

Differential Support of Lake Food Webs by Three Types of Terrestrial Organic Carbon

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**Abstract**

Organic carbon inputs from outside of ecosystem boundaries potentially subsidize recipient food webs. Four, whole-lake additions of dissolved inorganic  $^{13}\text{C}$  were made to reveal the pathways of subsidies to lakes from terrestrial dissolved organic carbon (t-DOC), terrestrial particulate organic carbon (t-POC) and terrestrial prey items (t-prey). Terrestrial DOC, the largest input, was a major subsidy of pelagic bacterial respiration, but little of this bacterial C was passed up the food web. Zooplankton received < 2% of their C from the t-DOC to bacteria pathway. Terrestrial POC significantly subsidized the production of both zooplankton and benthic invertebrates, and was passed up the food web to *Chaoborus* and fishes. This route supplied 33% to 73% of carbon flow to zooplankton and 20 to 50% to fishes in non-fertilized lakes. Terrestrial prey, by far the smallest input, provided some fishes with >20% of their carbon. The results show that impacts of cross-ecosystem subsidies depend on characteristics of the imported material, the route of entry into the food web, the types of consumers present, and the productivity of the recipient system.

## INTRODUCTION

Ecosystems typically receive materials, including organic matter, from outside of their boundaries. This loading of externally produced (allochthonous) organic matter can subsidize ecosystem metabolism and support the production of consumers of the receiving ecosystem (Vanni et al. 2004). Although early ecologists recognized the importance of cross-boundary inputs (Summerhayes and Elton 1923), recent work has focused on quantifying both the magnitudes and significant direct and indirect effects of subsidies on food webs (e.g. Power and Rainy 2000; Polis et al. 2004) and ecosystem metabolism (below). The largest allochthonous inputs and hence potential subsidies to most communities and ecosystems is detrital organic matter in dissolved and particulate forms (Polis et al. 1997). This material may be directly available or may require transformation by microorganisms prior to supporting animal consumers in recipient systems. In contrast, smaller fluxes of living organisms across boundaries are often directly available to consumers and numerous studies demonstrate their importance in food webs (e.g. Nakano and Murakami 2001; Sabo and Power 2002). However, for entire ecosystems the relative magnitude and utilization of various types of subsidies remains a poorly understood but significant problem. Theory indicates subsidies can stabilize population dynamics, predator-prey interactions, and food webs (DeAngelis 1992; Huxel and McCann 1998; Takimoto et al. 2002; Loreau and Holt 2004). Subsidies also indicate interdependence and important connections among ecosystems that are significant for management and conservation (e.g. Ehrenfeld and Toth 1997; Power et al. 2004; Douglas et al. 2005).

The organic matter imported across ecosystem boundaries can also affect the metabolic balance of the receiving system by providing a substrate for microbial respiration in excess of local primary production (Odum 1956; Webster and Meyer 1999). While these connections and subsidies have had a long history of study in stream ecosystems (e.g. Cummins et al. 1973; Fisher and Likens 1973; Hynes 1972) there has been far less work in lakes. Nevertheless, lakes are examples of ecosystems that receive large inputs of allochthonous organic matter with inputs often equal to or exceeding internal primary production (Caraco and Cole 2004). Even though only a small fraction of this allochthonous material is respired, the consequence, for many lakes, is that total respiration exceeds gross primary production so that net ecosystem production is negative (del Giorgio et al. 1999; Cole et al. 2000; Jonsson et al. 2003; Hanson et al. 2003). Thus, ecosystem metabolism in lakes suggests allochthonous support of food webs could be significant if degradation of terrestrial carbon is also coupled to consumer production (Cole et al. 2002). Studies of lake zooplankton using natural abundances of stable isotopes support this view and indicate zooplankton acquire some of their carbon from terrestrial sources (Meili et al. 1996; Jones et al. 1999; Grey et al. 2001; Karlsson et al. 2003).

Terrestrial organic matter may be incorporated into aquatic food webs by several mechanisms. Terrestrially-derived dissolved organic carbon (t-DOC) enters lakes in flowing water and is degraded by bacteria that are subsequently consumed by predators (Tranvik 1998; Hessen 1998). Terrestrially-derived particulate organic carbon (t-POC) enters lakes by both fluvial and aeolian transport. T-POC may be available to bacteria through decomposition and to other consumers through direct ingestion (Cole et al. 1990;

Hessen and Nygaard 1992). Terrestrial-prey items (t-prey) include insects, amphibians, and small reptiles and mammals, which either intentionally or accidentally enter lakes. Fish actively consume these items so t-prey constitutes a variable but significant resource at least in some small lakes (e.g. Carlton and Goldman 1984; Hodgson et al. 1993; Hodgson and Hansen 2005). Each of these terrestrial subsidies provides partial support to consumers which also serve as prey to predators.

