

An Inverse Model Analysis of Planktonic Food Webs in Experimental Lakes

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Vézina, A.F., and M.L. Pace. 1994. An inverse model analysis of planktonic food webs in experimental lakes. *Can. J. Fish. Aquat. Sci.* 51: 2034–2044.

We used inverse methods to reconstruct carbon flows in experimental lakes where the fish community had been purposely altered. These analyses were applied to three years of data from a reference lake and two experimental lakes located in Gogebic County, Michigan. We reconstructed seasonally averaged flows among two size groups of phytoplankton, heterotrophic bacteria, microzooplankton, cladocerans, and copepods. The inverse analysis produced significantly different flow networks for the different lakes that agreed qualitatively with known chemical and biological differences between lakes and with other analyses of the impact of fish manipulations on food web structure and dynamics. The results pointed to alterations in grazing pressure on the phytoplankton that parallel changes in the size and abundance of cladocerans and copepods among lakes. Estimated flows through the microbial food web indicated low bacterial production efficiencies and small carbon transfers from the microbial food web to the larger zooplankton. This study demonstrates the use of inverse methods to identify and compare flow patterns across ecosystems and suggests that microbial flows are relatively insensitive to changes at the upper trophic levels.

Nous avons appliqué des méthodes inverses pour reconstruire les flux de carbone dans des lacs expérimentaux dans lesquels les communautés de poisson ont été altérées. Ces analyses ont été appliquées à trois années de données d'un lac de référence et de deux lacs expérimentaux situés dans le comté Gogebic, Michigan. Nous avons reconstruit les flux saisonniers entre deux classes de taille de phytoplancton, les bactéries hétérotrophiques, le microzooplancton, les cladocères et les copépodes. L'analyse inverse a produit des réseaux de flux entre les compartiments qui sont significativement différents entre les différents lacs et qui s'accordent qualitativement avec des différences connues dans la chimie et la biologie de ces lacs et avec d'autres analyses de l'impact des manipulations des communautés de poissons sur la structure et la dynamique des réseaux trophiques. Les résultats montrent des altérations de la pression de broutage sur le phytoplancton en parallèle avec des changements dans la taille et l'abondance des cladocères et des copépodes. Les flux estimés à travers le réseau microbien indiquent des efficacités de croissance des bactéries faibles et de petits transferts de carbone du réseau microbien au zooplancton. Cette étude démontre l'utilité des méthodes inverses pour identifier et comparer entre les écosystèmes les patrons de transferts trophiques. Nous suggérons à partir de notre analyse que les flux microbiens sont relativement insensibles aux changements aux niveaux trophiques supérieurs.

Received September 17, 1993

Accepted April 8, 1994

(J12095)

Reçu le 17 septembre 1993

Accepté le 8 avril 1994

Mass fluxes in aquatic ecosystems are related to the structure of food webs and the supply of energy and nutrients to primary producers. Numerous studies in lakes have focused on the differences in food web dynamics in communities dominated either by piscivorous or planktivorous fishes (DeMelo et al. 1992). Shifts in fish community structure may induce changes in the structure, biomass, and productivity of lower trophic levels (Carpenter et al. 1985). The changes in lower trophic levels that result from cascading trophic interactions may have either transitory or long-term effects on the dynamics of aquatic ecosystems (e.g., Leavitt et al. 1989; Carpenter et al. 1993b). Few studies of trophic cascades have considered how material fluxes in pelagic systems change with differing food web structure (but see Carpenter et al. 1992). In addition, few studies have considered how modifications in organisms at the top of the food web might impact heterotrophic microbial

processes, despite considerable research indicating that these organisms account for much of the energy flow and nutrient recycling in planktonic systems (Stockner and Porter 1988; Sherr and Sherr 1991).

A crucial problem in assessing the response of aquatic systems to cascading trophic interactions is that most of the flows between food web constituents are difficult to measure. These unknown flows may be assessed by inverse modeling, which has been used extensively in the analysis of physical systems (e.g., Wunsch 1978; Bolin et al. 1983) and has recently been applied to food webs (Vézina and Platt 1988; Jackson and Eldridge 1992). Inverse modeling is closely related to multidimensional parameter optimization techniques that have been suggested or applied to estimate energy or material transfers in food webs (Halfon 1979). G. Radach (p. 48 in Platt et al. 1981) concluded that the utility of optimization techniques (which he called inverse methods) is

limited by the rarity of the long multivariate time series required to reliably estimate parameters. Vézina and Platt (1988) proposed to circumvent this difficulty by following practices in geophysical inverse methodology and directly incorporating a priori knowledge along with the data to constrain the parameter estimates. Inverse methods are formal procedures to estimate parameters of models that cannot be fully constrained by the available observations (under-determined models).

The other novel aspect of this approach is that prior knowledge is incorporated as ranges of possibilities (i.e., a flow can take any value within a defined range) that reflect the uncertainties concerning many biological processes. The method calculates the "best" solution that falls within those ranges. This allows us in particular to circumvent the exact specification of nonlinear interactions in the food web models. We rely on ranges to bound possible excursions of the parameters. For example, if the standing stock of compartment P varied by a factor of 2 between lake A and lake B, we would expect the flows from this compartment to also change by a factor of 2 in a linear model. However, inexact constraints in a multidimensional linear system allow nonlinear differences (by a factor other than 2) between the flows estimated for lakes A and B.

In summary, the inverse techniques we apply here rely heavily on inexact constraints to compensate for sparse or missing data and to deal implicitly with nonlinear variations. Typically, the ratio of inexact constraints to "hard" data in our models is 3 to 1, reflecting the general state of knowledge for many ecological systems. Our application of inexact constraints to this problem is a significant difference from the bulk of optimization procedures that have been applied in ecology in the past, which rely more on the data and on exact constraint rules. In any case, the use of formal procedures for estimating food web parameters is not widespread and the techniques available to do so need to be demonstrated and refined.

The inverse technique is described in detail in Vézina and Platt (1988) and was modified slightly by Jackson and Eldridge (1992). The general approach is to develop a compartmental food web model and constrain the model with measured flows. Unmeasured flows are bounded by a series of constraint conditions that are derived from prior knowledge of general allometric trends, limits to production efficiencies, and the partitioning among energetic pathways (e.g., respiration and excretion). A solution for all the flows is then computed that is consistent with the data and the constraint conditions. The inverse modeling approach addresses the typical situation where direct flow measurements are much fewer than the total number of flows within a given food web.

In this paper, we combine data from whole-lake fish manipulations with a simple compartmental model of the planktonic food web to examine changes in carbon flows in response to cascading trophic interactions. Weekly measures of the standing stocks of all components of the food web as well as some of the major flows (e.g., primary and bacterial production) over three years in three different lakes provide an extensive data set for inverse model analysis. Our study has two purposes. First, we use the data sets to examine the utility of inverse modeling as a method for analyzing food webs; inverse modeling is a relatively new and untested method in ecological studies. Data from the experimental manipulations provide

a variety of food web conditions. We examine whether the inverse modeling method can produce plausible flow structures that also discriminate between the major results of the ecosystem experiments. Our second interest is to assess carbon flows as revealed by the inverse model solutions. We evaluate how flows may have changed in response to the fish community manipulations. We focus on two types of flows that are particularly difficult to measure empirically: zooplankton grazing on phytoplankton and carbon uptake and loss by heterotrophic bacteria.

