

# Methods for constructing and balancing ecosystem flux charts: new techniques and software

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We describe a general computer program which employs novel techniques to analyze carbon (energy) and nutrient flows in complex food webs. The program uses estimates of metabolic/physiological parameters and ecosystem fluxes to simultaneously calculate the most likely balanced flux charts for carbon and a nutrient. We give an example of how the model can explore the theoretical issues involved with nutrient limitation and recycling.

**Keywords:** flux chart, ecosystem model, food web, nutrient limitation

## 1. Introduction

An understanding and quantification of the flows of energy and nutrients passing through and between organisms and trophic levels of an ecosystem is a necessary prerequisite for any serious ecological study of the system. Unfortunately, even this minimum requirement is very difficult to achieve with any reasonable degree of accuracy, simply because of the scarcity of reliable empirical data. A typical ecosystem contains a large number of flux “pathways” that interconnect the many biotic components of the food web, and this complexity increases substantially when one takes into account the presence of the “microbial loop” [1]. Most of these fluxes change significantly both in space and time, and many are rarely systematically measured in the field. Without a reasonably complete knowledge of the individual fluxes, it becomes hard to attain a clear picture of ecosystem structure and function. Largely because of this difficult situation, a number of elegant mathematical models have been devised over the last decade in order to maximize the use of the little empirical information that is generally available concerning ecosystem energy and nutrient flows (see, e.g., [7,10,14,17,18]). These models generally divide up an ecosystem into a set of (mostly) biotic compartments (e.g., phytoplankton, zooplankton, bacteria, etc.) and attempt to estimate and mass balance the network of flows so that the sum of inputs to each compartment is equal to the sum of its outputs in terms of carbon or nutrient flows. These procedures take advantage of known information which include: direct estimates of particular fluxes, literature values of various metabolic and feeding preference parameters, and reasonable boundary conditions that constrain the maximum and minimum values of particular fluxes or other parameters of the compartments.

In this article, we describe a general purpose computer program we have developed to construct, balance and analyze compartmental food web flux diagrams. This program,

which is described in section 2, will be available to the public from the authors upon request. The program has two methods for obtaining mass-balanced flux charts. The first uses the “inverse” approach of [7] and [12] to balance flux charts when prior estimates of the fluxes have already been obtained. It can also be used for some theoretical purposes as discussed in [7,12] and in an example given in the last section here. We have also included in the program a new method for constructing flux charts using information about metabolic, physiological and food preference parameters, without necessarily any prior information about the fluxes. Our technique extends previous methods [2–4,8–10,16,17], and is designed to be as flexible as possible. This method is discussed in detail in section 3.

One of the novel aspects of our program is its ability to balance carbon (energy) and nutrient (e.g., phosphorus or nitrogen) flows simultaneously. The approach takes into account the possibility that a consumer compartment can be limited by a nutrient rather than by the availability of carbon alone. In section 4, we give a theoretical example of a food web with a partially nutrient limited consumer compartment, and show the increased importance of the microbial community under these circumstances. Accurate knowledge of both energy and nutrient fluxes is not only important for the theoretical understanding of ecosystems, but also has practical implications for the proper management of such systems. We conclude this article by giving a discussion of some of these implications.

## 2. Program methodology and description

This section describes a computer software package that we have developed for the purpose of constructing, balancing and analyzing compartmental food webs. Figure 1, for example, displays a four compartment food web chart (phytoplankton, zooplankton, microbial organisms, detri-