Despite some understanding of utilization mechanisms and carbon budgets for lakes, the pathways of utilization and relative magnitudes of the major subsidies have not been compared. Here, the carbon subsidy for the food webs of several lakes is estimated accounting for three terrestrial sources: t-DOC, t-POC and t-prey. Inputs and fates of these sources along with autotrophic production were examined in four, whole-lake  $^{13}\text{C}$  additions. Prior work has documented that internal primary production provides only partial support to consumer production in small, low-nutrient lakes (Pace et al. 2004; Kritzberg et al. 2004; Carpenter et al. 2005). This paper adds to a growing literature on terrestrial subsidies by specifically analyzing the pathways and relative importance of the three ultimate sources of terrestrial subsidies, t-DOC, t-POC, and t-prey, in supporting ecosystem respiration and consumer consumption. The analysis demonstrates that the three kinds of terrestrial carbon make important contributions to aquatic consumers through distinctly different pathways.

## **METHODS**

### *$^{13}\text{C}$ Additions and Study Lakes*

$\text{NaH}^{13}\text{CO}_3$  was added daily to upper mixed layer of Paul, Peter, and Tuesday lakes during summer for five to six weeks (Pace et al. 2004; Kritzberg et al. 2004, 2005; Carpenter et al. 2005). The enrichments elevated the  $\delta^{13}\text{C}$  of the dissolved inorganic C (DIC) creating a large contrast between the organic matter produced by (or derived from) primary producers within the lake and terrestrially-derived organic sources. The lakes were chosen to provide contrasts in dissolved organic carbon concentrations (an indicator of allochthonous inputs), fish assemblages, and nutrient enrichment. The latter contrast was created by fertilizing one of the lakes (Peter Lake) with inorganic nitrogen and phosphorus to stimulate primary production and autochthonous food web pathways.

Paul, Peter, and Tuesday lakes are located at the University of Notre Dame Environmental Research Center (89°32'W, 46°13'N) and described in detail in Carpenter and Kitchell (1993). The lakes are small (0.9-2.5 ha), soft water systems with negligible growth of rooted aquatic vegetation (macrophytes), moderate to high dissolved organic C (DOC; 0.3 to 0.7 mmol C liter<sup>-1</sup>; or 4 to 8 mg C liter<sup>-1</sup>) and low concentrations of dissolved inorganic C (DIC) from 80 to 140  $\mu\text{M}$ . All lakes are strongly stratified with shallow thermoclines (3-4 m), anoxic hypolimnia, and primary production dominated by phytoplankton and periphyton.

Peter Lake was enriched twice with  $^{13}\text{C}$  in separate years. Peter Lake was fertilized in the second  $^{13}\text{C}$  manipulation (hereafter Peter +N&P) with additions of inorganic N ( $\text{NH}_4\text{NO}_3$ ) and P ( $\text{H}_3\text{PO}_4$ ) at an N:P atomic ratio of 25 (details in Carpenter et al. 2005). Primary producers were stimulated prior to  $^{13}\text{C}$  addition by adding 0.69 mmol P m<sup>-2</sup> and 18.9 mmol N m<sup>-2</sup> in a single dose on June 3, 2002. Daily additions of 0.11 mmol P m<sup>-2</sup> d<sup>-1</sup> and 2.7 mmol N m<sup>-2</sup> d<sup>-1</sup> were subsequently made from June 10 to

August 25. For the other three manipulations only the  $\delta^{13}\text{C}$  of DIC was elevated. Loadings were 0.24, 0.35, 0.25, and 0.61 moles  $^{13}\text{C d}^{-1}$  to Paul, Peter, Tuesday, and Peter +N&P lakes, respectively. In all cases the  $\delta^{13}\text{C}$  increased the total DIC by less than 1% and had no measurable effect on pH.

### *Measurement of $^{13}\text{C}$*

$^{13}\text{C}$  content of the major carbon pools was measured before, during and after the tracer addition, at either daily (DIC, POC), weekly (zooplankton, *Chaoborus* spp., small fish, benthic algae [periphyton], DOC, or at longer intervals (larger fish, benthic invertebrates). Detailed methods for sampling and preparation of materials for  $^{13}\text{C}$  analysis are summarized elsewhere (Cole et al. 2002; Pace et al. 2004; Kritzberg et al. 2004; Carpenter et al. 2005). The isotopic values for some key components came from specialized studies. For example the measured isotopic signals for pelagic bacteria were obtained from *in situ* growth experiments in dialysis cultures during the  $^{13}\text{C}$  additions (Kritzberg et al. 2004). The isotopic values for phytoplankton were obtained from the  $\delta^{13}\text{C}$  of the  $\text{CO}_2$  moiety of the DIC and estimates of isotopic discrimination during photosynthesis by phytoplankton (Bade et al. 2006; Bade and Cole, 2006).  $^{13}\text{C}$  was measured using mass spectrometers as previously described and reported here as  $\delta^{13}\text{C}$  (i.e. per mil values relative to a standard, see Carpenter et al. 2005).