Study Sites and Experimental Manipulations

The experimental studies on which the model analysis is based were conducted in Peter and Tuesday lakes located in Gogebic County, Michigan. A third lake, Paul, served as a reference system. These lakes, the experimental manipulations conducted, and the results from these studies have been previously described (Carpenter and Kitchell 1993). Here, we only briefly sketch the manipulations and major responses of the lakes for the years 1988–90. All data used to develop the model were based on weekly samples taken during the summer stratified season.

The experiment in Tuesday Lake involved observing the recovery of planktivorous minnow populations after the removal of largemouth bass (*Micropterus salmoides*). Minnow populations (principally the northern redbelly dace (*Phoxinus eos*)) underwent exponential growth over the period 1988–90 (Hodgson et al. 1993). In response to the increase in planktivory from minnows, the zooplankton community structure shifted abruptly at the end of 1988 when the large-bodied species of *Daphnia* declined. Subsequently, the zooplankton community was dominated by an assemblage of small species, and phytoplankton biomass and productivity increased about 30% (Carpenter et al. 1993b).

The experiment in Peter Lake was designed to simulate the effects of piscivore removal on a system containing both planktivores and piscivores (Carpenter and Kitchell 1993). Planktivores were added to the lake each year in the spring and piscivore populations were reduced. In 1988 and 1989, 3000 fingerling rainbow trout (*Oncorhynchus mykiss*) were introduced and 2000 golden shiner (*Notemigonus crysoleucas*) were introduced in 1990 (Hodgson et al. 1993). Piscivores, including largemouth bass and rainbow trout (age 1+), were almost completely removed in 1989 and 1990 by a combination of electroshocking, angling, and gillnetting (Hodgson et al. 1993). This experiment resulted in periods of increased planktivory that varied among years and resulted in large oscillations in zooplankton size structure and biomass (Soranno et al. 1993b). Phytoplankton biomass and production were also affected by shifts in the size of cladocerans (Carpenter et al. 1993b).

Methods

Model Description

We developed a compartmental model of carbon flows for the photic zone during summer (Fig. 1). The model structure and flows represent a compromise between the model complexity required to represent the interactions of interest and the need to keep the number of flows to be estimated as small as possible. The compartments are nano (<30 μm) and net (>30 μm) phytoplankton, heterotrophic

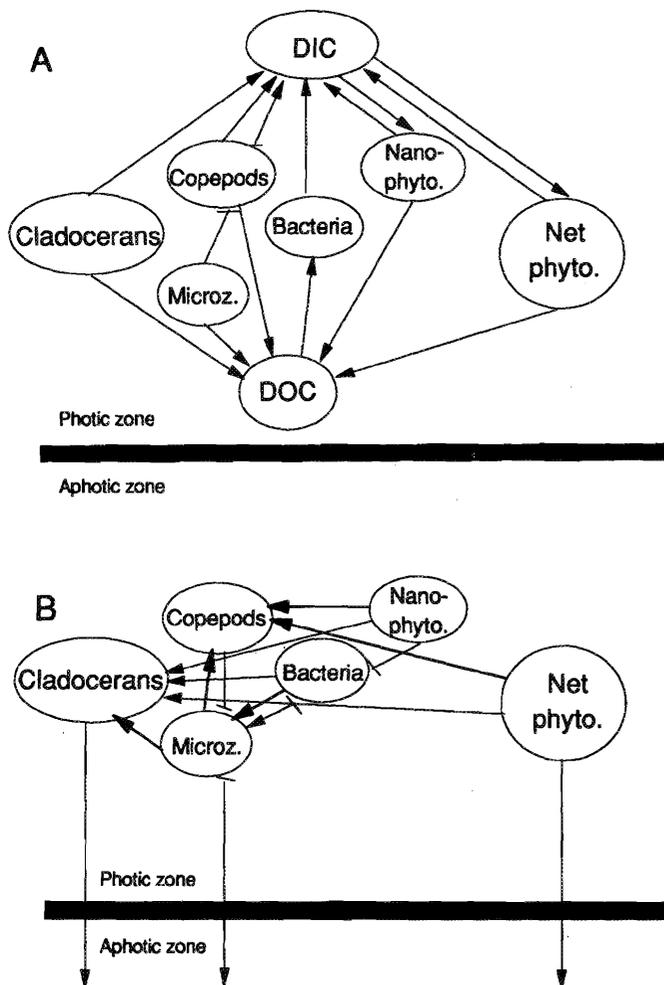


FIG. 1. Compartmental model of carbon flows in an epilimnetic food web. (A) Flows of DIC and DOC; (B) flows of particulate carbon.

bacteria, microzooplankton, cladocerans, and copepods. In the model, all living compartments add to the dissolved inorganic carbon (DIC) pool through respiration and contribute to the dissolved organic carbon (DOC) pool through excretion. We assumed that DOC release by bacteria is negligible compared with their DOC uptake.

The microzooplankton compartment represents a composite of rotifers and heterotrophic flagellates. We did not include ciliates in the microzooplankton estimates because complete data on these organisms were not available. Estimates using data from 1990 only indicate that ciliates account for 9–18% of the total microzooplankton biomass in the three lakes; excluding them from the model probably does not lead to serious underestimates of flows through the microzooplankton.

Trophic flows are limited by the prevalent feeding mode and by the relative sizes of predator and prey. In the model, cladocerans can graze on all the smaller-sized compartments, copepods are not allowed to consume bacteria, and the microzooplankton are restricted to feeding on bacteria and nanophytoplankton.

Representation of the production and fate of detrital material was highly simplified in the model. We assumed that bacteria, nanophytoplankton, and microzooplankton do not produce particulate detritus. Instead, detrital flows from these compartments move directly to the DOC pool (Fig. 1).

Net phytoplankton, cladocerans, and copepods produce DOC or particulate detritus. The latter is considered to sink directly out of the photic zone without significant recycling.

Conservation of mass equations were written for each compartment:

$$(1) \quad \sum_{\substack{i=1 \\ i \neq j}}^n f_{ij} + z_{0j} - \sum_{\substack{k=1 \\ k \neq j}}^n f_{jk} - y_{j0} = 0$$

where f_{ij} and f_{jk} represent intercompartmental flows (from compartment i to compartment j or from j to k) and z_{0j} and y_{j0} are, respectively, inflows and outflows across the boundaries of the food web. An external input of allochthonous DOC was introduced in the model as an additional source of heterotrophic activity (see below). Sedimentation of the detritus generated by phytoplankton and the large heterotrophs is the only net loss from the food web.

The mass flows among compartments are linear and determined strictly by the source compartment (donor controlled). Two-way interactions between source and sink compartments are not explicitly treated in the model. Top-down effects should appear as differences between the reference and treatment data sets that then affect the inverse solutions. This linear model by itself cannot simulate top-down interactions; however, comparisons among site- and time-specific solutions of the model should reveal these nonlinear interactions.

