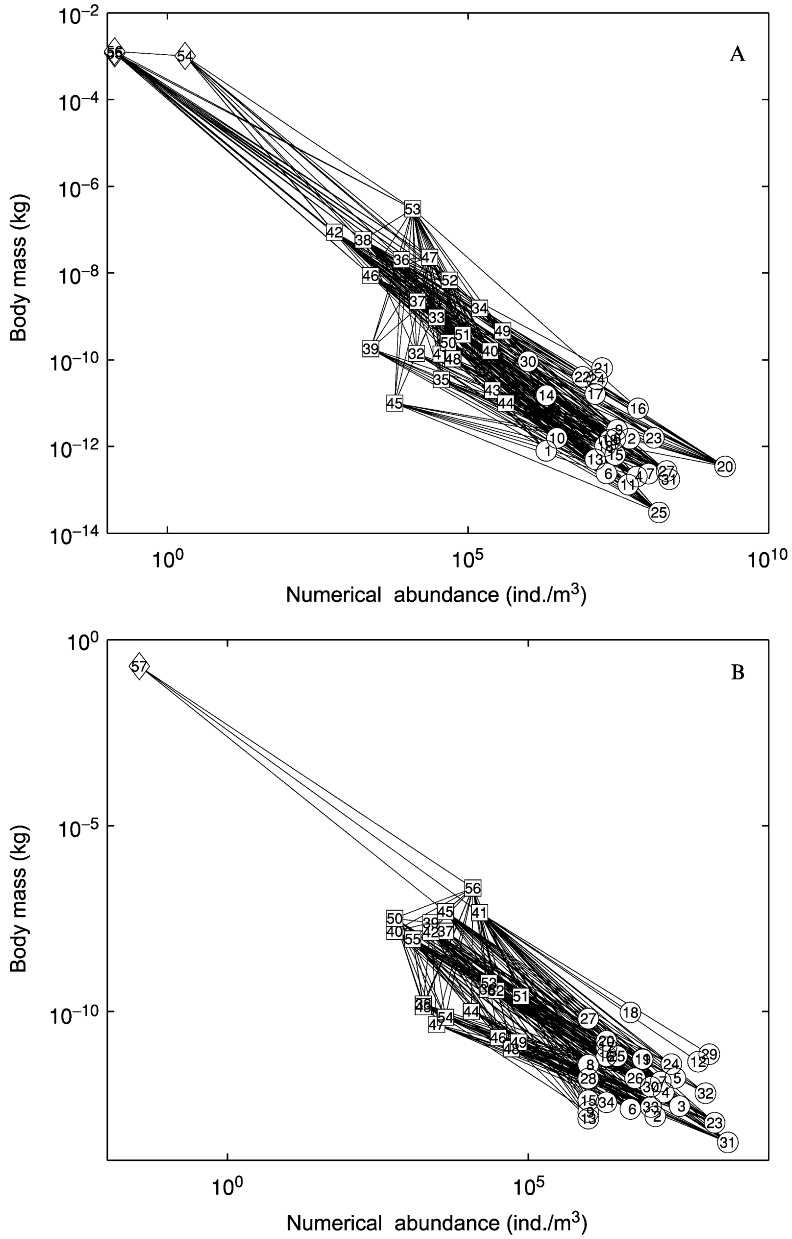

Figure 3 The Tuesday Lake food web in (A) 1984 and (B) 1986, plotted in the plane with abscissa measured by numerical abundance (individuals/m^3 in the epilimnion where species eat) and ordinate measured by body size (kg) on logarithmic scales for both axes. The center of a node locates the species identified by the number within

a. Predator-Prey Body Size Allometry

In aquatic and terrestrial habitats, if parasites and terrestrial herbivores are ignored, a predator is usually larger than its prey (Vézina, 1985; Warren and Lawton, 1987; Cohen *et al.*, 1993) and predator size is in general positively correlated to prey size. In some systems, the ratio in body size of two predators that differ in body size is typically less than the ratio in body size of the prey of those predators, that is, comparatively speaking, prey body size increases faster than predator body size, so that the larger the prey is, the more similar its size is to the size of its predators (Vézina, 1985; Cohen *et al.*, 1993).

These general patterns are predicted by the cascade model (Section III.A.I) if the ordering assumed in that model is interpreted as an ordering by body size. Under that interpretation, the cascade model assumes that predators are larger than their prey. The cascade model predicts that the larger the prey is, the more similar in size its average predator should be. The larger the predator, the less similar in size its average prey should be.

These relationships hold for Tuesday Lake (Fig. 4, Table 5). However, contrary to an assumption of the cascade model, the points that represent pairs of predator and prey in Fig. 4 are not randomly distributed above the diagonal. Rather, the data points lie in a wide band above the diagonal. The largest consumers (fish) do not eat the smallest prey (phytoplankton). Though Tuesday Lake conforms well to the predictions of the cascade model for the qualitative relationships between predator and prey size, the trophic links are not distributed, as the cascade model assumes, with equal probability between each predator and any species smaller than the predator.

In this deviation from the "equiprobability assumption" of the cascade model, Tuesday Lake is not alone. In 16 published food webs for which estimates of adult body masses were available, Neubert *et al.* (2000) found some evidence of departure from the equiprobability assumption in 7 of the 16 webs (at a significance level of $p \leq 0.06$). In six of these webs, the probability of a trophic link was affected by the identity of the predator species. This deviation from the original cascade model is captured in some generalizations (Cohen, 1990).

If species are sorted by their body size and isolated species are discarded, the resulting predation matrix has 269 nonzero entries (trophic links), of which 262 are from smaller prey to larger consumers. This finding must be interpreted cautiously because, as noted above, relative body sizes were

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the node. Edges connect consumer species to the species they eat. Isolated species (see Appendices 1 and 2) are omitted. Circles = phytoplankton, squares = zooplankton, diamonds = fish.

Table 4 Correlations among body size, abundance and trophic height in Tuesday Lake[a]

		Phytoplankton			Zooplankton			Total		
Variables	Year	*r*	*p*	*n*	*r*	*p*	*n*	*r*	*p*	*n*
$\log_{10}(BM)$ vs.	1984	−0.5615	$p < 0.002$	31	−0.5366	$p < 0.02$	22	−0.9175	$p < 0.001$	56
$\log_{10}(NA)$	1986	−0.2723	$p > 0.1$	35	−0.4843	$p < 0.05$	21	−0.8665	$p < 0.001$	57
$\log_{10}(BM)$ vs.	1984	0.7028	$p < 0.001$	31	0.7982	$p < 0.001$	22	0.4343	$p < 0.001$	56
$\log_{10}(BA)$	1986	0.6885	$p < 0.001$	35	0.8740	$p < 0.001$	21	0.5212	$p < 0.001$	57
$\log_{10}(BM)$ vs.	1984	0			0.6398	$p < 0.002$	22	0.9135	$p < 0.001$	50[b]
TH	1986	0			0.6152	$p < 0.005$	21	0.8804	$p < 0.001$	51[b]
$\log_{10}(NA)$ vs.	1984	0			−0.1238	$p > 0.5$	22	−0.8734	$p < 0.001$	50[b]
TH	1986	0			−0.3254	$p > 0.1$	21	−0.8546	$p < 0.001$	51[b]
$\log_{10}(BA)$ vs.	1984	0			0.6673	$p < 0.001$	22	0.3079	$p < 0.05$	50[b]
TH	1986	0			0.5224	$p < 0.02$	21	0.3044	$p < 0.05$	51[b]

[a] All connected phytoplankton have a trophic height of 1, hence correlation must be 0. For fish, no correlations were calculated because there are too few data points (3 species in 1984, 1 in 1986). *r* is the correlation coefficient, *p* is the significance level (null hypothesis is no correlation), and *n* is the number of species.

[b] Isolated species excluded (6 species of phytoplankton in both 1984 and 1986, see Appendices 1A and 2A).

BM: body mass (kg), NA: numerical abundance (individuals/m^3 in the epilimnion where species eat), BA: biomass abundance (kg/m^3 in the epilimnion where species eat), TH: trophic height (see text).

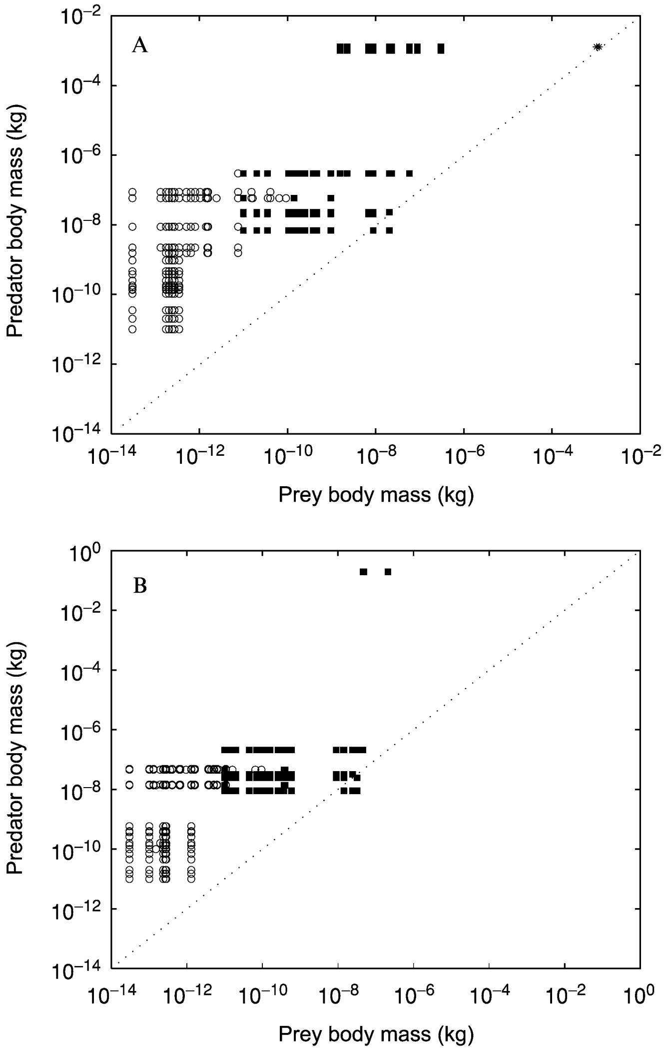

Figure 4 Prey and predator body mass (kg) in Tuesday Lake in (A) 1984 and (B) 1986, one marker for every trophic link in the unlumped food web. Cannibalistic links are excluded. Dotted line indicates equal prey and predator body mass. The links are coded according to the prey. For explanation of symbols see legend to Fig. 2. For correlations and regressions see Table 4. Figure 4A is reprinted from Cohen *et al.* (2003) with permission from the National Academy of Sciences.

Table 5 Correlations and linear least square regressions for prey and predator body size or abundance in Tuesday Lake[a]

Variables	Year	r	p	n	a	b
$X = \log_{10}$ (Prey BM)	1984	0.7859	$p < 0.001$	263	1.5598	0.8445
$Y = \log_{10}$ (Predator BM)	1986	0.6094	$p < 0.001$	233	−1.4108	0.5928
$X = \log_{10}$ (Prey BM)	1984	0.8832	$p < 0.001$	49	0.5073	0.7350
$Y = \text{mean}(\log_{10}$ (Predator BM))	1986	0.6885	$p < 0.001$	49	−0.4782	0.6440
$X = \log_{10}$ (Predator BM)	1984	0.9104	$p < 0.001$	25	−5.4342	0.7265
$Y = \text{mean}(\log_{10}$ (Prey BM))	1986	0.8479	$p < 0.001$	22	−6.5149	0.6063
$X = \log_{10}$ (Prey NA)	1984	0.5016	$p < 0.001$	263	0.8226	0.4299
$Y = \log_{10}$ (Predator NA)	1986	0.3434	$p < 0.001$	233	2.5262	0.1790
$X = \log_{10}$ (Prey NA)	1984	0.6489	$p < 0.001$	49	0.3126	0.4869
$Y = \text{mean}(\log_{10}$ (Predator NA))	1986	0.3805	$p < 0.01$	49	1.9720	0.2565
$X = \log_{10}$ (Predator NA)	1984	0.6899	$p < 0.001$	25	4.3406	0.6838
$Y = \text{mean}(\log_{10}$ (Prey NA))	1986	0.5458	$p < 0.01$	22	4.3272	0.6120
$X = \log_{10}$ (Predator NA)	1984	0.6807	$p < 0.001$	25	6.2032	0.5997
$Y = \log_{10}$ (Total prey NA)	1986	0.6111	$p < 0.005$	22	5.4433	0.6799

$X = \log_{10}$ (Prey NA)	1984	0.6078	$p < 0.001$	49	1.5684	0.4753
$Y = \log_{10}$ (Total predator NA)	1986	0.3682	$p < 0.01$	49	2.6109	0.2786
$X = \log_{10}$ (Prey BA)	1984	−0.0123	$p > 0.5$	263	−4.2699	−0.0147
$Y = \log_{10}$ (Predator BA)	1986	0.1029	$p > 0.1$	233	−3.7555	0.1574
$X = \log_{10}$ (Prey BA)	1984	−0.0253	$p > 0.5$	49	−3.9616	−0.0174
$Y = \text{mean}(\log_{10}$ (Predator BA))	1986	0.5000	$p < 0.001$	49	−1.9612	0.3930
$X = \log_{10}$ (Predator BA)	1984	0.0888	$p > 0.5$	25	−4.4113	0.0281
$Y = \text{mean}(\log_{10}$ (Prey BA))	1986	0.3987	$p > 0.05$	22	−4.4338	0.1525
$X = \log_{10}$ (Predator BA)	1984	0.4304	$p < 0.05$	25	−2.3378	0.1308
$Y = \log_{10}$ (Total prey BA)	1986	0.8013	$p < 0.001$	22	−2.1778	0.3462
$X = \log_{10}$ (Prey BA)	1984	−0.2110	$p > 0.1$	49	−3.6997	−0.1551
$Y = \log_{10}$ (Total predator BA))	1986	0.0807	$p > 0.5$	49	−2.7089	0.0293

[a] r is the correlation coefficient, p is the significance level (null hypothesis is no correlation), and n is the number of species. In the regression equation $Y = a + bX$, a is the intercept and b is the slope.

BM: body mass (kg), *NA*: numerical abundance (individuals/m^3 in the epilimnion where species eat), *BA*: biomass abundance (kg/m^3 in the epilimnion where species eat).

considered in establishing grazer-phytoplankton links (circles in Fig. 4). In only two links, a predator consumes a larger prey. Five links are cannibalistic. Trophic links are not distributed randomly in the upper triangular part of this sorted predation matrix ($p < 0.001$, along rows, columns, or diagonals, using the χ^2 approach described by Neubert *et al.*, 2000). In the trophic-species web, for which the cascade model was originally developed, links are not distributed randomly among columns or rows ($p < 0.001$) but are among diagonals ($p > 0.5$). Because species are, with few exceptions, consumed by species larger than themselves (Fig. 4), prey body mass is positively correlated with predator body mass (Table 5). On log-log scales, prey size increases faster than predator body mass (Table 5). If the variance in log predator size decreases with increasing prey size as Fig. 4 suggests, the assumed homogeneity of variance for hypothesis testing in linear least square regression analyses would be violated. Nevertheless, the data indicate that the ratio of body masses between predator and prey decreases as prey size increases, so that predators and prey on average become more similar in size as prey size increases.

