Pathways of organic carbon utilization in small lakes: Results from a whole-lake $^{13}$C addition and coupled model

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Abstract

In many small aquatic ecosystems, watershed loading of organic C exceeds autochthonous primary production. Although this allochthonous organic C has long been thought of as refractory, multiple lines of evidence indicate that substantial portions are respired in the receiving aquatic ecosystem. To what extent does this terrestrial C support secondary production of invertebrates and fish? Do current models adequately trace the pathways of allochthonous and autochthonous C through the food web? We evaluated the roles of allochthonous and autochthonous organic C by manipulating $^{13}$C content of dissolved inorganic C in a small, softwater, humic lake, thereby labeling autochthonous primary production for about 20 d. To ensure rapid and sufficient uptake of inorganic $^{13}$C, we enriched the lake with modest amounts of N and P. We constructed a carbon flow model based on the ambient and manipulated levels of $^{13}$C in C compartments in the lake, along with information on key rate processes. Despite the short nature of this experiment, several results emerged. (1) Fractionation of photosynthetically assimilated $^{13}$C-CO$_2$ by phytoplankton ($\epsilon$) is lower ($\approx 6\%$) than physiologic models would estimate ($\approx 20\%$). (2) Bacteria respire, but do not assimilate, a large amount of terrestrially derived dissolved organic C (DOC) and pass little of this C to higher trophic levels. (3) The oxidation of terrestrial DOC is the major source of dissolved inorganic C in the lake. (4) Zooplankton production, a major food of young-of-year fishes, is predominantly derived from current autochthonous carbon sources under the conditions of this experiment.

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Whole-lake $^{13}$C addition

The purpose of this study was to create and experimentally test a C model of a lake ecosystem that would encompass the fates of both allochthonously loaded and autochthonously produced organic matter.

**Materials and methods**

**Site description**—East Long Lake is part of the University of Notre Dame Environmental Research Center (UNDERC) near Land o’ Lakes, Wisconsin (89°32’W; 46°13’N) and is the eastern basin of Long Lake. A neoprene curtain deployed in 1991 separated this basin from the rest of the lake. East Long Lake has been extensively studied in the context of whole-lake manipulations of nutrients and food web structure (Carpenter et al. 2001). The lake is small (2.3 ha), relatively deep (mean depth = 4.9 m), well stratified, and darkly stained with DOC (1.100 μM; Fig. 1). The mixed depth of the epilimnion is about 1 m. East Long Lake has modest fish populations and low rates of zooplanktivity. Zooplankton are generally dominated by large-bodied Daphnia (Carpenter et al. 2001). The hydrologic residence time of East Long Lake, measured by whole system LiBr addition, is about 1.5 yr (Cole and Pace 1998). DIC averages ~80 μM, and the lake is acidic (mean pH 5.2; Fig. 1). Phytoplankton are typical of humic lakes in the region and are dominated by small flagellates, mostly Chrysophytes. Surface water chlorophyll a (Chl a) concentrations in the absence of fertilization are moderate, averaging 10 to 20 μg L$^{-1}$.

To insure sufficient and rapid uptake of $^{13}$C, we also enriched the lake with inorganic N and P. Beginning 2 weeks prior to the addition of $^{13}$C (below) we added NH$_4$NO$_3$ and H$_2$PO$_4$ at a rate of 1.02 and 0.05 mmol m$^{-2}$ d$^{-1}$, respectively. These additions, which are in the low end of the range used in previous long-term eutrophication experiments in this lake, were made at a weekly time step and continued for 3 weeks during the 2 weeks prior to and 1 week of $^{13}$C addition (Carpenter et al. 2001). The goal was to reduce nutrient limitation and thereby ensure labeling of phytoplankton with $^{13}$C. Thus, the nutrient enrichment was modest and brief.

**Stable isotope addition**—On 23 June 1999 we added 4 mol of NaH$^{13}$CO$_3$ (Isotech; $^{13}$C content > 99%) to the epilimnion of East Long Lake. The addition was accomplished

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*Fig. 1.* Time series of selected constituents in the surface water of East Long Lake in 1999. (A) Temperature ($^\circ$C). (B) pH. (C) pCO$_2$ (μatm) in the surface water (open circles) and in the air 1 m above the lake surface (crosses, dotted line). (D) DOC in surface water (mg C L$^{-1}$). The arrow shows the point at which $^{13}$C-DIC was added; the dotted line shows the extent of the nutrient addition (see text).
by dissolving aliquots of the isotope in a gas-tight carboy of lake water and feeding this water by gravity into the propeller wash of an electric outboard motor at a depth of 0.25 m. We kept the boat moving to achieve maximal initial mixing into the lake. Prior experience with other tracer additions in this lake demonstrated complete mixing of the epilimnion within 24 h. Furthermore, LiBr added to the epilimnion did not enter the hypolimnion until thermocline deepening occurred 50 d after the addition (Cole and Pace 1998). The stable isotope addition greatly changed the δ13C of DIC (below) but increased the total DIC concentration by only 0.2% and acid neutralizing capacity by 0.18 μeq L⁻¹.

