

Estimating Relative Energy Fluxes Using the Food Web, Species Abundance, and Body Size

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I. SUMMARY

Given the food web, mean body sizes, and numerical abundances of species in an ecological community, four new models to estimate the relative flux of energy along any pair of links were developed. The models were tested using the data collected by Stephen R. Carpenter and colleagues in Tuesday Lake,

Michigan, to describe the pelagic food web together with mean body mass (M) and population density (N) of each species. In the metabolic action model, flux was proportional to the product of prey population production times predator population consumption, using allometric formulas for these quantities. This model tested marginally better than the other models and was more easily visualized and applied. Two other models were based on the same allometric formulas, and the fourth was based on an allometric relationship of Emmerson and Raffaelli (2004) between predator impact on prey and the ratio of predator and prey body mass. A new graphical summary of a food web took the $\log(M)$ versus $\log(N)$ plot of Cohen, Jonsson and Carpenter (2003) and added equiproduction and equiconsumption lines, making it possible to visualize species M and N data, trophic data, allometric data, and relative flux data under any of the four models, all from a single plot. The flux models were used to compare several definitions of trophic height; some definitions were more likely than others to correspond to methods of measuring trophic height based on stable isotope analysis. The flux models were also used to develop an ecosystem sampling theory that associated p-values to statements that a given trophic link did not occur in a system. This theory may assist in choosing ecosystems for study that are likely to yield the highest-quality data with the least sampling effort.

II. INTRODUCTION

This report proposes, evaluates, and applies some methods of estimating relative energy fluxes through the trophic links of a community food web, given the average body mass (M) and the numerical abundance per unit of habitat (N) of each species in the web. Previous efforts to estimate fluxes in food webs based on demographic and metabolic data include Moore *et al.* (1993), deRuiter *et al.* (1995), Rott and Godfray (2000), Ulanowicz (1984), Bersier *et al.* (2002), and others.

The combination of food web data with species' M and N data—hereafter called an (M, N)-web—has been explored by Cohen *et al.* (2003), Jonsson *et al.* (2005), and Reuman and Cohen (2004). Those studies and the current study used data collected by Stephen R. Carpenter and colleagues from the community in the nonlittoral epilimnion in Tuesday Lake, Michigan, a small temperate lake that is further described in the Data section below. To our knowledge, Tuesday Lake is the only system with complete, published data on the community food web and the mean body mass and numerical abundance of each species.

Four new models of relative flux through the trophic links of an (M, N)-web were developed in this study, and the models were illustrated using the data of Tuesday Lake. Three models were based on standard allometric

formulas of population production and population consumption (Peters, 1983). The first, called the metabolic action (MA) model, set flux through a link proportional to the product of the production of the prey times the consumption of the predator. The fourth flux model was based on an empirical allometric formula from Emmerson and Raffaelli (2004) that related numbers of prey eaten by a predator per unit time to the body mass ratio of predator to prey.

Since direct, empirical measurements of the fluxes in Tuesday Lake were not available, the models were tested indirectly. The first testing method computed, for each intermediate species, the ratio of the total estimated flux into that species divided by the total estimated flux out of that species. Models were judged on their ability to produce ratios greater than 1. Ratios less than 1 were considered unrealistic because they indicated more estimated energy flux out of a species than into it. The second testing method considered the models' ability to estimate fluxes that agreed with allometric estimates of population production and population consumption for all species simultaneously. The MA model performed slightly better than the others on these tests, but its victory was not decisive enough to discard the other models. The main weakness of this study was its inability to compare model-estimated fluxes to empirically measured fluxes, which were unavailable for Tuesday Lake. It may be possible to use the unpublished data of the Broadstone Stream ecosystem (Woodward *et al.*, 2005) and the Ythan Estuary system (Emmerson and Raffaelli, 2004) to test the present models directly.

The MA model was more simply defined, and more easily visualized and applied, than the other models. Starting from the food web plot of Cohen *et al.* (2003) and Jonsson *et al.* (2005) on $\log(M)$ (vertical) versus $\log(N)$ (horizontal) axes, this study added equiproduction and equiconsumption lines using the standard allometric formulas of Peters (1983) for population production and consumption. These lines had slopes of $-1/\alpha$ and $-1/\beta$, where α and β are the exponents of M in the allometric formulas for production and consumption, respectively. The strength of flux under the MA model could be easily visualized using these lines. The resulting single plot summarized many aspects of the food web data: body masses, numerical abundances, trophic relations, population production and consumption, and estimated fluxes.

The MA and other models were also applied to a flux-based definition of trophic level (Adams *et al.*, 1983; Winemiller, 1990). These definitions of trophic level gave values that were on average less than the chain-length-based definitions of Cohen and Luczak (1992), Cohen *et al.* (2003), Jonsson *et al.* (2005), and Reuman and Cohen (2004). The flux-based definitions would probably produce values more similar to the stable isotope analysis measurements of trophic height of Jennings *et al.* (2002a,b), and Post (2002).

The flux models were also used to create a model of sampling effort. Assuming sampling methods with certain properties, this model associates a p-value with a claim that a given link did not occur in a web, or that, if it did occur, its flux was less than a certain value. If this model was tested and verified experimentally, it could be used to attach p-values to statistical descriptions of food web topology and (M, N) -web structure. The model could be a new tool for understanding how food web structure varies with varying sampling intensity. The model may also be useful in identifying which ecological systems can be sampled for relatively complete community food webs with minimal sampling effort.

Laboratory biologists have a tradition of choosing a few model organisms in which to study general phenomena. Some of these organisms are carefully chosen for the ease with which they can be manipulated or for the ability to generalize the results of study. In recent years, several model food webs and some model (M, N) -webs have emerged (including, but not limited to, Tuesday Lake, Ythan Estuary, Broadstone Stream, and Little Rock Lake). These webs and others may be the current food web theorists' analog to the laboratory biologists' *E. coli*, *C. elegans*, *Drosophila*, zebrafish, and mouse. The data on some of these systems were gathered expressly to completely document a community food web. The data of others were gathered with other goals in mind. To our knowledge, the completeness of food web information that can be expected from a given sampling effort has not been analyzed mathematically before. To produce better data on model ecosystems, such analysis should be combined with the usual considerations of the practicalities of observation and sampling.

Flux estimates have been used in other studies to generate Lotka-Volterra coefficients and to address questions of stability (Moore *et al.*, 1993; Neutel *et al.*, 2002; Emmerson and Raffaelli, 2004). We declined to do this because a flux estimate f_{ij} can be used to generate the corresponding Lotka-Volterra coefficient α_{ij} , but estimating the coefficients α_{ji} or α_{ii} would require making additional tenuous assumptions.

III. FLUX ESTIMATION METHODS: DEFINITIONS AND THEORY OF EVALUATION

A. Notation, Definitions, and Assumptions

The following were taken as given: a list of S species, $S \geq 2$; the predation matrix $W = (w_{ij})$, where $w_{ij} = 1$ if species j eats species i , and $w_{ij} = 0$ otherwise; the average body mass M_i and the numerical abundance N_i per unit habitat of species i . These data were taken as independent of time and space, representing either a steady state or an average of fluctuating states.

The (possibly null) sets of resources and consumers of each species k were defined as $R_k = \{i : w_{ik} = 1\}$ and $Q_k = \{j : w_{kj} = 1\}$. The number of species in R_k was called the generality of species k . The number of species in Q_k was called the vulnerability of species k (Schoener, 1989). Species k was called a consumer if R_k was not empty, and was called a resource if Q_k was not empty. An intermediate species i was one such that both R_i and Q_i were nonempty. An isolated species i was one such that both R_i and Q_i were empty. We assumed that no species was isolated and that the web had a single connected component; if the web had multiple connected components, our methods could be applied to each connected component one at a time.

The outputs of the models in this paper were estimates of the relative flux matrix $F = (f_{ij})$, where f_{ij} was the (average or steady state) flow of energy per unit time from species i to species j , expressed as a dimensionless fraction of all energy fluxes measured in units of calories per unit of time and per unit of habitat (surface area or volume).

Allometric assumptions were: for each species i , the population production P_i and population consumption C_i (in energy units) were approximated by the allometric functions

$$P_i = pN_iM_i^\alpha \quad (1)$$

$$C_i = cN_iM_i^\beta \quad (2)$$

where p , c , α , and β are all positive constants independent of i , and $\alpha < 1$ and $\beta < 1$ (Peters, 1983). These allometric assumptions implied that, in the plane with horizontal axis $\log(N)$ and with vertical axis $\log(M)$, the locus of points with constant population production P is a straight line with slope $-1/\alpha$ and the locus of points with constant population consumption C is a straight line with slope $-1/\beta$. (To prove this, let $pNM^\alpha = k_1$. Then $\log N + \alpha \log M = k_2$, so $\log M = k_3 - 1/\alpha \log N$. The argument for constant population consumption is similar.)

B. Methods of Estimating Fluxes

We analyzed five methods of estimating fluxes.

Method 0 was an equal flux model (EF). All fluxes were taken to equal $1/L$, where L was the total number of links in the web.

Method 1 was a metabolic action model (MA). Let

$$f_{ij} = \frac{P_i C_j}{\sum_{\substack{\text{trophic} \\ \text{links (g,h)}}} P_g C_h} \quad (3)$$

where the sum is over all prey-predator species pairs (g = prey species, h = predator species). The flux from i to j was set proportional to the product of the population production of i and the population consumption of j . This assumption is similar to mass-action laws used in chemistry and in the Lotka-Volterra equations, but concentrations, biomasses or population densities were replaced here by estimates of population production and population consumption. This assumption differs notably from mass action laws based on the biomasses of consumer or resource species, as steady fluxes proportional to biomasses for species of different body sizes could be unsustainable if production scaled less than linearly with body size.

Method 2 was the consumer control model (CC). For each consumer species j with (non-null) resource set R_j , let

$$f2_{ij} = \left(\frac{P_i}{\sum_{g \in R_j} P_g} \right) \left(\frac{C_j}{\sum_{\text{consumers } h} C_h} \right) \quad (4)$$

The flux into consumer j was set by the population consumption of j , and was distributed over the resources of consumer j in proportion to the population production of each of its resource species.

Method 3 was the resource control model (RC). For each resource species i with (non-null) consumer set Q_i , let

$$f3_{ij} = \left(\frac{P_i}{\sum_{\text{resources } g} P_g} \right) \left(\frac{C_j}{\sum_{h \in Q_i} C_h} \right) \quad (5)$$

The flux out of resource i was set by the population production of i , and was distributed among the consumers of resource i in proportion to the population consumption of each of its consumer species.

Method 4 was the body mass ratio model (BR). Emmerson and Raffaelli (2004) inferred that in the Ythan estuary a power law relationship holds between per capita interaction strength of a predator j on its prey i , and the ratio of the predator's body size to the prey's body size:

$$I_{ij} = \lambda \left(\frac{M_j}{M_i} \right)^\gamma \quad (6)$$

Emmerson and Raffaelli estimated γ near 0.66. This study used 0.66 exactly. The interaction strengths measured by Emmerson and Raffaelli were equivalent to the coefficients of the quadratic terms in the Lotka-Volterra equations with numerical abundance (not biomass abundance) as the variables. According to these equations, the rate of change of the abundance of resource species i due to species j was

$$\frac{dN_i}{dt} = I_{ij}N_iN_j \quad (7)$$

Our flux, f_{ij} , was a flux of energy proportional to $M_i dN_i/dt$ under the assumption that all species have the same caloric value per unit mass. We combined Eqs (6), (7), and this proportionality relation to obtain the estimate

$$f_{4ij} = \lambda(N_i M_i^{1-\gamma})(N_j M_j^\gamma) \quad (8)$$

We chose the value of λ so that the sum of all fluxes in the web was 1.

These methods shared several properties. The sum over all trophic links of all fluxes was 1, using any method. All of the relative flux estimates were dimensionless numbers. Empirical measurement of the absolute flux of any trophic link would identify the multiplier from which the theoretical estimates of relative flux along all remaining links could be converted to estimates of absolute flux. In addition, the relative flux along any trophic link under models MA, RC, and CC was independent of the constants p and c . Finally, the flux formulas in these three models could also be used given any positive P_i and C_j . The expressions for P_i and C_j need not necessarily be allometric formulas.

C. Evaluating the Methods: Theory

The relative flux estimates were evaluated using several tests.