In addition, log prey size increases with mean log predator size, while log predator size increases with mean log prey size (Table 5). The slopes of both of these relationships are less than 1, as predicted by the cascade model. The larger the prey, the more similar in size its average predator; the larger the predator, the less similar in size its average prey.

The relationship between prey and predator body sizes may have implications for ecosystem dynamics. For example, the resilience (the reciprocal of return time; e.g., Harrison, 1979; Pimm, 1982) of an ecosystem could be affected (Jonsson and Ebenman, 1998) if the per capita effects between predators and their prey are correlated to the predator-prey body mass ratio (as could be expected for energetic reasons).

b. Body Size versus Trophic Height

The trophic height of a species in the Tuesday Lake food web is significantly positively related to its body size across all species (Table 4, left rear walls in Fig. 2), and negatively related to its log rank (from large to small) in body mass ($r = -0.9139$). For zooplankton (the only group for which there is sufficient variation in trophic height), the relationship between body mass and trophic height is much weaker (but still significantly positive, Table 4) than for all species.

c. Trophic Vulnerability and Generality versus Body Size

On average, trophic vulnerability decreases with increasing body size across all species ($r = -0.4305$, $p < 0.002$) while trophic generality on average increases with body size ($r = 0.4142$, $p < 0.05$). Among phytoplankton, trophic vulnerability decreases significantly with body size ($r = -0.6933$,

$p < 0.001$), but not among zooplankton ($r = -0.2224$, $p > 0.2$). On the other hand, trophic generality increases significantly with body size among zooplankton ($r = -0.8882$, $p < 0.001$).

2. *Body Size and Abundance*

a. Abundance-Body Size Allometry

The negative relationship between body size and numerical abundance among all species of Tuesday Lake is highly significant (Table 4, Fig. 5A, B). Most species in Tuesday Lake fall near a diagonal with slope -1 at a biomass abundance of 10^{-4} or 10^{-5} kg/m^3 in the (log numerical

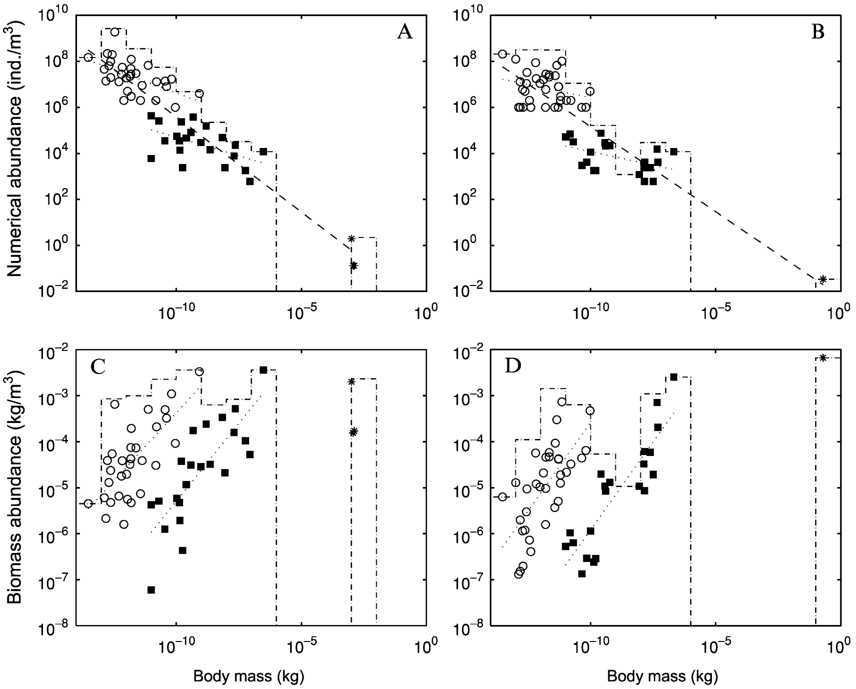

Figure 5 Body mass (kg) and abundance of the species in Tuesday Lake in 1984 (A & C) and 1986 (B & D). Numerical abundance (individuals/m^3 in the epilimnion where species eat) is shown in (A) and (B), and biomass abundance (kg/m^3 in the epilimnion where species eat) in (C) and (D). For explanation of symbols see legend to Fig. 2. Dashed line in (A) and (B) is the regression line using all species. Dotted lines are the regression lines for phytoplankton and zooplankton separately. Dash-dotted line shows the total numerical abundance (A & B) and biomass abundance (C & D; the biomass spectrum) in logarithmically increasing body mass classes. For correlations and regressions, see Tables 5 and 6.

abundance, log body mass) plane of Fig. 3. For all 56 species in 1984, including isolated species, the linear regression is

$$\text{log body mass} = -4.3510 - 1.0178 \text{ log numerical abundance}$$

with 95% confidence interval $(-1.14, -0.90)$ around the slope -1.0178. For all 57 species in 1986, including isolated species, the linear regression is

$$\text{log body mass} = -4.9058 - 1.0149 \text{ log numerical abundance}$$

with 95% confidence interval $(-1.1729, -0.8569)$ around the slope -1.0149. For both years, the confidence intervals include the slope -1 and exclude slopes equal to or greater than $-3/4$.

On the other hand, if the independent and dependent variables in these linear regressions are exchanged as in Fig. 5 and Table 6, then for all 56 species in 1984,

$$\text{log numerical abundance} = -2.6863 - 0.8271 \text{ log body mass}$$

with 95% confidence interval $(-0.92, -0.73)$ around the slope -0.8271. For all 57 species in 1986, the linear regression is

$$\text{log numerical abundance} = -2.2359 - 0.7397 \text{ log body mass}$$

with 95% confidence interval $(-0.85, -0.62)$ around the slope -0.7397. Only these models meet the assumptions of linear regression analysis for these data (Cohen and Carpenter, in press). For both years, the confidence intervals include the slope $-3/4$ and exclude the slope -1. The relationship is also significant for phytoplankton and zooplankton separately. At the 95% significance level, the slopes for these groups (Table 6) are considerably less steep than -1, $-3/4$, and $-2/3$, but not significantly different from each other.

Figure 5C and D visually confirms the quantitative conclusion (Table 6) that, across all species, the amount of biomass of each species increases only slightly from species of smaller body size to species of larger body size. Within the functional groups, however, larger species tend to have more biomass than smaller species.

The slopes of the body mass-numerical abundance relationships across all species are similar to the ones found by Marquet *et al.* (1990) in two rocky intertidal communities, and lie within the range reported by Cyr *et al.* (1997a) for 18 local aquatic communities. The slopes for these local communities lie in the range (-0.75 to -1) reported for most regional or global communities. The data of Tuesday Lake and Cyr *et al.* (1997a) contradict the finding (Blackburn and Gaston 1999, 1997) that at local scales, the relationship is more often polygonal and that the mean slope (-0.245) is less negative than at regional scales (mean, -0.692).

Cyr *et al.* (1997b) found algae and invertebrate slopes of -0.64 and -0.50, respectively (compared to -0.89 across all species) with data aggregated

Table 6 Linear least squares regression analyses of body size, abundance and trophic height in Tuesday Lake[a]

		Phytoplankton			Zooplankton			Total		
Relationship	Year	a	b	n	a	b	n	a	b	n
$\log_{10}(NA) =$	1984	2.5587	−0.4071	31	1.4664	−0.3242	22	−2.6863	−0.8271	56
$a + b \times \log_{10}(BM)$	1986	4.1239	−0.2297	35	1.7306	−0.2353	21	−2.2359	−0.7397	57
$\log_{10}(BA) =$	1984	2.5586	0.5929	31	1.4663	0.6758	22	−2.6863	0.1729	56
$a + b \times \log_{10}(BM)$	1986	4.1234	0.7703	35	1.7306	0.7647	21	−2.2359	0.2603	57
$\log_{10}(BM) =$	1984				−11.7863	1.1633	22	−13.6419	1.9423	50[b]
$a + b \times TH$	1986				−11.6845	1.1453	21	−13.8240	2.0539	51[b]
$\log_{10}(NA) =$	1984				4.7254	0.1361	22	8.7400	−1.6913	50[b]
$a + b \times TH$	1986				4.5390	−0.2944	21	8.2840	−1.7060	51[b]
$\log_{10}(BA) =$	1984				−7.0609	1.0273	22	−4.9019	0.2509	50[b]
$a + b \times TH$	1986				−7.1455	0.8510	21	−5.5416	0.3479	51[b]

[a] All connected phytoplankton have a trophic height of 1. For phytoplankton no regressions were calculated for the relationships between trophic height and any other variable due to lack of variation in trophic height. For fish, no regressions were performed because there were too few data points (3 species in 1984, 1 in 1986). In the regression equation $Y = a + bX$, a is the intercept b is the slope, and n is the number of species.

[b] Isolated species excluded (6 species of phytoplankton in both 1984 and 1986).

BM: body mass (kg), *NA*: numerical abundance (individuals/m^3 in the epilimnion where species eat), *BA*: biomass abundance (kg/m^3 in the epilimnion where species eat) and *TH*: trophic height (see text).

from 18 lakes worldwide. In Tuesday Lake, the much slower decrease in numerical abundance with increasing body size within functional groups (phytoplankton and zooplankton) than across all species (Table 6) is consistent with this finding. The slopes for the plankton groups in Tuesday Lake are considerably less negative than the corresponding slopes in Cyr *et al.* (1997b) and most previously reported slopes for restricted taxonomic groups (e.g., Peters and Wassenberg, 1983; Peters, 1983). If large and rare species within functional groups (e.g., phytoplankton and zooplankton) are missing more frequently from the data than small and rare species (as may be the case when using standard microscope counting techniques; Ursula Gaedke, personal communication, 2000), this selectivity could help to explain the shallower slope within the plankton groups than across all species.

The food web of Tuesday Lake makes it possible to refine the relationship between numerical abundance and body size. In Tuesday Lake across all *consumer* species, the slope of log numerical abundance as a function of body mass was -0.67 in 1984 and -0.50 in 1986. Because these slopes are greater than -1, consumer biomass increases from the bottom to the top of the food web. The intuitive explanation is that body mass increases from the bottom to the top of the food web and for each ratio of increase in consumer body mass, there is a smaller ratio of decrease in consumer numerical abundance, so consumer biomass (which is the product of body mass times numerical abundance) increases from the bottom to the top of the food web. Why might consumer biomass increase?

In Tuesday Lake in 1984, across all species on log-log scales, the amount of resource biomass per consumer species divided by the number of consumer species utilizing each prey increases significantly ($p < 0.001$) with consumer body size. For zooplankton separately, the amount of resource biomass increases with increasing body size ($p < 0.05$). Similar results are found in 1986. The increase in available resource biomass per consumer species with increasing consumer body size could help to explain why larger consumer species have more biomass.

As predicted in section 3.4, there is: (1) a positive correlation between the slope of the body mass-numerical abundance relationship (on log-log scales) for individual pairs of consumer and resource species on the one hand, and the number of prey species of the consumer species (i.e., trophic generality) on the other ($p < 0.001$ in both 1984 and 1986); and (2) a negative correlation between the slope of the body mass-numerical abundance relationship for individual pairs of consumer and resource species on the one hand, and the number of predator species of the prey species (i.e., trophic vulnerability) on the other ($p < 0.005$ in 1984 and $p < 0.001$ in 1986). The numerical abundance of a consumer species in Tuesday Lake is less than expected if the consumer shares its prey with other consumer species, but is greater than expected if the consumer has more species of prey. This finding supports the proposition that the slope of the body mass-numerical abundance relationship within a community can be (at least partly) explained by the amount of resources available to consumers.

However, resource supply rate is not the same as the standing stock of prey biomass. Smaller organisms typically have higher energetic and biomass turnover rates than larger organisms. In line with the findings of Carbone and Gittleman (2002), and as predicted in section III.D, the slope of numerical abundance of consumers divided by an estimate of the resource productivity available to each consumer (equation 2 in Section II.A), as a function of the body mass of the consumer, is closer to $-3/4$ on log-log scales than is the relationship using the unmodified numerical abundance of consumers (Fig. 6E and F, slope -0.70 versus -0.67 in 1984 and -0.69 versus -0.50 in 1986). Each prey's estimated productivity is divided by the prey's trophic vulnerability to adjust for the number of consumers utilizing each prey species (equation 2 in Section II.A). By contrast, using the *total* productivity of all prey species in the diet of a consumer, without dividing by the number of consumers that eat each prey species, hardly changes the regression slope or the goodness of fit of the log numerical abundance regression as a function of log body mass.

The slope of numerical abundance of consumers divided by an estimate of the resource biomass available to each consumer (see Section II.A), versus the body mass of the consumer, is closer to -1 on log-log scales than the relationship using the unmodified numerical abundance of consumers (Fig. 6C and D, -0.91 versus -0.67 in 1984 and -0.86 versus -0.50 in 1986), just as Carbone and Gittleman (2002) found for carnivores from many different communities. This scaling of consumer numerical abundance also reduces the variation in abundance not accounted for by the allometric relationship (r^2 increases from 0.79 to 0.86 for the data of 1984 and from 0.70 to 0.88 for the data of 1986). As above for productivity, the biomass abundance of each prey species must be divided by the number of consumers utilizing the prey, crudely assuming equal resource use by each of the consumer species. A slope of -1 for the log-log relationship between consumer numerical abundance divided by the available prey biomass (dependent variable) and consumer body mass (independent variable) means that one unit of prey biomass supports a constant amount of predator biomass, regardless of the body size of the consumer. To prove the above, let NA_c be the consumer's numerical abundance. BM_c is the consumer's body mass, $BA_c = NA_c BM_c$ is the consumer's biomass abundance, and BA_p is the prey's biomass abundance. If we assume a slope of -1, so that

$$\log(NA_c/BA_p) = k - \log(BM_c)$$

then

$$\log(NA_c) + \log(BM_c) - \log(BA_p) = k$$

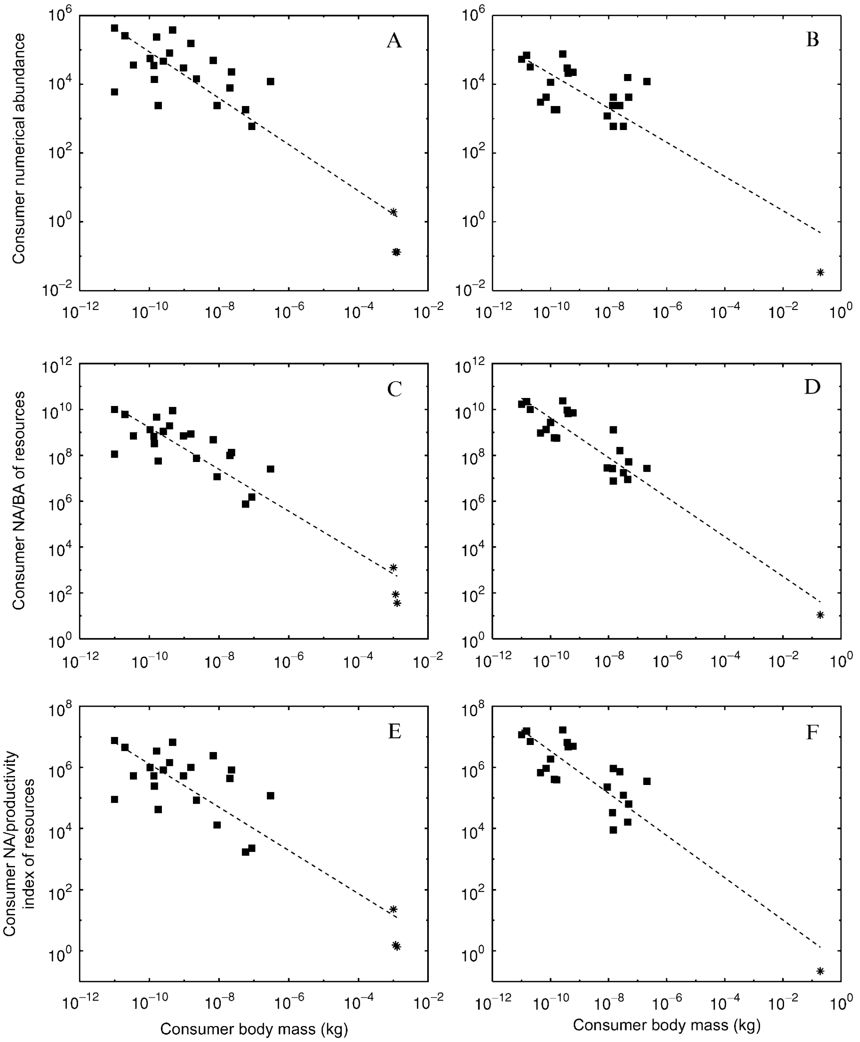

Figure 6 Body mass (kg) and abundance of the consumer species in Tuesday Lake in 1984 (A, C & E) and 1986 (B, D & F). Numerical abundance (individuals/m^3) as a function of consumer body mass (kg) is shown in (A) and (B). In (C) and (D) the numerical abundance (*NA*, individuals/m^3) of each consumer species is divided by the consumer's available resource biomass. The consumer's available resource biomass is computed as the sum, for every resource species in the diet of that consumer species, of the biomass abundance (*BA*, kg/m^3) of each resource divided by the number of consumer species that feed on that resource species (see equation (1) in Section II.A). The dimension of the ordinate in (C) and (D) is thus the number of consumers per kg of resources. In (E) and (F) the numerical abundance of each consumer species is divided by the consumer's available resource productivity.