Stable isotope samples and analyses—Samples for DIC were collected in two ways and sent to two different laboratories for analysis. Samples were collected at daily and twice-daily intervals during the initial phase of the 13C addition when concentrations changed rapidly. Prior to, and 2 weeks after, the addition samples were taken at weekly intervals. One-liter gas-tight bottles were completely filled with lake water, acidified to pH 2 with H₂SO₄, and sent to the Marine Biological Laboratory for analysis. Evacuated 100-ml serum vials were filled with 10 ml of N₂ and 90 ml of lake water, acidified to pH 2 with H₂SO₄, and sent to Cornell University’s Stable Isotope Facility for analysis. Replicate samples were sent to both laboratories. Samples for particulate organic C were collected by filtering water through precombusted Whatman GF/F filters that had been rinsed with dilute HCl (0.1%) prior to use. These filters were dried at 40°C and stored in a desiccator. Analysis was accomplished by in-line combustion to CO₂ followed by introduction to the mass spectrometer at Cornell. Samples for DOC were taken from the filtrate of the POC filtration, acidified to pH 2, and dried at 40°C. The dried residue was sent to the University of Alaska or Cornell University for combustion and 13C analysis. Samples of organisms were collected in various ways, sorted, dried (40°C), and sent to the University of Alaska for 13C measurement. Zooplankton were collected by oblique net tows within the epilimnion. Samples were sorted live, by hand, under a dissecting microscope. Two categories are used in this analysis: Daphnia (i.e., all species of D. magna combined) and total zooplankton, which included all crustacean zooplankton. Small fish (young of year) samples were entire fish. For larger fish, samples consisted of filets of muscle. Samples for periphyton were collected from submerged logs (epiphytic algae) and from clay tiles deployed for 7 d, allowing periphyton to colonize. These samples were taken both 1 week before and again 1 and 2 weeks following the 13C addition.

Other analyses—Sample collection and analysis followed protocols described for prior studies of these lakes (Pace and Cole 2000; Carpenter et al. 2001) Only a few key methods need be detailed here. Dissolved inorganic C and the partial pressure of CO₂ in the water and the atmosphere were measured directly using a Shimadzu GC-8 (see Cole et al. 2000). The CO₂ concentration of surface water in equilibrium with the air was calculated from Henry’s constant (Kₚ) and the partial pressure of CO₂ in the atmosphere. DOC was measured on Whatman GF/F filtered samples using a Shimadzu 5050 TOC analyzer. POC was measured on samples retained by Whatman GF/F filters using a Carlo-Erba CN analyzer. Each of these carbon pools was measured at weekly intervals.

GPP and respiration (Rₑtot) were estimated from continuous measurement of dissolved oxygen in the mixed layer of the lake using YSI-Endeco UPG-6000 sondes, which employed pulsed oxygen electrodes (see Cole et al. 2000). During 1999, sondes were deployed in East Long Lake 4 days of each week, and O₂ and temperature were recorded at 5-min intervals. Electrode drift and exchange with the atmosphere were calculated as in Cole et al. (2000). During night, the diffusion-corrected change in O₂ is a measure of ecosystem R (Rₑtot). During daylight, the diffusion-corrected change in O₂ is a measure of the difference between GPP and Rₑtot (NEP = GPP – Rₑtot) for the mixed layer of the lake. For these calculations, we assumed a gas piston velocity (kₚ) of 0.48 m d⁻¹, which is appropriate for wind speeds measured on these small lakes (Hesslein et al. 1980; Cole and Caraco 1998). Note that the mixed layer includes the water volume and sediment area to the depth of the mixed layer. We assume that Rₑtot in the dark and light are equal, and the respiratory quotient is 1 mol CO₂ mol⁻¹ O₂. We discussed the sensitivity of results to these assumptions in a prior paper (Cole et al. 2000). In the light, photooxidation is a potential component of Rₑtot that we cannot estimate directly. We assume that depth-integrated photooxidation is small in comparison to Rₑtot (Vahatalo et al. 2000) and discuss the effect of this assumption in the Discussion.

Pelagic respiration was measured during 24-h incubations of water in BOD bottles in the dark at ambient temperature at weekly intervals (Pace and Cole 2000). This measurement excludes the respiration of large zooplankton (below). Epilimnetic sediment respiration was estimated as the difference between Rₑtot and pelagic respiration. The water budget of East Long Lake was measured by experimentally adding a LiBr tracer in previous years (Cole and Pace 1998). This budget allows us to estimate the outflow coefficient of water. The outflow of any C pool is simply the product of the outflow of water and the concentration of that pool in the water. The input of DIC, POC, and DOC in groundwater were calculated from the water budget and the mass balance of each pool (below). The net exchange of DIC with the atmosphere was calculated as

\[
\text{Flux} = k(\text{CO}_2 \text{wat} - \text{CO}_2 \text{air})
\]

where k, the gas piston velocity, was obtained statistically from model fitting (below). Because of the low pH in East Long Lake, it was not necessary to consider chemically enhanced diffusion (Wanninkhof and Knox 1996).

Planktonic bacterial production (BP) was estimated using the 3H-leucine method of Smith and Azam (1993), conducted at weekly intervals. Conditions and assumptions for these measurements are well described for the UNDERC lakes (Pace and Cole 1996). Bacterial respiration (BR) was initially estimated from BP and an estimate of bacterial growth efficiency (del Giorgio and Cole 1998); we adjusted this estimate slightly to achieve mass balance for C. We assumed that DOC is the proximate substrate for pelagic bacteria.