1. Input-Output Ratio Test: Theory

For each intermediate species k in the Tuesday Lake system, the quantity

$$\lambda_k = \frac{\sum_{i \in R_k} f_{ik}}{\sum_{j \in Q_k} f_{kj}} \quad (9)$$

was calculated. This ratio was the sum of the fluxes of energy flowing into species k divided by the sum of the fluxes of energy flowing out of species k . Thus λ_k was expected to approximate the reciprocal of the ecological efficiency (Phillipson, 1966). Values were expected to be distributed around 10 when all species were considered. Values were expected to be higher for warm-blooded species and lower for cold-blooded species. If warm-blooded species generally occurred higher in a food web than cold-blooded species (barring parasites), then λ_k was expected to increase with body mass. If the sum of fluxes flowing into a species k equaled the allometric population

consumption of species k , and the sum of the fluxes flowing out of species k equaled the allometric population production of that species, then

$$\lambda_k = C_k/P_k = \frac{c}{p} M_k^{\beta-\alpha} \quad (10)$$

If $\alpha = \beta$, then a plot of $\log \lambda_k$ versus $\log(M_k)$ should have been flat. If $\beta = 0.75$ and $\alpha = 0.66$, then a plot of $\log \lambda_k$ versus $\log(M)$ should have been linear with the slightly positive slope $\beta - \alpha = 0.09$.

The input-output ratio was used to evaluate all methods of estimating fluxes, and the results are presented below.

2. Crosscheck Test: Theory

The aim of the crosscheck test is to check how nearly the estimated fluxes f_{ij} in Tuesday Lake satisfied the assumptions that $P_i = pN_iM_i^\alpha$ and $C_i = cN_iM_i^\beta$, where p and c are independent of i . The method required the computation of four vectors: the allometric production vector P_{allo} , the allometric consumption vector C_{allo} , the flux production vector P_{flux} , and the flux consumption vector C_{flux} . Specifically,

1. $P_{allo} = (P_1/p, \dots, P_R/p)$, where R was the number of resources in the web, so P_{allo} had i^{th} component $N_iM_i^\alpha$, which was independent of p ;
2. $C_{allo} = (C_1/c, \dots, C_Q/c)$, where Q was the number of consumers in the web, so C_{allo} had i^{th} component $N_iM_i^\beta$, which was independent of c ;
3. P_{flux} had i^{th} component equal to $\sum_{j \in Q_i} f_{ij}$, where i ranged over the resource species (this was the vector of estimated total fluxes out of each resource species);
4. C_{flux} had j^{th} component equal to $\sum_{i \in R_j} f_{ij}$, where j ranged over the consumer species (this was the vector of estimated total fluxes into each consumer species).

If the flux estimates were in perfect agreement with the allometric assumptions, then it would be possible to find constants π and χ such that

$$\pi P_{allo} = P_{flux} \quad (11)$$

$$\chi C_{allo} = C_{flux} \quad (12)$$

Fluxes estimated by the CC model were guaranteed to satisfy $\chi C_{allo} = C_{flux}$ for some χ , but not guaranteed to satisfy $\pi P_{allo} = P_{flux}$ for some π . Fluxes estimated by the RC model were guaranteed to satisfy $\pi P_{allo} = P_{flux}$ for some π , but not guaranteed to satisfy $\chi C_{allo} = C_{flux}$ for some χ . Fluxes

estimated by the MA model or the BR model were not guaranteed to satisfy either equation.

When the above equations were not satisfied perfectly, we could estimate π and χ by treating Eqs (11) and (12) as linear regression equations constrained to pass through the origin, that is, with zero y-intercept, with unknown slope coefficients π and χ :

$$P_{flux} = \pi P_{allo} + \varepsilon_1 \quad (13)$$

$$C_{flux} = \chi C_{allo} + \varepsilon_2 \quad (14)$$

To see how well the above equations were satisfied, we plotted $\log(P_{allo})$ (on the vertical axis) versus $\log(P_{flux})$ (on the horizontal axis) and $\log(C_{allo})$ versus $\log(C_{flux})$. Then multiplicative scaling of the allometric vector became vertical translation of the data points, and multiplicative scaling of the flux vector became horizontal translation. Neither change affected the residuals of the data from the line of slope 1 which best fitted the points (still in log-log coordinates). We measured the quality of the fit of such a line by means of the standard deviation of these residuals. If the same analysis were repeated with P_{flux} on the vertical axis and P_{allo} on the horizontal axis (or C_{flux} and C_{allo} , respectively), the analogous standard deviation statistic would have been precisely the same as the one just described, because horizontal and vertical residuals to a line of slope 1 are the same. The standard deviation of the residuals to the fitted line of slope 1 was the same as the standard deviation of the residuals to any line of slope 1 because vertical or horizontal translation of the line of slope 1 uniformly adds a constant to all residuals, and this addition does not affect the standard deviation of these residuals, though it changes the mean. So an easily-calculated summary statistic was the standard deviation of the residuals to the line $y = x$, or $\text{std}(\log(P_{allo}) - \log(P_{flux}))$ or $\text{std}(\log(C_{allo}) - \log(C_{flux}))$.

IV. DATA FOR EMPIRICAL EXAMPLE: TUESDAY LAKE, MICHIGAN

Tuesday Lake is a small, mildly acidic lake in Michigan (89°32' W, 46°13' N). The data used in this study were gathered by Stephen R. Carpenter and colleagues from Tuesday Lake in 1984, and again in 1986. In 1985, the three species of planktivorous fish that lived in the lake were removed, and a single species of piscivorous fish was added. In 1984 and 1986, the fish populations had not previously been exploited and the drainage basin had not previously been developed. The data (given in full by Jonsson *et al.*, 2005) consist of the following for each year (1984 and 1986): a list of species; for each species, its predator species and its prey species (for the body sizes

and life stages that were present in the lake); its average body mass M (kg fresh weight per individual); and its numerical abundance N (individuals/m³ in the epilimnion where the trophic interactions take place). The biomass abundance B (kg/m³) is M times N . The data represent seasonal averages during summer stratification. Most numerical variables, reported as mean values, were estimated by continuing sampling until the standard error of the mean was less than 10% of the mean. Here only the un lumped web of Tuesday Lake using biological species is described. Data for 1984 and 1986 are treated separately.

V. METHODS

All computations and plotting were done with Matlab version 6.5.0.180913a (R13). Linear regressions were done with the Matlab function “regress”. All p-values associated with linear regressions were returned by that function. Normality testing was done with the Jarque-Bera test (Matlab statistics toolbox function “jbtest”) and the Lilliefors test (Matlab statistics toolbox function “lillietest”). The Lilliefors test is a simulation-based test that returns p-values only between 0.01 and 0.2. Lilliefors p-values above this range have been reported as >0.2 , and values below this range have been reported as <0.01 . Both the Lilliefors test and the Jarque-Bera test are composite tests of normality (Lilliefors, 1967; Jarque and Bera, 1987). They are based on qualitatively different aspects of the data, so a set of data was called “normal” only if it passed both tests at the 5% level.

VI. FLUX ESTIMATION METHODS: EVALUATION

Each flux method was tested with the input-output ratio test, the crosscheck test, and other tests using the data of Tuesday Lake. All results below assume $\alpha = 0.75$, $\beta = 0.75$ and $\gamma = 0.66$.

A. Direct Comparison Between Models

Figure 1A plots the log flux of each link according to CC against the log flux of each link according to MA in Tuesday Lake, 1984. Figure 1B does the same for models BR vs. MA in 1984. The log flux of trophic links estimated by each of the five models was also plotted versus the log flux from each of the other models, but the remaining plots are not shown. All plots not involving EF had a general linear trend of slope 1. Plots not involving BR were similar to Fig. 1A, and plots involving BR were similar to Fig. 1B. The sum of the squares of the residuals of these plots from the line $y = x$ (Table 1)

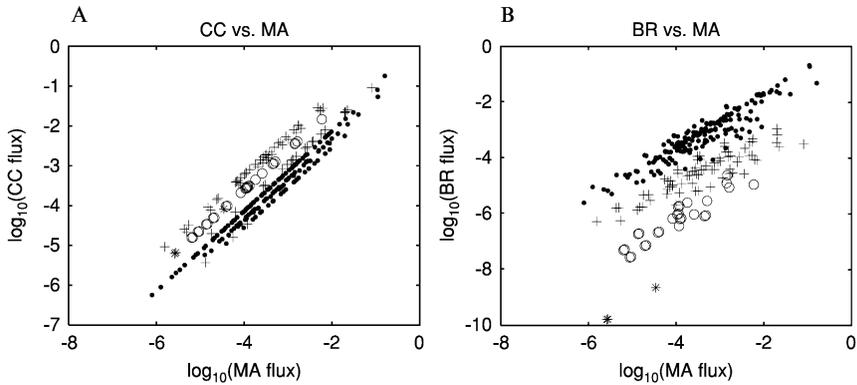


Figure 1 Typical plots of log flux under one model versus log flux under another model, for all trophic links in 1984. Dots denote links with zooplankton predator and phytoplankton prey. The + symbols denote links with zooplankton as both predator and prey. The \circ symbols denote links with fish as predator and zooplankton as prey. The * symbols denote links with fish as both predator and prey.

Table 1 Sums of squares (rounded to the nearest integer) of residuals for links from the line $y = x$ of log of the flux under the model in the column label versus log of the flux under the model in the row label

	Model			
	MA	RC	CC	BR
1984				
EF	556	608	563	1137
MA	0	60	47	323
RC		0	158	369
CC			0	510
1986				
EF	856	991	428	892
MA	0	14	132	169
RC		0	201	173
CC			0	317

Order of the axes is not important since vertical and horizontal residuals to the line $y = x$ are the same.

showed that MA was similar to RC and CC. RC and CC were also similar to each other, but not as similar as they were similar to MA. None of these models were as similar to BR as they were to each other in 1984, and EF was even more dissimilar from all the other models in both years. In 1986, RC was more similar to BR than it was to CC. Plots with EF on the y-axis had general linear trend of slope 0. Plotting fluxes of any model on the y-axis

versus those of the EF model on the x-axis yielded a vertical line, since EF fluxes were all the same.

Exactly linear subtrends of slope 1 occurred in log-log plots of the fluxes under one model versus the fluxes under another model if both models were chosen from among the MA, RC, and CC models (see Fig. 1A). These subtrends can be explained by taking the log of the definitions of flux under these three models:

For MA:

$$\log(f1_{ij}) = \log(P_i C_j) - \log(D) \quad (15)$$

For RC:

$$\log(f3_{ij}) = \log(P_i C_j) - \log\left(\sum_{k \in Q_i} C_k\right) - \log(E) \quad (16)$$

For CC:

$$\log(f2_{ij}) = \log(P_i C_j) - \log\left(\sum_{g \in R_j} P_g\right) - \log(F) \quad (17)$$

where D , E and F are constants. The constant D is the sum over all links of $P_i C_j$, the constant E is the sum of P_i over all resources in the whole web, and the constant F is the sum of C_i over all consumers in the whole web. When plotting MA versus CC, all links for which the predator species had a fixed set of prey sat on a line of slope 1. When plotting MA versus RC, all links for which the prey species had a fixed set of predators sat on a line of slope 1. When plotting RC against CC, any two links for which the two predators had the same prey set and the two prey had the same predator set sat on a line of slope 1.

The links in both Tuesday Lake food webs were grouped according to whether the predator was a fish (F) or a zooplankton (Z), and whether the prey was a zooplankton or a phytoplankton (P). So all links were classified as (P,Z), (Z,Z), (Z,F) or (F,F) links, where the first letter in the pair gives the group that the prey was in and the second gives the group that the predator was in (Reuman and Cohen, 2004). All of the exactly linear slope 1 subtrends found in plots involving MA, RC, and CC consisted entirely or almost entirely of links from a certain group, as expected, given the characterizations of these exactly linear subtrends found in the previous paragraph (which involved classification by diet and/or predator set).

Exactly linear subtrends were absent in log-log plots of BR-flux versus any one of the MA-, RC-, and CC-fluxes. However, an approximate overall slope-1 trend was visible, and within each group of links there was a clear nonexact linear subtrend. Taking the log of the definition of the BR flux gives:

$$\log(f_{4ij}) = \log(P_i C_j) + \log(M_i^{1-\gamma-\alpha} M_j^{-\beta+\gamma}) + \log(\lambda) \quad (18)$$

This relation explains the existence of approximate group-based subtrends and the lack of exact subtrends. The variance term (the second one on the right) was not constant for any particular group of links, nor was the difference between this term and the analogous terms in the RC and CC equations. However, the second term in the above equation took a very different distribution of values over links from different groups. Since the two exponents in that term were both negative for the assumed values of α , β and γ , for groups (A, B) where A and B both contain heavy species, we should expect linear subtrends below the overall linear trend. For groups in which A and B were both comparatively light, we should expect linear subtrends that are above the overall trend. These expectations are confirmed in Fig. 1B.

Histograms (not shown) of the flux in the links of the 1984 and 1986 webs under each model except the EF model confirmed the general expectation that a web should have many weak links and few strong links (Paine, 1992; Raffaelli and Hall, 1996; McCann *et al.*, 1998; Kokkoris *et al.*, 1999). Woodward *et al.* (2005) recently confirmed this phenomenon experimentally. In Tuesday Lake in 1984, for each model except the EF model, the sum of the 14 strongest fluxes under that model (14 of 269 links was a little more than 5%) made up at least 65% of the total flux in all links under that model. The top three fluxes (a little more than 1% of the links) made up at least 29% of the total flux for each model.