but

$$\log(NA_c) + \log(BM_c) = \log(BA_c)$$

Therefore

$$\log(BA_c/BA_p) = k,$$

meaning that the consumer biomass per unit of prey biomass is constant, regardless of the consumer's body size. A slope greater than -1 (less steep) would mean that one unit of prey biomass will support more predator biomass, the larger the body size of the consumer. The data of Carbone and Gittleman (2002) pool many different communities while our allometric exponents are derived from observations of a single community. Both analyses indicate that the productivity of the prey determines the numerical abundance of consumers and that the conversion efficiency of prey to predator biomass is roughly similar over a wide range of predator body sizes.

Energetic mechanisms appear to explain much of the observed relation between body mass and numerical abundance in Tuesday Lake. Food web data enrich understanding of a superficially bivariate relationship between consumer numerical abundance and consumer body mass. Food webs with energy flow estimates further enrich understanding of how trophic structure affects the relationship between body mass and numerical abundance.

b. Biomass-Body Size Spectrum

The biomass-body size spectrum studied in aquatic ecology describes the amount of biomass within logarithmic size intervals, with no attention paid to the species identity of the individuals. In many aquatic and pelagic communities, the distribution of biomass is approximately uniform (e.g., Sheldon *et al.*, 1972; 1977; Witek and Krajewska-Soltys, 1989; Gaedke, 1992). In some oceanic planktonic systems, the biomass may decrease with increasing body size (Rodriguez and Mullin, 1986). For other communities,

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The consumer's available resource productivity is computed as the sum, for every resource species i in the diet of that consumer species, of $NA_i \times BM_i^{3/4}/n_i$, where NA_i is the numerical abundance of resource species i, BM_i is the body mass of resource species i and n_i is the number of consumer species that feed on resource species i (see equation (2) in section II.A). The dimension of the ordinate in (E) and (F) is thus the number of consumers per kg of resources per unit time. For explanation of symbols see legend to Fig. 2. Dashed lines are the regression lines using all consumer species. (A) $Y = -0.67X - 1.80$, $r = -0.8908$ (B) $Y = -0.50X - 0.67$, $r = -0.8395$, (C) $Y = -0.91X+0.10$, $r = -0.9264$, (D) $Y = -0.86X+1.00$, $r = -0.9382$, (E) $Y = -0.71X - 0.96$, $r = -0.8769$, (F) $Y = -0.69X - 0.37$, $r = -0.9030$.

the few studies available suggest a flat spectrum (Janzen and Schoener, 1968) or a spectrum with several peaks (Schwinghammer, 1981). A uniform biomass spectrum means that the amount of biomass summed over logarithmically-equal size intervals is constant over a large size range. To infer from the biomass spectrum how individual species' biomass changes with increasing body size requires additional information on how the number of species in logarithmically increasing size classes changes with body size.

Conversely, the shape of the biomass spectrum can be deduced from the relationship between numerical abundance and body size only if the frequency distribution of species by body mass is known. For example, with a log-uniform distribution of body size (i.e., constant numbers of species in logarithmically increasing size classes), the slope of the biomass spectrum is equal to 1 plus the slope of the (straight-line) relationship between log numerical abundance and log body mass. To prove the above, let log S be the log number of species as a function log body mass (log BM, here assumed to be a constant k), let log NA be the log numerical abundance as a function of log body mass log BM, and let log T be log total biomass abundance of all species as a function of their log body mass log BM. The biomass spectrum plots log T as a function of log BM. If

$$\log S = k$$

$$\log NA = a + b \log BM$$

then by definition

$$T = S \cdot NA \cdot BM$$

which implies

$$\begin{aligned}\log T &= \log S + \log NA + \log BM = k + \log NA + \log BM \\ &= (k + a) + b \log BM + \log BM = (k + a) + (b + 1) \log BM\end{aligned}$$

Borgman (1987) reviews models of the slope of the biomass size spectrum and Vidondo *et al.* (1997) discuss how to analyze size spectra.

In Tuesday Lake, across all species, biomass abundance increases slightly with increasing body size (Tables 4 and 6). With a log-uniform distribution of body size, this means that the biomass spectrum should have a positive slope. Across all species, the actual spectrum (dash-dotted lines in Fig. 5C and D) has several peaks and does not seem to have a positive slope because species body masses are more log-normal or right-log skewed in distribution (Fig. 9). Within the phytoplankton and zooplankton categories, biomass of the species increases with body size (Table 6). Although the body size distributions of the phytoplankton and zooplankton are skewed as well, the slope of the biomass spectrum is positive within these groups (Fig. 5C and D). The larger species within each category tend to dominate the biomass. In summary, with no clear trend in the biomass spectrum with increasing size, the data of Tuesday Lake conform reasonably well with the flat spectrum found in other studies of pelagic communities.

c. Species Richness, Numerical Abundance and Body Size

The total number of individuals in logarithmically increasing body size classes is the numerical abundance-body size spectrum. Since biomass is the product of numerical abundance and body mass, a flat biomass spectrum implies a decreasing spectrum of numerical abundance. By dividing the log body size axis into size classes that are equal on a logarithmic scale, then counting the number of species (S_i) and the number of individuals (I_i) within each class (i), the body size distribution of species (section V.C.2) is combined with the numerical abundance-body size spectrum of individuals.

Tuesday Lake's numerical abundance-body mass spectrum (dash-dotted lines in Fig. 5A and B) decreases with increasing body size over most of the range in body size, as expected from Tuesday Lake's nearly flat biomass spectrum.

Siemann *et al.* (1996) studied the numerical abundance-body size spectrum and linked it to the body size distribution. In a grassland insect community, Siemann *et al.* (1996) found that both species richness and the number of individuals per body size class were unimodally distributed with respect to body size. The body size class with the largest number of individuals also had the largest number of species. Species richness was positively correlated to the number of individuals per body size class, roughly $S_i \propto I_i^{1/2}$. Consequently, the average number of individuals per species (A_i) scaled as $I_i^{1/2}$, and the size class with the largest number of individuals also had the largest expected numerical abundance of the species.

Tuesday Lake partially replicates the results in Siemann *et al.* (1996). In Tuesday Lake, species richness and numerical abundance per body size class are weakly positively correlated across all species ($r = 0.5312$, $p > 0.2$), as well as within the phytoplankton ($r = 0.7202$, $p > 0.1$) and the zooplankton ($r = 0.8141$, $p > 0.05$). Across all species, the number of species (species richness) and number of individuals peak at a similar (but not identical) body size class (Figs. 5A, B and 9). This size class is located close to the smallest body size class. To the right of this peak, with larger body sizes, the number of species and the number of individuals per size class decrease. For phytoplankton, both species richness and the number of individuals per size class are unimodally distributed with respect to body size, peaking at a similar (but not identical) intermediate body size class. Zooplankton show a similar, but less clear-cut, trend. In general, the number of species and number of individuals per size class co-vary, so that both increase up to a certain body size and then decrease with further increases in body size. These findings are qualitatively consistent with those of Siemann *et al.* (1996).

Contrary to Siemann *et al.* (1996), however, species richness is not allometrically related to the number of individuals in Tuesday Lake. The size class with the largest number of individuals and species was near the smallest size class in Tuesday Lake, not in the middle of the body size range. In the data of Siemann *et al.* (1996), it appeared at first that body size had no effect on the relationship between the number of individuals and the species richness per size class. However, on more careful examination of their data, the relationship between the number of individuals and species richness turns out to be a narrow parabola. Both species richness and the number of individuals per size class increase up to a certain body size and then decrease as body size increases further. In the data of Tuesday Lake, the effect of body size on this relationship is evident, since the parabola is more asymmetrical and its two legs lie further apart than in the data of Siemann *et al.* (1996).

The differences between these two studies may perhaps be understood by analyzing how numerical abundance and species number are associated with body size in a guild versus an entire community. Section V.C.2 suggests that log-normal or log-uniform distributions of species by body size may be a good approximation for a guild or taxonomic group. For a whole community, a right-log skewed or log-hyperbolic distribution may be more likely, and the smallest species tend to have the highest numerical abundance. When the smallest species are the most numerically abundant and the most species-rich in a community, they will dominate the numerical abundance-body size spectrum. For a guild or taxonomic group, numerical abundance and species richness could instead peak at an intermediate body size, which may increase the likelihood that species richness and total numerical abundance per body size class are allometrically related, as found by Siemann *et al.* (1996). Ritchie and Olff (1999) develop a theory of species diversity that predicts the distributions of body size and productivity within a group of species that use the same resource (i.e., a guild).

3. Food Web and Abundance

a. Predator-Prey Abundance Allometry

In Tuesday Lake, the numerical abundance of predators is mostly smaller than that of their prey (Fig. 7A and B). Prey numerical abundance is positively correlated to predator abundance on log-log scales (Table 5). Prey and predator numerical abundances tend to be less similar as prey becomes more abundant (Table 5). Hence, there is a larger relative difference in numerical abundance between phytoplankton and their zooplankton predators (on average) than between zooplankton and their predators.

In Fig. 7A and B, one distinct cluster of points represents phytoplankton prey (circles to the right); another represents zooplankton prey (squares to

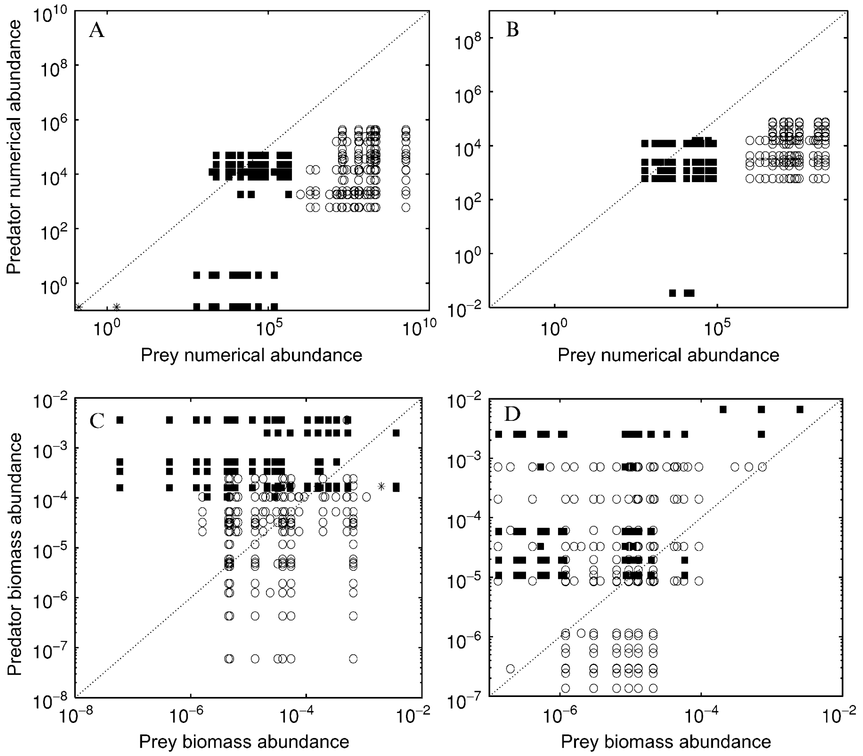

Figure 7 Prey and predator abundance in Tuesday Lake in 1984 (A & C) and 1986 (B & D). Numerical abundance (individuals/m^3 in the epilimnion where species eat) is shown in (A) and (B), and biomass abundance (kg/m^3 in the epilimnion where species eat) in (C) and (D). Dotted line indicates equal prey and predator abundance. Markers are coded according to the prey. Cannibalistic links have not been plotted, but other cyclic links are included. For explanation of symbols see legend to Fig. 2. For correlations and regressions see Table 4. Figure 7A and C reprinted from Cohen *et al.* (2003) with permission from the National Academy of Sciences.

the left). Within the zooplankton prey category, one cluster of data points displays a large difference in numerical abundance between prey and predator (bottom of the graph), while another displays more similar numerical abundance of prey and predator (middle of the graph). These two groups correspond, respectively, to zooplankton consumed by fish and to zooplankton consumed by other zooplankton.

No convincing relationship between predator and prey biomass abundance (Fig. 7C and D) emerges across all species (but see below), even though there is a statistically significant negative correlation between prey and predator biomass abundance (Table 5). The biomass abundance of predators that consume zooplankton was, in most cases, larger than that of their prey (squares in Fig. 7C and D). No clear trend for the biomass abundance of predators that consume phytoplankton (circles in Fig. 7C and D) could be seen.

b. Abundance versus Trophic Height

There is a significant negative correlation between trophic height and numerical abundance (projection on right rear wall in Fig. 2A and B, Table 4) across all species. For the zooplankton, the relationship is nonsignificant. The relationship between trophic height and biomass abundance (Fig. 2C and D, Table 4) across all species and for zooplankton is significantly positive.

c. Trophic Vulnerability and Generality versus Abundance

Trophic generality is weakly negatively correlated ($r = -0.1962$, $p > 0.2$) and trophic vulnerability is positively correlated ($r = 0.4210$, $p < 0.005$) to numerical abundance. With biomass abundance, trophic generality is positively correlated ($r = 0.5609$, $p < 0.005$) and trophic vulnerability is weakly negatively correlated ($r = -0.1228$, $p > 0.2$).

d. Trophic Pyramids

As described later, the three capital letters P, Z, and F in the upper right corner of Fig. 12B plot the aggregated biomass abundance of phytoplankton, zooplankton, and fish, respectively, in 1986 as a function of their values in 1984. The aggregate biomass abundance increased from fish to zooplankton to phytoplankton in 1984, but decreased along this sequence in 1986.