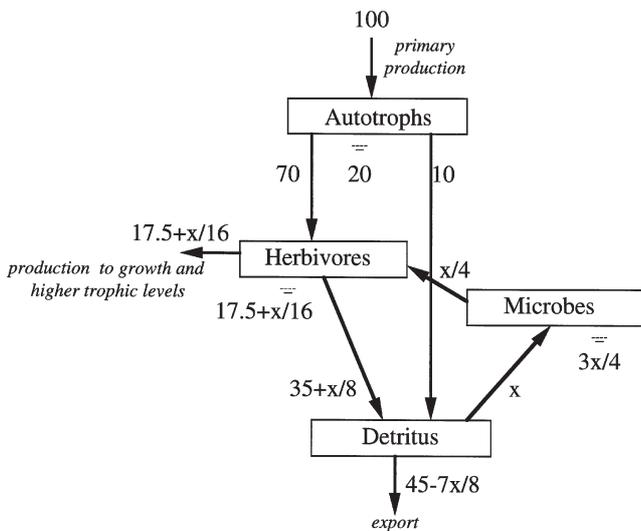


Figure 1. Carbon flux chart for four compartment model. The symbol  $x$  denotes the amount of recycled carbon.

tus) and the carbon fluxes that flow between each compartment. The chart is mass balanced since the sum of carbon entering any particular compartment is equal to the sum of carbon leaving that compartment. The program can accommodate changes in biomass that might occur over a given time period, and thus in particular is capable of constructing seasonal rather than just annual flux charts. Another important feature of the program is that it can use stoichiometric relationships (e.g., C:P ratios) to obtain flux charts that are simultaneously balanced for two different flux currency units (e.g., carbon and phosphorus). For example, the carbon chart in figure 1 has an associated phosphorus chart which is derived from C:P ratios (see below) and is also in balance, i.e., with the sum of phosphorus flows entering any particular compartment equal to the sum of phosphorus leaving that compartment.

The computer program was designed specifically for the study of lake food webs and is being tested as part of a large scale comparative study of Lake Kinneret (Israel) and Lake Constance (Germany) foodwebs. Nevertheless, the computer program is quite general and can be applied to almost any ecosystem. The program has a user friendly pull-down menu user interface with a spreadsheet-like main display. Data can be entered directly into the program or can be read from a disk from several different file types. Output from the program can be displayed in either spreadsheet or graphical form and can be saved in several file formats, including the NETWK input file format, which allows for further network analysis of the output using the NETWK program [13].

Our software has two methods for obtaining balanced charts. One is based on the “inverse” approach of [7,12]; the second will be discussed in the next section. In the inverse method, estimates of all fluxes are input into the program, together with upper and lower bounds on each of these fluxes. Respiration fluxes are treated somewhat differently than the other fluxes; they are entered as a percentage

of either the intake or production of a given compartment. This is a simple way of reflecting the fact that the amount of respiration depends on the activity of the compartment, and has been used in many similar investigations (e.g., [2–4,8,9,12]).

The program then, using a linear programming approach (see [12] for details), outputs the mass balanced flux chart that is closest to the initial estimates. It does so by minimizing a selected “objective function” that measures the distance between any hypothetical flux chart and the known initial flux estimates. The objective function can be put in terms of the deviations relative to either the absolute magnitudes of the fluxes or weighted depending on the uncertainty of each flux.

Physiological quantities such as production to biomass ( $p/b$ ) and gross growth efficiency ( $k_1$ ) are usually known to lie within a certain range. Thus, the program has the option of adding initial estimates and constraints on these quantities, and incorporates the distances of these parameters from their initial estimates into the objective function.

To summarize this method, initial estimates for each of the fluxes  $f_i^*$  and physiological or metabolic parameters  $p_j^*$  are specified, and the program finds the mass balanced chart with fluxes  $f_i$  and physiological parameters  $p_j$  which minimizes the objective function:

$$d = \sum_i w_i |f_i - f_i^*| + \sum_j v_j |p_j - p_j^*| \quad (1)$$

subject to the constraints  $f_{i \min} \leq f_i \leq f_{i \max}$  and  $p_{i \min} \leq p_i \leq p_{i \max}$  on the fluxes and parameters. Here, the  $w_i$  and  $v_j$  are weights expressing the confidence in the estimate of the  $i$ th flux and  $j$ th physiological parameter, respectively. Different levels of confidence in these fluxes and parameters can arise if, for example, some were directly measured, while others were estimated from literature values obtained under conditions possibly different from those of the study site. A proper choice of weightings can therefore improve the robustness of model results over models which do not include such weightings.