Lorenz curves (Fig. 2 for the MA model; Lorenz curves for other models except EF look similar) measure the level of inequality in flux distributions. The horizontal axis of the Lorenz plot shows the cumulative fraction of

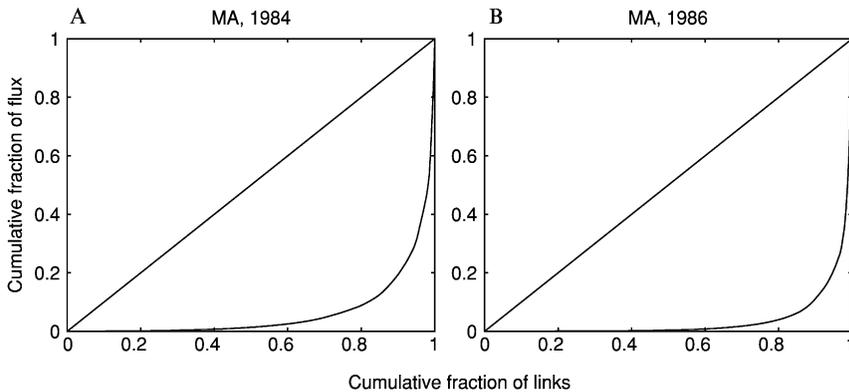


Figure 2 Lorenz curves for the flux distributions from the MA model in 1984 and 1986. The horizontal axis is the cumulative fraction of links, when the links are ranked from lowest to highest flux. The vertical axis is the cumulative fraction of total flux that flows along the links included so far.

Table 2 Gini indices for the flux distributions from each model in each year

Year	MA	RC	CC	BR
1984	0.874	0.871	0.864	0.910
1986	0.925	0.936	0.875	0.892

links, when the links are ranked from lowest to highest flux, while the vertical axis shows the cumulative fraction of total flux that flows along the links included so far. A highly unequal flux distribution would have a Lorenz curve lying far below the line $y = x$, while a hypothetical flux distribution with all fluxes equal would have Lorenz curve coinciding with the line $y = x$. The inequality in a flux distribution is quantified by the Gini index, which is twice the area between the Lorenz curve and the line $y = x$. The Gini index ranges from 0 when all links have equal flux to 1 in the limit when all flux in the system passes along a single trophic link and all remaining links have vanishingly small flux. The Gini indices (Table 2) for the flux distributions of each model were all greater than 0.85. The Gini index and Lorenz curve were not changed when all fluxes were multiplied by any positive constant, and were therefore useful for relative flux distributions.

The log-flux distributions in both years (histograms in Fig. 3) for the MA, RC, and CC models were normal at the 5% significance level, according to the Jarque-Bera and Lilliefors composite tests of normality. The BR distribution was not normal in 1984, but was in 1986. The p-values for these tests are in Table 3.

To summarize, direct comparison of the four models revealed that the MA, RC, and CC models were more similar to each other than they were to the BR model. All models produced very unequal distributions of fluxes with many weak fluxes and a few strong fluxes. Distributions of log-flux were approximately normal for the MA, RC, and CC models in 1984 and 1986, but normal for the BR model only in 1986.

B. Input-Output Ratio Test: Results

The results of applying the input-output ratio test to the five models were as follows.

1. Distributions of Flux Ratios

The log of the input-output flux ratio was computed for each intermediate species for each year and for each model. A species whose only predator was

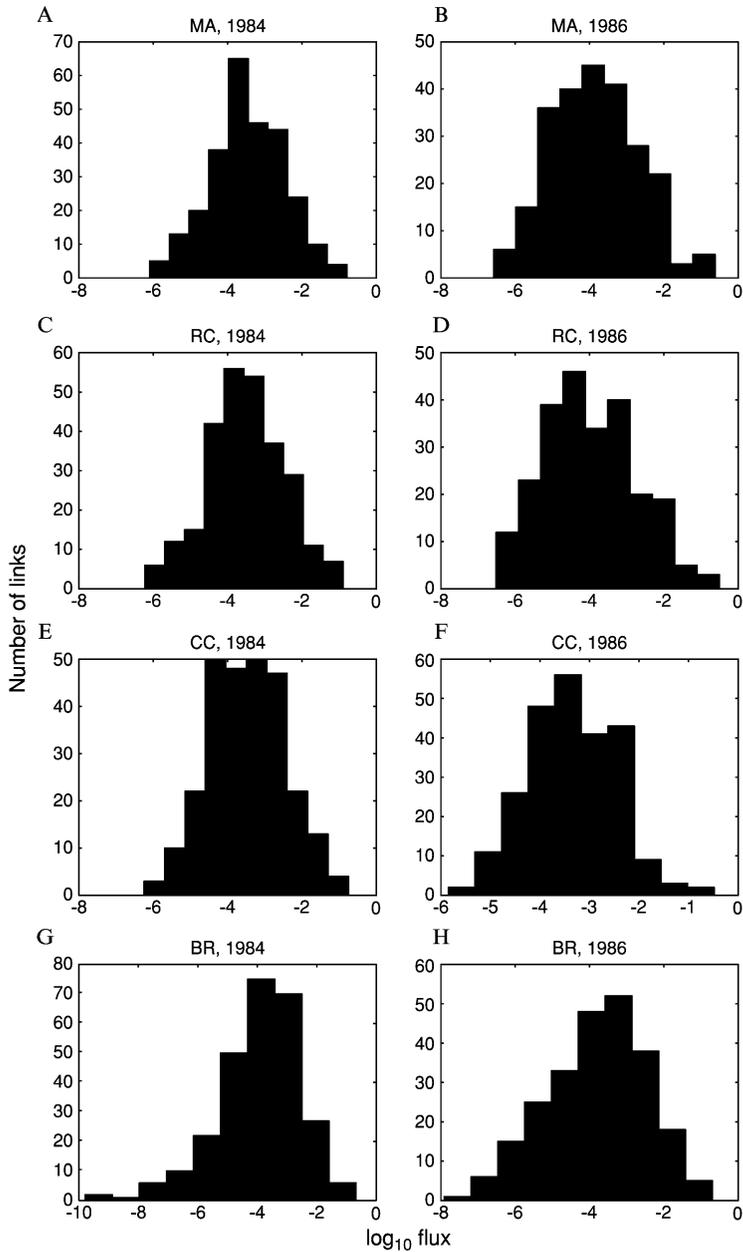


Figure 3 Histograms of the number of links according to the logarithm of flux for all models (except EF) in both years. Distributions are not statistically distinguishable from normal except BR in 1984.

Table 3 Tests of normality of the distribution of the logarithm of flux over links

Species	Year	MA	RC	CC	BR
Strict upper triangular	1984	0.95/>0.2	0.82/>0.2	0.70/>0.2	<0.001/<0.01
	1986	0.20/0.20	0.20/>0.2	0.51/0.05	0.15/>0.2
Upper triangular	1984	0.93/>0.2	0.83/>0.2	0.62/>0.2	<0.001/<0.01
	1986	0.18/0.19	0.16/>0.2	0.82/0.17	0.11/0.13
All	1984	0.95/>0.2	0.85/>0.2	0.59/>0.2	<0.001/<0.01
	1986	0.16/0.09	0.13/>0.2	0.86/0.10	0.10/0.09

Top two rows refer to links in the strict upper triangle in a body mass indexed predation matrix. Middle two rows refer to links in the upper triangle in a body mass indexed predation matrix. Bottom two rows refer to all links. Jarque-Bera (on the left in each cell) and Lilliefors (on the right in each cell) p-values assess normality of log-flux distributions of Tuesday Lake data using each flux model. Low values of p reject lognormality. Only the BR model rejects lognormality, and only in 1984.

Table 4 Minimum and maximum input-output flux ratios for each model in each year, and the number of the 25 intermediate species in 1984 and 21 in 1986 that had input-output flux ratio less than 1

Model	Number of species with flux ratio <1, 1984	Number of species with flux ratio <1, 1986	Minimum flux ratio, 1984	Minimum flux ratio, 1986	Maximum flux ratio, 1984	Maximum flux ratio, 1986
EF	0	0	1.20	1.00	12	23
MA	3	15	0.48	0.16	350	32
RC	3	14	0.50	0.15	156	23
CC	0	2	1.08	1.00	350	19
BR	0	1	1.71	0.67	40940	12035

Cannibalistic species were counted as intermediate.

itself through cannibalism was included as an intermediate species. Ratios < 1 indicated a greater flux out of a species than into it, and were the strongest indicator of fault in a model. Table 4 shows the number of intermediate species with input-output flux ratio <1 for each model and how much less than 1 these ratios were. Maximum ratios are also shown. From plots of log input-output flux ratio versus log body mass for intermediate species (Fig. 4), the distribution of log input-output flux ratios is easily seen by looking only at the ordinate (y-axis value) of each plotted point. An input-output flux ratio <1 appears in Fig. 4 as a log ratio <0.

Although the MA and RC models had many intermediate species with input-output flux ratios less than 1 in 1986, these ratios were rarely much less

than 1, and therefore did not represent a serious inaccuracy of the model (Table 4, Fig. 4).

In 1984, the three species with input-output flux ratio less than 1 under the MA model were the same as those with input-output flux ratio less than 1 under the RC model, and these were the only species with ratio less than 1 in

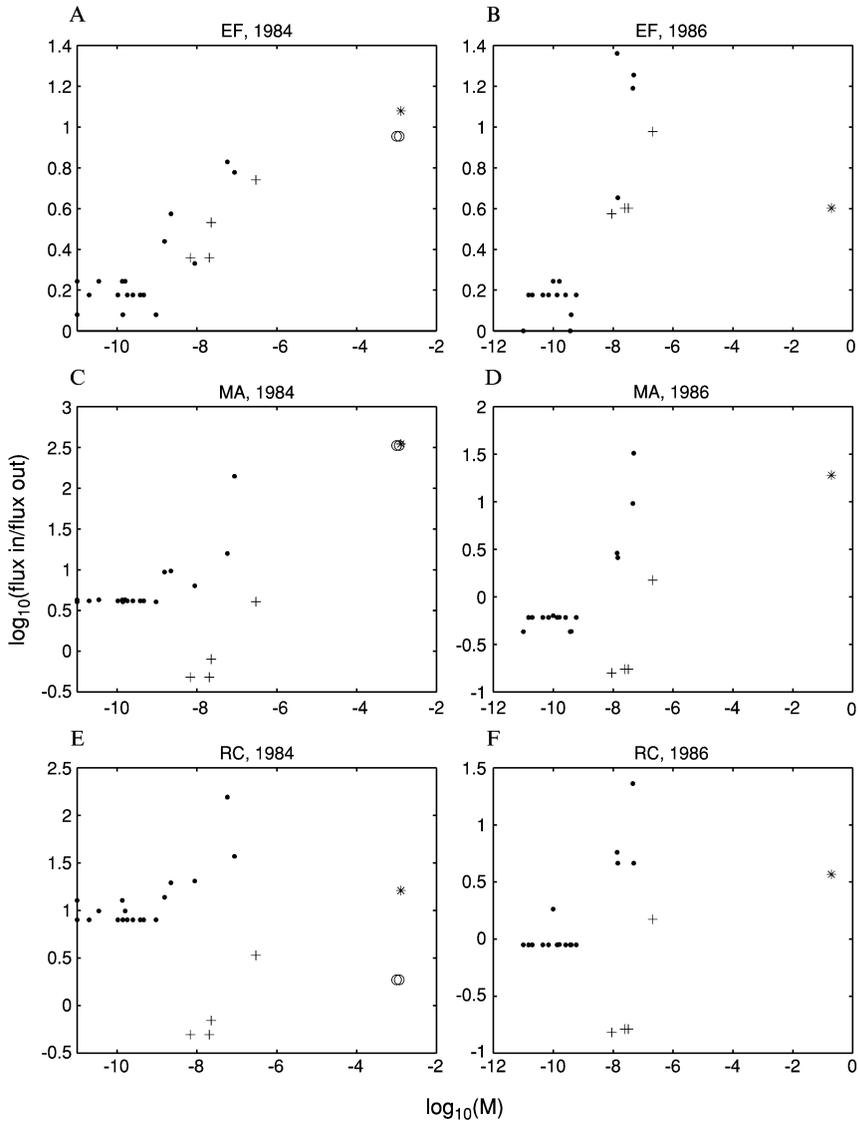


Figure 4 (Continued)