A descriptive pyramid may be constructed by putting species into discrete trophic levels [1 2), [2 3), [3 4), [4 5), [5 6), where, for example, the range of trophic heights [2 3) includes any species with trophic height greater than or equal to 2, up to 2.999999 (i.e., less than 3). Once species are categorized in this way by trophic height, the width of a bar can represent the sum of any characteristic that can be summed over species, such as numerical abundance or biomass abundance. Such a bar plot is merely a histogram turned on its side.

Numerical abundance decreases with increasing trophic height in Tuesday Lake in both years, but biomass abundance is much less regular as a function of trophic height (Fig. 8). In 1984, trophic level 4 has the largest total biomass abundance of all trophic levels (Fig. 8C). In 1986, the distribution of biomass abundance is hourglass-shaped with a biomass minimum on trophic level 3 (Fig. 8D). In retrospect, Figs. 1, 2, 3, and 7 all indicate a pyramid of numbers but not a (monotonic decreasing) pyramid of biomass in Tuesday Lake. Numerical abundance decreases, and biomass abundance sometimes increases, with increasing trophic height (Figs. 1 and 2, Table 4).

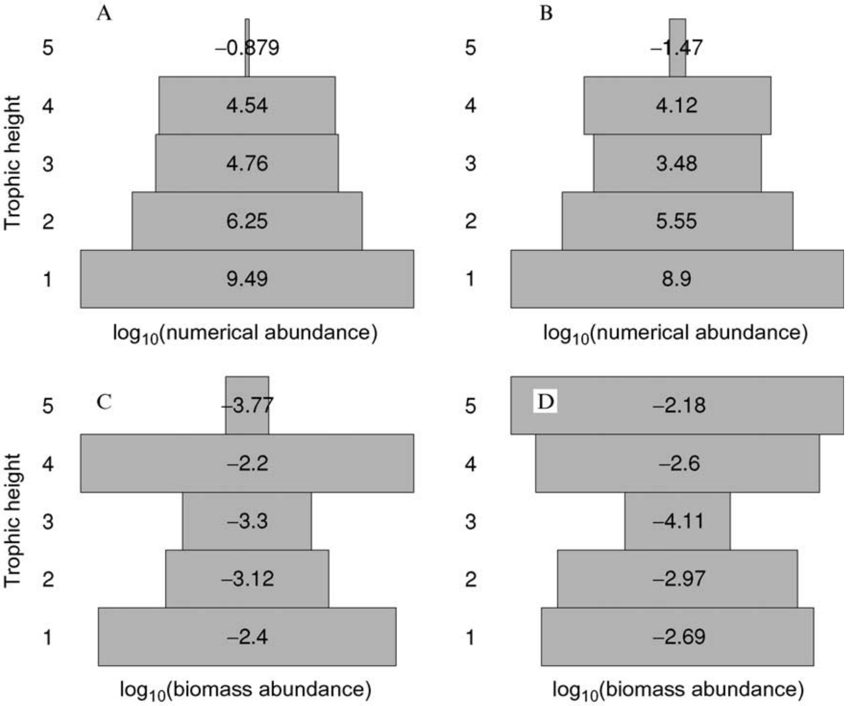

Figure 8 Total abundance by trophic height in Tuesday Lake in 1984 (A & C) and 1986 (B & D). Numerical abundance (individuals/m^3 in the epilimnion where species eat) is shown in (A) and (B), and biomass abundance (kg/m^3 in the epilimnion where species eat) in (C) and (D). Total abundance was calculated as the sum of the species abundance after species were put into discrete trophic height categories [1 2), [2 3), . . . , [4 5). The width of the bars and numbers in bars is the log$_{10}$(abundance).

We hypothesized in Section III.E that the changes in numerical and biomass abundance from one trophic level to the next could be inferred from the corresponding changes in average body mass. In 1984, the difference in average trophic level body mass is large between trophic levels 1 and 2 and between trophic levels 3 and 4, but very small between trophic levels 2 and 3 and between trophic levels 4 and 5. Our hypothesis suggests a large decrease in biomass abundance from trophic level 2 to trophic level 3 and from level 4 to level 5 as well as a small decrease, or even increase, in biomass abundance from trophic level 1 to 2 and from trophic level 3 to 4. In 1986, the difference in average trophic level body mass is large between trophic levels 1 and 2 and between trophic levels 4 and 5, but very small between trophic levels 2 and 3 and between trophic levels 3 and 4, suggesting a large decrease in biomass abundance from trophic level 2 to trophic level 3 and from trophic level 3 to trophic level 4 as well as a small decrease, or even increase, in biomass abundance from trophic level 1 to 2 and from trophic level 4 to 5. As can be seen in Fig. 8, these predictions are only partly true. Trophic levels are, however, crude descriptions of the interactions in a community. In Tuesday Lake, many species feed on multiple trophic levels. Hence, we now focus on individual consumer species.

Only 22 of 264 trophic links that are not cannibalistic connect a predator species and a prey species where predator numerical abundance exceeds prey numerical abundance (Fig. 7A and B), but 163 of 264 noncannibalistic links connect a predator species and a prey species where predator biomass exceeds prey biomass (Fig. 7C and D). Only 1 of 25 predator species has larger biomass abundance than the *total* biomass of all of its prey species.

As predicted in Section III.E, on log-log scales: (1) the ratio between predator and prey numerical abundance is positively correlated to the prey-predator body mass ratio in Tuesday Lake ($p < 0.001$ in both 1984 and 1986); and (2) the ratio between predator and prey biomass abundance is positively correlated to the predator-prey body mass ratio ($p < 0.05$ in 1984 and $p < 0.001$ in 1986). At the level of the individual consumer species, the change along a single trophic link in numerical and biomass abundance can be inferred on average from the body mass ratio of a consumer to its prey. Furthermore, the ratio of consumer biomass to an index of the available resource biomass previously described changes only slightly with increasing consumer size on log-log scales.

Therefore, the larger the relative differences in body size between a predator and its prey, the greater the ratio of consumer to resource biomass abundance will be. The amount of consumer biomass per unit of available prey biomass changes little with increasing consumer size. Despite the lack of complete success in explaining the distribution of biomass abundance across trophic levels in Tuesday Lake by average differences in body mass across trophic levels (Fig. 8), at the level of the individual consumer species the ratio of consumer to resource biomass abundance can be related to the ratio of consumer to resource body mass.

De Ruiter *et al.* (1995) and Neutel *et al.* (2002) analyzed the local asymptotic stability of Lotka-Volterra–type models of real food webs and pointed out some dynamic implications of the shape of biomass pyramids in communities. Instead of drawing the interaction strengths of such models at random from the same distribution for all species as in the work of May (1972), they estimated the interaction strengths from observed abundance data and assumptions of equilibrium feeding rates (de Ruiter *et al.*, 1994). DeRuiter *et al.* (1995) showed that this approach gives rise to interaction strengths that promote local asymptotic stability in some soil ecosystems. Neutel *et al.* (2002) showed that the increase in local asymptotic stability is caused by long trophic loops that contain relatively many weak links and can be inferred from the existence of biomass pyramids in communities. They conclude that a marked decrease in biomass with increasing trophic levels, together with predators feeding on several types of prey, caused weak links to aggregate in long loops, thereby preventing complex food webs from being unstable. That is, compared to communities where interaction strengths are distributed randomly, communities that display pyramids of biomass, and thus a characteristic pattern in the distribution of interaction strengths, are much more likely to have a low maximum loop weight, a characteristic that is shown to increase the probability of local asymptotic stability.

Raffaelli (2002, in his commentary on Neutel *et al.*, 2002) suggested that the slope of the side of the biomass pyramid in a community (assuming such a slope exists) could be an indicator of the stability of that community. Tall, thin pyramids with a high ratio of consumer to resource biomass should be less likely, he suggested, to be stable than short, relatively flat pyramids with a smaller ratio of consumer to resource biomass.

Tuesday Lake does not have a traditional pyramid of biomass when biomass abundance is summed within discrete trophic levels. The significance, if any, of the shape of the biomass distribution by trophic levels for the stability of Tuesday Lake's populations remains unclear. A remaining challenge is to try to parameterize and analyze a dynamical model of the pelagic community of Tuesday Lake.

C. Univariate Distributions

1. The Food Web

Table 3 summarizes and compares the Tuesday Lake pelagic food web in 1984 and 1986. The food web graphs of Tuesday Lake (Fig. 1A and B) show a high density of links and many species of autotrophs, fewer primary consumers, and many fewer secondary consumers.

In the unlumped web, a connected species interacts trophically with roughly 5 to 15 other species (resources and consumers). The zooplankton species are more highly connected than both the phytoplankton and the fish (since the zooplankton have both prey and predators, but the phytoplankton only predators and the fish mainly prey). In both the unlumped web and the lumped or trophic-species web, the number of resources per consumer species is greater than the number of consumers per resource species, as would be expected in a food web of pyramidal structure. The number of species, the number of food chains, food chain length, and linkage density are greater, but connectance is lower, in the unlumped webs than in the trophic-species webs.

The connectance of the food web of Tuesday Lake is considerably greater than that in the catalogues of Cohen *et al.* (1990), Schoenly *et al.* (1991) and Havens (1992), particularly when compared to webs with similar numbers of species. The connectance and number of trophic species of the Tuesday Lake food web are similar to those in the webs described by Warren (1989) and Polis (1991), but connectance is considerably higher than in the more species-rich webs of Hall and Raffaelli (1991), Martinez (1991) and Goldwasser and Roughgarden (1993). Warren (1994) reviews mechanisms affecting the connectance of food webs and the relationship between connectance and web size. In Tuesday Lake, food chains are longer (but not dramatically so) than in many previous studies.

Two empirical findings suggest that real food webs should have a pyramidal trophic structure. First, most species in communities have small bodies. Second, trophic position increases on average with body size. Consequently, food webs should have many species at low trophic heights and few species at high. This conclusion ignores the existence of parasites for which trophic position increases with decreasing body size.

The food web of Tuesday Lake differs from cascade model webs in two important aspects: the web has a pyramidal trophic structure and links are not distributed randomly among species categories, trophic levels, or among species. The pyramidal structure of the webs causes food chains to be shorter than expected under the cascade model for such a highly connected food web. For example, most intermediate species in the Tuesday Lake food web have a trophic height of 2. A food web of the same size and connectance, but in which the intermediate species have more widely varying trophic heights, should have longer food chains.

A pyramidal structure also partly explains the difference between the observed web and the cascade model webs in the distribution of links among basal, intermediate, and top species. By definition, with equal predation probabilities between any potential predator and any potential prey, a high number of basal and a low number of top species, as in the observed web, will lead to a high number of basal-intermediate links and a low number of intermediate-top links (contrary to cascade model predictions). Second, a χ^2-test of the distribution of links shows that the links are not distributed randomly ($p < 0.001$) among the species categories (basal, intermediate, and top species) in the unlumped web or in the trophic-species web. There are more observed than predicted basal-intermediate links and fewer observed than predicted intermediate-intermediate and basal-top links. If species are put into discrete trophic levels as before [1 2), [2 3), . . . , [5 6), then the null hypothesis that the fraction of realized links is constant among trophic levels can be rejected by a χ^2-analysis for the unlumped web ($p < 0.001$). Compared to a random distribution, there is an excess of links between nearby trophic levels. There is also a deficit of links within the second trophic level and between the first trophic level and any level above the second. Links between distant trophic levels not involving the first level occurred approximately as often as expected. Some modifications of the cascade model (Cohen, 1990) have suggested that links could be more confined to species at nearby trophic levels, as seems to be the case here.

Schoener (1989) discussed how average vulnerability and generalization vary with the number of species in a community. He argued that the number of predator species a prey species can effectively defend against could be constrained, as well as the number of prey species a predator species can consume. Schoener (1989) predicted that vulnerability would increase with the number of species in a web, but that generalization would be unaffected by the number of species.

The same arguments predict that *within* a web, vulnerability should increase with *de*creasing trophic height, since the lower the trophic height of species the more potential consumers there are. Generality should increase and then possibly level off with increasing trophic height, since the number of potential prey species of a consumer should increase with the trophic height of the consumer, but the consumer's capacity to feed on the potential prey species is limited. The cascade model also predicts that vulnerability should decrease with increasing trophic height within a web, but does not predict any upper limit to the number of prey species a predator species can consume.

The predictions of the cascade model for the relationships between trophic height on the one hand and trophic generality and trophic vulnerability on the other agree with the observations in the food web of Tuesday Lake. Trophic vulnerability is weakly negatively correlated and trophic generality is weakly positively correlated to trophic height (but not significantly so, $p > 0.05$). Species low in the food web tend to have more predators and fewer prey than species high in the web. Across all species, generality was more weakly correlated to trophic height than vulnerability; generality does not seem to increase without limits with increasing trophic height. It is not clear from these data whether or not there is an upper limit to trophic generality. The data of Tuesday Lake do not refute the hypothesis of unconstrained vulnerability and constrained generality within a food web, but are hardly decisive.

a. The Distribution of Species

The number of basal species slightly exceeds the number of intermediate species, which is far greater than the number of top species in the unlumped web of Tuesday Lake (Table 3). Basal, intermediate, and top species correspond, with a few exceptions, to phytoplankton, zooplankton, and fish. However, in the trophic-species (lumped) web, the number of intermediate trophic species exceeds the number of basal trophic species, which is greater than the number of top trophic species.