Use of Measured Flows in the Model

Primary production, bacterial production, and total respiration were measured weekly during the growing season (Carpenter et al. 1993b; Pace 1993). Seasonal averages of these measurements were included in the model with equations of the form

$$(2) \quad p(f, z, y) = \bar{q}$$

where \bar{q} is a seasonally averaged measured flow and $p(f, z, y)$ is a linear function that specifies the model flows (Fig. 1) that add up to the measured flow. Each equation was divided by the seasonal variance to insure that the weight of each measured flow in determining the global solution was inversely related to its variability.

Sedimentation losses of net phytoplankton from the photic zone for each lake and year were calculated by the formula

$$(3) \quad f_{\text{sed}} = \frac{s \cdot P_{\text{net}}}{z_e}$$

where f_{sed} is the carbon flux sedimenting as net phytoplankton (milligrams per square metre per day), s is the average net phytoplankton sinking rate (metres per day) assumed constant for all lakes and all seasons (Baines and Pace 1994), P_{net} is the integrated carbon biomass of net phytoplankton (milligrams per square metre), and z_e is the seasonally averaged depth of the euphotic zone in each lake (metres). A constant variance of 10^4 was applied to calculated sedimentation fluxes as an indicator of the low precision of this estimate.

Use of Inequality Constraints in the Model

Vézina and Platt (1988) introduced a number of constraints for inverse modeling of aquatic food webs that are mostly size-dependent limits to energetic processes (e.g., respiration, ingestion) and limits on the efficiency of biological

TABLE 1. Constraints applied to biological flows in the inverse model. The same constraints apply to both phytoplankton compartments (nano- and net) and to the heterotrophic compartments other than bacteria. The constraint equations give the upper or lower bound to the corresponding flow in $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Variables used in the constraint equations are gross primary production (PP), net primary production (NPP), respiration (R), excretion (E), ingestion (I), degradation of dead phytoplankton to DOC (D_{ph}), DOC input from the watershed (D_{allo}), carbon biomass of the compartment (B), average individual size (W, pgC), and mean temperature of the euphotic zone (T).

Process	Compartments	Type of bound	Equation	Reference
Respiration	Phytoplankton	Lower	$0.05\cdot\text{PP}$	Vézina and Platt 1988
Respiration	Phytoplankton	Upper	$0.30\cdot\text{PP}$	Vézina and Platt 1988
Respiration	Heterotrophs	Lower	$0.03\cdot I$	Fasham 1985
Respiration	Bacteria	Lower	$0.30\cdot(\sum E + D_{\text{ph}} + D_{\text{allo}})$	Fasham 1985
Respiration	Heterotrophs	Upper	$(14\cdot W^{-0.25}\cdot e^{(0.0693\cdot(T-20))})\cdot B$	Moloney and Field 1989
Respiration	Bacteria	Upper	$(1.7\cdot W^{-0.25}\cdot e^{(0.0693\cdot(T-20))})\cdot B$	Moloney and Field 1989
Excretion	Phytoplankton	Lower	$0.02\cdot\text{NPP}$	Baines and Pace 1991
Excretion	Phytoplankton	Upper	$0.55\cdot\text{NPP}$	Baines and Pace 1991
Excretion	Heterotrophs	Lower	$0.10\cdot I$	Vézina and Platt 1988
Excretion	Heterotrophs	Upper	R	Vézina and Platt 1988
Ingestion	Heterotrophs	Upper	$(63\cdot W^{-0.25}\cdot e^{(0.0693\cdot(T-20))})\cdot B$	Moloney and Field 1989
Degradation to DOC	Phytoplankton	Lower	$0.10\cdot(\text{PP} - R - E)$	Pace et al. 1984

TABLE 2. Limits to growth and assimilation efficiencies for the heterotrophic compartments.

	Bacteria	Microzooplankton	Copepods	Cladocerans
Growth efficiency (%)	10–60	10–40	5–40	5–40
Assimilation efficiency (%)	—	—	50–80	50–80

transformations (e.g., growth efficiency, assimilation efficiency). These constraints are expressed in the general form

$$(4) \quad h_L \leq g(f, z, y) \leq h_U$$

where h_L and h_U are lower and upper bounds and $g(f, z, y)$ is a linear function that specifies the combination of flows that add up to the lower and upper bounds.

We made a number of modifications to these original constraints. We updated the size-dependent constraints on respiration and ingestion with new empirical models from the literature (Table 1). The lower and upper bounds on the proportion of net primary production released as DOC were recalculated from a new literature review (Table 1). Constraints on phytoplankton respiration, DOC release by heterotrophs (Table 1), and metabolic efficiencies are basically the same as in Vézina and Platt (1988) (Table 2).

Vézina and Platt (1988) did not introduce any constraints on the specific grazing flows. As a result, some grazing flows can be set to zero by the inverse solution technique (see below), and the relative sizes of grazing flows may bear little relationship to the relative biomass of the prey compartments. We sought to correct this problem by introducing simple grazing functions based on the assumption that consumers graze in proportion to resource availability:

$$(5) \quad G_{kj} > \frac{B_k}{\sum B_i} \cdot \sum G_{ij}$$

where G_{kj} is the grazing flow from prey compartment k to consumer compartment j , B_k is the biomass of compartment k , $\sum G_{ij}$ is the total grazing by compartment j across

all prey compartments, and $\sum B_i$ is the total biomass of the prey compartments. This is equivalent to assuming that the consumer compartments do not select against any prey.

Two exceptions were recognized. An unpublished study indicates that copepods filter nanophytoplankton about half as fast as net phytoplankton (H. Cyr, University of Toronto, Toronto, Ont., unpublished data). In addition, a recent study of cladoceran particle utilization (Brandelburger 1991) yields a filtration efficiency of 0.625 on bacteria relative to larger particles. Therefore, in both those cases, the grazing flows were bounded by

$$(6) \quad G_{kj} < \alpha_{kj} \cdot \sum_{i \neq k} G_{ij}$$

where α_{kj} is the ratio of the filtering rate on prey compartment k to the maximum filtering rate.

Finally, some limits on the biomass turnover (grams of carbon per gram of carbon per day) of the heterotrophic compartments were imposed. Lake- and year-specific limits on the turnover of cladocerans were calculated from birth rate data (Soranno et al. 1993a). Upper and lower bounds on the turnover rate were set at ± 2 standard errors of the mean. Microzooplankton and copepod compartments were assumed to turn over at least once per 10 d and once per 20 d, respectively.

The constraints were calculated based on seasonal averages of the mean size and mean biomass of the compartments for each lake and year. The calculated means were substituted into the constraint equations (Tables 1 and 2), and these were used to obtain lake- and year-specific solutions.