The program can also balance a nutrient flux simultaneously with the carbon flux. Carbon fluxes to consumer compartments are converted to nutrient units using the carbon to nutrient ratio of the prey compartment, while fluxes to primary producers and bacteria are converted using the carbon to nutrient ratio of the producer compartment. The difference between nutrient inflow to a compartment and nutrient outflow from this compartment to predators is sent to the detrital (non-living) compartment. The compartment can of course only be mass balanced if the flux excreted to detritus is non-negative; the program by default constrains the fluxes to satisfy this. Consumers are typically not completely efficient in assimilating ingested nutrients. For this reason, the program has an option to put a bound on the maximum possible nutrient assimilation efficiency of each consumer compartment, i.e., to require that at least a certain percentage of ingested nutrient be sent to the detrital compartment.

By changing the objective function (1), the linear programming approach can be used for other purposes as well. For example, the program can maximize or minimize any given flux or physiological parameter, which indicates whether and how much the constraints on all the fluxes and parameters further constrain that particular flux [7]. Another possible objective function instead of (1) minimizes the sum of all fluxes, subject to the given constraints [17]. While this method of balancing charts has achieved some popularity [6,16], it is not clear to us what the biological meaning of the criterion is, nor do we see evidence that ecosystems should tend to minimize the sum of fluxes.

The method described in this section can be used to balance and analyze flux charts for which prior estimates of the fluxes have already been made. However, when few measured estimates of fluxes exist, as is often the case, the inverse approach is less successful. To overcome this, we describe another approach in the next section, which can be used to construct balanced flux charts even when there are no prior estimates of the various fluxes.

### 3. Quantitative estimation of food web flux diagrams

The problem of estimating fluxes between compartments in a food web has received less attention than the subsequent network analysis of the constructed food web. This is unfortunate since many of the fluxes are not directly known, and the validity of the network analysis depends on an accurate knowledge of the flows through the food web. In this section, we describe a general technique for constructing mass-balanced food webs from the commonly available information described below.

The following information is needed for each living compartment: (a) production, or equivalently biomass and the production to biomass ( $p/b$ ) ratio; (b) the gross growth efficiency (production/intake) ratio  $k_1$  (for our purposes, “intake” includes not only ingested food, but also food lost by sloppy feeding); (c) the net growth efficiency  $k_2 = \text{production}/(\text{production} + \text{respiration})$ . Production of phytoplankton and bacteria are often regularly measured; literature values can usually be found for the  $p/b$  values of other compartments, as well as the efficiency ratios  $k_1$  and  $k_2$ . For the non-living compartment(s) (typically POC and/or DOC) only export fluxes (e.g., sedimentation) and estimates of any fluxes between these compartments are needed.

From the values of production,  $k_1$  and  $k_2$ , the food requirements as well as respiration and egestion of each compartment can be inferred (e.g., respiration = production  $\times (1/k_2 - 1)$ ). It remains only to partition the demands of each compartment among its potential prey. Our method is derived from two general observations: (i) Most consumers are *opportunistic*. That is, they will shift the food composition of their diet depending on what types of food are available (this is incorporated into the food web models of [3,4,16]). (ii) In spite of (i), most consumers have some preferences or differential rates of consumption of

various potential food sources (this is used in the food web models of [2–4,10]). Differential consumption rates for individuals can result from, for example, differential filtration rates for filter feeders, or differences in capture success for carnivores. Apparent compartmental preferences can also be a result of heterogeneity of a compartment. For example, in Lake Kinneret, the majority of fish are zooplanktivores. However, there are a few fish (e.g., the St. Peters fish *Sarotherodon galilaea*) which feed primarily on phytoplankton. Hence, the fish compartment as a whole shows a preference for zooplankton, even though most of the individual fish either eat only zooplankton, or eat primarily phytoplankton.