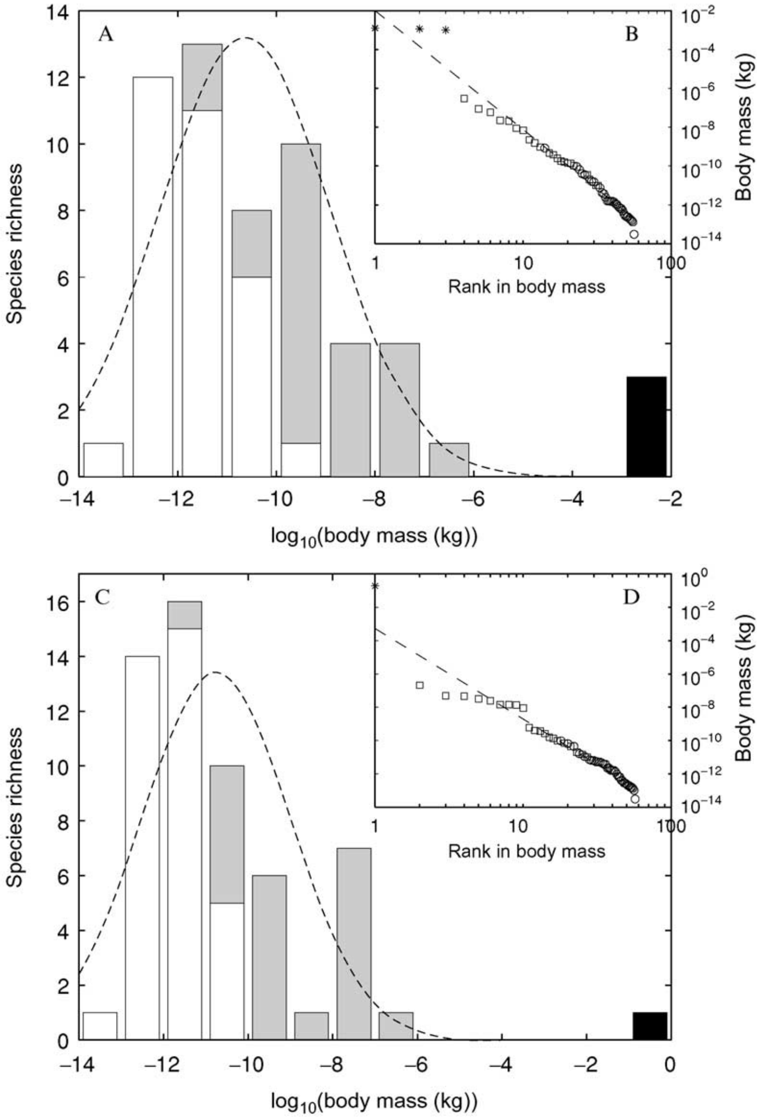

Figure 9 (A & C) The frequency distribution of the number of species (species richness) by log$_{10}$ body mass (kg) in Tuesday Lake in (A) 1984 and (C) 1986. White bars = phytoplankton, gray bars = zooplankton, black bars = fish. Dashed line is the log-normal distribution with the same mean and variance as the observed distribution with fishes excluded. (B & D) Body mass vs. the rank in body mass for the species in Tuesday Lake in (B) 1984 and (D) 1986. Rank goes from largest body mass to smallest. Dashed lines are the ordinary least squares regression lines, using all species. (B) $Y = -6.16X - 1.99$, $r = -0.9861$, (D) $Y = -5.43X - 3.27$,

The cascade model (Section III.A.1) predicts equal numbers of basal and top trophic species. The observed distribution of trophic species in Tuesday Lake (Table 3) is significantly different ($p < 0.01$, χ^2-test) from that predicted by the cascade model, primarily because of a large number of basal trophic species.

b. The Distribution of Trophic Links

In Tuesday Lake, the number of links between basal and intermediate species is approximately twice the number of links between intermediate and intermediate species. These numbers are much greater than the number of links between intermediate and top species. Links between basal and top species are absent. The trophic-species webs have more basal-intermediate links, and fewer basal-top and intermediate top-links, than predicted by the cascade model (Table 3).

c. The Distribution of Chain Lengths

Food chain lengths are more or less normally distributed in both the unlumped web and in the trophic-species web. However, observed food chains are on average (Table 3) much shorter than expected ($p < 0.001$, using the normal deviate as described in Zar, 1999) if links were distributed randomly among the species. To make this comparison, observed noncannibalistic links were randomly redistributed in the upper triangular part of the predation matrix and the observed mean chain length was compared to the distribution of simulated means in 100 replicates.

2. Body Size

The distribution of log body mass of the species in Tuesday Lake (Fig. 9A and C) is skewed and deviates significantly from a normal distribution ($p < 0.001$). The absence of species between the largest zooplankton species and the fish gives a wide gap in the distribution. Other potential gaps are located between 10^{-9} and 10^{-8} kg in both years and between 10^{-10} and 10^{-11} kg in 1984. Holling (1992) reviewed mechanisms that may lead to gaps in the body size distribution in communities. If fish are excluded, the null hypothesis of normality of log body size cannot be rejected ($p > 0.1$). The distributions of log body size do not deviate significantly from normal distributions

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$r = -0.9714$. Y is $\log_{10}$(body mass) and X is $\log_{10}$(rank in body mass). A straight-line relationship between Y and X represents a power-law distribution of body mass. For explanation of symbols, see legend to Fig. 2.

for phytoplankton and zooplankton separately ($p > 0.1$ and $p > 0.25$, respectively).

The slope of the right tail of the body size distribution in Tuesday Lake (fish excluded) is approximately linear on log-log scales and considerably less steep than $-2/3$ both for phytoplankton and zooplankton combined and separately. While the shape and slope of the tail of any distribution can be affected by the choice of histogram intervals, and the tail of the body size distribution need not necessarily be linear on log-log scales (Loder *et al.*, 1997), these possibilities are not of concern here. Tuesday Lake has relatively fewer small species and/or more large species than, for example, the studies reviewed by May (1986). We predict that combining data from a number of similar pelagic systems would add relatively more small species and would decrease the slope of (i.e., make steeper) the right tail of the distribution.

Another way of looking at the distribution of body sizes is to plot the body mass data by their rank. In Tuesday Lake, both allometric and exponential models are good approximations to the relationship between body mass and body mass rank. However, an allometric or power-law model (Fig. 9B and D) fits slightly better than an exponential model for all species ($r = -0.9861$ versus $r = -0.9064$) and for phytoplankton only ($r = -0.9805$ versus $r = -0.9543$), but not for zooplankton only ($r = -0.9620$ versus $r = -0.9855$).

The nearly linear relationship between log body mass and log rank in body mass argues against the log-normality of the distribution of body sizes. If body mass is allometrically related to rank ($BM \propto \text{rank}^{\alpha}$), then the frequency distribution of body mass may be more log-hyperbolic than log-normal. This pattern in Tuesday Lake differs from that reported for North American land mammals (Brown and Nicoletto, 1991), which suggests nearly log-uniform body size distributions at local geographical scales.

3. *Abundance*

Figure 10A and B shows the distributions of numerical abundance and the rank-numerical abundance relation in Tuesday Lake. The numerical abundance of phytoplankton exceeds that of zooplankton on average by approximately 3 orders of magnitude and their distributions do not overlap (Appendices 1A and 2A). The excess of zooplankton over fish numerical abundance is even greater. Across all species, the distribution of numerical abundance consists of three separate distributions, and the deviation from a normal distribution of log numerical abundance is statistically significant ($p < 0.001$). The distributions of phytoplankton and zooplankton abundance do not deviate significantly from log-normal distributions, separately ($p > 0.5$)

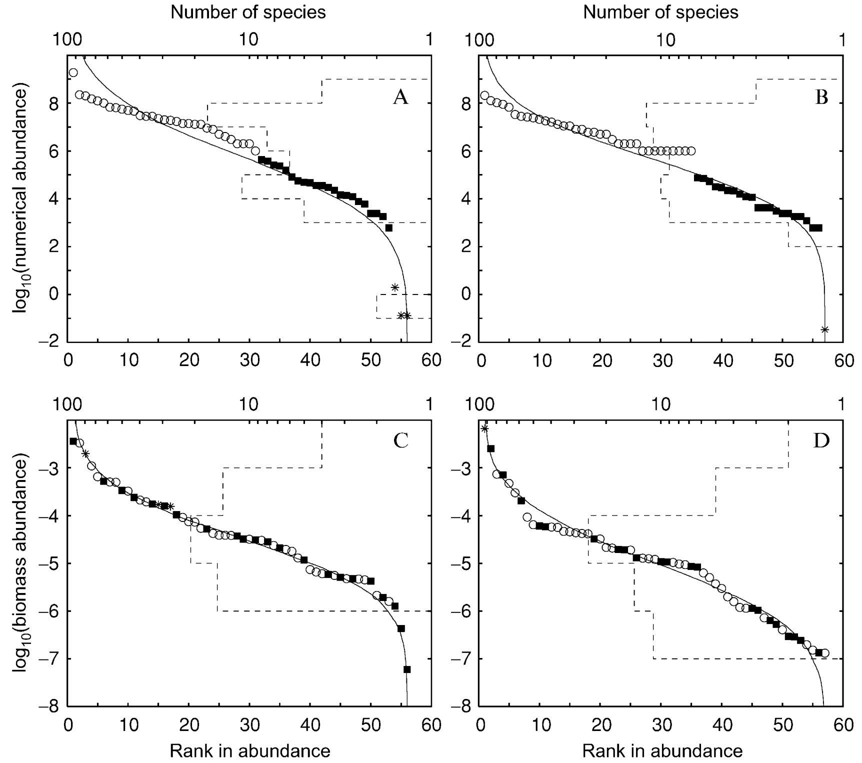

Figure 10 Abundance vs. the rank in abundance for the species in Tuesday Lake in 1984 (A & C) and 1986 (B & D). Rank goes from greatest abundance to smallest. Numerical abundance (individuals/m^3 in the epilimnion where species eat) is shown in (A) and (B), and biomass abundance (kg/m^3 in the epilimnion where species eat) in (C) and (D). For explanation of symbols see legend to Fig. 2. Solid line is the expected rank-abundance relationship assuming that abundance is lognormally distributed. (Drawing 10,000 values from a normal distribution with the same mean and variance as the observed distribution of log abundance and plotting abundance vs. rank in abundance produced the line.) Dashed line is the (log scale) frequency distribution of the number of species (top horizontal axis) by (log scale) numerical abundance in (A) and (B), and by (log scale) biomass abundance in (C) and (D).

or combined ($p > 0.2$). A log-normal distribution of numerical abundance across all species is a reasonable, but not perfect, approximation of the data (solid line in Fig. 10A, using the same mean and variance of log numerical abundance as that in the observed distribution). The observed decrease in log numerical abundance with increasing rank is close to linear within the two plankton categories, indicating departures from log-normality but, on the contrary, agreement with a power-law distribution. The slope of rank-log numerical abundance is shallower for phytoplankton than for zooplankton. Abundance declines more slowly with increasing rank in phytoplankton than in zooplankton. At least in 1984, the plot of log numerical abundance by rank is nearly concave, as predicted in Section III.C for pyramidal food webs. Thus, as predicted, the pyramidal shape of the food web of Tuesday Lake is reflected in the rank-numerical abundance relationship.

Figure 10C and D shows the distributions of biomass abundance and the rank-biomass abundance relations in Tuesday Lake in 1984 and 1986. The ranks of phytoplankton, zooplankton and fish by biomass abundance are mixed so that there are no gaps in the distribution. The difference in biomass abundance between phytoplankton and zooplankton is not significant (one-way ANOVA: $p = 0.33$). A few species dominate the distribution of biomass abundance. The frequency distribution of biomass abundance does not differ significantly from a log-normal distribution, considering all species together (dashed line in Fig. 10C and D, $p > 0.7$) or phytoplankton and zooplankton species separately ($p > 0.25$ and $p > 0.69$, respectively). The observed rank-biomass abundance relationship conforms well, by visual inspection, to that predicted using a log-normal distribution of biomass with the same mean and variance of log biomass abundance as that in the observed distribution (solid line in Fig. 10C and D).

Other models of the rank-numerical abundance relationship include the log-series and broken-stick distributions (for review, see May, 1975). A log-normal distribution is symmetrical and sigmoid in shape when log abundance is plotted as a function of rank, whereas a log-series distribution displays a linear decrease in log abundance with increasing rank. The broken-stick distribution, intermediate between these two, shows an almost linear decrease in log abundance over a large part of the range in rank.

Across all species in Tuesday Lake, the rank-log abundance relationship is not linear for numerical or biomass abundance. However, the relationship is very close to linear for numerical abundance within the species categories (phytoplankton and zooplankton), suggesting a broken-stick or log-series relationship within these species categories.

These results are in line with expectations. A broken-stick relationship is expected when a homogenous group of species (e.g., a guild) divides a limiting resource (or niche space) randomly and each species' numerical abundance is proportional to its share of the resource (MacArthur, 1957), although the same relationship can be derived from quite different assumptions (Cohen, 1968). Empirically, the broken-stick distribution of numerical abundance is usually found in small, homogeneous taxa of similar body size where the numerical abundance is thought to be governed by one (or a few) factors or limiting resources. The log-series distribution is expected when abundance is governed by one or few factors (as in the broken-stick model), but where the partitioning of the resource or niche space is highly hierarchical. Harsh environments with low resource levels or high levels of disturbance are thought to lead to log-series distributions. This distribution is also expected in early successional stages of communities (Gray, 1987). The log-normal distribution applies to larger, more heterogeneous groups where many independent factors affect the abundance. Log-normal distributions of numerical abundance should be associated with undisturbed whole communities in equilibria, where competitive species interactions are abundant (May, 1975; Tokeshi, 1993; but see Nummelin, 1998; Watt, 1998; and Section VI.H).

In Tuesday Lake, the numerical abundance of phytoplankton and zooplankton is not log-normally but rather broken-stick distributed or concave as a function of rank in abundance, and the biomass abundance of all species is approximately log-normally distributed. This result suggests that the numerical abundance of phytoplankton and zooplankton may be affected by a few factors only, but the numerical and biomass abundance across all species may be determined by many independent factors.

The four trophic groups of Tuesday Lake—namely, phytoplankton, herbivorous zooplankton, carnivorous zooplankton, and fish—are fairly distinct with respect to body size. Since numerical abundance is well correlated with body size, these groups separate in a rank-numerical abundance plot. In other communities as well, the rank-numerical abundance plot could be composed of several broken-stick-like distributions. As the number of trophic groups increases and their body sizes overlap, the relationship may increasingly resemble a log-normal distribution.

The relationship between body mass and body mass rank (Section V.C.2) can be used to predict the numerical abundance of the species. Accepting an allometric relationship $BM_i = \alpha i^\beta$ between body mass BM_i and body mass rank i (Fig. 9B and D) and accepting that numerical abundance is allometrically related to body mass (Fig. 5A and B), it follows that numerical abundance is allometrically related to body mass rank as well. The data of Tuesday Lake (Fig. 11A and B) indicate a reasonable approximation to this prediction ($r = 0.9026$). Further, if body mass and numerical abundance are allometrically related to body mass rank, then so is biomass abundance, with an exponent that is determined by the exponents for body mass and numerical abundance. With $BM \propto \text{rank}^{-6.16}$ and $NA \propto \text{rank}^{+5.08}$ in 1984, it follows that $BA \propto \text{rank}^{-1.08}$. That the exponent -1.08 is negative is a prediction that higher ranked (smaller bodied) species will have smaller biomass abundance. As predicted, in Tuesday Lake, smaller species (with higher body mass ranks) tend to have smaller biomass than larger species (Fig. 11C and D).