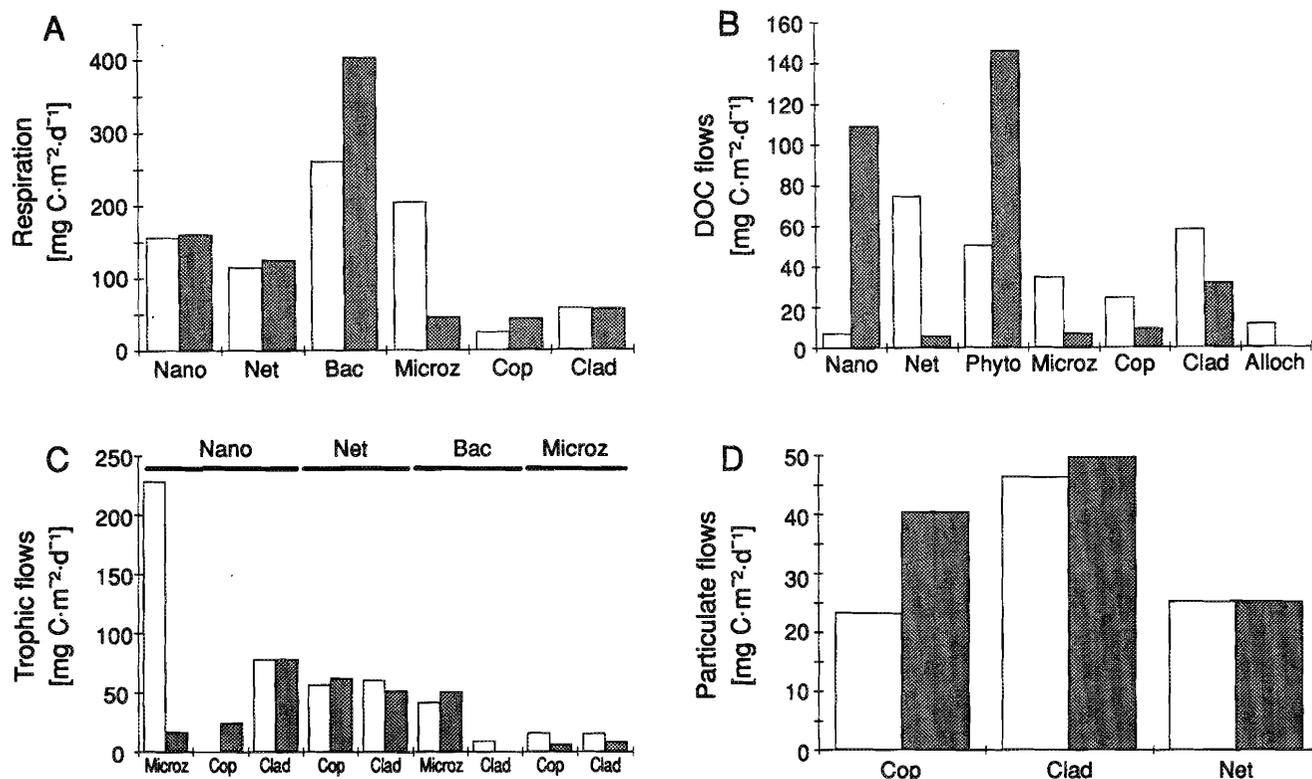


FIG. 2. Carbon flows calculated by the inverse method for Paul Lake, 1988. White bars are the estimates from the standard model and gray bars are those from the M-R model. The flows are grouped into (A) respiration flows, (B) DOC flows, (C) trophic flows, and (D) particulate detrital flows. For Fig. 2A, 2B, and 2D, the bar labels are the source compartment; for Fig. 2C, the bottom bar labels are the receiving compartments (grazers) and the top bar labels are the source compartments (prey). Abbreviations for compartments: Nano, nanophytoplankton; Net, net phytoplankton; Bac, bacteria; Microz, microzooplankton; Cop, copepods; Clad, cladocerans; Alloch, allochthonous source. Phyto in Fig. 2B refers to dissolution of detritus from both nano- and net phytoplankton.

Model Solution and Analysis

The conservation of mass (Eq. 1), flow specification (Eq. 2), and constraint (Eq. 4) equations can be collected into matrix form

$$(7) \quad \mathbf{Ax} = \mathbf{b}$$

$$(8) \quad \mathbf{h}_U \geq \mathbf{Gx} \geq \mathbf{h}_L$$

where $\mathbf{x} = [\mathbf{f} \ \mathbf{z} \ \mathbf{y}]'$, $\mathbf{b} = [\mathbf{0} \ \bar{\mathbf{q}}]'$, prime means matrix transpose, and \mathbf{A} and \mathbf{G} are matrices of constant coefficients. A priori weights on the conservation of mass and measured flows (\mathbf{b}) and on the flows to be estimated (\mathbf{x}) can be introduced as follows:

$$(9) \quad \mathbf{S}^{-1/2} \mathbf{A} \mathbf{W}^{1/2} \mathbf{W}^{-1/2} \mathbf{x} = \mathbf{S}^{-1/2} \mathbf{b}$$

$$(10) \quad \mathbf{G} \mathbf{W}^{1/2} \mathbf{W}^{-1/2} \mathbf{x} \geq \mathbf{h}$$

where \mathbf{S} and \mathbf{W} are diagonal matrices that contain weights for \mathbf{b} and \mathbf{x} , respectively. The diagonal of \mathbf{S} has the form $[\mathbf{1} \ \sigma^2]'$ where σ^2 are the variances of the measured flows. The diagonal of \mathbf{W} contains weights that control the relative importance of the flows based on a priori expectations. We used a biomass-weighted scheme, where the flows are assumed proportional to the biomass of the compartments ($w_i = B_i$). The effect of these weights is to control the relative importance of the different compartments in determining the flow structure.

Equations 9 and 10 can be solved for \mathbf{x} by quadratic programming (Lawson and Hanson 1974). The solution obtained minimizes the L2 norms of the residuals ($\mathbf{Ax} - \mathbf{b}$) and of the

flows (\mathbf{x}), that is, it minimizes the squared errors of the measured flows and the sum of the squared flows. Equations 9 and 10 together specify over 60 constraints on 27 parameters. These constraints are not necessarily compatible and there may not be feasible solutions. We have systematically modified some of the constraints either to allow feasible solutions to be computed or to explore alternative solutions to the mass balance problem. These modifications are described in the next section.

Results

Initial Model Solutions

We first describe some general features of the inverse solutions using the flow network for Paul Lake, 1988 (Fig. 2). Gross primary production is split about equally between nano- and net phytoplankton. Respiration by the phytoplankton is high, constituting about 20–30% of gross primary production. Bacterial respiration is the most important respiration flow, followed by microzooplankton respiration; contributions of large grazers to total respiration are small. Except for nanophytoplankton, DOC flows from the biota (hereafter, recycled DOC) are spread relatively uniformly among the various compartments. Allochthonous DOC inputs make a small contribution to bacterial energy demand. Consumption of nanophytoplankton by microzooplankton is a major grazing pathway whereas the flow from nanophytoplankton to copepods is zero. Cladoceran grazing is split about equally between nano- and net

phytoplankton and is an important loss term for both compartments. Microzooplankton dominate bacterial grazing, and the utilization of microzooplankton by cladocerans and copepods are minor trophic pathways. Cladocerans are an important source of sinking detrital material; the direct contribution of autotrophic material to sinking fluxes is smaller than material produced by zooplankton.