### *Additional Measurements of Standing Stocks and Fluxes*

To support the dual isotope flow model (described below), the standing stocks of carbon pools and many of the fluxes among these pools were measured. These

measurements included: daily concentrations of DIC and  $p\text{CO}_2$ ; weekly concentrations of chlorophyll *a* (an indicator of phytoplankton biomass), DOC, POC, the abundance and species composition of crustacean zooplankton and the phantom midge, *Chaoborus*, (several species), bacterial production, and dark-bottle pelagic respiration. The abundance, size structure and growth rates of the dominant fish species were also measured in each lake. Dissolved organic C is measured as organic C which passes a 0.7  $\mu\text{m}$ -pore glass fiber filter; Particulate organic C is organic C  $<153 \mu\text{m}$  that is retained by the glass fiber filter. Terrestrial prey items are identified to species and life stage from the stomach contents of fishes. Methods for these measurements are described elsewhere (Carpenter et al. 2005) and provided in an on-line manual (<http://ecostudies.org/cascade/manual.htm>). Gross primary production (GPP) and total system respiration ( $R_{\text{tot}}$ ) were derived from continuous deployment of YSI sondes that recorded oxygen concentration and temperature (along with pH) at 5 minute intervals following methods in Cole et al. (2000, 2002) and Hanson et al. (2003). GPP estimates include the production of both phytoplankton and benthic microalgae integrated to the bottom of the upper mixed layer.  $R_{\text{tot}}$ , measured this way, includes the respiration of all autotrophs and heterotrophs in both the water column and sediments to the bottom of the mixed layer. Mixed layer depths were estimated from depth profiles of temperature made weekly. The rate of gas exchange was obtained from direct measurements of the gas piston velocity ( $k_{600}$ ) using a whole-lake  $\text{SF}_6$  addition and wind-based estimates from continuous lake-side wind measurements (Wanninkhof et al. 1985; Cole and Caraco 1998; Bade and Cole 2006).

### *The Dual Isotope Flow Model*

A dual isotope flow (DIF) model was developed to simulate the flow of C ( $^{12}\text{C}$  +  $^{13}\text{C}$ ) and  $^{13}\text{C}$ . The ecosystem was partitioned into twelve compartments: DIC, DOC, pelagic bacteria, phytoplankton, detrital POC, zooplankton, *Chaoborus*, periphyton, and three fish compartments specific to the dominants in each lake. Two differential equations, one for C (i.e.  $^{12}\text{C}$  +  $^{13}\text{C}$ ) and one for  $^{13}\text{C}$ , describe the mass balance of carbon for each compartment (Appendix). Model parameters were derived for each lake either from direct measurements, calculations from measurements, literature estimates, or in some cases by fitting to observed  $^{13}\text{C}$  time series (Appendix). The boundaries of the ecosystem for the purposes of the model were the air-water interface to the base of the mixed layer encompassing all sediments above the mixed layer of the lake.

Three fish compartments were modeled in each lake. In Paul Lake the three compartments were age classes (young of year, juveniles (age 1+), and adults) of a single dominant species largemouth bass (*Micropterus salmoides*). In Peter Lake the fish compartments were pumpkinseeds (*Lepomis gibbosus*), sticklebacks (*Gasterosteus aculeatus*), and fathead minnows (*Pimephales promelas*). The dominant species of Tuesday Lake were golden shiners (*Notemigonus chrysoleucas*), sticklebacks, and fathead minnows. Some terms in the fish carbon balances (e.g. ingestion of prey items, respiration, egestion) were obtained using a bioenergetics model (Hanson et al. 1997) augmented in some cases by measured diets (Appendix). Growth and biomass dynamics were measured directly and interpolated to daily values input to the bioenergetics model.

Performance of the model was evaluated in several ways. First, fluxes simulated by the model were checked for reasonableness given extensive measurements and knowledge of rates and processes in the lakes. Second, where possible, the DIF model estimates of some parameters (e.g. photosynthetic fractionation) were compared to estimates based on other methods. Third, modeled values of  $\delta^{13}\text{C}$  for the compartments were compared against measured values using least squares regression of predicted versus observed  $\delta^{13}\text{C}$ . The values of fitted parameters were arrived at by minimizing the SSE of the predicted versus observed  $^{13}\text{C}$  regressions.

#### *Terrestrial Inputs and Pathways*

The DIF model provides several pathways for the input and utilization of terrestrial organic carbon (Fig. 1). Analysis of these pathways is the central focus of this paper. Terrestrial DOC (t-DOC) is an input to the DOC compartment and hence this compartment contains carbon of both terrestrial and lake origin. This mixture of DOC is consumed by bacteria that are in turn consumed by zooplankton who are the prey of fish and *Chaoborus*. Thus, t-DOC can potentially move through the food web to fish. Terrestrial POC (t-POC) is an input to the detrital POC compartment. This compartment is a potential resource for zooplankton. Detrital POC is also lost by sedimentation where it becomes food for benthos. Thus, t-POC can move through the food web to fish via zooplankton and benthos (Fig. 1). Finally, terrestrial prey is a food resource for the fish compartments (Fig. 1). All fish compartments except young of year largemouth bass (in Paul Lake) consume terrestrial prey as supported by diet observations (e.g. Hodgson et al. 1993; Hodgson and Hansen 2005).