As approximate linear or allometric relations are compounded by these theoretical calculations, the scatter of data points with respect to the predicted linear relationships noticeably increases (e.g., compare successively

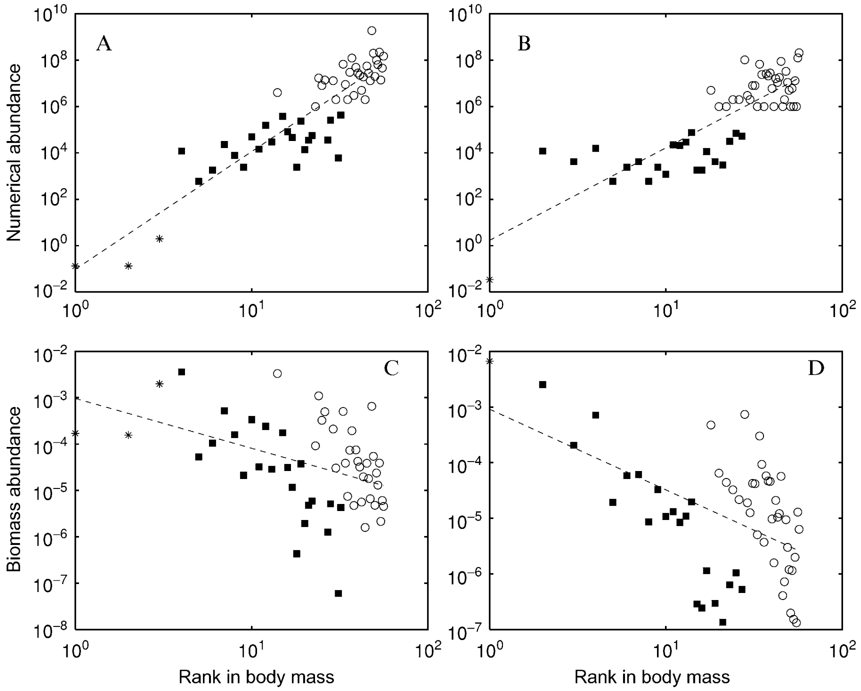

Figure 11 Numerical abundance (A and B, individuals/m^3 in the epilimnion where species eat) and biomass abundance (C and D, kg/m^3 in the epilimnion where species eat) of the species in Tuesday Lake in 1984 (A and C) and 1986 (B and D) plotted as a function of the rank in body mass (where rank goes from largest body mass to smallest). For explanation of symbols see legend to Fig. 2. Dashed lines are the ordinary least squares regression lines, using all species, with $Y = \log_{10}$(abundance) and X = $\log_{10}$(rank in body mass). (A) $Y = 5.08X - 1.02$, $r = 0.9026$ (B) $Y = 3.99X + 0.23$, $r = 0.8344$, (C) $Y = -1.08X - 3.02$, $r = -0.4331$, (D) $Y = -1.45X - 3.04$, $r = -0.5187$.

Figs. 5A and 9B with 12A and finally 12C). A theory of variability is needed along with a theory of expected relationships.

VI. EFFECTS OF A FOOD WEB MANIPULATION ON COMMUNITY CHARACTERISTICS

This section compares Tuesday Lake in 1984 and 1986, one year before and after the 1985 manipulation that removed three species of fish and introduced another species of fish (Section IV.A). Some conclusions on the effect of a food web manipulation on community patterns are suggested.

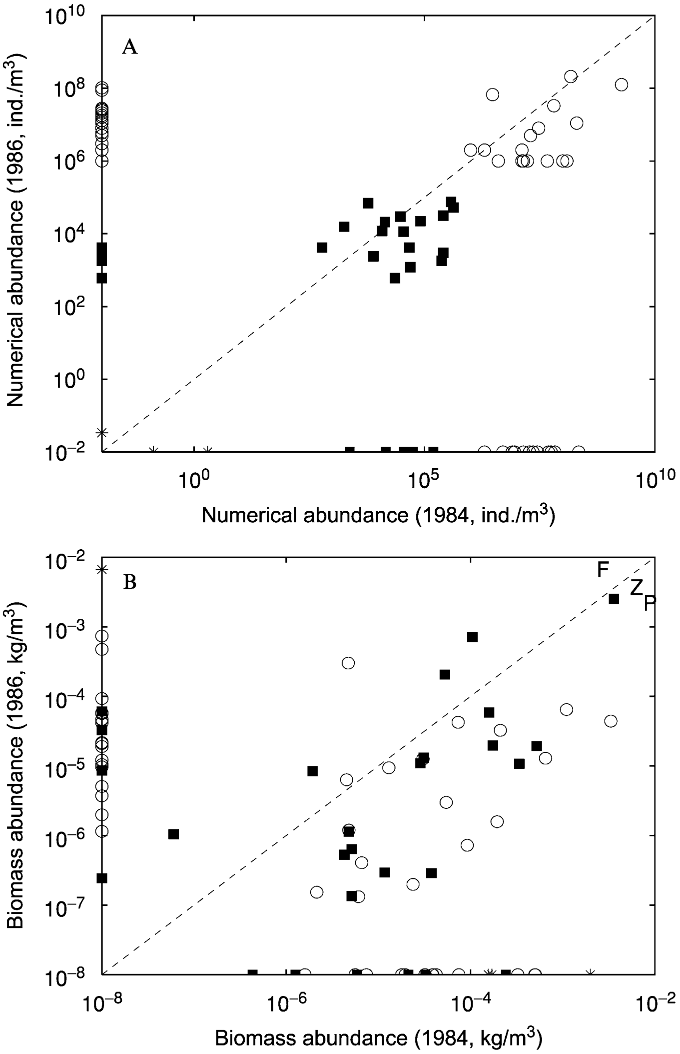

Figure 12 The abundance of the species in Tuesday Lake in 1984 and in 1986. (A) numerical abundance (individuals/m^3 in the epilimnion where species eat) and (B) biomass abundance (kg/m^3 in the epilimnion where species eat). For explanation of symbols see legend to Fig. 2. Symbols on the line $Y = 10^{-2}$ in (A) and $Y = 10^{-8}$ in (B) denote species that were present in 1984 only, those on the line $X = 10^{-2}$ in (A) and $X = 10^{-8}$ in (B) denote species present in 1986 only. Dashed line indicates equal abundance in 1984 and 1986. Letters in (B) indicate the total biomass abundance of all phytoplankton species (P), all zooplankton species (Z) and all fish species (F).

A. Species Composition and Species Turnover

The total number of species remained almost the same, but the species composition changed (Appendices 1A and 2A, Table 3). There were more species of phytoplankton in 1986 than in 1984, but fewer zooplankton and fewer fish species. Most species were phytoplankton in both years. Approximately 60% of the species present in 1984 were also present in 1986. Of the number of phytoplankton species present in a particular year, approximately one-half occurred in that year only. Approximately one-quarter of the zooplankton species were unique to a particular year. Thus, the zooplankton species present were more similar between 1984 and 1986 than the phytoplankton species present. The turnover rate of the phytoplankton species was 32 of 49, or approximately 65.3% (14 species disappeared and 18 species appeared between 1984 and 1986). The turnover rate of zooplankton species was 11 of 27, or approximately 40.7% (6 species disappeared and 5 species appeared).

We lack a theory for what appear to be high rates of species turnover. We do not know if the apparent changes in species composition result from insufficient sampling in both years, or from real local extinctions and introductions, or from both.

B. Food Web, Body Size, and Abundance

Unlike 1984, body mass and trophic height explain approximately equal amounts of variation in numerical abundance in 1986 (Table 4). Multiple regression slightly increases the proportion of variation explained. The food web manipulation decreased the predictive power of body mass for abundance to about the same level as that of trophic height.

C. Food Web and Body Size

Most patterns that involve body size and trophic interactions were similar in 1984 and 1986. In both years, predators generally consumed smaller prey (Fig. 4), trophic vulnerability decreased, and trophic height increased on average with body size (Fig. 2). Unlike 1984, trophic generality did not increase significantly ($p > 0.1$) with body size in 1986. Geometric mean predator size increased more slowly (but not significantly so, $p = 0.2057$) with prey size in 1986 than in 1984 (Table 5), and geometric mean prey size increased with predator size more slowly in 1986 than in 1984, but again not significantly more slowly ($p = 0.1368$). As predicted in Section III.A.2, trophic height is better predicted by log rank in body mass in 1984 than in 1986 ($r_{84}^2 = 0.84$ versus $r_{86}^2 = 0.76$).

D. Food Web and Abundance

In both years, the numerical abundance of predators was generally smaller than that of their prey. But in 1986, fewer zooplankton species than in 1984 were consumed by a predator with a much lower numerical abundance (squares in lower middle part of Fig. 7A and B). The fish predator in 1986 consumed fewer zooplankton species than the fish predators in 1984. In both years, the biomasses of predators consuming zooplankton were mostly higher than that of their prey (squares in Fig. 7C and D). In 1986, there was more variation in both predator and prey biomass (i.e., the squares are more scattered in Fig. 7D than in C). The same is true for the interaction between phytoplankton and their consumers (circles in Fig. 7C and D).

In both years, the food web of Tuesday Lake showed an approximate pyramid of numbers for species in discrete trophic levels (Fig. 8A and B) and for phytoplankton, zooplankton, and fish. Unlike 1984, fish biomass in 1986 exceeded zooplankton biomass, which exceeded phytoplankton biomass (letters F, Z, and P in Fig. 12). For species in discrete trophic levels, the bar plot is hourglass-shaped in 1986 (Fig. 8D). In 1986, of the 236 trophic links that are not cannibalistic, only 17 connected a predator and a prey where predator numerical abundance exceeded prey numerical abundance (3 of these links are involved in cycles), but 157 of 236 noncannibalistic links connected a predator and a prey where predator biomass abundance exceeded prey biomass abundance (3 of these links are involved in cycles). However, only three of 22 predators have larger biomass abundance than the *total* biomass of their respective prey. Thus, as in 1984, numerical abundance of consumers was in general less than that of their prey, whereas biomass abundance of consumers can be either larger or smaller than the biomass abundance of their resources. In general, the biomass abundance of a consumer was smaller than the total biomass of its prey.

E. Body Size and Abundance

The shapes of the abundance-body size relationships are similar in both years. The slope of log numerical abundance as a function of log body size is less steep in 1986 than in 1984 for phytoplankton, zooplankton, and all species (Table 6), but the differences in slope are not significant among the phytoplankton ($p = 0.16$) or zooplankton ($p = 0.28$) or for all species

($p = 0.12$). The abundance-body size spectra (dash-dotted lines in Fig. 5) are also similar in shape in the two years.

Marquet *et al.* (1990) analyzed the effect of human disturbance on the abundance-body size relationship in two rocky intertidal communities. Despite considerable effects of the perturbation on the species composition and food web, the abundance-body size relationship was not influenced. Similarly, in Tuesday Lake, the slopes of the numerical abundance-body size relationship in 1986 and 1984 (Table 6, Fig. 5A and B) are not significantly different.

We speculated in Section III.A.2 that body size and abundance could be better predicted by the rank in body mass in a community before than after a disturbance. For Tuesday Lake, this prediction holds on log-log scales for body mass ($r^2_{84} = 0.97$ versus $r^2_{86} = 0.94$, Fig. 9B and D) and numerical abundance ($r^2_{84} = 0.81$ versus $r^2_{86} = 0.70$, Fig. 11A and B) but not for biomass abundance ($r^2_{84} = 0.19$ versus $r^2_{86} = 0.27$, Fig. 11C and D). However, since the amount of variation in log biomass abundance that is explained by variation in log rank in body mass is very low in both years, this relationship may not be appropriate for detecting effects of disturbance.

F. Food Web

The food webs of Tuesday Lake in 1984 and 1986 are on the whole very similar. However, the unlumped food web in 1986 is a bit less connected, has somewhat fewer trophic links and many fewer food chains and slightly shorter food chains on average than the food web in 1984 (Table 3). Similarly, in the trophic-species web, connectance and the number of trophic links and food chains are lower, and food chains shorter on average, in 1986 than in 1984. Unlike 1984, the food web of 1986 has a few links between basal and top species because, in 1986, one species of zooplankton (*Chonochilus* colonial) was not consumed by any other species.

Connectance decreased between 1984 and 1986, mainly because the three zooplanktivorous fishes removed had a higher connectance to the rest of the web than the introduced, mainly piscivorous, species. The planktivorous fishes consumed 9.7 other species on average, while the piscivorous fish consumed 3 other species. For all other categories, the differences between years were minor.

Unlike 1984, in 1986 the observed distribution of *trophic* species in the categories basal, intermediate, and top (Table 3) was not significantly different ($p > 0.25$, χ^2-test) from that predicted by the cascade model. Furthermore, the null hypothesis of equal fractions of realized links among the different categories could not be rejected ($p > 0.25$) for the trophic-species web in 1986. In neither year were the trophic links randomly distributed in the *unlumped* webs, neither among trophic levels nor among basal, intermediate, and top species. For both the unlumped web and the trophic-species webs, the χ^2-values were considerably smaller in 1986 than in 1984, suggesting that the manipulation of the food web to some extent randomized the distribution of trophic links. As in 1984, the trophic links are not distributed randomly among the species in the upper triangular part of the predation matrix ($p < 0.001$) in the unlumped web.

G. Body Size

The distributions of body size in Tuesday Lake (Fig. 9A and C) are similar and right-log skewed in both years (but do not deviate significantly from a log-normal distribution for phytoplankton or phytoplankton and zooplankton combined). Contrary to 1984, the distribution of log body size of zooplankton in 1986 shows a significant deviation ($p < 0.005$) from normality. Furthermore in 1986, the larger zooplankton species are more horizontally positioned in the rank-body size relationship (Fig. 9B and D) than in 1984.

Holling (1992) proposed that clumps in body size distributions may reflect discontinuities in habitat texture and do not result from, for example, historical or trophic factors. Raffaelli *et al.* (2000) tested the proposition of Holling (1992) by examining the sensitivity to perturbations of the body size distribution in a benthic invertebrate community. Despite large-scale changes in the composition of the community and the abundance of the organisms as a result of the treatments, the locations of the gaps and clumps in the body size distributions were little affected. This finding supports the view that habitat architecture may be responsible for the shape of the body size distribution. That the body size distribution of Tuesday Lake was changed little by the manipulation could indicate that, despite a well-documented ‘‘trophic cascade,’’ trophic factors alone are not the dominating force affecting the distribution of body sizes in this community. This conclusion is corroborated by the analyses of Havlicek and Carpenter (2001), who found that clumps and gaps in plankton size distributions were robust to food web perturbations.

H. Abundance

Total biomass abundance of all species is similar in 1984 and 1986 (1.51×10^{-2} kg/m^3 versus 1.25×10^{-2} kg/m^3). The 1984 total phytoplankton biomass is larger (7.44×10^{-3} kg/m^3 versus 2.19×10^{-3} kg/m^3), the total zooplankton biomass slightly larger (5.38×10^{-3} kg/m^3 versus 3.68×10^{-3} kg/m^3), and the total fish biomass less (2.32×10^{-3} kg/m^3 versus 6.64×10^{-3} kg/m^3) than the corresponding biomass in 1986. An unexpected finding is that, both before and after the 1985 manipulation, the biomass abundance of these three categories of organisms were all within less than one order of magnitude of each another, despite the variation in biomass abundance of individuals species over roughly six orders of magnitude.

Most single species had lower numerical and biomass abundance in 1986 than in 1984 (Fig. 12). For phytoplankton, both log numerical abundance and log biomass abundance of the species are greater in 1984 than in 1986 (one-way ANOVA: $p < 0.02$). For zooplankton, log numerical abundance of the species, but not log biomass abundance, is greater in 1984 than in 1986 (one-way ANOVA: $p < 0.02$). Species that were present in both 1984 and 1986 are, on average, less abundant in 1986 than in 1984, in both numerical abundance (binomial test, $p = 0.002611$) and biomass abundance (binomial test, $p < 0.001$). However, two species of phytoplankton (*Chromulina* sp. and *Dinobryon cylindricum*) and four species of zooplankton (*Ascomorpha eucadis, Daphnia pulex, Holopedium gibberum*, and *Keratella testudo*) had a higher numerical and biomass abundance in 1986 than in 1984. One species of phytoplankton (*Synedra* sp.) had a higher numerical abundance, but not biomass abundance, in 1986 than in 1984.