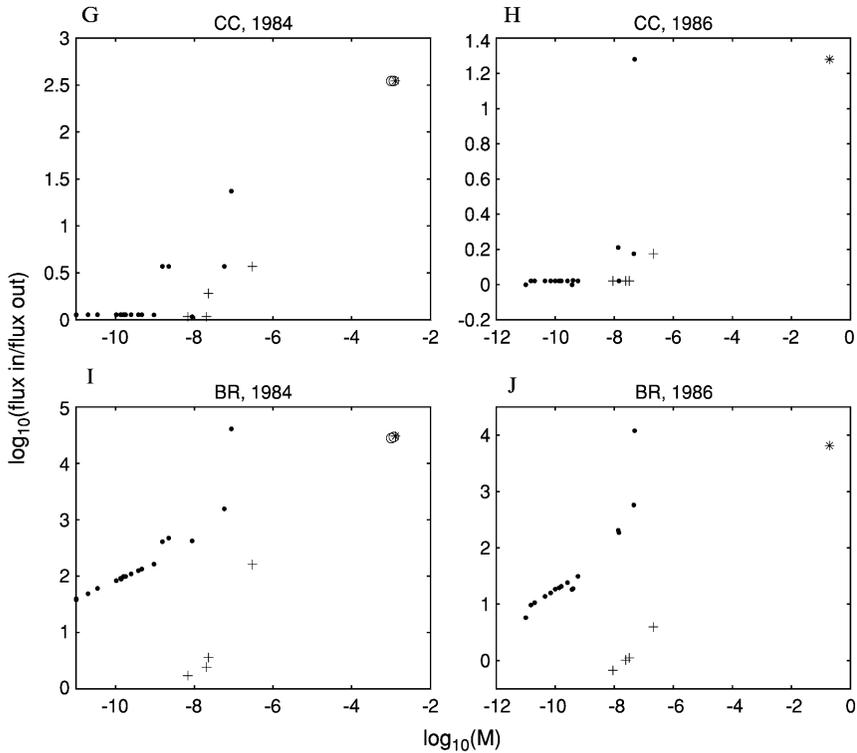


Figure 4 Log of input-output flux ratios versus log of intermediate species body mass for each model in each year. Asterisks (*) represent cannibalistic fish, \circ non-cannibalistic fish, + non-fish cannibals, and dots other intermediate species.

any model in that year. These three species, all cannibals, were *Cyclops varians rubellus*, *Orthocyclops modestus*, and *Tropocyclops prasinus*. They were the only three species from the Cyclopoida order (in the class of Copepods) found in Tuesday Lake in either year. It is plausible that cannibalism occurred between different size classes within each species. These three species were also all present in 1986. If one discounts these species in 1986, then the minimal input-output flux ratios were 1.0000, 0.4314, 0.8903, 0.9981, and 3.9439 for the EF, MA, RC, CC, and BR models, respectively. These values are better than the minima reflected in Table 4, and are either greater than 1 or just slightly less than 1.

The models with the fewest species with input-output flux ratios less than 1 were the BR and CC models, but because flux ratios that were less than 1 for the other models were usually not much less than 1, the input-output flux ratio data did not strongly favor the BR and CC models.

2. Flux Ratios versus Body Mass

Input-output flux ratios were plotted against species body mass on log-log scales (Fig. 4). Sometimes cannibalistic species and/or fish were outliers on these plots, so they have been marked separately. Table 5 contains linear regression statistics for these plots, with separate statistics computed without fish and/or cannibalistic species.

One species in 1984 and each of two in 1986 took fewer than 15% and greater than 0% of its prey species from the animal kingdom. None of these were counted as being primarily carnivorous. Any other species that ate any meat at all took at least 95% of its prey species from the animal kingdom. All species that were primarily carnivores were also either fish or cannibals (or both) in both years, so excluding fish and cannibals was the same as excluding all mainly carnivorous species.

The slopes of the regressions in Table 5 were always slightly positive, or not statistically different from zero. This is consistent with the allometrically predicted input-output flux ratios (see the section on Input-output ratio tests: Theory). The EF model had positive regressions in both years, regardless of which outliers were removed. The MA model also had positive regressions unless only fish were removed. The RC model never had slope statistically different from zero unless both fish and cannibals were removed (the only fish in 1986 was also a cannibal, so removing only cannibals was the same as removing fish and cannibals). The CC model always gave positive slopes, except when only fish were removed in 1986. The BR model always gave positive slopes except both years when only fish were removed.

The flux ratio versus body mass trends supported all models because the regressions in the Table 5 were of the correct order of magnitude (theory predicted slope $\beta - \alpha$, so regression slopes should have been between about -1 and 1 , which they were). These slopes did not appear to support one model over the others.

C. Flux Differences versus Species Metabolism

The difference between flux in and flux out should equal the amount of metabolic energy consumed by an intermediate species, neglecting energy lost through feces. Log of (flux in minus flux out) was plotted versus the log of allometrically estimated species metabolism using the formula NM^δ for metabolism, where $\delta = 0.75$ and 0.80 were both tried (Peters, 1983). It was expected that the line $y = x$ would fit the resulting plot well, but on the contrary there was no visible linear relationship. The noise in both the independent and dependent variables on this plot appeared to overwhelm any pattern that may exist.

Table 5 Linear regression statistics for plots of log(flux in/flux out) versus log(body mass)

	EF	MA	RC	CC	BR
All species					
1984 slope	0.12 (0.09,0.14)	0.24 (0.14,0.34)	-0.05 (-0.15,0.05)	0.32 (0.26,0.38)	0.34 (0.18,0.50)
r ²	0.83	0.52	0.04	0.84	0.45
p-value	0.00	0.00	0.32	0.00	0.00
1986 slope	0.10 (0.03,0.18)	0.16 (0.05,0.27)	0.07 (-0.04,0.18)	0.12 (0.07,0.18)	0.25 (0.04,0.45)
r ²	0.31	0.34	0.08	0.53	0.25
p-value	0.01	0.01	0.21	0.00	0.02
No fish					
1984 slope	0.14 (0.10,0.19)	0.04 (-0.14,0.22)	-0.05 (-0.25,0.16)	0.16 (0.06,0.25)	0.16 (-0.16,0.48)
r ²	0.67	0.01	0.01	0.38	0.05
p-value	0.00	0.65	0.64	0.00	0.32
1986 slope	0.27 (0.18,0.35)	0.16 (-0.03,0.35)	0.08 (-0.11,0.27)	0.09 (-0.07,0.18)	0.14 (-0.20,0.49)
r ²	0.70	0.15	0.04	0.17	0.04
p-value	0.00	0.09	0.41	0.07	0.40
No cannibals					
1984 slope	0.12 (0.08,0.15)	0.27 (0.22,0.32)	-0.05 (-0.13,0.04)	0.33 (0.27,0.39)	0.39 (0.31,0.47)
r ²	0.78	0.87	0.08	0.89	0.86
p-value	0.00	0.00	0.24	0.00	0.00
1986 slope	0.33 (0.22,0.44)	0.38 (0.25,0.52)	0.30 (0.20,0.41)	0.15 (0.03,0.27)	0.63 (0.46,0.81)
r ²	0.74	0.72	0.72	0.33	0.82
p-value	0.00	0.00	0.00	0.02	0.00
No fish or cannibals					
1984 slope	0.16 (0.09,0.22)	0.26 (0.14,0.37)	0.22 (0.12,0.32)	0.22 (0.11,0.34)	0.57 (0.43,0.72)
r ²	0.64	0.58	0.57	0.53	0.82
p-value	0.00	0.00	0.00	0.00	0.00
1986 slope	0.33 (0.22,0.44)	0.38 (0.25,0.52)	0.30 (0.20,0.41)	0.15 (0.03,0.27)	0.63 (0.46,0.81)
r ²	0.74	0.72	0.72	0.33	0.82
p-value	0.00	0.00	0.00	0.02	0.00

See Fig. 4. Only intermediate species were included in the first regression. All cannibalistic species were counted as intermediate. The "No fish" and "No cannibals" regressions considered only non-fish and non-cannibalistic intermediate species, respectively. In parentheses are 95% confidence intervals.

D. Crosscheck Test: Results

For each model in each year, $\log(C_{flux})$ was plotted versus $\log(C_{allo})$, and $\log(P_{flux})$ was plotted versus $\log(P_{allo})$. Figure 5 shows the MA and BR plots in 1984. For these plots, the C_{flux} , C_{allo} , P_{flux} , and P_{allo} vectors were multiplicatively normalized (before taking logs) so that each had a Euclidean length of 1. Table 6 has the summary statistic $\text{std}(y_{\text{data}} - x_{\text{data}})$ discussed in the section on Crosscheck test: Theory, including or excluding cannibals and (independently of cannibals) fishes (cannibals and fishes were frequently outliers). The assessment number in the last part of that table, an overall description of each models' performance, is the mean of the nonzero P and C

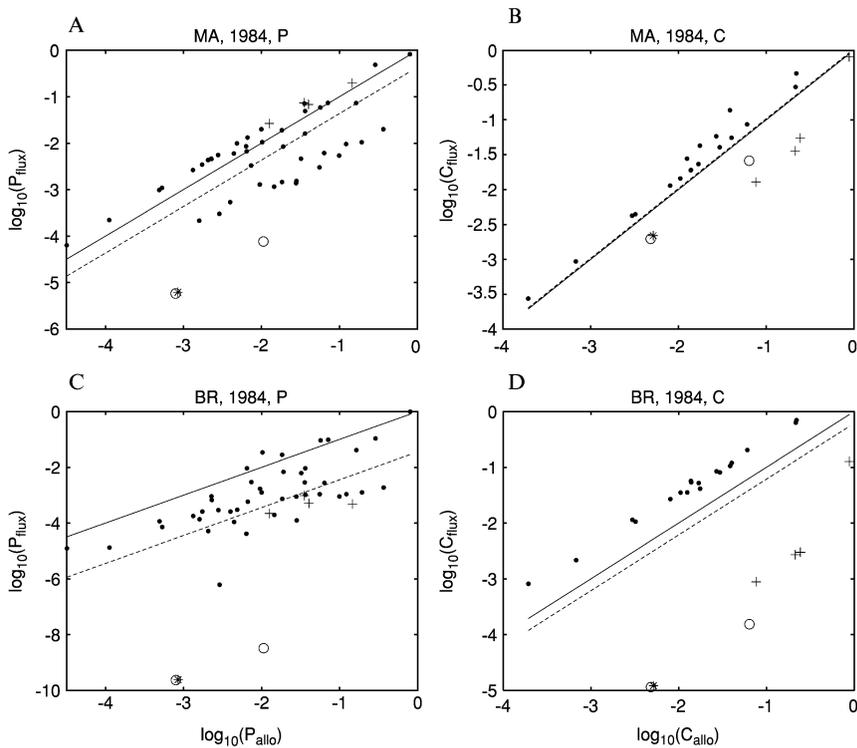


Figure 5 Plots of $\log(C_{flux})$ versus $\log(C_{allo})$ and $\log(P_{flux})$ versus $\log(P_{allo})$ for the MA and BR models in 1984. The proximity of the data on the C plots to a line of slope 1 measures how well the allometric population consumption agreed with total flux into each species. The proximity of the data on the P plots to a line of slope 1 measures how well the allometric population production agreed with total flux out of each species. The solid line is the line $y = x$, and the dashed line is the least squares line of slope 1. Asterisks (*) are cannibalistic fish, o non-cannibalistic fish, + non-fish cannibals, and dots other species.

Table 6 Assessments of fit of C_{flux} with C_{allo} and of P_{flux} with P_{allo} by means of the standard deviation of the residuals of the data from the line of slope 1 which best fitted the points in log-log coordinates

		EF	MA	RC	CC	BR
All species						
P	1984	0.96	0.75	0.00	1.00	1.54
	1986	1.10	0.32	0.00	0.58	1.08
C	1984	0.76	0.36	0.56	0.00	1.22
	1986	0.80	0.42	0.52	0.00	1.03
No fish						
P	1984	0.98	0.62	0.00	0.96	0.85
	1986	1.11	0.29	0.00	0.57	0.75
C	1984	0.78	0.35	0.57	0.00	0.88
	1986	0.77	0.42	0.52	0.00	0.90
No cannibals						
P	1984	0.99	0.72	0.00	0.99	1.41
	1986	1.12	0.30	0.00	0.57	0.70
C	1984	0.73	0.22	0.40	0.00	0.97
	1986	0.74	0.36	0.42	0.00	0.13
No fish or cannibals						
P	1984	1.01	0.62	0.00	0.97	0.85
	1986	1.12	0.30	0.00	0.57	0.70
C	1984	0.75	0.12	0.33	0.00	0.07
	1986	0.74	0.36	0.42	0.00	0.13
Overall assessment numbers						
All species		0.91	0.46	0.54	0.79	1.22
No fish		0.91	0.42	0.54	0.77	0.84
No cannibals		0.90	0.40	0.41	0.78	0.80
No fish or cannibals		0.90	0.35	0.38	0.77	0.43

The lower the standard deviation, the better the fit. The overall assessment number of each model is the mean of the nonzero P and C statistics from 1984 and 1986. The overall assessments favor the MA model.

table values in 1984 and 1986 for that model. Lower assessment numbers indicated models for which allometric and flux vectors can be better reconciled. The MA model was consistently best by this standard.