## RESULTS

The addition of  $^{13}\text{C}$  resulted in a large increase in the  $^{13}\text{C}$  content of the DIC in the lakes and, consequently, in both primary producers and consumers (Fig. 2). In all cases primary producers (phytoplankton and benthic algae) became highly labeled but the degree of labeling in the consumer organisms, relative to the primary producers, was quite different among the lakes and type of consumer (Figs. 2, 3). This labeling suggests that an alternative food source such as unlabeled terrestrial carbon is supporting some consumers. The DIF was used model to quantify the use of these alternative sources.

Plots of modeled versus measured values of  $^{13}\text{C}$  for the 12 compartments are shown in Figure 3. The agreement of modeled with measured values supports the plausibility of the actual fluxes of autochthonous and allochthonous C calculated by the model. The best fits of the DIF model were for the Peter and Paul additions ( $R^2 = 0.98$ ,  $n = 136$  and  $R^2 = 0.97$ ,  $n = 149$ , respectively) and the regressions slopes ( $\pm 1$  SE) were close to unity ( $0.97 \pm 0.02$  and  $0.94 \pm 0.02$ , respectively). The fit for the Peter +N&P addition was also very only slightly lower ( $R^2 = 0.92$ ,  $n = 144$ , slope =  $0.90 \pm 0.03$ ) an encouraging results considering the rapid dynamics of  $^{13}\text{C}$  observed in the lower food web compartments (Figure 3). While Tuesday had a lower fit the model still explained nearly 80% of the variability in measured values. ( $R^2 = 0.79$ ,  $n = 151$ , slope =  $0.96 \pm 0.04$ ).

### *Loading of Allochthonous and Autochthonous Organic C*

The model provided estimates of organic carbon loading and respiration of the biotic compartments that can be compared to measured values of  $\text{GPP}_{\text{tot}}$  and  $\text{R}_{\text{tot}}$  (Table

1). Model-derived loading of terrestrial DOC and POC ranged from 21 to 67 mmol C m<sup>-2</sup> d<sup>-1</sup> (Table 1) and differences in loading followed measured differences in concentrations among Paul, Peter, and Tuesday lakes. Although t-DOC dominated loading, t-POC accounted for a substantial portion, averaging 19.5% of total terrestrial loading among the lakes (4.6 to 15.8 mmol C m<sup>-2</sup> d<sup>-1</sup>). Total autochthonous primary production (GPP<sub>tot</sub>) was dominated by phytoplankton and ranged from 34 to 103 mmol C m<sup>-2</sup> d<sup>-1</sup> in the lakes. GPP<sub>tot</sub> was highest in nutrient-enriched Peter Lake where it was 4-fold larger than terrestrial loading (Table 1). In the unenriched lakes GPP<sub>tot</sub> was 1.7 times terrestrial loading in Paul Lake, co-equal to it in Peter Lake (without added nutrients) and only 0.6 times terrestrial loading in Tuesday Lake. The potential importance of a terrestrial subsidy to consumers is larger than the above comparisons suggest because a fraction (13 to 21% among lakes) of GPP<sub>tot</sub> is respired by the algae themselves (Table 1).

#### *Respiratory Losses of Allochthonous and Autochthonous C*

The three types of terrestrial inputs considered by the DIF model subsidize consumer respiration in different ways (Table 1). t-DOC was the most important terrestrial subsidy to the respiration of pelagic heterotrophs (pelagic R<sub>h</sub>) supporting from 28 (Paul Lake) to 68% (Tuesday Lake) of their respiration. Since pelagic bacteria are the only consumers of t-DOC in the model, this result reflects their significance in overall heterotrophic respiration. Overall, t-POC supported less respiration (2 to 26% of R<sub>h</sub>), but this material constituted a respiratory subsidy, especially to zooplankton which are the major users of t-POC in the water column (below). In Paul Lake t-POC supports nearly as much (5.5 mmol C m<sup>-2</sup> d<sup>-1</sup>) pelagic R<sub>h</sub> as does t-DOC (6.8 mmol C m<sup>-2</sup> d<sup>-1</sup>; Table 1).

Terrestrial prey supported only a very small fraction of respiration in all lakes (Table 1), but were highly significant C sources to fishes (below).