This solution concentrated the grazing of nanophytoplankton and bacteria through the microzooplankton. We compared microzooplankton filtering rates estimated from the inverse solution with filtering rates measured in the field (Vaqué and Pace 1992) and found that the inverse estimates were on the order of 10 times higher than the field measurements. The estimated filtering rates for the other grazers were consistent with rates expected in the field (Peters and Downing 1984). This led us to limit the grazing activity of microzooplankton by restricting the size range of particles available to $<5 \mu\text{m}$ for microflagellates and $<20 \mu\text{m}$ for rotifers. The effect of this restriction on the inverse solution (microzooplankton restricted, or M-R hereafter) is shown in Fig. 2 for Paul Lake, 1988. Respiration flows through the bacteria were increased at the expense of microzooplankton, whose contribution to total respiration became comparable with that of the large grazers. DOC flow was routed mostly through the phytoplankton, especially through dissolution of phytoplankton detritus, and contributions by heterotrophs became much smaller. Nanophytoplankton grazing by microzooplankton fell by an order of magnitude whereas the other trophic flows remained basically unchanged. Finally, sinking flows through the large grazers were increased. The overall impact of this model change was that phytoplankton excretion losses and increased defecation by crustaceans compensated for the smaller loss term through microzooplankton.

The M-R model gave microzooplankton filtering rates on nanophytoplankton that agreed with the field estimates; however, the microzooplankton filtering rates on bacteria remained high. We tried decreasing this rate by forcing bacterial flows through the cladocerans with empirical estimates of bacterial grazing by cladocerans (Porter et al. 1983). This version of the model, however, did not work for cases where the cladoceran densities were quite high (Paul Lake, 1989, and Peter Lake, 1989 and 1990) and, in the other cases, only reduced microzooplankton filtering rates on bacteria by a factor of 2 instead of the factor of 10 needed to reconcile inverse and field estimates. Therefore, we kept the M-R model for comparison with the initial (standard) model. We recognized that the M-R model did not yield completely accurate trophic flows through the microzooplankton, but we considered it as the best model given existing information.

Consistency of Inverse Flow Networks

We computed solutions based on the standard and M-R models for the nine lake-year data sets. Feasible solutions (i.e., compatible with all the constraints) were obtained in all but one case: the M-R model for Paul Lake, 1990. To determine if the solutions were consistent and discriminated among the nine data sets, we used a principal component analysis of all the flows from all the solutions (27 flows \times 17 solutions). The first two components accounted for 46% of the total variability in flows among models and data sets and were used to map the solutions

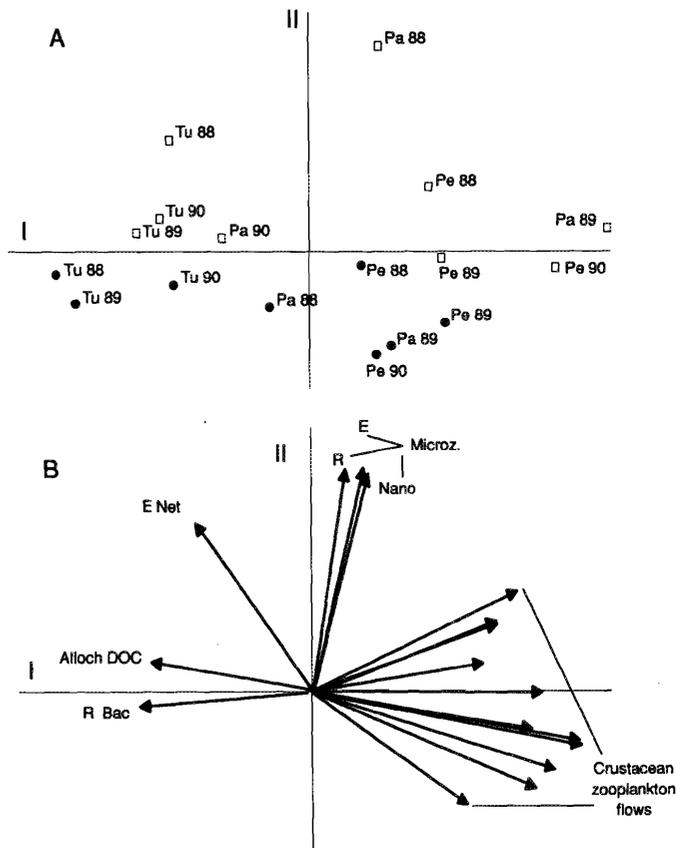


FIG. 3. (A) Positions of multidimensional inverse solutions (27 flows) on the plane formed by the first and second principal components and (B) positions of the flows that weigh most heavily on these components. Squares represent the solutions of the standard model and circles are the solutions of the M-R model. Abbreviations in Fig. 3A: Tu, Tuesday Lake; Pa, Paul Lake; Pe, Peter Lake; solutions for 1988, 1989, and 1990 are shown. Abbreviations for flows in Fig. 3B: E, excretion; R, respiration; compartments are identified as in Fig. 2. Crustacean zooplankton flows are not identified individually. Flows tend to increase in the direction of the arrows.

and the flows that were most strongly correlated with the variations among solutions.

The inverse solutions for the experimental lakes, Tuesday and Peter, map in different parts of the reduced space formed by the first two components. The solutions for Paul Lake tend to be more dispersed, as might be expected for the reference lake. Solutions for Peter Lake are found on the positive side of the first principal component (Fig. 3A), reflecting higher flows through the large consumers (Fig. 3B). Solutions for Tuesday Lake fall on the negative side of the first principal component (Fig. 3A), toward higher bacteria respiration, allochthonous DOC inputs, and phytoplankton excretion flows (Fig. 3B). The first component is largely driven by changes in the grazing and metabolic flows of the crustacean zooplankton compartments; except for bacterial respiration, the microbial flows are not strongly involved in the differences in flow patterns.

The standard solutions for Paul and Tuesday lakes fall on the positive side of the second component whereas the M-R solutions for these lakes fall on the negative side (Fig. 3A). The positive side of component 2 is related to increases in flows through the microzooplankton (Fig. 3B).