In the model (Tables 1, 2), some of the fluxes are calcu-
involving the mass balance for zooplankton, assuming steady state. We also assumed that zooplankton feed nonselectively on the particulate material in proportion to the masses of each pool. The total consumption of organic C by zooplankton is derived from the assimilation and respiratory coefficients for consumer \( n \). (e.g., respiratory flux = \( r_n \cdot X_n \)). \( x_n \) is total consumption of all material by consumer \( n \). \( n \) is the proportion of material in pool \( n \) consumed by consumer \( n \). \( \alpha_m \) is the consumption coefficient of material \( m \) by consumer \( n \) (e.g., flux from \( m \) to \( n = c_{nm} \cdot X_n \)). \( \beta_{tot} \) is total consumption of all material by consumer \( n \). \( \beta_{nm} \) and \( \beta_{mn} \) are the assimilation and respiratory coefficients for consumer \( n \) (e.g., respiratory flux = \( \beta_{mn} \cdot X_n \)). \( \beta_{mn} \) is the sedimentation flux from compartment \( m \) to \( \beta_{mn} \) is the input flux to compartment \( m \).

**Table 1.** Mass balance equations and definitions for the carbon model. Other abbreviations are explained in Table 2. In these equations, there are six carbon compartments: DIC = 1, DOC = 2, Bacteria = 3, Phytoplankton = 4, Dead POC = 5, Zooplankton = 6. Units: All pools are mmol C m\(^{-2}\), and all fluxes are mmol C m\(^{-2}\) d\(^{-1}\). \( X_n \) and \( x_n \) are the total C and \(^{13}\)C in compartment \( n \). \( \beta_n \) is the ratio of \(^{13}\)C to total C in compartment \( n \). \( \alpha_m \) is the proportion of material in pool \( m \) consumed by consumer \( n \). \( \beta_{nm} \) is the consumption coefficient of material \( m \) by consumer \( n \) (e.g., flux from \( m \) to \( n = c_{nm} \cdot X_n \)). \( \beta_{tot} \) is total consumption of all material by consumer \( n \). \( \alpha_m \) and \( \beta_{mn} \) are the assimilation and respiratory coefficients for consumer \( n \) (e.g., respiratory flux = \( \beta_{mn} \cdot X_n \)).

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\begin{align*}
\text{Dissolved inorganic carbon} & \quad \frac{dX_1}{dt} = -k\left[\left(X_1/\text{zmix}\right) - \text{aircon}\right] - GPP + R_{tot} + in \cdot X_1 - \text{out} \cdot X_1 \\
\text{Dissolved organic carbon} & \quad \frac{dX_2}{dt} = in - \text{out} \cdot X_2 - c_{32} \cdot X_2 + c_{24} \cdot X_4 \\
\text{Bacteria} & \quad \frac{dX_3}{dt} = c_{32} \cdot X_2 - r_3 \cdot X_3 - c_{63} \cdot X_3 \\
\text{Phytoplankton} & \quad \frac{dX_4}{dt} = (1 - \text{BPP}) \cdot GPP - c_{24} \cdot X_4 - r_4 \cdot X_4 - c_{54} \cdot X_4 - c_{64} \cdot X_4 - \text{physed} \cdot X_4 \\
\text{Dead POC} & \quad \frac{dX_5}{dt} = \text{in} 5 + \left(\text{1 - fecesed}\right) \cdot \left(1 - \text{as6}\right) \cdot c_{64} \cdot X_4 + \left(\text{1 - fecesed}\right) \cdot \left(1 - \text{as6}\right) \cdot c_{63} \cdot X_3 + \left(\text{1 - fecesed}\right) \cdot \left(1 - \text{as6}\right) \cdot c_{65} \cdot X_5 + c_{54} \cdot X_4 - \text{sed5} \cdot X_5 - \text{out} \cdot X_5 - c_{65} \cdot X_5 \\
\text{Zooplankton} & \quad \frac{dX_6}{dt} = c_{66} \cdot X_3 + c_{66} \cdot X_4 + c_{66} \cdot X_5 - r_6 \cdot X_6 \\
\end{align*}
\]

This model also includes some assumed relationships. We assumed that zooplankton feed nonselectively on the particles available to them (nonliving POC, phytoplankton, bacteria) in proportion to the masses of each pool. The total consumption of organic C by zooplankton is derived from the mass balance for zooplankton, assuming steady state. We also assumed that bacterial assimilation depletes all of the primary production. Thus we calculated the area of the rotational torus of sediments that is above the mixed layer depth of the lake (9.4% of the area of East Long Lake) and assumed that benthic GPP equaled pelagic GPP per unit area of sediment.

The loss of phytoplankton C into the DOC (c24) pool was estimated as 10% of phytoplankton C per day and is comparable to literature-based estimates, which are usually normalized to phytoplankton production (Baines and Pace 1991). The \(^{13}\)C content of atmospheric CO\(_2\) was assumed to be \(7\%\). The \(^{13}\)C content of DIC in groundwater was assumed to be equal to that of the lake at ice out (\(28\%\)). The \(^{13}\)C of terrestrial DOC and POC entering the lake was estimated as \(10\%\) of terrestrial DOC and POC entering the lake was assumed to be \(28\%\), a typical value for the C-3 vegetation (maples, birch, aspen, and conifers) in the watershed of East Long Lake.