While terrestrial inputs were a major source of the carbon ultimately supporting consumer respiration, autochthonous organic carbon from primary production supported a large share of heterotrophic respiration in all cases. In Peter Lake +N&P autochthonous carbon supported 88% of pelagic  $R_h$  ( $38.5 \text{ mmol C m}^{-2}\text{d}^{-1}$ ) or 7 times that supported by terrestrial inputs. Even in the absence of nutrients, the autochthonous component of respiration was significant, ranging from 28% of total pelagic  $R_h$  in Tuesday L., to about 60% in Paul and Peter lakes (without nutrient additions).

Epilimnetic sediment respiration (sediment  $R_h$  = benthic microorganisms plus meiofauna) comprised 29 to 47% of total heterotrophic R (water column plus sediments; Table 1). Because the model did not explicitly include the dynamics of the microbial and meiofaunal benthos, it is not possible to partition this respiration among the three terrestrial sources, but can calculate the relative amount supported by total allochthonous and autochthonous sources (Carpenter et al. 2005). The DIF model estimated 30 to 50% of sediment  $R_h$  is supported by terrestrial C in the unfertilized lakes. The fertilization of Peter Lake greatly increased the supply of autochthonous C to the benthos and decreased the importance of allochthonous C to <4% (Table 1).

#### *Support of Consumers by Allochthonous and Autochthonous C*

The DIF model allows the computation of key flows of terrestrial and autochthonous C sources to consumers including both direct and indirect pathways (Fig. 1; Appendix).

Zooplankton and *Chaoborus*. For all the additions, the flow of t-DOC to bacteria to zooplankton was a very minor pathway, accounting for 1 to 2% of zooplankton C (Fig. 4A). Carbon of phytoplankton origin was a variable but large source to zooplankton in all cases comprising 25% in Tuesday Lake, about 60% in Peter and Paul lakes and nearly 90% in Peter Lake +N&P (Fig 4). Terrestrially-derived POC was also an important C source for zooplankton ranging from 73% in Tuesday Lake to near 35% for both Peter and Paul lakes. In nutrient enriched Peter Lake, t-POC accounted for more than 10% of zooplankton demand (Fig. 4). *Chaoborus*, an important prey for many fish, consumed only zooplankton in the model and the terrestrial subsidy of *Chaoborus* tracks that of zooplankton (data not shown).

Pelagic bacteria. Pelagic bacteria obtain their C entirely from DOC of either terrestrial or in-lake (autochthonous) origin. Terrestrially-derived DOC was a more important C source for bacteria than autochthonously-produced DOC in all the additions except Peter +N&P where allochthonous t-DOC supplied 39% of bacterial demand (Fig 4B). In the other lakes t-DOC ranged accounted for 60 to 76% of pelagic bacterial demand (Fig 4B).

Benthic invertebrates. t-POC was the dominant source of C supporting benthic macroinvertebrates comprising 60 to 85% of macroinvertebrate production. In the Peter Lake +N&P addition benthic algal production was greatly stimulated (Table 1) and the importance of t-POC was reduced to only 6% of macroinvertebrate production (Fig. 4C).

Fish. In the model fish had access to t-DOC and t-POC indirectly by preying on the consumers of these sources and their predators (Fig. 1). Fish also consumed t-prey directly. There were large differences in the importance of terrestrial sources and autotrophic C to fishes among lakes and among the different types of fish. In no case was

t-DOC an important ultimate C source to any of the fish groups (Fig 5), reflecting the minor importance of this source to zooplankton. Prey items of terrestrial origin (t-prey) were a significant component for fish in all lakes.

In Paul Lake where the three fish compartments were age classes of a single species (largemouth bass), autotrophic C was a dominant C source only for YOY fish (Fig. 5a). These YOY fish feed primarily on zooplankton before switching to benthic prey as they develop (Post et al. 1997). The model indicates that about 40% of YOY C derived from t-POC reflecting the importance of this material to zooplankton, *Chaoborus*, and benthos. For juvenile bass which are more benthivorous and piscivorous, t-POC and autotrophic C were co-equal (about 40% each) with the remainder from t-prey (Fig. 5a). In adult fish t-prey, t-POC and autotrophic C are all about co-equal in importance (Fig 5A). For largemouth bass, then, t-POC was always an important subsidy and t-prey became more important as fish increased in size.

Pumpkinseeds and sticklebacks in Peter Lake (without nutrients) used t-POC, t-prey and autotrophic C about equally. Fathead minnows were less dependent on t-prey (Fig.5B). Fertilization of Peter L (+N&P) greatly increased GPP (Table 1) and the standing stock of phytoplankton (about 10x, see Carpenter et al. 2005). The nutrient fertilization resulted in greater use of autochthonous C in most components of the food web (Fig 4) and decreased importance of the terrestrial subsidies for all three of the fish species (Fig 5b&d). Fertilization did not consistently increase the rate of utilization of terrestrial C by any component of the food web.

In Tuesday Lake t-prey was the dominant source of C supporting golden shiners and sticklebacks accounting for 60 to 70% of their C consumption (Fig 5c). For fathead

minnows, t-prey were less important than t-POC, as in Peter Lake (above). Overall, fish in Tuesday Lake were only weakly supported by autochthonous C.