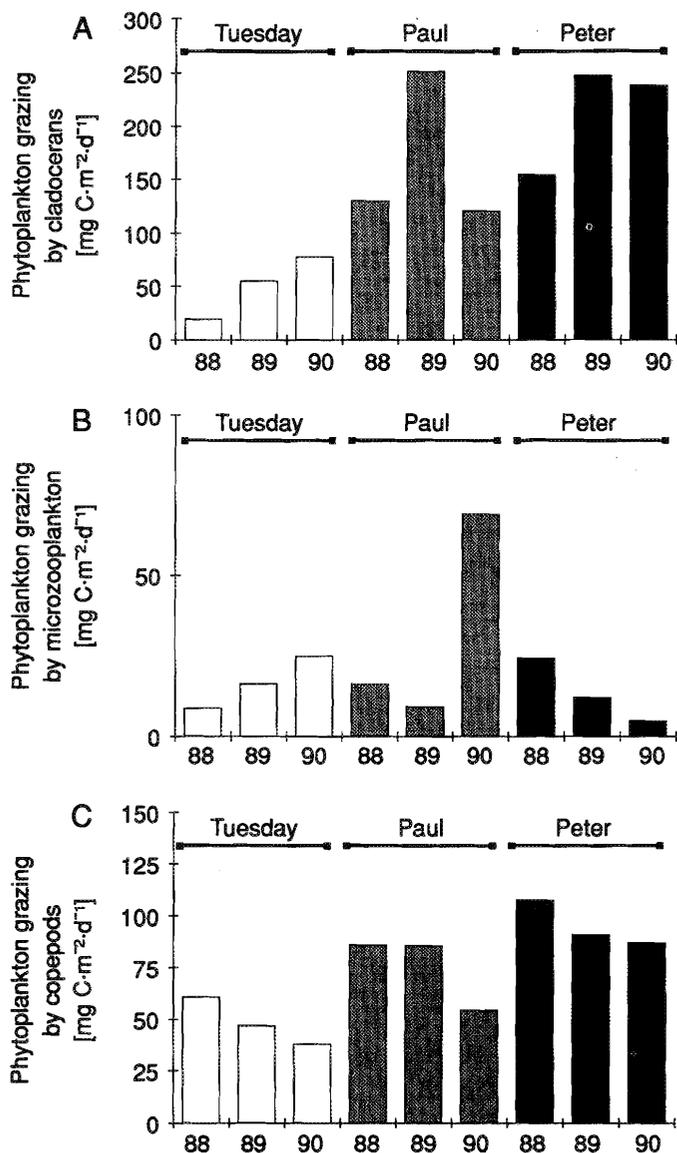


FIG. 4. Phytoplankton grazing rates inferred by the inverse models.

This generalizes the tendency, already noted for Paul Lake, 1988, of the standard model to route the flows preferentially through the microzooplankton.

Analysis of Flows

Using the microzooplankton restriction model, we analyzed the flows of carbon through the food webs for all lakes and years except for Paul Lake, 1990, where the standard model was used. We focused on the phytoplankton grazing flows and on the flows through the microbial food web. These flows have not been measured directly in the experimental lakes and we feel that it is in those areas that the inverse solutions can make the strongest contribution.

Patterns of grazing on phytoplankton

One of the intentions of the experimental manipulations was to induce shifts in zooplankton community structure that would change the grazing pressure on phytoplankton. The inverse solutions provided estimates of the various grazing flows (Fig. 4) that were difficult to measure directly. We used the model flows to evaluate how grazing may have

changed in response to the manipulations. In addition, we assessed the modeled grazing flows for their consistency with other data and analyses of the ecosystem responses.

In the reference system, Paul Lake, cladocerans were the most important grazers in all three years, and grazing by cladocerans was particularly high in 1989 (Fig. 4A). This was because the large cladoceran *Holopedium gibberum* was very abundant during this year; zooplankton biomass reached the highest level recorded in Paul Lake over a 7-yr period (Soranno et al. 1993a, 1993b). Microzooplankton grazing was low except during 1990 (Fig. 4B). However, only the standard model could fit the 1990 Paul Lake data and we have no evidence to support this high estimated microzooplankton grazing. Neither rotifers nor heterotrophic flagellates occurred at higher abundances and there were no significant changes in size structure of either community in 1990 relative to other years in Paul Lake.

In Peter Lake, crustacean zooplankton grazing was a large component of the total flow in the food web. For example, crustacean zooplankton grazing accounted for 53–68% of the net primary production in Peter Lake compared with 39–57% in Paul Lake and 25–33% in Tuesday Lake over the three years. Grazing by cladocerans increased in 1989 and 1990, while copepod grazing remained stable (Fig. 4A and 4C). Microzooplankton grazing was a minor flow in all three years and declined over time (Fig. 4B). These patterns agreed with large increases in both the size and biomass of the cladocerans during 1989 and 1990, but not with shifts in the biomass of copepods (Soranno et al. 1993a).

We suspect that the magnitude of the interannual changes in grazing in Peter Lake was actually higher than that portrayed in the model. This is because, for 1989 and 1990, the upper limit on the biomass turnover of the copepods and the cladocerans had to be relaxed to obtain a feasible solution. The turnover times for these compartments reached 2–3 mo in the model. The high turnover times were needed because the model could not satisfy the high zooplankton demand given the available production. This agrees with lower measured birth rates for cladocerans (1989–90) as well as with the sharp population declines observed after an initial biomass maximum.

Modeled flows for Tuesday Lake suggested that grazing by microzooplankton and cladocerans was low in 1988 and then increased in 1989 and 1990 (Fig. 4A and 4B). In general, microzooplankton were a more important component of the total grazing in Tuesday Lake than in the other lakes. Increased microzooplankton grazing in 1989 and 1990 (Fig. 4B) was consistent with increases in rotifer populations observed over this period (Soranno et al. 1993a). Cladoceran grazing was especially low in 1988 (Fig. 4A). This result seemed surprising, as cladoceran biomass was highest in 1988 and the mean size of cladocerans declined from 1988 to 1990 as planktivory from the recovering minnow populations increased (Soranno et al. 1993a). Nevertheless, this result was consistent with the allometric formulations we used in the model. The shift to smaller zooplankton in Tuesday Lake led to a higher metabolic demand by the zooplankton in 1989 and 1990. This resulted in a solution that partitioned more of the phytoplankton carbon through the cladoceran compartment.

Microbial flows

The changes induced by the experimental manipulations offer the opportunity to analyze the sensitivity of microbial