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Table 2. Parameters and variables of the carbon model. Shown are the symbol for each parameter as used in the code (Table 1), the value and units of each parameter, a descriptive name for each parameter and the source for each values.

| Symbol   | Value | Units       | Name                                                   | Source*          |
|----------|-------|-------------|--------------------------------------------------------|-------------------|
| k        | 0.45  | m d⁻¹       | Gas piston velocity                                    | Fitted           |
| Zmix     | 1     | m           | Mixed layer depth                                      | Measured         |
| CO₂(sat) | 13    | mmol m⁻³    | CO₂ concentration in equilibrium with atmosphere       | Measured, used mean |
| GPP      | 57    | mmol m⁻² d⁻¹| Gross primary production                               | Measured         |
| Rrot     | 82    | mmol m⁻² d⁻¹| Total ecosystem respiration                            | Measured         |
| in1      | 0.83  | mmol m⁻² d⁻¹| DIC inflow                                             | Estimated from water budget and mass balance |
| out      | 0.0027| d⁻¹         | Outflow coefficient                                    | Measured         |
| Patm     | −7    | δ¹³C        | Proportion of ¹³C in atmosphere                        | Literature       |
| f₁₃      | Dynamic | Unitless | Ratio of ¹³C in photosynthate to ¹³C in DIC            | Calculated from fitted fractionation factor for GPP (5.4 per mil) |
| Pgw      | −28   | δ¹³C        | Proportion of ¹³C in groundwater DIC                   | Assumed          |
| sedresp  | 49    | mmol m⁻² d⁻¹| Sediment respiration                                   | Calculated by difference |
| Psed     | −31   | δ¹³C        | Proportion of ¹³C in sediment                          | Measured         |
| in2      | 23.3  | mmol m⁻² d⁻¹| Influx of DOC                                          | Estimated from water budget and mass balance |
| c₃₂      | 0.0178| d⁻¹         | DOC consumption coefficient of bacteria                 | Estimated from measured bacterial production |
| c₄₂      | 0.1   | d⁻¹         | DOC release coefficient by phytoplankton               | Literature       |
| Pter     | −28   | δ¹³C        | Proportion of ¹³C in terrestrial DOC                   | Literature       |
| r₃       | 6.27  | d⁻¹         | Respiration coefficient of bacteria                     | Estimated based on measured BP; literature |
| c₆₃      | 0.054 | d⁻¹         | Consumption coefficient of bacteria by zooplankton     | Calculated from zooplankton mass balance assuming nonselective grazing |
| BPP      | 0.094 | Dimensionless | Proportion of GPP due to benthos                      | Estimated from morphometry and measured benthic PP; literature |
| r₄       | 0.073 | d⁻¹         | Phytoplankton respiration coefficient                  | Literature       |
| c₆₄      | 0.19  | d⁻¹         | Consumption coefficient of phytoplankton by zooplankton | Calculated from zooplankton mass balance assuming nonselective grazing |
| physed   | 0.5   | Unitless    | Proportion of phytoplankton that sediment directly without entering dead POC pool | Fitted           |
| in5      | 1.8   | mmol m⁻² d⁻¹| Input flux of dead POC                                 | Estimated from water budget and mass balance |
| fececesed| 0.9   | Unitless    | Proportion of zooplankton feces that sediment directly without entering dead POC pool | Fitted           |
| as₆      | 0.7   | Unitless    | Proportion of zooplankton consumption that is assimilated | Literature       |
| c₆₅      | 0.054 | d⁻¹         | Consumption coefficient of dead POC by zooplankton     | Calculated from zooplankton mass balance assuming nonselective grazing |
| sed₅     | 0.37  | d⁻¹         | Sedimentation coefficient of dead POC                  | Calculated from mass balance |
| r₆       | 0.3   | d⁻¹         | Respiration coefficient for zooplankton               | Fitted           |

* Measured, the value was measured in East Long Lake as part of this study or calculated from one or more measured values (see text for explanation); Literature, an estimate was taken from the literature (see text); Fitted, the value was arrived at by statistical fit of the model (see text).
**Whole-lake $^{13}$C addition**

**Results**

**Ecosystem metabolism**—As in many DOC-rich lakes, whole-lake respiration ($R_{tot}$) exceeded gross primary production and the lake was undersaturated on O$_2$ (Fig. 2) and was net heterotrophic (Fig. 3). Averaged for the entire season and using the continuous O$_2$ data from the sondes (Fig. 3), NEP was $-32 \pm 7$ mmol m$^{-2}$ d$^{-1}$ (mean ± SD). Using the weekly CO$_2$ data (Fig. 1), NEP was $-32 \pm 12$ mmol m$^{-2}$ d$^{-1}$. Both estimates were in good agreement with each other and prior measurements in East Long Lake at comparable nutrient loading (Cole et al. 2000). During the period of the $^{13}$C addition, NEP was slightly less negative: $-27$ mmol m$^{-2}$ d$^{-1}$. Calculated values of GPP and R were $57 \pm 4$ and $82 \pm 7$ mmol m$^{-2}$ d$^{-1}$. The mean ratio of GPP/R was $0.66 \pm 0.05$.