## **DISCUSSION**

### *The DIF Model*

Our estimates of carbon flows derive from a model that is subject to error because of uncertainty in parameters and in model structure. Nevertheless, there are multiple reasons to have some confidence in the model. First, the model includes a detailed accounting of carbon flows among the major pools of the mixed layers of the lakes. The modeled connections among pools and corresponding estimates of flows are consistent with current understanding of lake carbon cycles (Appendix; Figure A1 and Table A3). Second, most of the pools and flows of the model were directly measured, and those not measured were estimated by fitting the model to the measured pools and flows as well as the time series of  $^{13}\text{C}$  in the pools (Appendix Table A4A). Thus, the model output is strongly constrained by field observations. Third, there is agreement between independent estimates of parameters that were also fit by the model. For example Bade et al. (2006) estimated phytoplankton fractionation in these lakes by physical separation and obtained results in the same range (12 to 16 per mil in the unenriched lakes and near 0 in Peter Lake +N&P as estimates from the DIF model. (f13\_4 in Appendix Table A4B). Kritzberg et al. (2004, 2005) using in situ dialysis culture measured the fraction of algal DOC that supported the growth of pelagic bacteria and obtained very similar results to the DIF model (pX3\_auto in Appendix Table A4A). Further, model-fit values for parameters not measured (for example, zooplankton coefficients of assimilation) were

within the range of literature values. (Appendix Table A4B). Fourth, the model predictions of  $^{13}\text{C}$  dynamics closely match the observations (Fig. 3). Fifth, estimates of allochthony (i.e. the proportion of the carbon flow to a compartment supported by terrestrial carbon) from this model were corroborated by two different, independent models fit to the same data (Carpenter et al. 2005). Although these other models cannot be used to estimate the specific sources of allochthony presented in this paper, the corroboration of total allochthony lends some confidence to the more detailed accounting of carbon sources presented here. Finally, the estimates of allochthony in the DIF model are robust and not greatly affected by altering the values of key parameters away from those fit by the model. Table A6 and Figure A2 show the effect on model performance of altering values of a few key parameters.

#### *t-DOC*

DOC is the dominant input of terrestrial organic carbon into lakes in general and inputs were similar to gross primary production in the study lakes except when nutrients were added (Table 1). While pelagic bacteria respire large amounts of t-DOC, they pass very little up the food web. Where allochthony in zooplankton has been reported in other studies, it is often assumed that the pathway is via microbial utilization of t-DOC with subsequent consumption of microbes by zooplankton (Grey et al. 2001; Karlsson et al. 2003). The present study suggests that zooplankton acquire only a minor terrestrial subsidy by this route. This result is consistent with measured rates of bacterial production and estimated bacterial feeding rates by cladocerans that indicate only a small fraction (4-7%) of zooplankton carbon demand can be supported by bacteria in these

lakes. Further, a large fraction (about half) of the DOC acquired by bacteria is of autochthonous rather than allochthonous origin (Kritzberg et al. 2004, 2005). Pelagic bacteria, then, pass only a small amount of C up the food web in these lakes and a substantial fraction of that C is not of terrestrial origin.

#### *t-POC*

If the pathway from t-DOC to bacteria to zooplankton is small, how do zooplankton acquire terrestrial C? Both the DIF model and two independent modeling approaches demonstrate that zooplankton in these lakes were heavily subsidized (22-75%) by terrestrial C unless primary production was stimulated by nutrient addition (Cole et al. 2002; Carpenter et al. 2005). The DIF model suggests that allochthonous support of zooplankton is dominated by direct consumption of terrigenous POC and this subsidy is large in comparison to C of autotrophic origin. Through consumption of zooplankton, their predators (*Chaoborus* and planktivorous fish) also derive a significant subsidy from terrigenous POC. Terrestrial POC was the single largest C source for pumpkinseeds and sticklebacks in Peter Lake (unfertilized). Terrestrial POC was also the largest source of organic carbon to benthic invertebrates, except during experimental enrichment of Peter Lake (Fig 4). Some unlabeled sediment consumed by benthos may be autochthonous production that occurred prior to the labeling of DIC. However, terrestrial POC is still a major organic carbon source for benthos when sediment carbon is corrected for old autochthonous production (Carpenter et al. 2005).

*t-prey*

Fish also derive subsidies by directly consuming terrestrial prey items and through piscivory on other fish that consume t-prey. While t-prey is a very minor C input to these lakes, it is a large subsidy to some the studies fish (Hodgson and Hansen 2005). Only YOY largemouth bass, which are highly planktivorous, were not significantly subsidized by t-prey. In Tuesday Lake t-prey were the dominant C source for both golden shiners and sticklebacks.