In plots of C_{flux} versus C_{allo} and P_{flux} versus P_{allo} , linear subtrends were visible for some of the models. For the EF model, these linear subtrends had a slope of 0. Some of the other models had linear subtrends of slope 1. Fish and cannibals were also sometimes outliers from the general trend on some plots for some models (Fig. 5).

The following equations helped to explain these phenomena. For the EF model,

$$\log(C_{flux,i}) = \log(g_i) - \log(L) \quad (19)$$

$$\log(P_{flux,i}) = \log(v_i) - \log(L) \quad (20)$$

where g_i is the generality of species i , v_i is the vulnerability of species i , and L is the total number of links in the web.

For the BR model,

$$\log(C_{flux,i}) = \log(C_{allo,i}) + \log\left(M_i^{\gamma-\beta} \sum_{j \in R_i} N_j M_j^{1-\gamma}\right) + \log(\lambda) \quad (21)$$

$$\log(P_{flux,i}) = \log(P_{allo,i}) + \log\left(M_i^{1-\gamma-\alpha} \sum_{j \in Q_i} N_j M_j^\gamma\right) + \log(\lambda) \quad (22)$$

For the MA model,

$$\log(C_{flux,i}) = \log(C_{allo,i}) + \log\left(\sum_{j \in R_i} P_j\right) - \log(D) \quad (23)$$

$$\log(P_{flux,i}) = \log(P_{allo,i}) + \log\left(\sum_{j \in Q_i} C_j\right) - \log(D) \quad (24)$$

The second term on the right of (23) is the log of the sum of the productions of the species that i ate, and the second term on the right of (24) is the log of the sum of the consumptions of the species that ate i .

For the RC model,

$$\log(C_{flux,i}) = \log(C_{allo,i}) + \log\left(\sum_{j \in R_i} \frac{P_j}{\sum_{k \in Q_j} C_k}\right) - \log(E) \quad (25)$$

There is no need for an equation relating $P_{flux,i}$ and $P_{allo,i}$ because the RC model forced them to be equal.

For the CC model,

$$\log(P_{flux,i}) = \log(P_{allo,i}) + \log\left(\sum_{j \in Q_i} \frac{C_j}{\sum_{k \in R_j} P_k}\right) - \log(F) \quad (26)$$

There is no need for an equation relating $C_{flux,i}$ and $C_{allo,i}$ because the CC model forced them to be equal.

Each of Eqs (21) through (26) has three terms on the right side. The last term is always constant, and the first term is always either $\log(P_{allo,i})$ or $\log(C_{allo,i})$, depending on whether the left side of the equation is $\log(P_{flux,i})$ or $\log(C_{flux,i})$. As a result, there is an underlying linear relationship of slope 1 between $\log(P_{flux,i})$ and $\log(P_{allo,i})$, and between $\log(C_{flux,i})$ and $\log(C_{allo,i})$. This first term will be called the main term. The second term on the right side expresses the variance of the data from the trend. This second term will be called the variance term. In the EF Eqs (19) and (20), the first term on the

right side will be called the variance term. The main term is zero for the EF equations because in this case, the underlying trend is a slope 0 trend.

The variance terms are useful in understanding observed linear subtrends, and observed tendencies of certain classes of species to lie far from the linear trend of slope 1 (or slope 0, in the case of the EF model). Two species for which the variance terms were equal sat together on a line of slope exactly 1 (or for the EF model, exactly 0). So exactly linear subtrends in the data arose from classes of species that all shared the same variance term. In the case of the EF model, such species all had the same generality or vulnerability. There were only 11 distinct nonzero generalities in the 1984 web, and nine in the 1986 web. There were eight distinct nonzero vulnerabilities in the 1984 web and seven in the 1986 web. Each of these corresponds to an exactly flat subtrend in the EF plots.

The variance term in the consumption equation (23) for the MA model represents the log of the sum of the productions of the species that species i ate. If two species had identical diets, their variance terms in that equation were the same, and they sat on a line of slope exactly 1 in the plot of $\log(C_{flux})$ versus $\log(C_{allo})$. There were only 14 distinct columns in the 1984 predation matrix, and 11 in the 1986 predation matrix. Because many species shared the same diet, exactly linear subtrends of slope 1 appeared in the MA plots of $\log(C_{flux})$ versus $\log(C_{allo})$ (e.g., Fig. 5B).

In the production Eq. (24) for the MA model, the variance term represents the log of the sum of the consumptions of the species that ate species i . There were 16 distinct rows in the 1984 predation matrix and 13 in the 1986 predation matrix. Because many species shared the same predator set, exactly linear subtrends of slope 1 appeared in the MA plots of $\log(P_{flux})$ versus $\log(P_{allo})$ (e.g., Fig. 5A).

The variance term in the RC Eq. (25) was also the same for two species that had the same prey set, and the variance term in the CC Eq. (26) was the same for two species that had the same predator set. This explains the appearance of exactly linear subtrends of slope 1 in those plots.

The variance terms in the BR equation are not the same for species that had the same prey set or predator set. As expected, the BR plots have no exactly linear subtrends.

Species that were eaten only by fish were outliers on the BR model production plots in 1984 (Fig. 5C) and 1986. The variance terms in the BR model Eqs (21) and (22) explain why. If we assume that all species in Tuesday Lake had the same biomass abundance B (which is a rough but reasonable approximation for present purposes), then we can write the variance terms as

$$\log\left(M_i^{\gamma-\beta} \sum_{j \in R_i} \frac{B}{M_j^\gamma}\right) \quad (27)$$

and

$$\log\left(M_i^{1-\gamma-\alpha} \sum_{j \in Q_i} \frac{B}{M_j^{1-\gamma}}\right) \quad (28)$$

in the consumption (21) and production (22) equations, respectively. If species i was eaten only by fish, then the production variance term was very negative. So we expect species that were eaten only by fish to lie significantly below the overall linear trend of slope 1 on the production plot. The only species that were eaten only by fish were the fish themselves, and one other species in each year (a single species that survived from 1984 to 1986). The fish and this other species deviated from the general trend more than any other species in both years (Fig. 5C, D).

Fish and cannibals were outliers on the BR model consumption plots in 1984 and 1986, and they lay below the overall trend (Fig. 5C, D). These were the same species, in both years, as those with diets that consisted predominantly of meat. For the other models also, though to a lesser extent, the species that lay significantly below the overall linear trend on $\log(C_{flux})$ versus $\log(C_{allo})$ plots had predominantly meat diets. For the MA, RC, and BR models in each year, Fig. 6 plots species' residuals from the line $y = x$ on $\log(C_{flux})$ versus $\log(C_{allo})$ axes, versus the percent of the species' diet that consisted of meat (as calculated using the flux model in question). Species with more meat in the diet generally had more negative residuals. Why?

Consumption of zooplankton (meat) may have been more beneficial to the growth and reproduction of a consumer than consumption of phytoplankton, if zooplankton contained a higher proportion of fat than phytoplankton. Fat has more calories per unit mass than protein or carbohydrate. However, for stoichiometric reasons, zooplankton consumption may have been more beneficial to consumer growth and reproduction even if zooplankton fat content was no higher than that of phytoplankton. The zooplankton of Tuesday Lake may have contained limiting growth reagents in greater abundance than the phytoplankton. In either case, one would expect mainly carnivorous species to fall below the general linear trend on $\log(C_{flux})$ versus $\log(C_{allo})$ plots because less consumption (C_{flux}) of richer food was needed to meet fixed allometric requirements (C_{allo}).

A modified method of evaluating the five flux models was considered. Instead of plotting normalized C_{flux} versus normalized C_{allo} on log-log axes, a normalized alternate C_{flux} (called AC_{flux}) versus a normalized C_{allo} was plotted. The new AC_{flux} was the sum of inbound fluxes as calculated by the flux model under study, but with the fluxes coming from nonphytoplankton species multiplied by some fixed "meat benefit ratio" which was greater than or equal to 1. A summary statistic of the quality of the new plots is $\text{std}(\log(AC_{flux}) - \log(C_{allo}))$. This summary statistic was plotted as a function

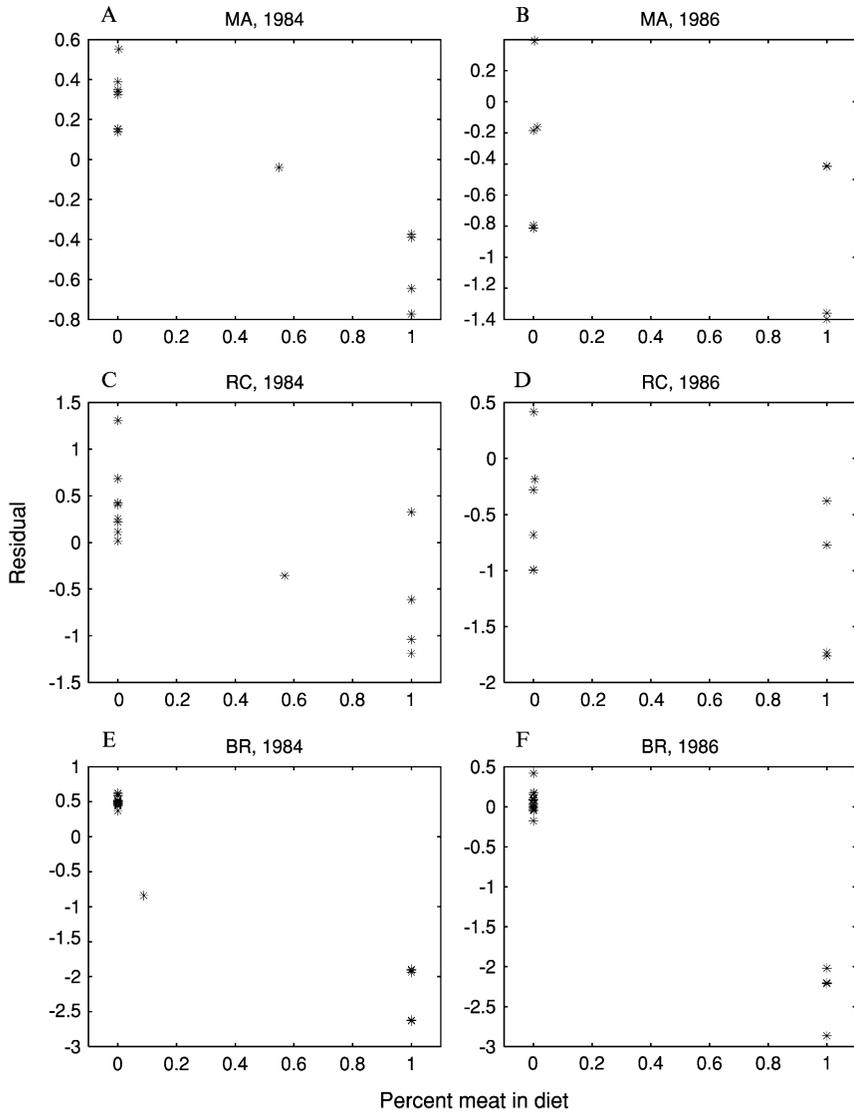


Figure 6 Plots of the residuals from the line $y = x$ in $\log(C_{flux})$ versus $\log(C_{allo})$ plots versus percent of the species' diet that was meat (as calculated using each flux model), for nonbasal species, for models MA, RC and BR in 1984 and 1986.

of the meat benefit ratio, increasing from a meat benefit ratio of 1, for each of the models MA, RC, and BR. For all models in both years, the summary statistic decreased initially as the meat benefit ratio increased from 1, until it reached some minimum after which it increased. Table 7 gives summary

Table 7 Assessments of fit of $\log(C_{flux})$ with $\log(C_{allo})$ and of $\log(AC_{flux})$ with $\log(C_{allo})$ ^a

Model	Year	Standard deviation with MBR = 1	MBR for minimal summary stat.	Minimal standard deviation
MA	1984	0.36	5.4	0.15
	1986	0.42	2.3	0.39
RC	1984	0.56	8.3	0.38
	1986	0.52	3.2	0.47
BR	1984	1.22	536	0.20
	1986	1.03	218	0.19

^aBy means of the standard deviation of the residuals of the data from the line of slope 1 which best fitted the points in log-log coordinates. Values in column 5 are for the optimal meat benefit ratios (MBR) shown in column 4.

statistics with meat benefit ratio 1, as well as meat benefit ratios that minimized the summary statistic, and the accompanying minimal statistic. The meat benefit ratio that minimized the summary statistic was called the minimizing meat benefit ratio.