Despite the nutrient enrichment, whole-system R was considerably larger than GPP and exceeded our estimate of pelagic R based on dark-bottle O$_2$ consumption (22 mmol m$^{-2}$ d$^{-1}$). Thus by difference, benthic R was about 73% of system R (60 mmol m$^{-2}$ d$^{-1}$).

**$^{13}$C natural abundances**—Prior to the addition of the isotope, the ambient levels of $^{13}$C in the various C pools were low (moderately depleted in $^{13}$C) and typical for values in humic, softwater lakes (Fig. 4). DIC averaged $-28.2\%e$; POC, $-30.2\%e$; DOC, $-29\%e$; and Daphnia $-28.4\%e$. Benthic algae collected from pile recolonization experiments were also highly depleted ($-26.5\%e$), whereas epixylic algae collected from logs in the lake were somewhat less depleted $-22\%e$. With the exception of epixylic algae, these $^{13}$C values all are close to that of terrestrial primary production and soils (about $-28\%e$).

**Response to $^{13}$C-DIC addition**—The addition of $^{13}$C-DIC resulted in an immediate, large, and transient increase in several of the major C pools (Fig. 4). At the time of the addition the DIC pool rose to approximately +197% because of rapid atmospheric exchange, by day 3 DIC was at $-16\%e$, and by 10 d after the addition, DIC was only slightly

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**Table 1.** Model parameters and initial conditions. The values for DIC, POC, DOC, and zooplankton respiration were measured directly (in Matlab, Shampine and Reichelt 1997) to compare model results with observations of isotope dynamics during the experiment.

| **Parameter** | **Value** |
|---------------|-----------|
| DIC (mmol m$^{-2}$) | 10.2 |
| POC (mmol m$^{-2}$) | 5.4 |
| DOC (mmol m$^{-2}$) | 1.8 |
| Zooplankton respiration (mmol m$^{-2}$ d$^{-1}$) | 0.5 |

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**Fig. 2.** Continuous measurements of dissolved O$_2$ in East Long Lake. Four days of measurements are plotted during the $^{13}$C addition 1999; the x-axis shows day of year. The top of the scale (240 $\mu$M) is close to 100% saturation.

**Fig. 3.** Estimates of whole system metabolism for East Long Lake during summer 1999. The data are derived from continuous O$_2$ measurements as in Fig. 2. (A) Gross primary production (GPP). (B) Ecosystem respiration ($R_{tot}$) plotted as a negative value to aid visualization. (C) Net ecosystem production (NEP, GPP $- R$). Negative values of NEP mean that respiration exceeds gross photosynthesis (see text).
Fig. 4. Measured and modeled (lines) values of δ¹³C in three key carbon pools. (A) Dissolved inorganic carbon. (B) Zooplankton (filled circles are *Daphnia*; clear circles are total zooplankton). (C) Particulate organic C. The open diamonds are the ambient (prespike) values of δ¹³C arrived at by the model. The ¹³C addition occurred on day 173 on this scale.

Fig. 5. Measured versus modeled values of δ¹³C in DIC, POC, *Daphnia*, and total zooplankton. The dashed line is *Y* = *X*. The actual regression is *Y* = 1.065 (±0.075) *X* + 1.8 (±1.63), *r*² = 0.81; *P* < 0.0001; *n* = 50. Excluded from this regression is the initial value of DIC at the time of addition. Including this value (δ¹³C = 197) improves the *r*² to 0.98 and does not alter the slope (see Table 3).

Elevated over prespike levels. Peak ¹³C was measured in zooplankton at −5% 5 d after the spike. The elevated values in zooplankton persisted much longer than in the DIC and did not decline to prespike levels until about 20 d following the spike. The POC pool had peak values (+12%) on day 3. Like the zooplankton, POC returned to prespike values within about 20 d. We have too few samples of periphyton to accurately chart the time course, but peak measured values were near −12%, 9 d after the spike and were very close to the values in POC on the same day. The ¹³C of DOC was not changed measurably by the ¹³C addition.

**Model results and analysis**—Using these values, along with those in Table 1, the model produced a steady-state solution for C fluxes that agreed well with the baseline (prespike) ¹³C values in the lake (diamonds in Fig. 4). The fitted parameters agreed reasonably well with estimations of those parameters from other approaches. For example, in order to achieve an overall balance for C and initial ¹³C in the model, we estimated *k*, the gas piston velocity, at 0.45 m d⁻¹. Based on the equation in Cole and Caraco (1998), the wind-based calculation estimated *k* at 0.48 m d⁻¹. Both estimates were very close to that obtained by whole-lake ¹³C addition to a small lake in Canada (Hesslein et al. 1980). The best fit of the model was obtained when a fairly large proportion of phytoplankton biomass (50% d⁻¹) sedimented without being grazed. In the 1-m mixed layer of East Long Lake, this is equivalent to a settling velocity for phytoplankton of 0.5 m d⁻¹, which is reasonable (Baines and Pace 1994). On the other hand, the fitted fractionation factor for photosynthesis was 5.4%, which is considerably lower than the 15 to 20% in much of the literature (below). The fitted value for the sedimentation of zooplankton feces (0.9, feces variable in Table 2) is equivalent to a sinking rate of 0.9 m d⁻¹. The fit value for zooplankton respiration is 30% of biomass per day (R6 in Table 2), which is within the range of literature values (Lampert 1984).