*Primary Production*

While most consumers utilize one or more of the three terrestrial subsidies, consumer utilization of primary production from either phytoplankton or benthic algae is important and in many cases larger than all terrestrial sources combined (e.g. zooplankton in Peter and Paul Lakes; YOY fish in Paul Lake; fathead minnows in Peter Lake). With a few exceptions (most groups in Tuesday Lake, benthic invertebrates in unenriched Peter Lake) primary production accounted for 30% or more of C demand. The nutrient fertilization of Peter Lake demonstrated that increases in primary production lead to increases in the autotrophic support of secondary production. These results are consistent with the generalization from many comparative studies that consumer biomass and/or productivity increase with primary production (summarized in Kalff 2002). As fertilization had no effect on the rate of processing of allochthonous inputs, this analysis does not support the idea that nutrients or labile co-metabolites from primary production increase the utilization of more recalcitrant terrestrial detritus (Carpenter and Pace 1997; Tranvik 1998). Taken together, the present results in concert with these studies, suggest

that terrestrial support of consumers is likely to be most important in low-nutrient, oligotrophic systems. Further, it is possible that the degree of terrestrial subsidy may explain some of the residual variation in regressions between consumer biomass and primary production.

#### *Terrestrial subsidies of ecosystem metabolism*

Terrestrial DOC provides substantial support to microbial respiration in the water column in these experiments (e.g. Fig 4B). As these lakes are often net-heterotrophic ( $R > GPP$ ), respiration of this terrestrial source would be expected to be significant. While t-POC supports less respiration than does t-DOC, the respiration of t-POC is nevertheless significant and in some cases nearly as large as the respiration of t-DOC (Paul Lake). The respiration of zooplankton is typically co-equal with that of pelagic bacteria (Cole et al. 1988) and in these lakes t-POC is an important substrate respired by zooplankton.

#### *General Implications*

The impacts of subsidies depend on a number of features of the subsidy and the food web including the type of material (e.g. t-DOC vs. t-prey), the flux rate into the recipient system (e.g. large inputs of DOC, small inputs of t-prey), the mode of utilization (e.g. via microbial degradation versus direct ingestion), the route of entry into the food web, and the temporal variation in the rate of input (e.g. steady loading of t-DOC versus episodic loading of t-prey). In the present study different consumers were dependent on different forms of terrestrial organic carbon: bacteria on t-DOC; benthos and zooplankton on t-POC; and fishes on t-POC (through consumption of benthos and

zooplankton) and terrestrial prey. These subsidies also provided differential support in terms of respiration (primary fate of t-DOC) and production. Hence, assessment of the impact of subsidies on ecosystems requires considering a variety of sources, modes of utilization, and food web interactions.

Our study raises several questions concerning how variation in subsidies affects ecosystems. For example, increasing primary production in Peter Lake increased the proportion of autotrophic C supporting consumers. This study does not reveal, however, if increasing terrestrial C inputs to lakes would lead to a similar increase in the terrestrial support of consumers. In addition, while terrestrial organic carbon partially fuels the food webs of the small lakes studied here, would terrestrial carbon be equally important in larger lakes of similar nutrient status? Factors such as watershed size, lake size, loading rates, water residence time, and riparian vegetation may be important, and support of food webs might differ considerably among systems.

Our results add to a growing literature on cross-ecosystem subsidies by quantifying the magnitude and pathways by which terrigenous DOC, POC and animal prey subsidize aquatic food webs (Huryñ 1996, Nakano and Murakami 2001, Polis et al. 2004). The pathways are complex (Fig. 1) and similar complex pathways of subsidization may occur in other ecosystems (Polis et al. 2004, Loreau and Holt 2004, McCann et al. 2005). It is not known if all pathways have equal impacts on structure, processes and stability of receiving ecosystems. However, the sensitivity of model ecosystems to network structure (Huxel and McCann 1998, Ives et al. 2003, Polis et al. 2004) suggests that different pathways of subsidization could have important effects on

fundamental properties of food web dynamics and carbon cycling. Elucidation of such effects seems to be an expanding frontier of ecological research.

## **ACKNOWLEDGEMENTS**

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## Figure Legends

Figure 1. Simplified diagram of pathways for the entry and trophic transfer of terrestrial organic carbon in the dual isotope flow (DIF) model. Each box represents a compartment in the DIF model; the connections of these compartments to the terrestrial inputs are highlighted with arrows. The boxes shown are: DOC (dissolved organic C) which is a mixture of autochthonous and terrestrial sources; dPOC (detrital particulate organic C), also a mixture of autochthonous and terrestrial sources; Bacteria (pelagic bacteria); Zooplankton (crustacean zooplankton); *Chaoborus*; and Benthos (benthic macroinvertebrates). Only the compartments that are connected to terrestrial inputs are shown here. A complete diagram for the DIF model is in Appendix Figure 1. The three terrestrial C subsidies are: t-DOC (terrestrial DOC); t-POC (terrestrial POC); and , t-prey (terrestrial prey). Each of these terrestrial inputs is connected to the aquatic food web in different ways. The heavy solid arrows show the pathway of entry of t-DOC through the pelagic bacteria. The dashed arrows follow the input and fate of t-POC through zooplankton. The dash-dot arrow follows the consumption of t-prey by fishes. Where more than one kind of arrow is shown (e.g. zooplankton to *Chaoborus*), more than one terrestrial source is utilized. To simplify the diagram pathways of C of autochthonous origin (phytoplankton and benthic algae; see Appendix Fig. 1) are not shown here.