The MA and the RC models had reasonable minimizing meat benefit ratios (between 2.3 and 8.3). The BR did not (its minimizing meat benefit ratio was over 200), but given these unreasonable meat benefit ratios, this model produced good summary statistics, bettered only by the MA model in 1984. The BR model may have improved so much with the implementation of a meat benefit ratio because it was the only model originally posed as a model of biomass flux. The BR model's assumption that all species had the same caloric value per unit mass is precisely the assumption that a nonunit meat benefit ratio seeks to correct. The other models were based on allometric formulas with energy units, and were therefore direct models of energy flux.

Excluding mainly carnivorous species was the same, in both years, as excluding fish and cannibals. The "no fish or cannibals" section of Table 6 shows how well each model performs, considering only species whose diet did not consist mainly of meat. In the two consumption *C* rows of this part of the table, the BR model outperformed the other models.

VII. APPLICATION: TROPHIC LEVEL AND TROPHIC HEIGHT

Adams *et al.* (1983) proposed and Winemiller (1990) among others used a recursive definition of trophic level τ as follows. Species that ate no other species were assigned trophic level of $\tau = 0$. The trophic level τ_j of any

consumer j was defined as

$$\tau_j = 1 + \sum_{i \in R_j} \tau_i F_{ij} \quad (29)$$

where F_{ij} was the fraction of the consumed food of species j consisting of species i . Adams *et al.* (1983) measured the fraction in terms of volume (equivalent to energy under the assumption that all species had the same energy per unit of volume). Using energy flux here, F_{ij} for the Tuesday Lake data was computed from the fluxes f_{ij} by

$$F_{ij} = \frac{f_{ij}}{\sum_{g \in R_j} f_{gj}} \quad (30)$$

The trophic level τ was not constrained to be an integer, and was defined regardless of cannibalism, omnivory, or loops in the food web, although in some of these cases, linear algebraic equations had to be solved.

The fluxes of the five flux models gave five different measures of trophic level. However, the fluxes from the metabolic action and consumer control models gave the same trophic levels for all species. This identity held because if i_1 and i_2 were two prey of species j , then

$$f_{i_1 j} / f_{i_2 j} = P_{i_1} / P_{i_2} \quad (31)$$

for both the MA fluxes and the CC fluxes. So the normalized fluxes F_{ij} in the trophic level equation were the same in both cases. Therefore, for all analyses of trophic level, results were computed for all models except the CC model.

Reuman and Cohen (2004) defined trophic height in a way that did not depend on fluxes, but only on the food web, as follows. The *trophic position* of a species in a food chain was defined to be the number of species below it. (In a recursive definition, species A was said to be *below* species $B \neq A$ in a food chain if species A was eaten by species B , or if species A was below any species that was below species B .) The *trophic height* (H) of a species was the average trophic position of the species in all food chains to which it belonged, only considering food chains with no repetitions of species. Excluding repetitions of species ruled out chains that went all the way around a loop in the food web (even a loop of length one, i.e., a cannibalistic link). Chains that went any part of the way around a loop were allowed. This definition was the same as one of the definitions in Cohen and Luczak (1992) and Yodzis (1989).

The trophic level of each species was computed under each of the five flux models, and the trophic height of each species was also computed using the method of Yodzis (1989), Reuman and Cohen (2004) and others. Trophic height and trophic level generally increased with increasing species body mass according to any method of calculation.

The trophic height was greater than or equal to the trophic level as measured using the EF or BR flux models, for all species in both years. The trophic height was greater than or equal to the trophic level as measured under the other flux models except for two species in 1984 (the same two species for all three models). This consistent inequality can be understood mathematically in the following way. The trophic height of a species was a weighted average of the trophic heights of its prey, plus one. Prey with more chains entering them from below in the web were weighted more heavily. However, higher trophic height prey tended to have more chains entering them than lower trophic height prey. Thus, the weighted average that produced the trophic height of a species more heavily weighted prey of greater trophic height. This weighting inflated results compared to trophic level, using any one of the flux estimate methods. While trophic level also used a weighted average of the prey of a species, the weighting was based on the percentage of the diet that each prey represented.

In the absence of flux measurements or estimates, one could replace trophic height with trophic level, using the EF model. The assumptions of this model are false, but this method avoids the overestimation problems of trophic height.

The data of Tuesday Lake provided a weak basis for comparing methods of calculating trophic height or level because only a few species in Tuesday Lake had trophic height or level greater than 1 under any method. All basal species had height or level 0 under any method. Basal species were at least half of all species in Tuesday Lake. Species that ate only basal species had height or level equal to 1 under any method. Very few species remained in Tuesday Lake after species of height or levels 0 or 1 were eliminated. Larger webs with more species of height or level greater than 1 are needed to make better comparisons among the methods.

Stable nitrogen isotopes have been widely used to estimate trophic height or level (Peterson and Fry, 1987; Kling *et al.*, 1992; Zanden and Rasmussen, 1999; Post *et al.*, 2000; Post, 2002; Jennings *et al.*, 2002a). The method is based on the fact that the index $\delta^{15}\text{N}$ of the ratio of the stable isotopes of nitrogen (see Jennings *et al.*, 2002a for a definition of $\delta^{15}\text{N}$) in a predator is approximately 3–4‰ more than the weighted mean of the $\delta^{15}\text{N}$ values of its prey species, where the weighting is according to the ease with which the predator absorbs nitrogen from each of its prey species (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Peterson and Fry, 1987; Post, 2002). Assuming that absorption of nitrogen is proportional to absorption of energy, the mean can be calculated with weighting given by the energy fluxes from each prey to the predator. Stable isotope methods of measuring trophic position were judged to be more likely to correspond closely to trophic level than to trophic height, and such measurements should correspond most closely to the trophic level estimate that is based on the

Table 8 Trophic heights or levels of all nonbasal, nonherbivorous species using six methods of measuring height

Species	Height	EF Level	MA Level	RC Level	CC Level	BR Level
1984						
<i>Cyclops varians rubellus</i>	2.50	2.14	2.67	2.64	2.67	2.15
<i>Daphnia pulex</i>	1.43	1.11	1.00	1.00	1.00	1.00
<i>Orthocyclops modestus</i>	3.20	2.21	3.01	3.05	3.01	2.23
<i>Tropocyclops prasinus</i>	2.50	2.14	2.67	2.64	2.67	2.15
<i>Chaoborus punctipennis</i>	3.60	2.17	2.04	2.08	2.04	1.10
<i>Phoxinus eos</i>	4.17	2.53	3.09	2.93	3.09	2.47
<i>Phoxinus neogaeus</i>	4.17	2.53	3.09	2.93	3.09	2.47
<i>Umbra limi</i>	4.84	2.80	3.13	3.87	3.13	2.47
1986						
<i>Cyclops varians rubellus</i>	3.19	2.23	2.50	2.55	2.50	2.08
<i>Daphnia pulex</i>	1.39	1.10	1.00	1.00	1.00	1.00
<i>Daphnia rosea</i>	1.47	1.13	1.01	1.00	1.01	1.00
<i>Orthocyclops modestus</i>	3.19	2.23	2.50	2.55	2.50	2.08
<i>Tropocyclops prasinus</i>	3.22	2.25	2.55	2.59	2.55	2.09
<i>Chaoborus punctipennis</i>	3.97	2.27	3.75	3.78	3.75	2.38
<i>Micropterus salmoides</i>	4.86	2.79	3.86	3.33	3.86	2.70

most realistic flux model. Therefore, it may be possible to test the flux models using stable isotope analysis, once community-wide (M , N)-food web data are gathered in conjunction with stable isotope analysis data from all or several species in a community.

The trophic heights and levels (under each of the five flux models) of all nonbasal, nonherbivorous species are in Table 8.

VIII. APPLICATION: EQUIPRODUCTION AND EQUICONSUMPTION LINES

Using the allometric formulas for population production in Eq. (1) and population consumption in Eq. (2), the equiproduction and equiconsumption curves on $\log(M)$ (ordinate) versus $\log(N)$ (abscissa) coordinates were lines of slope $-1/\alpha$ and $-1/\beta$, respectively. Including these lines on the food web plot in the plane of $\log(M)$ versus $\log(N)$ (Cohen *et al.*, 2003; Jonsson *et al.*, 2005) made the resulting plot even more powerful for visualizing food webs (Fig. 7B, which assumes $\alpha = \beta = 0.75$, making the equiproduction and equiconsumption lines the same). If $\alpha \neq 1$ and $\beta \neq 1$, the equiproduction and equiconsumption lines do not coincide with the equal biomass lines of slope -1 . Hence, there may exist pairs of species i and j such that i has more

biomass than j , but j has greater population consumption than i , and similarly for population production.

Under the MA model, the flux along a link was proportional to the product of the population consumption of the predator times the population production of the prey. When equiproduction and equiconservation lines were added to the $\log(M)$ versus $\log(N)$ plot of the food web, links that had a predator on a high equiconservation line and a prey on a high equiproduction line had a strong flux under the MA model. For instance, the flux from species 17 (unclassified flagellates) to species 47 (*Chaoborus punctipennis*) in Fig. 7B was very strong under the MA model, while the flux from species 22 (*Chromulina* sp.) to species 39 (*Keratella testudo*) was weak.

Under the CC and MA models, the relative strengths of the fluxes into a consumer were determined by the relative productions of the respective prey. Under either of these models, one could see which of two fluxes into a fixed consumer was stronger (and therefore which of two prey was more important for that consumer) by looking at a $\log(M)$ versus $\log(N)$ plot of the food web, with added equiproduction lines. The more important prey was on a higher equiproduction line. In Fig. 7B, the flux from 47 to 48 (*Phoxinus eos*) was stronger than the flux from 36 (*Holopedium gibberum*) to 48, so species 47 was probably a more important food source for species 48 than species 36 was.

Under the RC and MA models, the relative strengths of fluxes out of a resource were determined by the relative consumption of the respective predators. One could see which fluxes were stronger, and therefore which predators of a given prey consumed the most, using $\log(M)$ versus $\log(N)$ plots with equiconservation lines. The most consumptive predator was the one on the highest equiconservation line.

If $\alpha \neq \beta$, the equiproduction and equiconservation lines of Fig. 7B would no longer coincide, but relative flux strengths could still be visualized in a similar way. Under the BR model, the strength of a flux was proportional to the product of $N_i M_i^{1-\gamma}$ times $N_j M_j^\gamma$, for prey i and predator j . Lines of equal $N M^{1-\gamma}$ and $N M^\gamma$ would make possible similar visual comparisons of flux strength.

IX. APPLICATION: ESTIMATING REQUIRED LEVEL OF SAMPLING EFFORT

Cohen *et al.* (1993) suggested that food web data should be accompanied by yield-effort curves, which have units of sampling effort along the x-axis, and either number of observed species or number of observed links along the y-axis. Woodward *et al.* (2005) implemented this suggestion in their study of the Broadstone Stream ecosystem. Their species-yield-effort curves

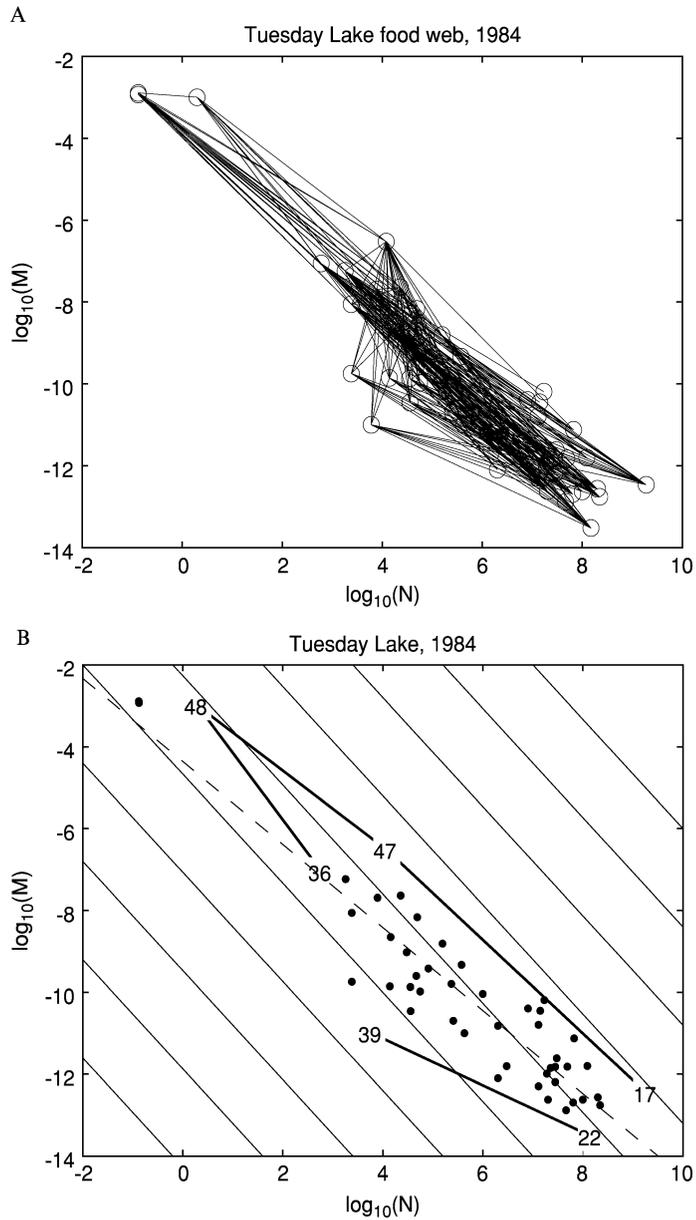


Figure 7 The Tuesday Lake food web in 1984. (A) As plotted by Cohen *et al.* (2003) and Jonsson *et al.* (2005). (B) With added equiproduction and equiconsumption lines (light solid lines), but only selected trophic links (heavy lines that join species numbers). Allometric formulas $P_i = pN_iM_i^{0.75}$ and $C_i = cN_iM_i^{0.75}$ have been assumed, so each equiproduction line coincides with an equiconsumption line. The dashed line