With these fitted and measured parameters in the model, we then simulated the ¹³C addition and its distribution into the various C pools. The model reproduced both the dynamics and the magnitudes of change in ¹³C as it moved into and out of the various pools (Fig. 4). A plot of measured versus modeled ¹³C in the DIC, POC, and zooplankton pools (Fig. 5) is highly significant (*P* < 0.001) has a slope indistinguishable from 1 (1.065 ± 0.075)) and accounts for much of the variance (*r*² = 0.81). Looking at the pools independently reveals significant fits for each pool and little evidence of bias (Table 3).

**Fractionation of ¹³C-DIC by phytoplankton**—The best fit of the model occurred when the fractionation factor for photosynthesis was low (5.4%). We varied this parameter from 0 (no fractionation) to 20%, a value near the high end of fractionation factors from the literature (Laws et al. 1995). As we increased the fractionation factor, the overall fit of the model to the data decreased (i.e., the standard error increased, Fig. 6A). Furthermore, increasing the fractionation factor caused the predicted ambient (prespike) ¹³C levels to diverge away from measured values (Fig. 6B). With increasing fractionation, the model predicted δ¹³C in DIC that was less depleted than we measured and zooplankton ¹³C that was more depleted than we measured. Thus, if the fractionation factor was set larger than about 10%, the model no longer produced plausible predictions.
Table 3. Measured and modeled values of $\delta^{13}C$ in various categories. Shown are the linear regressions of modeled (as the independent variable) versus measured value of $\delta^{13}C$ as in Fig. 5.

| Data* | $n$ | $r^2$ | $P$ | Slope | SE slope |
|-------|-----|-------|-----|-------|----------|
| All   | 51  | 0.98  | <0.001 | 1.01 | 0.015    |
| All – initial DIC spike | 50  | 0.81  | <0.001 | 1.07 | 0.08     |
| All DIC | 12  | 0.99  | <0.001 | 1.00 | 0.02     |
| All DIC – initial spike | 11  | 0.62  | <0.03 | 0.76 | 0.20     |
| POC   | 11  | 0.89  | <0.001 | 1.20 | 0.14     |
| Daphnia | 15  | 0.90  | <0.001 | 1.23 | 0.11     |
| Total zooplankton | 13  | 0.77  | <0.001 | 0.766 | 0.13     |

* All, the entire data set, which includes the DIC value at the time of addition; All—initial DIC spike, excludes the DIC value at the time of addition and is the regression shown in Fig. 4. The other four categories of DIC—with and without the initial spike value, POC, Daphnia, and total zooplankton—are as in Fig. 4.

† $n$ is the number of samples in each data set; SE slope is the standard error of the slope.

**Fig. 7** Results of C model for East Long Lake. (Upper panel) Box and arrow diagram of the C flow model. Shown are the ecosystem boundaries (heavy dashed line) and the C flux (mmol m$^{-2}$ d$^{-1}$) across these boundaries for the steady-state fit of the model. The simplified internal structure of the model is shown by the boxes and arrows within the ecosystem boundaries. The left side shows inputs and the right side outputs of flowing water. Littoral benthos include both autotrophic (periphyton) and heterotrophic (benthic invertebrates, microbes, etc.) components for the torus of sediments that intersects the mixed zone of the water column (see text). The exchange with the atmosphere includes both invasion and evasion terms; this is necessary to calculate the $^{13}$C-CO$_2$ fluxes across the air–water interface. (Lower panel) Detail of some of the internal part of the model to highlight the fluxes of organic C to pelagic bacteria and zooplankton. The bold numbers inside the boxes are standing stocks (mmol C m$^{-2}$); the numbers associated with arrows are fluxes (mmol m$^{-2}$ d$^{-1}$). The values shown are for the best fit of the model (minimum SSE). The fluxes from organisms to DIC denote respiration; the flux of DIC to phytoplankton plus benthos denotes gross primary production. Phyto-DOC is DOC of phytoplankton origin; detrital POC is nonliving POC (see text) and could be of autochthonous or allochthonous origin.

**Carbon budget of East Long Lake**—The model reproduced the measured distribution of added $^{13}$C to East Long Lake with high fidelity. The model is tightly constrained by data that includes total C fluxes and $^{13}$C values prior to, during, and following the spike. The overall goodness of fit gives us some confidence that flux estimates are realistic. Carbon flows based on the model are illustrated in Fig. 7. Several general points emerge. First, despite the moderate nutrient addition, East Long Lake remained net heterotrophic and system R exceeded system GPP by large amounts, implying that terrestrial organic matter fuels much of heterotrophic respiration (see upper panel, Fig. 7). Second, DIC in the lake is derived largely from this internal respiration, which is much larger than the external inputs of DIC in groundwater. Third, although externally supplied DOC supports a large part of system R, zooplankton, a key component of pelagic food, is predominantly supported by phytoplankton primary production under the conditions of this experiment (see lower panel, Fig. 7). Finally, pelagic bac-
teria appear to respire large amounts of terrestrially derived DOC but pass very little of this organic C up the food web.