Relative abundance changed also, but by less than one order of magnitude, for the aggregated major groups. The ratio of phytoplankton biomass to zooplankton biomass to fish biomass (P:Z:F) is 1:0.72:0.31 in 1984 and 1:1.68:3.04 in 1986. The pelagic community is dominated by phytoplankton in 1984 and by fish in 1986. The ratio of isolated species biomass (all phytoplankton) to total phytoplankton biomass is 0.46 in 1984 and 0.071 in 1986. The biomass ratio of small zooplankton (<0.001 mm) to large zooplankton is 0.43 in 1984 and 0.12 in 1986. Larger bodied zooplankton decreased much less than smaller bodied zooplankton. The biomass of isolated phytoplankton decreased more between 1984 and 1986 than the biomass of nonisolated phytoplankton. In summary, between 1984 and 1986, a community with a large amount of "inedible" phytoplankton and a significant amount of small zooplankton shifted to a community dominated by one species of fish, with a much smaller amount of both inedible phytoplankton and small zooplankton. Decreasing absolute abundance for both phytoplankton and zooplankton could result from some abiotic factor. Changes in relative abundance are more likely due to biotic factors.

The slope and shape of the rank-abundance curves (Fig. 10) are similar in 1984 and 1986. The 1984 curve consistently lies above the 1986 curve for biomass abundance, and slightly above for numerical abundance for most ranks, because the abundance in 1984 was greater than in 1986 for most species. The slope of the rank-biomass relationship is initially steeper in 1986 than 1984, mainly due to the dominance of the introduced bass.

The difference in slope between the years is gradually reduced as more species are included.

In communities that have been disturbed, a few dominating, disturbance-resistant, or resilient species may account for the majority of the individuals present. Some studies have proposed that more even or log-normal distributions are typical of undisturbed, species-rich systems (May, 1975; Gray, 1987; Tokeshi, 1993) and that a lack of fit of species' numerical abundance to a log-normal distribution could indicate ecosystem disturbance (Hill *et al.*, 1995). However, Nummelin (1998), analyzing data of forest floor vegetation and four insect groups in logged and unlogged rainforest sites in Uganda, found no support for the hypothesis that undisturbed, but not disturbed communities, are characterized by log-normal distributions of abundance. Irrespective of whether they came from disturbed or undisturbed sites, the distributions of numerical abundance fitted a log-normal distribution. Watt (1998) criticized the use of species-abundance models as indicators of ecosystem disturbance by pointing out that conclusive empirical support for the hypothesis is lacking, that there may be far better ways to assess whether a community has been disturbed or not and that the method provides no quantitative measure of the degree of the disturbance.

In Tuesday Lake, the relative abundance of species was less even in 1984 before the manipulation than in 1986. Regardless of the effects of disturbance on the distribution of abundance, *which* species appear or disappear and *which* species increase or decrease significantly, as a result of a disturbance, could be more interesting and informative than a change (or lack of change) in the shape of a rank-abundance relationship, which ignores species identity or characteristics other than abundance.

I. Conclusions Regarding the Manipulation

The manipulation of the fish species in 1985 gives this study a comparative aspect with the advantage that major parts of the system remained the same before and after the intervention. If we were to compare Tuesday Lake with say, a forest, there would be no way of knowing which of the many differences between the two systems were responsible for any difference in community characteristics observed.

The manipulation produced at most minor differences between 1984 and 1986 in the relationships analyzed in Sections V and VI. The food webs, the rank-abundance relationships, and abundance-body size relationships are similar in shape. In both years, the distribution of body size was right-log skewed, the biomass spectrum across all species flat, and consumers were with few exceptions larger and less numerically abundant than their prey. Species composition changed, as did the numerical and biomass abundance of the species and relative abundance among species categories.

At least three possibilities could explain why the manipulation did not have major effects on community characteristics. First, the lake could be constantly perturbed by natural climatic and biotic fluctuations, so that the human manipulation in 1985 was not different in kind from major upheavals experienced prior to 1984. According to this possibility, nothing much changed because the manipulation was business as usual. Second, the manipulation was not severe enough to affect the community characteristics analyzed here. Third, the major effects of the disturbance take longer than one year to appear.

Testing the first and third alternatives requires a longer time series of detailed observations than the two years available here. We do not know if 1986 represents a transient stage or a new steady state of the system. If the lake is constantly perturbed, all states are transient. The question of dynamics lies beyond the data, and therefore beyond the scope, of the article. Our results do not bear directly on questions of complexity and stability.

If the second alternative is correct, then even though the species changed, many of the constraints on species imposed by ecological interactions did not change. The range in body size and abundance of the species in a whole community is very large compared to the variation in these variables that a food web manipulation may cause for individual species. Effects of a perturbation that is noticeable at the species level could make little difference at the community level.

VII. DATA LIMITATIONS AND EFFECT OF VARIABILITY

The data on Tuesday Lake used here have at least seven limitations that could affect the relationships analyzed.

First, the community boundaries are defined to include the pelagic food web of Tuesday Lake, and to exclude the littoral zone and *Sphagnum* bog that surround the lake. Feedbacks between the littoral and pelagic zones are well documented in other lakes (Boers *et al*., 1991; Persson *et al*., 1992; Carpenter *et al*., 1992). Since Tuesday Lake is a small lake, it has a large ratio of perimeter to lake area and a large ratio of surface to volume. Stomach contents showed that some food of fish was littoral (and even terrestrial in a few cases). These extrapelagic sources may help to explain the high biomass of fish relative to their pelagic food base, and inclusion of the lake's benthic fauna might fill some of the gap in the body size distribution (Fig. 9). The littoral zone in Tuesday Lake could be important. On the other hand, the littoral zone is small and sparsely vegetated, macrophytes are nearly absent, and the few invertebrates (e.g., dragonfly larvae and beetles) are associated with the bog edge. We infer a low benthic production and a minor role for the littoral zone when compared to many other lakes.

Second, the community is incompletely described within its defined boundaries. Two potentially important groups are missing: microbes and parasites. Molecular methods of determining bacterial diversity were not available at the time of this study. Studies of protozoa in Tuesday Lake began in 1988 (Pace, 1993). Bacteria are consumed by mixotrophic phytoplankton, protozoans, and zooplankton. Protozoans are consumed by zooplankton. These feeding relationships constitute the microbial loop, which may be important for nutrient recycling (see Stockner and Porter, 1988; Porter *et al.*, 1988 for reviews). Including the microbial food web may affect the zooplankton body size distribution and related measures, and will probably affect the trophic positions of the zooplankton. Better understanding of the microbial food web in lakes and its linkages to the metazoan food web reported here is an important topic for future research.

Parasites are potentially important regulators of the numerical abundance of species, but are absent from most food web descriptions (except Huxham *et al.*, 1995; Memmott *et al.*, 2000). Since parasites can affect many food web properties (e.g., create looping and increase chain lengths), incorporation of these organisms in food web descriptions is an important goal for future studies (Marcogliese and Cone, 1997).

Despite the extensive sampling, our data are a sample and other species than microbes and parasites may have been missed. However, sampling efforts were similar in the two years, and the same microscopist counted the phytoplankton in both years. Any differences in phytoplankton between the two years are not likely to be an artifact of sampling intensity or analytical bias.

Third, although a community changes in time, the data are static. They represent averages over some time and space. The food web is an accumulated web, not a snapshot of the pelagic community of Tuesday Lake. In reality, many species shift diets in response to their developmental stage and to changing prey availability. The abundance data represent seasonal averages during summer stratification (May to September). In reality, there is a succession of phytoplankton and zooplankton species during a year. Different species gain dominance and peak at different times. The body sizes are average sizes. In reality, a species is composed of a mix of juvenile and adult individuals. The body size of some organisms may range over several orders of magnitude during the growth of individuals. The average depends on the age structure of the population. If body mass increases monotonically with age, then a slowly growing or declining population has a higher concentration of older individuals and therefore a greater mean body mass than a rapidly growing population, which will have a higher proportion of young individuals even if the schedule of body mass as a function of age is the same in both populations. Further, the hypothesis in the previous sentence that body mass increases monotonically with age is not universally valid; on the contrary, individuals in some species shrink on starvation. Our analysis ignores all these complications of change.

An alternative to the approach taken here would be to have data averaged over smaller intervals of time and space. But weekly and even daily data are also averages. To obtain and to analyze temporally better resolved data of the type analyzed here are challenges for future studies (see Schoenly and Cohen, 1991; Closs and Lake, 1994; Tavares-Cromar and Williams, 1996 for studies of temporal variation in food web structure). The connectedness of different static descriptions of a community applies equally well to dynamic data, and dynamic data create many new possibilities for interesting patterns and relationships.

Fourth, not all the data analyzed were independently obtained. Since relative sizes of consumers and potential prey were used in some cases to infer trophic relations, any pattern in the distribution of trophic links (such as the food web) or relationships involving trophic relations and body size (such as predator-prey size relationships) must be interpreted cautiously. Relationships involving body size and abundance (such as rank-abundance or abundance-body size allometries) are unaffected by inferences about the food web.

Fifth, the area or volume where the zooplankton species of Tuesday Lake feed, namely the epilimnion, is not identical to the area or volume where the species live, which is about six times deeper. In which volume should abundance be expressed? We chose here to express the abundance of all species as the number of individuals per cubic meter of water in the epilimnion, where the trophic interactions take place. (The zooplankton migrate daily to the epilimnion to feed.) The zooplankton species live and were sampled in a water volume that is larger by a factor of 6. Appendices 1 and 2 express zooplankton concentrations in the larger volume where they live. For all statistical calculations reported here, we multiplied (only!) zooplankton abundance by 6 to convert the counts of zooplankton to numerical abundance per cubic meter of epilimnion. This adjustment will not qualitatively change our results for numerical abundance because zooplankton numerical abundance is on average three orders of magnitude less than that of phytoplankton. Without multiplying zooplankton numerical abundance by 6, the biomass abundance of phytoplankton would exceed that of zooplankton. After the multiplication by 6, zooplankton biomass abundance is roughly equal to phytoplankton biomass abundance. For the other relationships involving abundance, such as the abundance-body size allometry, there are no qualitative changes. Slopes and intercepts are quantitatively, but not qualitatively, affected by adjusting the abundance of zooplankton, because the adjustment factor is small compared to the range in abundance in the community.

Sixth, despite attempts to make highly reliable measurements (see Section IV.B), uncertainty remains over how well the estimates of body size and abundance reflect the mean values of temporally variable quantities. We tried to analyze the effect of data variability on the relationship between body size and numerical abundance (Fig. 5). To simulate variation in the data, we randomly and independently perturbed the 1984 estimates of body mass and numerical abundance of each species simultaneously. The perturbed values were drawn from a log-normal distribution with a mean equal to the observed log value and a standard deviation of 0.25 (approximately 95% of the perturbed values will be found within an order of magnitude of the observed values). The variance of the slopes of the linear regression of log numerical abundance as a function of log body mass in 10,000 replicates was 3.38×10^{-4} (CV = 2.25%, mean ± 95% CI: -0.8187 ± 0.00036). This pattern is rather robust to moderate random variation, given the particular model assumptions used here. A different distribution of perturbed values or allowing correlated variation in the data (so that a larger than observed value for body size is associated with a larger than observed abundance) may alter the conclusion. The approach outlined here may in principle be used to analyze effects of variation on other patterns. The primary reason for the robustness of the relationship to variation in the data is the large range of body size and abundance of the species in Tuesday Lake. Body mass and numerical abundance span approximately 12 and 10 orders of magnitude, respectively. Variation within an order of magnitude at the species level will have small effects at the level of the community.

Seventh, this study has a sample size consisting of just one ecosystem, Tuesday Lake. We do not know which relationships described here are unique to Tuesday Lake and which hold in other communities. It would be highly desirable to carry out parallel analyses to test the generality of the patterns described here using data for several different ecosystems, for example, above-ground terrestrial, pedologic, pelagic, and benthic marine, estuarine, and limnic ecosystems (Chase, 2000; Jan Bengtsson, personal communication, 2002). While our present sample size of one ecosystem is not a persuasive basis for generalization, it represents a first step. Our example is intended as a challenge to experts who know the data on other ecosystems.

In summary, the extent to which the data limitations mentioned above affect the patterns reported here is unknown. We therefore call for improved data from similar and different ecosystems to corroborate or challenge the relationships reported here.

VIII. CONCLUSIONS

This study has analyzed the relationships among species abundance, body size, and the food web in the pelagic community of Tuesday Lake. This analysis illustrates a new integrated approach, using a new data structure for the description of ecological communities. A traditional food web (Camerano, 1880) is a directed graph in which each node is associated with a species' name and each arrow (link or directed edge) indicates a flow of nutrients from a resource species to a consumer species. The new data structure introduced here associates with each node a vector of quantitative attributes of the named species (Fig. 1). In this study, the attributes are body size and abundance (numerical and biomass). Since the relationship among these community characteristics affects many other aspects of the community, awareness of these connections is needed for a better understanding of the ecological constraints acting on species assemblages.

In the famous tale of the blind men and the elephant, the blind men cannot agree because they are experiencing different parts of the strange animal. The diverse patterns analyzed here are like the trunk, ears, legs, and tail of the elephant: they all follow from the food web and the body size and abundance of the species in the community (Cohen, 1991). A clear vision of these three features, and their connectedness, gives a more comprehensive picture of the ecological elephant (Table 1). We have identified some relationships that rarely have been analyzed for entire communities before (e.g., trophic generality and vulnerability with respect to trophic height, body size, and abundance of the species within a food web; abundance-body size allometry; predator-prey abundance allometry). The relationship between the trophic height of a species and its body size or abundance has, to our knowledge, not been analyzed quantitatively in a community before. Many previously reported patterns have been confirmed. Furthermore, body size and abundance are often claimed to be allometrically related, but the exact form of the relationship is disputed. Whole communities have rarely been analyzed before. New insights have been gained from a knowledge of the trophic relations among the species. Many of the relations appear to be very robust to a major perturbation (Section VI). If this finding for Tuesday Lake applies generally, then communities may have properties that are fairly consistent and predictable.

Different fields of ecology have focused on different sets of the bivariate relationships in Table 1. For example, the biomass abundance-body size spectrum (Section V.B.2.b) has mainly been studied by limnologists (Kerr and Dickie, 2001), while studies of rank-abundance and predator-prey body size relationships mainly are confined to the field of terrestrial ecology.

Integration of the relationships as suggested here could bring these fields together.

At least three major tasks remain: (1) to test the generality of the present findings by analyzing comparable or better data on other communities, including temporal and spatial variation and heterotrophic microorganisms and parasites; (2) to explain whatever patterns consistently emerge with persuasive quantitative theory; and (3) to extend and apply the data structure introduced here, which is formally a directed graph with vector-labeled nodes.

Here are some examples of how the data structure introduced here could be extended and applied. If dates and places of observation were added to data on body size and abundance associated with each node of a food web, a dynamic, spatially explicit description would become possible. If each node also had an associated Leslie matrix, in which fertility coefficients depended on the abundance of species consumed by the nodal species, and in which the survival coefficients depended on the abundance of the species that consume the nodal species, then dynamic modeling of age- or stage-structured populations (Caswell, 2001) could be integrated with dynamic food web modeling. Such modeling would promote the general integration of population biology and community ecology. If chemical compositions of each species were added to the vector of attributes (Sterner *et al.*, 1996; Sterner and Elser 2002) and if all coefficients of the Leslie matrix also took explicit account of abiotic environmental variables (such as chemical concentrations of nutrients and toxins), then population biology and community ecology could move toward an integration with biogeochemistry. Additional future prospects are suggested by Brown and Gillooly (2003).