measured effort by the number of examined 25 cm by 25 cm quadrats of habitat. The species-yield-effort curves flattened out with increasing effort, indicating that the listed collection of species would probably not become much more complete with more sampling effort. Woodward *et al.* (2005) presented nine link-yield-effort curves for the nine most common predator species in their ecosystem, with the number of predator guts visually inspected as the measure of effort, and the number of prey species discovered in the guts as the measure of yield. Their link-yield-effort curves did not flatten out, except for some very common and very exhaustively sampled predators (for which hundreds of guts were examined). This finding supported the suspicion that typical reported food webs probably have not documented all links in the system (Martinez, 1991, Martinez *et al.*, 1999). We developed a theory for estimating the probability with which an unobserved link could be said not to exist, or not to represent a flux of more than a given strength. We also developed a theory for estimating the probability of absence of an undetected species.

Woodward *et al.* (2005) captured and counted all species that were larger than a certain size in each sampled 25 cm by 25 cm quadrat. Our model assumed that one unit of species sampling effort (quadrat) was sufficient to observe all species larger than a fixed size that were in a sampled habitat volume or area A . The model ignored species too small to be observed via the sampling method, although such species (e.g., microbes) may be biologically very important. The model also assumed that some version of gut content analysis of predators was used to detect links. Analysis of one gut was considered one unit of link sampling effort. The expected number of individuals of a given species in volume or area A was NA , where N was the numerical abundance (population density) of the species, as before, assuming that the species' presence or absence was independent of the presence or absence of other species in the sampled quadrats. The probability of finding the species in one unit of species-sampling effort was

$$p_s = 1 - P_{NA}(0) \quad (32)$$

where $P_{NA}(0)$ was the probability of 0 in a Poisson distribution with parameter NA . The probability of not finding the species after n units of sampling effort was therefore $(P_{NA}(0))^n = e^{-NA n}$. This probability was less than a fixed acceptable probability of failure p_f if and only if

is a least squares fit (in log-log coordinates) to all the plotted species. Most species are indicated with a dot, but the ones involved in a pictured trophic link are indicated with their species index as given in the appendix of Reuman and Cohen (2004): 17, unclassified flagellates; 22, *Chromulina* sp.; 36, *Holopedium gibberum*; 39, *Keratella testudo*; 47, *Chaoborus punctipennis*; 48, *Phoxinus eos*.

$$n \geq \frac{-\ln(p_f)}{NA} \quad (33)$$

After n units of sampling effort, each species with density N greater than

$$\frac{-\ln(p)}{nA} \quad (34)$$

would have been detected with probability at least $1 - p$. If after n units of sampling effort a species was not observed, then with probability $1 - p$ its numerical abundance was less than the quantity in Eq. (34).

Rare species that required many units of sampling effort to detect with reasonable probability were probably also large (because of the negative correlation between size and abundance). A second sampling method could be used to detect the presence of any such species that may have been missed using the first sampling method (e.g., nets with bigger mesh size that could be dragged over a larger area or volume of habitat).

Let V be a predator's gut volume, and let J be its consumption rate in volume units per unit time (which is assumed proportional to M^β , with M the average body mass of the predator, under the assumption that all species had equal energy density). If gut residence time of food particles is proportional to V/J (Kooijman, 2000, p. 81), and if V is proportional to the predator's mass M , then gut residence time is proportional to $M^{1-\beta}$. Let φ_{ij} be the aggregate (over all individuals) absolute energy flux per unit time from species i to species j . This energy flux is proportional to biomass flux under the assumption that all species have roughly the same energy content per unit mass. If prey species i was recognizable for a fixed proportion of the time it spent in its predator's gut, then the average number of individuals of species i that could be recognized in the gut of a randomly chosen individual of species j was proportional to

$$\eta = \frac{\varphi_{ij}M_j^{1-\beta}}{M_iN_j} \quad (35)$$

Let k denote the constant of proportionality. An italic f will be used to denote a relative flux, and a φ will be used to denote an absolute flux. Then the probability of having found evidence of species i in the gut of an individual of species j was

$$p_l = 1 - P_{k\eta}(0) = 1 - e^{-k\eta} \quad (36)$$

If n was the number of guts that were examined and p_f was the acceptable probability of not finding a link that exists, then $e^{-kn\eta} \leq p_f$ if and only if

$$n \geq \frac{-\ln(p_f)M_iN_j}{k\varphi_{ij}M_j^{1-\beta}} \quad (37)$$

Under the MA model, the right side of Eq. (37) became

$$\frac{-\ln(p_f)M_i^{1-\alpha}}{kpcN_iM_j} = \xi \quad (38)$$

If M_i increased, then N_i tended to decrease, and therefore ξ (the required sampling effort for a given probability of finding the link) increased. Modifying M_j had the opposite effect. The links most difficult to detect (in terms of the number of guts that had to be examined) had relatively small consumer M_j and relatively large resource M_i . These same conclusions held for the BR model.

After n units of sampling effort, each link with flux greater than

$$\frac{-\ln(p)M_iN_j}{knM_j^{1-\beta}} \quad (39)$$

would have been detected with probability at least $1 - p$, as a consequence of Eq. (37). If after n units of sampling effort a link had not been observed, then with probability $1 - p$, its flux was less than Eq. (39).

The MA and other proposed flux models are models of relative flux, but Eqs (35)–(39) use absolute flux. If a link from species i to species j was detected, one could estimate from experimental data the probability of having found evidence of species i in a single gut of species j by counting the percentage of guts of species j in which species i was found. Setting this relative frequency equal to the probability in Eq. (36) yields an estimate of $k\varphi_{ij}$. Doing this for all detected fluxes and fitting the estimates to

$$k\varphi_{ij} = kpcN_iN_jM_i^\alpha M_j^\beta \quad (40)$$

yields absolute estimates of $k\varphi_{ij}$ for unsampled or undetected links. In addition, the quality of the fit of the right side of Eq. (40) to the empirical estimates of $k\varphi_{ij}$ would be a valuable test of the MA model (or another model, if one replaces Eq. (40) with the flux definition for another model). Then the sentence that contains Eq. (39) gets replaced with the statement that each link for which the absolute $k\varphi_{ij}$ estimate was greater than

$$\frac{-\ln(p)M_iN_j}{nM_j^{1-\beta}} \quad (41)$$

would have been detected with probability at least $1 - p$ after n units of link-sampling effort. If after n units of sampling effort a link had not been observed, then with probability $1 - p$ its $k\varphi_{ij}$ estimate was less than Eq. (41).

This analysis makes it possible to identify in advance a food web that will have links and species that can be easily detected. Before a link is observed, its predator species must be observed, and predators tend to be rarer than

prey. Several predator guts may have to be examined before a given link is detected. So an ecosystem with no extremely rare species, and especially no extremely rare predators, can be more easily studied. A reviewer suggested that species-poor ecosystems may be good examples of systems with few extremely rare species because their species body mass distributions may have shorter upper tails. Tuesday Lake, Broadstone Stream, and Skipwith Pond—three of the most detailed webs currently available—are all relatively species-poor acid systems.

The probability of a link being detected, given the predator's gut, is given by Eq. (36). In a web that is well-suited for study, this probability must be large for all links. Therefore, the web must have large η and large $\log(\eta)$ for all links. Assuming the MA model, taking $\log(\eta)$, throwing out constant terms, and making use of the allometric relationship $\log(N) = -s\log(M) + \kappa$ (Peters, 1983), an easily studied web would have only links with large values of

$$\log(M_j) - (s + 1 - \alpha)\log(M_i) = \log\left(\frac{M_j}{M_i^\epsilon}\right) \quad (42)$$

where $\epsilon = s + 1 - \alpha$, which is close to 1. Therefore, the most easily sampled ecosystems will only have links with large predator to prey mass ratios, and no very rare predators.

This condition may be satisfied in an ecosystem with a classification of species into groups of very different body masses, with all members of each group feeding only on members of other groups of smaller body mass. The existence of such a classification would imply a block structure in a body mass indexed predation matrix, but is not equivalent to such a block structure. The Tuesday Lake body mass indexed predation matrix has a block structure in both 1984 and 1986 (Reuman and Cohen, 2004), and the species in Tuesday Lake can be classified into phytoplankton, zooplankton (which feed mainly on the phytoplankton), and fish (which feed mainly on the zooplankton). However, the gap in body mass between zooplankton and phytoplankton is not large enough in Tuesday Lake to ensure that all trophic links have large predator-to-prey body mass ratios. Moreover, some zooplankton feed on other zooplankton of similar size, and some fish feed on other fish. One reviewer suggested that pelagic systems may have exclusively high predator-to-prey body mass ratios because of the common trophic and size separation among the categories of phytoplankton, zooplankton, and fish. Other pelagic systems should be examined to see if it is possible to find a system with a clear size gap between phytoplankton and zooplankton, in which all zooplankton are herbivores, and no fish eat other fish. The same reviewer pointed out that benthic systems in freshwater tend not to have well-separated size and trophic classifications of species, due to the commonness of insects.

A similar contrast between marine systems and some terrestrial systems has been noticed (Pauly *et al.*, 2002). The size spectrum of some pelagic systems can be manipulated for experimental purposes through the use of nets of variable mesh size. The condition of large predator-to-prey body mass ratios in every trophic link may also be satisfied by a community in which all species have dentition and feeding practices that allow them only to eat species much smaller than themselves.

Conclusions similar to Eq. (42) hold for the BR model, but with exponents $1 - \beta + \gamma$ on M_j and $s + \gamma$ on M_i on the right side. Qualitative characterization of easily studied webs using the RC or CC models is more difficult.

The above approach is equally applicable when the link-sampling method is traditional visual gut-content analysis or a more sophisticated and sensitive method of gut content analysis. The only change would be the value of the constant k in Eqs. (36)–(40). Polymerase chain reaction (PCR) has been used to identify mosquito larvae in the gut contents in dragonfly nymphs (Morales *et al.*, 2003) and to distinguish among three prey species in the guts of spiders (Greenstone and Shufuran, 2003). To our knowledge, PCR has not been used community-wide to improve identification of prey species in the guts of predators. Use of PCR in this way might increase the interval after predation within which gut contents can still be identified, decreasing the total number of guts that have to be examined to detect a link with a fixed probability of success. Considering that the yield-effort curves for the number of links of Woodward *et al.* (2005) flattened out only for predators for which hundreds of guts were sampled, some such improvement may be essential to gather complete data on any food web of reasonable complexity.

X. APPLICATION: MEAN TRANSFER EFFICIENCIES

Jennings *et al.* (2002b) and Gaedke and Straile (1994) calculated mean transfer efficiencies in the following way. They grouped individual organisms into bins of log body mass (with no regard to the species of the organism). They then created a “production-size-spectrum,” which is a histogram with $\log(M)$ bins on the x-axis, and log of the amount of production occurring in the organisms within that weight class on the y-axis. This log production can be computed for each bin as α times the central $\log(M)$ value for that bin plus the log of the number of organisms in that bin. The “central” $\log(M)$ value of a bin is the arithmetic mean of the minimal and maximal $\log(M)$ values included in that bin. The log of the mean transfer efficiency was then the linear-regression slope of the production-size-spectrum times the mean of the logs of the predator-prey body mass ratios. These mean transfer efficiency estimation methods were adapted so that they could be applied to (M, N) -food webs by assuming that all individuals of a given

species have log-body-mass equal to $\log(M)$ given in the (M, N) -web data. The adapted methods were used to calculate the mean transfer efficiencies in Tuesday Lake.