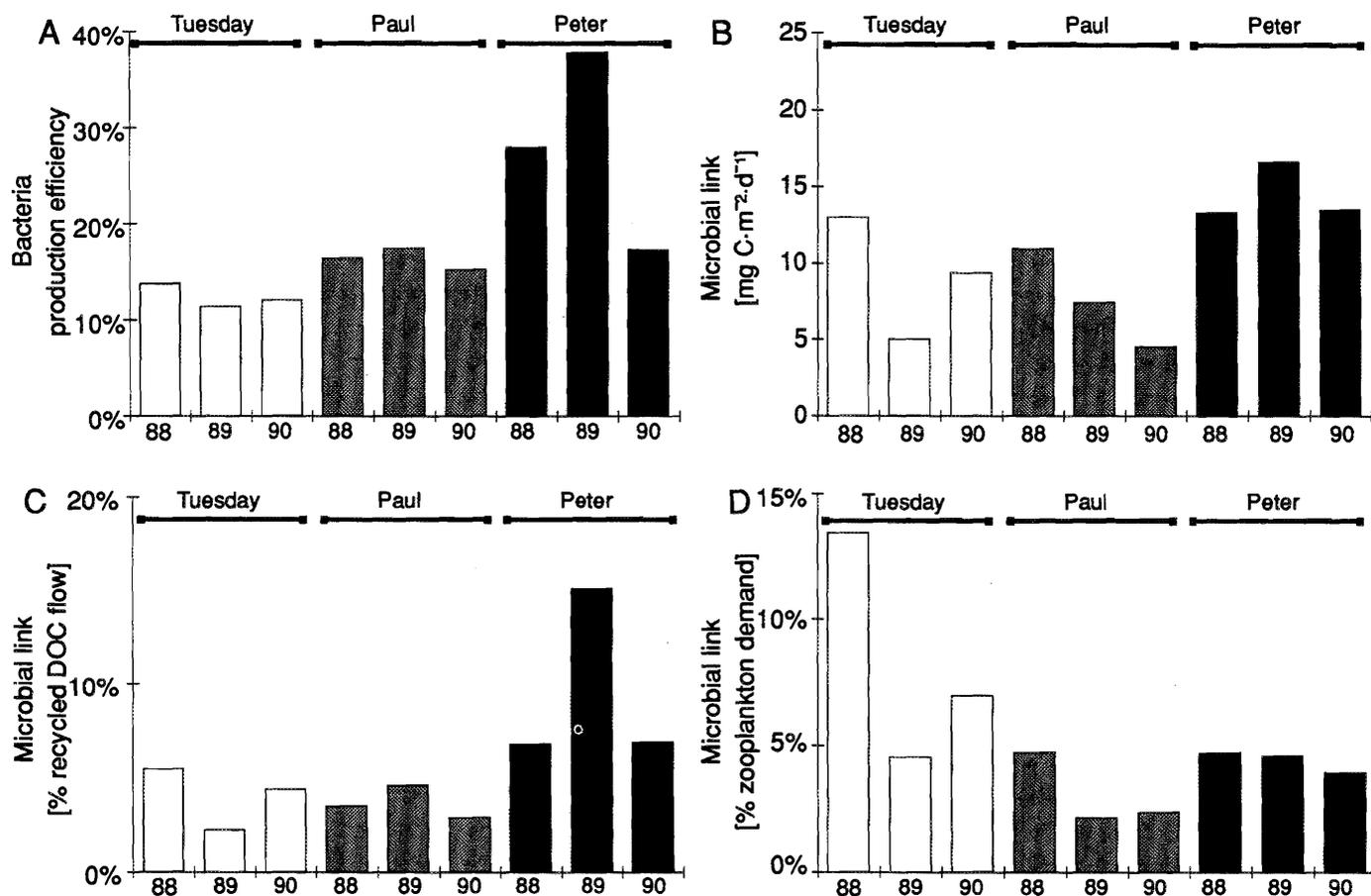


FIG. 5. (A) Bacterial production efficiency and (B–D) flows of particulate carbon from the microbial food web (bacteria and microzooplankton) to the zooplankton (copepods and cladocerans) in carbon units (Fig. 5B) and as a proportion of the gross DOC flow (Fig. 5C) and of the zooplankton carbon demand (Fig. 5D).

flows to shifts in food web structure. From the flow networks, we derived bacterial production efficiency, the amount of bacterial carbon transferred to crustacean zooplankton, and the ratios of this carbon transfer to DOC flow and zooplankton demand (Fig. 5). In the model, bacterial production efficiency was the ratio of predatory consumption to carbon input to this compartment. This efficiency was about 10–15% in Tuesday and Paul lakes and 20–40% in Peter Lake (Fig. 5A). The low production efficiencies in Tuesday and Paul lakes resulted from the relationship between measured rates of bacterial production and total community respiration. Bacterial production was low relative to primary production, while community respiration often exceeded net primary production (Pace 1993). As a consequence, bacterial respiration in model solutions was a major flow (Fig. 2) leading to low production efficiencies. In Peter Lake, the primary production to respiration ratio exceeded 1, so less material was funnelled through bacterial respiration in the model solutions. Production efficiencies were thereby higher, although not as high as the values of 50% often used as standards in modeling studies (e.g., Pace et al. 1984; Fasham et al. 1990).

The “microbial link” is the transfer of microbial carbon to crustacean zooplankton, either by direct consumption or indirectly through the microzooplankton compartment (Fig. 5B). In absolute terms, this quantity varied from about 5 to 15 mg C·m⁻²·d⁻¹ in the different solutions (Fig. 5B). This quantity represented a small percentage of the flow of

DOC derived from biotic compartments (=recycled DOC in Fig. 5C), meaning that most of the DOC produced by constituents of the food web was respired within the microbial food web (bacteria and microzooplankton). The microbial link was also a small fraction of the crustacean zooplankton carbon demand. Mean efficiencies for the different lakes and years are all <15% and are usually around 5%, indicating that only a small component of the carbon required by zooplankton was ultimately derived from bacterial production (Fig. 5D).

According to model solutions, flows through the microbial compartments were not strongly impacted by the food web shifts. For example, despite the large changes in zooplankton biomass in Peter Lake, there was little change in the quantity of microbial production moving to larger zooplankton (Fig. 5B and 5D). Similarly, in Tuesday Lake, there was little change in the modeled flows through the microbial components even though primary production, chlorophyll, and zooplankton size structure changed over the 3-yr period.

Discussion

Evaluation of Inverse Method Results

One initial goal of our investigation was to evaluate the ability of the inverse method to discriminate among different experimental situations. For Tuesday and Peter lakes, the differences were clear and were as expected from their

contrasting trophic structures. Large grazers were generally dominant in Peter Lake and the inverse solutions produced high grazing flows through the crustacean zooplankton. Small grazers were relatively more abundant in Tuesday Lake and more of the production moved through detritus and DOC to bacteria. The inverse solutions also suggested higher allochthonous DOC utilization in Tuesday Lake than in Peter Lake. This was an original result of the inverse analysis (there were no data or constraints on this flow) and it agreed qualitatively with the trophic status of Tuesday (dystrophic) and Peter (oligotrophic) lakes. In general, the inverse analysis discriminated flow networks between the experimentally manipulated lakes that involved plausible changes in flow patterns.

The inverse analysis did not discriminate interannual differences as well as differences between the experimental lakes. In Tuesday Lake, the production, biomass, and size structure shifts induced by the minnow population recovery between 1988 and 1990 were modest (on the order of 20–30%). In Peter Lake, shifts in crustacean zooplankton were strong but transient, and their impact was difficult to resolve with a seasonally averaged model. We would expect stronger and sustained manipulation effects to appear in the flow structures estimated by inverse analysis. In any case, the M-R solutions suggested a movement toward higher crustacean grazing in both Tuesday and Peter lakes in 1989 and 1990. This change in Peter Lake can be related to the effect of the manipulation on zooplankton biomass; the unexpected increase in grazing in Tuesday Lake is discussed later.

In Paul Lake, the trophic structure was not pushed to extremes by manipulations as in Tuesday or Peter Lake. For such undisturbed situations, the model choice was more critical because the data and constraints allowed a wider range of inverse solutions. The M-R model solutions appeared as more credible descriptions of flows in the reference lake. Not only were the estimated grazing flows more realistic, but the interannual differences in the solutions were much less pronounced than with the standard model, which was what we expected in the reference system. Nevertheless, the interannual differences in Paul Lake solutions were significant and related to significant year-to-year variations in the reference lake (e.g., the *Holopedium* bloom in 1989 and measured primary production in 1990 which was 20% below its 3-yr mean). Long-term records are needed to separate experimental effects from natural variability whatever the analysis techniques used, including inverse analysis.