To incorporate both properties (i) and (ii) into our methodology, we have devised the following scheme to estimate the flux  $t_{ij}$  from prey compartment  $j$  to consumer compartment  $i$ . Firstly, relative food preferences  $r_{ij}$  are estimated for each consumer; here  $r_{ij}$  indicates the preference of the consumer compartment  $i$  for prey compartment  $j$ . They represent the *relative* rate of consumption of the prey per unit time; the absolute rates are not necessary. The relative rates can be inferred from commonly available information such as relative filtration rates and indices of electivity. For each food compartment, its available production  $a_j$  (i.e., its production less its change in biomass over the given time period) is multiplied by the relative food preference  $r_{ij}$  to give a “consumption score”  $c_{ij} = a_j r_{ij}$  for consumption of the  $i$ th compartment on the  $j$ th compartment. The diet composition of the  $i$ th compartment is then taken to be proportional to the consumption score of each of its possible prey compartments. More precisely, if  $d_i$  is the intake demand of the  $i$ th compartment, its consumption  $t_{ij}$  on prey compartment  $j$  is taken to be:

$$t_{ij} = \frac{d_i c_{ij}}{\sum_k c_{ik}}, \quad (2)$$

where the sum is over all possible prey compartments of compartment  $i$ . This method takes into consideration opportunistic feeding in that it relates the availability of a potential prey with its fraction in the diet of a consumer compartment. But it also takes feeding preferences into account; for example, if the production of each possible prey was equal, the consumer’s diet composition would be proportional to its preference for each possible food source.

The  $t_{ij}$  calculated above specify all intercompartmental fluxes. It is not necessarily true however that the food web given by the  $t_{ij}$  is mass balanced. In particular, there may be more (or too little) demand by consumers for a particular compartment than the actual available production of that compartment. The derived set of flux estimates can now be mass-balanced using the balancing technique described in the last section.

Though not implemented at this time, we wish to mention an alternative method for not only achieving mass balance but obtaining optimized estimates of the metabolic and food preference parameters. This method directly adjusts the production, growth efficiency and food preference pa-

rameters (rather than the fluxes) to obtain a balanced chart. Unfortunately, this problem is intrinsically nonlinear and the linear programming software we provide (as described in the previous section) is incapable of directly obtaining the required optimization. However, as it is possible to implement such a nonlinear optimization routine, we sketch out the basic technique below.

The optimization of the parameters should be done in such a way that the initial estimates are changed as little as possible in some sense. More precisely, if  $p_i^*$  are the initial estimates of the metabolic and food preference parameters, we wish to find adjusted parameters  $p_i$  that minimize a weighted distance function of the form

$$d = \sum_i w_i |p_i - p_i^*|^n, \quad (3)$$

where  $n$  is typically taken to be either 1 or 2 and the  $w_i$  are weights reflecting the relative confidence in the  $i$ th estimate. This is to allow for the variation of the amount of uncertainty in the different parameters; some parameters may be directly measured and thus there is reasonable confidence in their values, while the estimates of other parameters may be based on unreliable literature values or are even just educated guesses. There is in addition a biologically realistic range for each parameter  $p_i$ ; that is, each parameter is constrained to some interval. The optimal parameters are the ones that minimize the distance (3) subject to mass-balance and the other constraints. In this way, the chart is not only balanced, but improved estimates of the initial parameter estimates can be made.

One special case of weighting choice in (3) deserves special mention, namely the possibility of setting some of the weights  $w_i$  to 0 (or perhaps to a number very close to zero). The optimization procedure will then, if possible, achieve a mass-balance by varying only those parameters whose weights have been set to zero while clamping the other parameters at (or near) their initial estimates. This takes advantage of the overdetermined nature of the problem to estimate unknown parameters whose weights have been set to zero from the estimates of the other parameters which can be estimated with more confidence. A similar idea to this was used in [3,4] to estimate  $k_1$  values of some consumer compartments in Lake Constance.