Given a relative flux model, mean transfer efficiencies were computed for Tuesday Lake by adding the relative fluxes coming out of all intermediate species, and dividing by the sum of the relative fluxes going into the same set of species. The quotient obviated any need for absolute fluxes. Comparison of the outputs of these two methods was used as a test of the relative flux models (Table 9).

To compute mean transfer efficiencies using the adapted methods of Jennings *et al.* (2002b), $\log(M)$ bins beginning at -14 in both years and ending at -2 in 1984 and 0 in 1986 were used. These values approximately delimited the values of $\log(M)$ in each year. Regression values for the slope of the resulting production-size spectrum depended slightly on the width of the $\log(M)$ bins that were used. Table 9 shows the resulting transfer efficiencies for a reasonable range of bin widths. All flux-model transfer efficiencies were comparable with the values obtained using the adapted methods of Jennings *et al.* (2002b), except for the BR model values, which were 1–2 orders of magnitude too small.

The main weakness of the methods of Jennings *et al.* (2002b), as those methods were adapted here to (M, N) -webs (not a shortcoming in the original methods), was that the choice of bin widths could affect the estimate of transfer efficiency. Jennings *et al.* (2002b) worked with a $\log(M)$ distribution of individuals, while the current study worked with the distribution of the logarithms of body mass means over species. The latter distribution was

Table 9 Mean transfer efficiencies in Tuesday Lake according to each of several computational methods

	1984	1986
EF flux	0.383	0.325
MA flux	0.257	0.273
RC flux	0.127	0.150
CC flux	0.491	0.629
BR flux	0.008	0.008
bin width 2	0.259	0.387
bin width 1	0.631	0.685
bin width 0.5	0.494	0.646

The methods marked with a flux model take the quotient of the fluxes out of intermediate species by the fluxes into intermediate species. The methods marked by a bin width use the adapted methods of Jennings (2002b), as described in the text.

much coarser and therefore more prone to yield different results with different bin choices. For Tuesday Lake data in both years, for reasonable $\log(M)$ bin widths, the latter distribution had some bins that contained no species. The resulting $-\infty$ log-production values for those bins were ignored for linear regressions of log-production versus $\log(M)$. If the original distributions of individual body masses over each species had been retained in addition to the means of these distributions, these shortcomings could have been remedied.

XI. DISCUSSION

Given the food web, mean body sizes, and numerical abundances of species in an ecological community, the relative flux of energy along any link was estimated in several plausible ways. Previous efforts to estimate fluxes include Moore *et al.* (1993), deRuiter *et al.* (1995), Rott and Godfray (2000), Ulanowicz (1984), Bersier *et al.* (2002), and others. Several new models of the flux of energy were proposed here. Models of relative energetic flux were also models of relative biomass flux if multiplication by a constant sufficed to convert biomass to energy. When resource species differed in their energetic value (Cousins, 2003), the conversion between biomass and energy would be conditional on both the resource and the consumer.

A. Which Model Is Most Plausible

A null model supposed all fluxes equal (EF model). Three models of relative flux were based on allometric relations between mean body mass and population production and population consumption (the MA, RC, and CC models). One model of flux was based on an allometric relation between the rate of consumption and the body mass ratio of predator to prey (the BR model, adapted from Emmerson and Raffaelli (2004)). Lacking direct empirical estimates of fluxes, in this paper we evaluated the relative merits of the models using two indirect methods based on the input-output ratio for each species and the cross-check of predicted fluxes against allometric assumptions.

The input-output ratios under any model in either year were never much less than 1, except for three problematic cannibalistic species from the order Cyclopoida in both years (these species were present in both years, and were the only species from that order). In 1984, no model had input-output ratios less than 1 at all, except for these three species under the MA and RC models. In 1986, only the MA and RC models had any input-output ratios less than 0.99, other than these three problematic cannibals, and these ratios

were also not much less than 1. The greater presence of input-output ratios less than 1 in 1986 could be a fault of the MA and RC flux models, or an indication that the system was not at equilibrium in 1986. Since the input-output ratios were only slightly less than 1, these results may also mean nothing. The BR and CC models were the best models (other than EF) for ensuring no input-output ratios less than 1 in Tuesday Lake. Plots of log flux ratios versus log body mass revealed either no trend or an increasing trend, fulfilling the predictions of theory.

The consumer crosscheck test measured the consistency between the population consumption of each consumer species predicted by each model and the population consumption predicted by an allometric formula. The resource crosscheck test similarly compared population production of each resource species to flux out of those species according to a given model. Ignoring any comparison that is guaranteed perfect by definition of the model, we found that the MA model was the most consistent (among the models considered here) with the underlying allometric assumptions, for the Tuesday Lake data. This superiority of the MA model is no guarantee that it will perform better than the other models when absolute or relative fluxes are measured directly, or that it will still be the most consistent model when applied to other (M, N)-food web data sets.

On plots of $\log(C_{flux})$ versus $\log(C_{allo})$, mainly carnivorous species frequently lay below the general slope 1 linear trend, especially under the BR model. This pattern may arise because zooplankton (meat) prey species had a caloric or stoichiometric advantage over phytoplankton prey species. When we multiplied meat fluxes by a meat benefit ratio, the plots improved (i.e., the scatter from a slope 1 linear trend diminished) as the meat benefit ratio increased from 1, for MA, RC, and BR models in both years ($\log(C_{flux})$ versus $\log(C_{allo})$ plots for the CC model were perfect by definition). Meat benefit ratios that maximized the quality of the plots seemed quantitatively plausible (between 2.3 and 8.3) for the MA and RC models, but did not seem quantitatively plausible (218 and 536) for the BR model, although the $\log(C_{flux})$ versus $\log(C_{allo})$ plots with minimizing meat benefit ratios were better for the BR model than for either the RC or MA models. Using the minimizing meat benefit ratio for each model, the mean qualities of $\log(C_{flux})$ versus $\log(C_{allo})$ plots and $\log(P_{flux})$ versus $\log(P_{allo})$ plots were still best for the MA model.

Theoretical predictions of relative fluxes could be converted to theoretical predictions of absolute fluxes if the absolute flux of one or more links were measured empirically. To test directly whether one model was more successful than another would require empirical estimates of the relative or absolute fluxes of at least two links (in addition to the assumed information about the food web, mean body sizes, and numerical abundance of all species in those links).

B. Applications, Implications, and Possible Future Directions

Plausible flux estimates promise a variety of applications. In this study, we used flux estimates to compare six measures of trophic height or trophic level: two measures based on the food web alone (or, for the EF model, the food web plus the assumption of equal fluxes in all links), and four measures based on the flux models proposed here. The measure based on mean lengths of food chains used by Cohen *et al.* (2003), Jonsson *et al.* (2005), Reuman and Cohen (2004), and others probably inflated results compared to plausible stable isotope measures of trophic level. The measures of trophic level based on the flux models would probably be more in tune with stable isotope measures of trophic level.

To see which flux model estimates trophic levels closest to those obtained from stable isotopes, complete (M , N)-food web data would have to be compared with stable isotope measurements of several species. The isotope analysis should be done on species high in a food web, because it is for such species that estimates of trophic height or level differ the most among alternative models. A web with some omnivory should be used, since omnivory gives rise to differences among methods of calculating trophic level and height.

All flux models considered here produced flux distributions that were extremely unequal (except the EF model). The MA, RC, and CC models produced normally distributed log-flux distributions in both years. The BR model did so only in 1986. These results suggested log-normality of fluxes as a testable null hypothesis to quantify the qualitative hypothesis of “many weak, few strong links.” Quantitative measures of community flux distribution should be produced for other webs using estimated and (when available) directly measured fluxes. The Lorenz curve and the Gini index are two convenient measures of inequality in flux distributions.

Plausible flux estimates also made possible a theory of the amount of sampling effort needed to detect links and species in a community, with a given probability of success, when using sampling methods with certain properties. The accuracy and usefulness of this sampling theory could be tested on any data that include summary (M , N)-food web data and detailed records of the sampling process, including amounts and timing of sampling effort and the fruits of each unit of sampling effort. The unpublished data of Woodward *et al.* (2005) on the Broadstone Stream ecosystem may contain these details. The sampling theory presented here related the sampling effort expended, the population density of a species to be measured, and the probability of detecting that species. The theory also provided a similar relationship between sampling effort, the strength of flux through a link, and the probability of detecting the link. An experimentally verified theory of sampling effort could be useful for associating levels of certainty with

observed statistical regularities in food webs. Such a theory may also be useful in selecting for study an ecosystem that could be sampled with minimal effort to provide comprehensive or near-comprehensive (M, N)-food web data.

Mean trophic transfer efficiencies computed using an adaptation of the methods of Jennings *et al.* (2002b) and Gaedke and Straile (1994) were found to be comparable to mean trophic transfer efficiencies computed using the flux models, except the BR model. Adapted methods had to be used because Tuesday Lake data included only the mean body mass for each species. By contrast, the original methods of Jennings *et al.* (2002b) and Gaedke and Straile (1994) use the masses of each individual organism captured. The adaptation created uncertainty in the resulting mean transfer efficiencies, so that results could not be used as evidence that one flux model is superior to the others, except in the case of the BR, where the disagreement between the two methods was pronounced. Data including body mass measurements for all individual organisms captured would be necessary for more precise comparison, and this comparison may provide a way of distinguishing among flux models.

Comparing the Ecosim and Ecopath fisheries models of Villy Christensen, Carl Walters, and Daniel Pauly (Pauly and Pitcher, 2000) with the models of this study may offer a way for future research to evaluate both the present models (with explicit, analytically tractable hypotheses about allometry, links, and fluxes) and the Ecosim and Ecopath models (programmed packages where the core assumptions and their implementation may be less transparent).

C. Weaknesses

If the production (increase in body mass per unit time plus reproduction) of an individual in species i of body mass M is pM^α and the population of species i contains $N(M)$ individuals of body mass M , then the species abundance is $N_i = \int_0^\infty N(M)dM$ and the average body mass is $M_i = (1/N_i) \int_0^\infty M * N(M)dM$. The aggregated production of all individuals of species i is then $\int_0^\infty N(M)pM^\alpha dM \leq pN_iM_i^\alpha$. The inequality follows from Jensen's inequality, because M^α is a concave function of M when $\alpha < 1$, as assumed. The inequality is strict as long as there are individuals of at least two different body sizes in species i . An identical argument and inequality apply to the population consumption of species i . If the allometric functions apply to individuals, then the allometric functions for population production and population consumption must overstate the production and consumption aggregated over all individuals, respectively. This overstatement has been ignored. The significance of intraspecific variation in body mass for

interspecific allometric estimates was independently recognized and has been analyzed significantly further by Savage (2004).

Another weakness of the study, as already mentioned, is the lack of empirical flux measurements to compare with the predictions of the flux models.

XII. CONCLUSIONS

All models presented (except the EF model) performed well enough on the tests done to be considered plausible. The MA was the most plausible because it performed slightly better than the other models and because it is conceptually simpler, more easily applied, and more readily visualized. A plot of an (M , N)-web on $\log(M)$ versus $\log(N)$ coordinates, with equi-production and equiconsumption lines based on the standard allometric formulas for production and consumption, yielded more visual information about the relative magnitude of fluxes under the MA model than under any other model. The MA and BR models were also the easiest to use in conjunction with the theory of sampling effort developed in the section on theory. Whether the MA model produces realistic flux estimates can be determined only by empirical measurements of flux in a real ecosystem.

From the perspective of this study, ideal community food-web data should include:

1. Time and location of capture of each individual organism, to test whether the system is temporally and spatially homogeneous.
2. M measurements for individual organisms, and N measurements for each unit of species sampling effort.
3. Age measurements or estimates for individual organisms.
4. Individual organism gut content analysis for nonbasal species, using visual analysis or PCR.
5. Individual organism stable isotope measurements and stoichiometry of at least C, N, P.

This list is not exhaustive and may not be entirely practical under all circumstances.

The choice of ecosystem and the sampling design should be made in light of the following considerations.

1. The ecosystem should be chosen to obtain a food web that is as nearly complete as possible with minimal sampling effort. This choice should be informed by the sampling theory of this study.
2. A system should be chosen for which an initial assumption of spatial homogeneity is reasonable, or separate sampling designs and evaluations

- should be constructed for clearly distinguishable major spatial components (e.g., pelagic versus benthic versus littoral, below ground versus above ground).
3. Sampling should be done speedily enough to justify assuming that the ecosystem has not changed much during the sampling, or separate sampling designs and evaluations should be constructed for clearly distinguishable major temporal components (e.g., major seasonal differences or different precipitation regimes).
 4. Within each spatial or temporal component, sampling should be intensive enough to reach the point of diminishing returns (i.e., until species yield-effort curves and link yield-effort curves nearly cease to increase with additional sampling effort).
 5. Sampling should be continued until M and N data for each species reach a specified coefficient of variation. The value of 10% was used in Tuesday Lake.

Additional desiderata for food-web data were discussed in Cohen *et al.* (1993).

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