Discussion

Before we interpret the experiment and model results, there are a few caveats. Numerous parameters and the pre-spike conditions were estimated by assuming steady state for total C. Most of the pools and fluxes that we actually measured did not vary greatly during this experimental period (e.g., Fig. 1). Furthermore, that this model is able to reproduce the dynamics of the $^13$C spike suggests that results were not greatly affected by the steady-state assumption. Second, we assumed in the model that the only way inorganic C could be converted to organic C was by photosynthesis. We have ignored several mechanisms whereby CO$_2$ can be reduced heterotrophically. Using energy from metabolism, some bacteria can carboxylate the C skeletons of the tricarboxylic acid cycle (anaplerotic reactions), resulting in a net production of CO$_2$. We can put an upper limit on heterotrophic consumption of CO$_2$. We can put an upper limit on heterotrophic CO$_2$ uptake in the pelagic region with respect to dark CO$_2$ uptake by pelagic bacteria. We have estimated that only 6% of bacterial secondary production is attributed to dark CO$_2$ uptake by bacteria (Jordan and Likens 1980). In the surface water of East Long Lake during summer 1999, H-leucine-based estimates of BP averaged 8.1 $\pm$ 5.1 $\mu$mol C L$^{-1}$ d$^{-1}$ or 0.67 mmol C m$^{-2}$ d$^{-1}$. “Dark” CO$_2$ uptake by pelagic bacteria should be no more than 0.04 mmol C m$^{-2}$ d$^{-1}$, which is less than 0.08% of GPP. Therefore, the heterotrophic route for CO$_2$ entry into the food web can be ignored. Finally, we have attributed CO$_2$ production and oxygen consumption to respiration. Photooxidation of DOC could be an additional and significant source of CO$_2$ and a sink for O$_2$ (e.g., Wetzel et al. 1995; Granéli et al. 1996) that we have not included in the model. Our estimate of ecosystem R, however, comes from night declines in O$_2$; our estimate of pelagic R comes from sedimentation of DOC but pass very little of this organic C up the food web.

This experiment was too short to provide a quantitative estimate of the amount of terrestrial C that might support the production of fishes. However, we can estimate the extent to which zooplankton, a major prey of small fishes, is supported by allochthonous and autochthonous sources in East Long Lake (Fig. 7). If zooplankton were supported entirely by terrestrial organic C (via bacterial uptake), there would have been no shift in the $\delta^{13}$C of zooplankton. The large increases in $\delta^{13}$C for both Daphnia and total zooplankton demonstrate unequivocally that newly photosynthesized autochthonous C is an important source for zooplankton under the conditions of this experiment. Using the model, we can calculate the quantity of C and the pathways supporting zooplankton in this experiment. Zooplankton assimilation is dominated by inputs from phytoplankton, with 59% coming from living phytoplankton and 31% from the nonliving POC of autochthonous origin. According to the model, only 8.4% of the C assimilated by zooplankton is of allochthonous origin. (Fig. 7).

The conclusion that allochthonous C is relatively unimportant to zooplankton can be corroborated by an independent calculation. If pelagic bacterial C demand were supported entirely by DOC of allochthonous origin, bacterial secondary production (BP; 0.67 mmol C m$^{-2}$ d$^{-1}$) would be a maximum estimate of allochthonous DOC available to zooplankton. This is only about 21% of zooplankton C assimilation. Furthermore, some BP is not directly available to zooplankton because it is grazed by protists and rotifers, and a portion of BP is supported by DOC of autochthonous origin (Fig. 7). Thus, if allochthonous C is available to zooplankton only via bacteria, we would expect that allochthonous organic C should support less than 21% of crustacean zooplankton assimilation, in agreement with the model and the isotope results, which suggest 8.4%. If zooplankton consumed allochthonous POC directly, the importance of allochthonous C could be larger than this estimate suggests.

Because zooplankton were labeled with autochthonous C, can we see this label in fast-growing fish that consume them? Prior to the addition, planktivorous, young of year (YOY) large-mouth bass (Micropterus salmoides) isotopically resembled many of the other C pools in the lake ($\delta^{13}$C $\approx$ $-30\%e$; Fig. 8). Following the addition, there was a 6% shift to the more positive value of $\sim$24%, indicating some connection of these fish to autochthonous production. In contrast, a benthivorous fish, adult yellow perch (Perca flavescens), remained at $\sim$30%e throughout the study. The experiment did not run long enough for us to make any strong conclusions about fishes. The lack of label in the yellow perch could simply be the result of slower growth rates in these adult fish and the time required for transfer of the label to the next trophic level. Although we cannot yet quantify the importance of autochthonous organic matter to fish, its presence in YOY bass suggests it is important in supporting the highest trophic levels.

Although pelagic bacteria pass relatively little allochthonous organic C up the food web, they assimilate a large amount of DOC of allochthonous origin (21 mmol m$^{-2}$ d$^{-1}$ according to the model). We do not have a way to separately estimate the growth efficiency of bacteria using allochthonous and autochthonous DOC sources, but we can estimate the combined growth efficiency. The model suggests that
in the lake. The model suggests that respiration of allochthonous DOC in the lake is a much larger source (>25-fold) of DIC than is groundwater input for this softwater lake (Fig. 7). In fact, the isotopic signature of the DIC is a result of a combination of the respiration of allochthonous DOC, primary production, and atmospheric exchange. This view of multiple controls is consistent with the large degree of variation in DIC $^{13}$C values among small lakes (Hesslein et al. 1991; Streigl et al. 2001).