#### 4. A theoretical example

We will present applications of this model to lake food webs elsewhere, but demonstrate here how the model can also be used to assist in theoretical studies, especially because of its ability to handle dual currencies. In particular we will focus on the problem of a model system in which a consumer compartment is partially constrained by a nutrient. While the importance of nutrient limitation of producers is well established, it is only recently that there has been awareness of the possibility of nutrient limitation of consumers (see, e.g., [5,11,15]). Nutrient limitation places

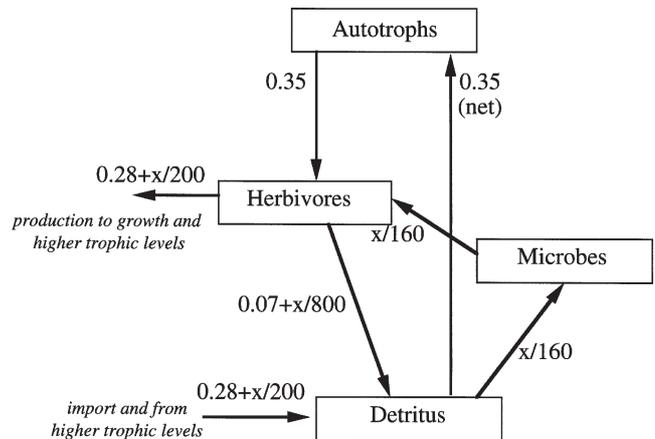


Figure 2. Phosphorus flux chart for four compartment model as derived from C:P ratios.

additional constraints on the growth of the consumer compartment, and thereby increases the importance of recycling via microbial activity.

Consider an ecosystem consisting of four compartments: autotrophs, herbivores, microbes (bacteria and protozoa), and a detrital compartment consisting of non-living matter. We assume primary production of 100 carbon units, with 20% of this respired, 10% sent to the detritus, and the remaining 70% grazed by the herbivores (see figure 1). Assuming sufficient nutrients, one quarter of the herbivores' intake goes to production, one quarter to respiration, and the remaining half to detritus. Now suppose that the microbes take up  $x$  carbon units from the detritus compartment; the remainder of the detrital carbon input is lost from the system. Three quarters of the microbial carbon uptake is respired, with the remaining one quarter being supplemental food to the herbivores. Figure 1 portrays this system when carbon flows are mass-balanced. Because herbivores are taken to be 25% efficient, one sees from the carbon chart that  $1/16$  of the microbial carbon uptake  $x$  is ultimately converted into herbivore production. Examine now the extreme condition that all detrital material is recycled. One has from figure 1, by setting  $\text{export} = 45 - 7x/8$  to zero, that  $x \approx 51.43$ . In this case the microbial compartment adds only about  $x/16 = 51.43/16 = 3.2$ , or less than 20%, additional carbon to the herbivore food supply. In other words, microbial secondary production is only a minor contributor of carbon to the herbivores.

Now consider the effect of the addition of a second currency, in this example phosphorus, to the system. We will take the weighted C:P ratios in a severely phosphorus limited system to be 200:1 for the autotrophs and 40:1 for the herbivores and microbes. We assume that the herbivores are capable of up to 80% efficiency in assimilating incoming phosphorus. Figure 2 gives the phosphorus flux chart corresponding to figure 1 under the above assumptions, which takes into allowance that no phosphorus is ever lost through respiration. Dividing the autotroph-herbivore carbon flux of 70 by the 200:1 (C:P) ratio of the autotrophs, herbivores consume 0.35 units of phosphorus from the autotrophs. At

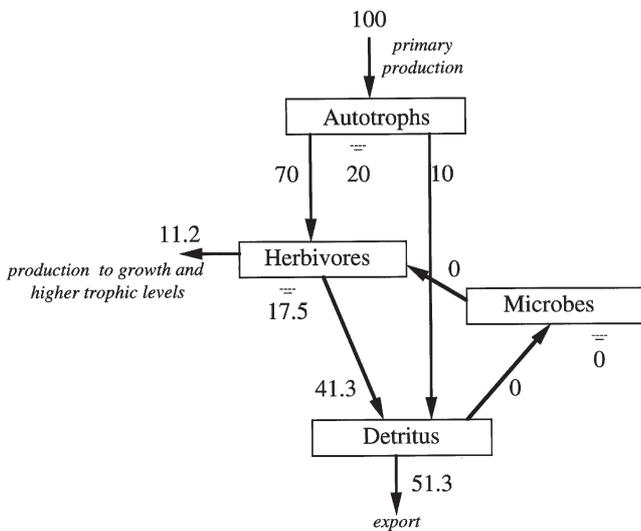


Figure 3. Carbon chart for four compartment model with no recycling, taking into account herbivore nutrient limitation.