A vector of attributes could be associated with each edge to quantify the flows of energy (Baird and Ulanowicz, 1989) and materials (nutrients and toxins and inert matter), including averages and measures of temporal and/or spatial variation. Empirically estimated energy flows in a community could be compared with the flows predicted by the mortality rates derived from the Leslie matrices, dynamically and at steady state.

The new data structure illustrated in this study and future extensions hold the potential to embed studies of food web structure in a general framework for analyzing communities and ecosystems.

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APPENDICES

Appendix 1A Species in Tuesday Lake in 1984

Id #	Species name (category)	*BM*	*NA*	*TS*	*TH*
1	*Nostoc* sp. (P)	7.97×10^{-13}	2.00×10^{6}	1	1
2	*Arthrodesmus* sp. (P)	1.52×10^{-12}	4.90×10^{7}	2	1
3	*Asterionella formosa* (P)	1.12×10^{-12}	5.00×10^{6}		
4	*Cryptomonas* sp. 1 (P)	2.03×10^{-13}	6.40×10^{7}	3	1
5	*Cryptomonas* sp. 2 (P)	1.51×10^{-12}	2.80×10^{7}	4	1
6	*Chroococcus dispersus* (P)	2.39×10^{-13}	2.00×10^{7}	3	1
7	*Closteriopsis longissimus* (P)	2.37×10^{-13}	1.00×10^{8}	5	1
8	*Chrysosphaerella longispina* (P)	8.31×10^{-10}	4.00×10^{6}		
9	*Dinobryon bavaricum*[†] (P)	2.44×10^{-12}	3.00×10^{7}	6	1
10	*Dinobryon cylindricum*[†] (P)	1.57×10^{-12}	3.00×10^{6}	1	1
11	*Dactylococcopsis fascicularis* (P)	1.32×10^{-13}	4.60×10^{7}	1	1
12	*Diceras* sp. (P)	1.53×10^{-13}	1.40×10^{7}		
13	*Dictyosphaerium pulchellum* (P)	5.07×10^{-13}	1.30×10^{7}	4	1
14	*Dinobryon sertularia* (P)	1.52×10^{-11}	2.00×10^{6}	7	1
15	*Dinobryon sociale* (P)	6.41×10^{-13}	2.80×10^{7}	4	1
16	*Glenodinium quadridens* (P)	7.54×10^{-12}	6.70×10^{7}	8	1
17	*Microcystis aeruginosa*[‡] (P)	1.62×10^{-11}	1.30×10^{7}	6	1
18	*Mallomonas* sp. 1 (P)	1.03×10^{-12}	1.90×10^{7}	7	1
19	*Mallomonas* sp. 2 (P)	1.41×10^{-12}	2.27×10^{7}	2	1
20	Unclassified *flagellates* (P)	3.46×10^{-13}	1.88×10^{9}	3	1
21	*Peridinium limbatum* (P)	6.46×10^{-11}	1.70×10^{7}	6	1
22	*Peridinium cinctum* (P)	4.06×10^{-11}	8.00×10^{6}	7	1
23	*Peridinium pulsillum* (P)	1.58×10^{-12}	1.23×10^{8}	4	1
24	*Peridinium wisconsinense* (P)	3.56×10^{-11}	1.40×10^{7}	6	1
25	*Chromulina* sp. (P)	3.03×10^{-14}	1.49×10^{8}	3	1
26	*Rhizosolenia* sp. (P)	6.86×10^{-13}	5.60×10^{7}		
27	*Selenastrum minutum* (P)	2.72×10^{-13}	2.00×10^{8}	3	1
28	*Spinocosmarium* sp. (P)	3.71×10^{-12}	2.00×10^{6}		
29	*Staurastrum* sp. (P)	4.30×10^{-12}	9.00×10^{6}		
30	*Synedra* sp. (P)	9.18×10^{-11}	1.00×10^{6}	6	1
31	*Trachelomonas* sp. (P)	1.75×10^{-13}	2.22×10^{8}	3	1

(*Continued*)

Appendix 1A (*Continued*)

Id #	Species name (category)	*BM*	*NA*	*TS*	*TH*
32	*Ascomorpha eucadis*[¥] (Z)	1.40×10^{-10}	2.30×10^{3}	9	2
33	*Synchaeta sp.*[¥] (Z)	9.50×10^{-10}	5.00×10^{3}	9	2
34	*Bosmina longirostris* (Z)	1.55×10^{-9}	2.59×10^{4}	10	2
35	*Conochilus* (solitary) (Z)	3.50×10^{-11}	6.00×10^{3}	11	2
36	*Cyclops varians rubellus* (Z)	2.04×10^{-8}	1.30×10^{3}	12	3
37	*Diaphanosoma leuchtenbergianum* (Z)	2.24×10^{-9}	2.40×10^{3}	13	2
38	*Daphnia pulex* (Z)	5.80×10^{-8}	3.00×10^{2}	14	2.42
39	*Filinia longispina* (Z)	1.80×10^{-10}	4.00×10^{2}	15	2
40	*Conochiloides dossuarius* (Z)	1.60×10^{-10}	3.91×10^{4}	11	2
41	*Gastropus stylifer* (Z)	1.35×10^{-10}	5.90×10^{3}	15	2
42	*Holopedium gibberum* (Z)	8.75×10^{-8}	1.00×10^{2}	16	2
43	*Kellicottia* sp.[∈] (Z)	2.00×10^{-11}	4.26×10^{4}	15	2
44	*Keratella cochlearis*[¥] (Z)	1.00×10^{-11}	7.11×10^{4}	9	2
45	*Keratella testudo* (Z)	1.00×10^{-11}	1.00×10^{3}	15	2
46	*Leptodiaptomus siciloides* (Z)	8.80×10^{-9}	4.00×10^{2}	17	2
47	*Orthocyclops modestus* (Z)	2.29×10^{-8}	3.80×10^{3}	18	4
48	*Ploesoma* sp. (Z)	1.05×10^{-10}	9.30×10^{3}	15	2
49	*Polyarthra vulgaris* (Z)	4.65×10^{-10}	6.26×10^{4}	15	2
50	*Trichocerca multicrinis* (Z)	2.50×10^{-10}	7.80×10^{3}	15	2
51	*Trichocerca cylindrica* (Z)	3.80×10^{-10}	1.36×10^{4}	15	2
52	*Tropocyclops prasinus* (Z)	6.85×10^{-9}	8.20×10^{3}	12	3.5
53	*Chaoborus punctipennis* (Z)	3.00×10^{-7}	2.00×10^{3}	19	4.40
54	*Phoxinus eos* (F)	1.01×10^{-3}	1.97×10^{0}	20	4.97
55	*Phoxinus neogaeus* (F)	1.17×10^{-3}	1.33×10^{-1}	20	4.97
56	*Umbra limi* (F)	1.29×10^{-3}	1.32×10^{-1}	21	5.64

[†]: eat bacteria.

[‡]: Can be egested by 37, but survives with nutrients absorbed from predator's digestive tract.

[¥]: Is killed by 37, but not consumed.

[∈]: *K. bostoniensis* + *K. longispina.*

Category P: phytoplankton, Z: zooplankton, and F: fish. *BM*: Body mass (kg), *NA*: Numerical abundance (individuals/m^3), *TS*: Trophic species number (Appendix 1B), *TH*: Trophic height of species (see text). All *NA* values for zooplankton species only should be multiplied by 6 to convert them to concentrations in the epilimnion, as in all statistical calculations reported here. Missing values indicate isolated species.

Appendix 1B Predation matrix of the trophic species web of Tuesday Lake in 1984 (isolated species not included). Biological species with identical prey and identical predators are aggregated into trophic species according to *TS* column of Appendix 1A

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0
3	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	0	0	0	0
4	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0
9	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
11	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
12	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
15	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
17	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Appendix 2A Species in Tuesday Lake in 1986

Id #	Species name (category)	*BM*	*NA*	*TS*	*TH*
1	*Anabaena circinalis* (P)	1.91×10^{-13}	6.00×10^{6}		
2	*Ankyra judayi* (P)	1.53×10^{-13}	1.30×10^{7}	1	1
3	*Cryptomonas* sp. 1 (P)	2.85×10^{-13}	3.30×10^{7}	2	1
4	*Cryptomonas* sp. 3 (P)	6.72×10^{-13}	1.80×10^{7}	3	1
5	*Cryptomonas* sp. 4 (P)	1.64×10^{-12}	2.80×10^{7}	3	1
6	*Chroococcus dispersus* (P)	2.39×10^{-13}	5.00×10^{6}	2	1
7	*Chroococcus limneticus* (P)	1.31×10^{-12}	1.60×10^{7}	2	1
8	*Cosmarium* sp. (P)	3.71×10^{-12}	1.00×10^{6}	3	1
9	*Closteriopsis longissimus* (P)	1.98×10^{-13}	1.00×10^{6}	4	1
10	*Chrysosphaerella longispina* (P)	4.40×10^{-11}	1.00×10^{6}		
11	*Dinobryon bavaricum* (P)	5.29×10^{-12}	8.00×10^{6}	5	1
12	*Dinobryon cylindricum* (P)	4.48×10^{-12}	6.70×10^{7}	5	1
13	*Dactylococcopsis fascicularis* (P)	1.32×10^{-13}	1.00×10^{6}	3	1
14	*Diceras* sp. (P)	1.53×10^{-13}	1.00×10^{6}		
15	*Dictyosphaerium pulchellum* (P)	4.07×10^{-13}	1.00×10^{6}	3	1
16	*Dinobryon sertularia* (P)	6.28×10^{-12}	2.00×10^{6}	3	1
17	*Sphaerocystis schroeteri*† (P)	1.08×10^{-11}	2.00×10^{6}	3	1
18	*Gloeocystis* sp.‡ (P)	9.46×10^{-11}	5.00×10^{6}	5	1

(*Continued*)

Appendix 2A (*Continued*)

Id #	Species name (category)	*BM*	*NA*	*TS*	*TH*
19	*Glenodinium pulvisculus* (P)	5.20×10^{-12}	8.00×10^{6}	3	1
20	*Microcystis aeruginosa*[‡] (P)	1.62×10^{-11}	2.00×10^{6}	5	1
21	*Mallomonas*-spiny sp. 1 (P)	2.22×10^{-12}	2.10×10^{7}		
22	*Mallomonas*-spiny sp. 2 (P)	2.22×10^{-12}	2.60×10^{7}		
23	unclassified *microflagellates* (P)	1.02×10^{-13}	1.26×10^{8}	2	1
24	*Oocystis* sp. 1 (P)	3.86×10^{-12}	2.40×10^{7}	3	1
25	*Oocystis* sp. 2 (P)	6.32×10^{-12}	3.00×10^{6}	3	1
26	*Oscillatoria* sp. (P)	1.61×10^{-12}	6.00×10^{6}	6	1
27	*Peridinium limbatum* (P)	6.46×10^{-11}	1.00×10^{6}	5	1
28	*Peridinium pulsillum* (P)	1.58×10^{-12}	1.00×10^{6}	3	1
29	*Quadrigula lacustris* (P)	7.13×10^{-12}	1.03×10^{8}	5	1
30	*Quadrigula* sp. 2 (P)	9.48×10^{-13}	1.10×10^{7}	5	1
31	*Chromulina* sp. (P)	3.03×10^{-14}	2.09×10^{8}	2	1
32	*Schroederia setigera* (P)	6.37×10^{-13}	8.90×10^{7}	3	1
33	*Selenastrum minutum* (P)	2.72×10^{-13}	1.10×10^{7}	2	1
34	*Synedra* sp. (P)	3.62×10^{-13}	2.00×10^{6}	5	1
35	*Synura* sp. (P)	5.07×10^{-12}	1.00×10^{6}		
36	*Ascomorpha eucadis* (Z)	4.00×10^{-10}	3.50×10^{3}	7	2
37	*Conochilus* (colonial) (Z)	1.46×10^{-8}	7.00×10^{2}	8	2
38	*Conochiloides dossuarius* (Z)	1.60×10^{-10}	3.00×10^{2}	9	2
39	*Cyclops varians rubellus* (Z)	2.44×10^{-8}	4.00×10^{2}	10	3
40	*Diaptomus oregonensis* (Z)	1.44×10^{-8}	1.00×10^{2}	11	2
41	*Daphnia pulex* (Z)	4.56×10^{-8}	2.60×10^{3}	12	2.39
42	*Daphnia rosea* (Z)	1.36×10^{-8}	4.00×10^{2}	13	2.47
43	*Gastropus hyptopus* (Z)	1.35×10^{-10}	3.00×10^{2}	14	2
44	*Gastropus stylifer* (Z)	1.00×10^{-10}	1.90×10^{3}	15	2
45	*Holopedium gibberum* (Z)	4.89×10^{-8}	7.00×10^{2}	16	2
46	*Kellicottia bostoniensis* (Z)	2.00×10^{-11}	5.30×10^{3}	14	2
47	*Kellicottia longispina* (Z)	4.50×10^{-11}	5.00×10^{2}	14	2
48	*Keratella cochlearis* (Z)	1.00×10^{-11}	8.80×10^{3}	17	2
49	*Keratella testudo* (Z)	1.50×10^{-11}	1.16×10^{4}	14	2
50	*Orthocyclops modestus* (Z)	3.22×10^{-8}	1.00×10^{2}	10	3.5
51	*Polyarthra vulgaris* (Z)	2.60×10^{-10}	1.26×10^{4}	14	2
52	*Synchaeta* sp. (Z)	3.70×10^{-10}	4.90×10^{3}	17	2
53	*Trichocerca cylindrica* (Z)	5.90×10^{-10}	3.70×10^{3}	14	2
54	*Trichocerca multicrinis* (Z)	7.00×10^{-11}	7.00×10^{2}	14	2
55	*Tropocyclops prasinus* (Z)	8.95×10^{-9}	2.00×10^{2}	18	4.02
56	*Chaoborus punctipennis* (Z)	2.10×10^{-7}	2.00×10^{3}	19	4.39
57	*Micropterus salmoides* (F)	1.95×10^{-1}	3.40×10^{-2}	20	5.24

[†]: Can be egested by its predators, but survives with nutrients absorbed from predators' digestive tract.

[‡]: Can be egested by 41, but survives with nutrients absorbed from predator's digestive tract.

Category P: Phytoplankton, Z: Zooplankton and F: Fish. *BM* Body mass (kg), NA: Numerical abundance (individuals/m^3), *TS*: Trophic species number (Appendix 2B), *TH*: Trophic height of species (see text). All *NA* values for zooplankton species only should be multiplied by 6 to convert them to concentrations in the epilimnion, as in all statistical calculations reported here.

Missing values indicate isolated species.

Appendix 2B Predation matrix of the trophic species web of Tuesday Lake in 1986 (isolated species not included). Biological species with identical prey and identical predators are aggregated into trophic species according to *TS* column of Appendix 2A

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
2	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1	0	0	0
3	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
4	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
10	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
11	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
14	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
15	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
17	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0
18	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

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