Inverse models of the experimental lakes did not always produce feasible solutions. Data collated within an inverse model were not necessarily consistent with the preconceptions built into the mass balance conditions (e.g., steady state) or the constraints. The steady-state assumption was probably inappropriate for Peter Lake in 1989 and 1990. Zooplankton biomass fluctuated dramatically during the growing season and inverse solutions tracking the week-to-week dynamic changes would probably have been required to properly account for the seasonal flows. Methods to do this are under development. That feasible solutions were obtained by increasing the turnover time of crustacean zooplankton confirmed that there was a shortage of energy for large grazers in Peter Lake, in accord with observations that the artificially high zooplankton biomass was not sustainable (Soranno et al. 1993a).

Although the basic model used was linear, some of the

differences in inverse solutions among lakes and years were nonlinear. For example, the proportion of the primary production grazed shifted dramatically among lakes, particularly between Tuesday Lake and both Paul and Peter lakes. There were also shifts in microbial flow patterns between Peter Lake and the other lakes. Contrary to our expectations, these shifts were more related to lake-to-lake differences than to specific experimental manipulations. Nevertheless, the inverse model was able to reveal nonlinear changes in the flow patterns implicit in the differences among data sets.

In this analysis, the interactions between nutrient and carbon flows were not considered. Phosphorus generally limits carbon production in lakes and phosphorus cycling is obviously a critical component of these food webs and of their response to manipulations. The inverse methodology can accommodate models with several materials or tracers flowing simultaneously through the system (Vézina and Platt 1988). Many of the phosphorus flows are simple stoichiometric transformations of carbon flows and do not add new information; nevertheless, the addition of cycling processes specific to phosphorus could further constrain the carbon flows. The detailed data on phosphorus cycling in these lakes were not available at the time of our analyses, but this information is now becoming available and will be used in future analyses.

Overall, the inverse analysis gave flow networks that qualitatively agreed with independent assessments of the interlake differences and of the effects of the manipulations. They also agreed with the magnitude and nature of interannual variations in the reference lake. The absence of a feasible solution could indicate either potential difficulties with the data (averaging out fluctuations), imbalances between trophic levels, or other incompatibilities between the data and the constraints. Inverse analysis proved a useful tool not only to produce flow networks, but also to verify the internal consistency of complex data sets.

Ecological Implications of Inverse Method Results

The inverse analysis provided a number of quantitative insights into flows that are not routinely measured in the field. Microbial flows and efficiencies, for example, are difficult to assess because bacterial utilization of the heterogeneous DOC pool that feeds the microbial food web is difficult to quantify *in situ*. The growth efficiency of bacteria in nature is uncertain (Pomeroy and Wiebe 1988) and some efficiency figure must be assumed in energy flow studies. Our inverse analysis circumvents this problem by calculating bacteria growth efficiencies that are consistent with global properties of the ecosystem. The results for these experimental lakes indicate that bacteria growth efficiencies must be low to simultaneously balance production, respiration, and the energy flows through the various trophic levels. The bacterial respiratory sink in these lakes is very high, particularly in dystrophic Tuesday Lake. Whether this result, obtained in these small lakes, can be generalized to other aquatic systems remains to be determined.

Given low bacterial efficiencies, microbial transfers to large consumers calculated by inverse modeling are small. These results are qualitatively consistent with tracer studies (Ducklow et al. 1986; Pernie et al. 1990; Wylie and Currie 1991) and with other modeling studies (Jackson and Eldridge 1992). From an ecosystem perspective, trophic links directly

from bacteria to large grazers or through micrograzers contribute little energy to the upper food web.

The efficiency of DOC utilization and transfer was highest in Peter Lake in 1989 and 1990, when there were high biomass of cladocerans and copepods. Under those conditions, the large grazers reduced the energy available to the microbial food web. The inverse models consistently calculated lower phytoplankton grazing by microzooplankton and lower DOC flows, particularly through the phytoplankton. Therefore, the inverse solutions suggested shifts from detrital to grazing pathways that may have been caused by perturbations at higher trophic levels. Nonetheless, the proportion of the zooplankton demand met by the microbial link remained negligible. Increases in microbial efficiencies did not compensate for lower absolute DOC flows or for increased zooplankton demand.

The inverse modeling also produced estimates of grazing flows that were difficult to measure in the field. The solutions gave the expected differences in grazing patterns between Tuesday and Peter lakes: relatively larger grazing flows through the microzooplankton and lower overall grazing pressure in Tuesday Lake. The only unexpected result was that overall grazing pressure in Tuesday Lake increased from 1988 to 1990 contrary to expectations based on time series analyses of cascading interactions. Specifically, the increase in phytoplankton biomass and production in Tuesday Lake between 1988 and 1990 was attributed to decreased grazing pressure by *Daphnia* (Carpenter et al. 1993a).

There are three possible explanations for this discrepancy. The first is that grazing did increase slightly as portrayed in the inverse solutions and that the increase in primary production is not a consequence of lower grazing pressure. The second is that time-averaged inverse models cannot detect the modest effect of the *Daphnia* population decline on primary production. The third possibility is that the models we used do not effectively simulate the grazing of large *Daphnia*. The standard and M-R models used in this study both predict higher metabolic demands for smaller organisms. Because they are based strictly on allometric relations, decreases in grazer size will to a certain extent compensate or even reverse the impact of decreases in grazer biomass. However, these allometric rules may not accurately portray the differences in actual feeding rates among grazers (Cyr and Pace 1992). Large *Daphnia* consume a broader spectrum of particles than most zooplankton (Burns 1968). Furthermore, while allometric models for zooplankton in general reveal that specific feeding rates decline with body size (Peters and Downing 1984), models of in situ cladoceran feeding predict that specific rates do not decline with size (Knoechel and Holtby 1986). The use of alternative formulations to parameterize this effect in inverse models, and other types of models as well, should be explored.

An important goal of ecosystem studies is to identify regular and repeatable patterns in the flows of energy and materials and to compare these flow properties within and among systems. Inverse methods were proposed as one way to move toward this objective (Vézina and Platt 1988). This study demonstrates the use of inverse methods to identify and compare flow patterns across ecosystems. From our analysis, we propose that the most fruitful directions for improvement of the inverse methodology would be (1) use of time series data to preserve dynamic information and (2) improved constraint equations to increase the ecological

realism of the solutions. We believe that inverse analysis can contribute greatly to the elucidation of energy flow patterns in aquatic ecosystems that remain difficult to assess by direct observational or experimental means.

Acknowledgments

We thank J. Cole for useful discussions on the inverse method results and S. Carpenter for providing data and commenting on the manuscript. L. Devine Castonguay edited the manuscript and worked on the figures. This study was supported by NSF grant DEB9019873 to M.L. Pace, by an NSERC operating grant to A.F. Vézina, and by the Department of Fisheries and Oceans.

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