80% efficiency, herbivore production (in units of phosphorus) is  $(0.8)(0.35) = 0.28$ , to which must be added  $x/200$ , i.e., 80% of recycled production. The detrital pool receives the remaining 20% of the phosphorus consumed by the herbivores, or  $0.07 + x/800$ .

Examine now more closely the interdependency of the dual currencies on herbivore production. The unusual effect we wish to convey can be seen by converting herbivore phosphorus production into units of carbon (by multiplying the phosphorus available for herbivore production by 40) to obtain  $11.2 + x/5$ , as compared to  $17.5 + x/16$  found in the carbon chart of figure 1. If there is no recycling ( $x = 0$ ), phosphorus limitation sets the limit to herbivore carbon production at a maximum of 11.2, which is much less than the predicted value of 17.5 one obtains by (wrongly) neglecting to consider possible phosphorus constraints. Thus, one sees that for low to moderate levels of microbial uptake  $x$ , herbivore growth is phosphorus limited. It is only when the recycling  $x$  is large enough that  $11.2 + x/5 > 17.5 + x/16$ , i.e.,  $x > 45.8$ , when microbial uptake is near maximum, that the herbivores become carbon limited. When dual currencies are considered, microbial production can thus increase herbivore production up to about 85%, from a minimum of 11.2 with no recycling to a maximum of about 20.7 with complete recycling. This is in contrast to the less than 20% predicted from considering carbon flows alone. Thus, the importance of microbial activity can be seen much more clearly and correctly through the use of dual currencies.

As an exercise to confirm the validity of the computer model, we entered the carbon chart given in figure 1 with  $x = 0$  (i.e., no microbial uptake) into the program, and imposed the phosphorus constraints and C:P ratios given above. The dual currency balanced chart output from the program is shown in figure 3. It is in agreement with our above discussion: herbivore production is reduced from 17.5 to 11.2, with a corresponding increase in the carbon flow from herbivores to the detritus.

## 5. Discussion

Though the food web investigated in the last section is simple enough to study analytically, the computer model can be used in more complex situations to similarly detect and analyze the effects of consumer nutrient limitation. As can be seen from this example, the detection of nutrient limitation when it exists can be crucial to comprehending the system as a whole.

More generally, the model output of energy and nutrient flows, together with subsequent network analysis of these flows, can be used to help understand both the direct and indirect relationships between compartments. In particular, it may help predict the ultimate effect that a change in one compartment will have on another. Besides being of theoretical interest, such knowledge has implications for many kinds of management decisions. For example, numerous lakes and reservoirs are at risk of eutrophication due to increased nutrient inputs, which can endanger safe drinking water supplies. Information on the interplay between nutrient and energy limitation, and the interconnections between components of an ecosystem, can help predict a system's response to changes in nutrient inputs. A better understanding of ecosystem function can thus help enable a more efficient allocation of resources to manage the problems associated with eutrophication.

Knowledge of food web fluxes is also important for the enhancement or control of individual species. For example, managers who wish to enhance the yield of a certain fish species, or to save an endangered species, need to know not only the diet composition of the species, but also the ultimate (or indirect) dependency of the species on the various components of the ecosystem. From such information, one can devise strategies to protect or enhance those components of the ecosystem which are important to the target species.

As can be seen from these examples, knowledge of ecosystem energy and nutrient fluxes and the direct and indirect links between system compartments is important for the understanding of individual components as well as the system as a whole. Thus, through our model and its techniques, we hope that better theoretical and practical understanding of ecosystem function can be achieved.

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