The model and experiment lead to an interesting conundrum about our knowledge of C cycling in lakes. If we had not added the $^{13}$C tracer, we could have come to the conclusion that the food web in East Long Lake was supported almost exclusively by allochthonously supplied organic C. The fractionation of $^{13}$C uptake by phytoplankton has been well studied in marine systems under both field and laboratory conditions (e.g., Laws et al. 1995; Bidigare et al. 2001; Rau et al. 2001). This fractionation is rarely measured for freshwater phytoplankton (see Yoshioka 1997; Jones et al. 1998). In marine systems, phytoplankton fractionation can be estimated from external CO$_2$ concentration, temperature, and growth rate of the phytoplankton—all known variables in East Long Lake. Applying one well-known estimator (Laws et al. 1995) to East Long Lake yields $\varepsilon = -25$‰ and an expected $^{\delta^{13}}$C value for phytoplankton of $-50$‰ if the growth rate of phytoplankton ($\mu$) is 1 d$^{-1}$. Letting the growth rate range from 0.25 to 8 d$^{-1}$ has only a small effect on $\varepsilon$, and the expected $^{\delta^{13}}$C would range from $-44$ to $-51$‰. Intriguingly, there are no measured components in the food web of East Long Lake that are this depleted in $^{13}$C (Figs. 4, 8), so in the absence of the manipulation, we might have erroneously concluded that the major C source for zooplankton was terrestrial organic matter and not phytoplankton production. Similarly, assuming $\varepsilon = 20$‰, one would conclude that POC could not be largely of autochthonous origin. The large shifts in the $^{\delta^{13}}$C values for POC and zooplankton clearly indicate a strong connection to the autochthonous food web. Our model suggests that the fractionation for phytoplankton in situ in this softwater lake is unexpectedly low and not well predicted by generic models largely developed for marine phytoplankton growing in bicarbonate-rich culture media or in marine systems in the field (Bidigare et al. 2001). Our values of $\varepsilon$, while low, are within the published range (Laws et al. 1995; Rau et al. 2001) but surprising in this CO$_2$-rich softwater lake.

Although we cannot yet explain the physiologic or species-specific basis for the low $\varepsilon$ implied by the model, we can constrain the bounds with a simple calculation. If all sestonic POC were of phytoplankton origin, then the contrast between the $^{\delta^{13}}$C of DIC and POC would be a direct measure of $\varepsilon$. The prespike values would produce $\varepsilon = 2.6$‰, the postspike values 6.3‰. Clearly this approach ignores the portion of the POC that is of allochthonous origin. We can approximate this portion in several ways. A maximum estimate of this fraction would be to assume that all nonliving POC is allochthonous, thus ignoring the contribution of formerly living phytoplankton to nonliving POC. We can calculate the algal fraction of POC from the C:Chl $a$ ratio and measured chlorophyll. The C:Chl $a$ ratio in UNDERC lakes was measured directly by Carpenter and Leavitt (1991) and averaged...
about 40:1—close to frequently assumed values in the literature. Because we know the $^{13}$C of POC, and assuming that the allochthonous portion has $\delta = -28\%_c$, we can solve algebraically for $\varepsilon$, which is $-6\%_c$. These two independent assessments of $\varepsilon$ produce similarly low values, in good agreement with the value obtained by best fit of the model.

Our model and experiment suggest that the zooplankton and, by extension, the YOY fish that prey on them are components of a food web that is not very dependent on the vast amount of allochthonous C loading to East Long Lake. The metabolism of allochthonous organic C by pelagic bacteria is either a direct respiratory sink for the allochthonous C or supports a microbial loop that does not strongly interact with the food chain supported by phytoplankton production (Ducklow et al. 1986).

The conclusions we can draw here about carbon cycling, although intriguing, pertain to this one lake and under a regime of N and P enrichment. We enriched the lake with nutrients, so that we would be assured of measurable assimilation of the added $^{13}$C into the autotrophic part of the food web, and used this enrichment to calibrate the model. Without this enrichment, it is possible that the autochthonous pathways would be less important than we estimated. Furthermore, we caution that our pulse experiment was too brief to effectively label DOC, benthic organisms, or longer lived fish. The large amount of benthic D derived from our model could suggest that allochthonously loaded C is important to benthic invertebrates and the larger fishes that prey on them. Finally, our experiment occurred during the summer growing season and with a particular zooplankton community. For example, using ambient stable isotopes in Loch Ness, Grey et al. (2001) found that the $^{13}$C content of *Daphnia* during summer was consistent with a phytoplankton origin. However, over the entire annual period, Loch Ness zooplankton were supported about 40% by terrestrial organic C. These unknowns might be resolved by a sustained $^{13}$C addition without the addition of nutrients. A sustained experiment would both shed light on benthic connections and help determine the roles of allochthonous and autochthonous C under ambient, nutrient-limited conditions.

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