Figure 2. Dynamics of  $\delta^{13}\text{C}$  for periphyton (solid diamonds) and zooplankton (open circles) in the 4 whole-lake  $^{13}\text{C}$  additions. Arrows on X-axis indicate the start and end dates of the daily additions of inorganic  $^{13}\text{C}$ . For Peter +N&P inorganic N and P were added to simulate primary production (see text).

Figure 3. Comparison of the  $\delta^{13}\text{C}$  predicted by the dual isotope flow (DIF) model with observed values for each lake. In the 12 compartments (Paul and Peter lakes) or 11 compartments (Peter +N&P; Tuesday Lake) are indicated by distinct symbols (below) along with a 1:1 line. Least square regressions of predicted versus observed values were significant at  $p < 0.0001$  (see text).

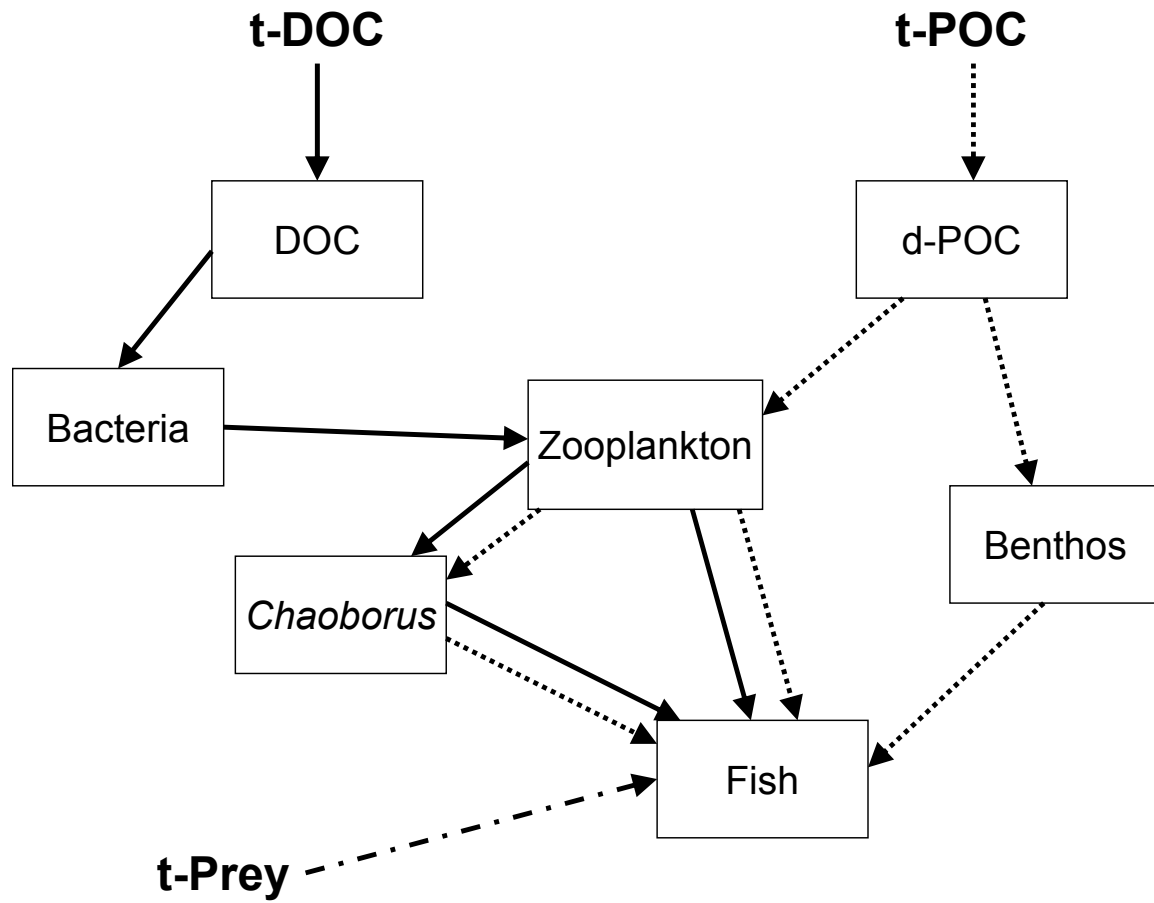
Figure 3 - Caption with embedded symbols below as jpg file to show symbols.

Figure 3. Comparison of the  $\delta^{13}\text{C}$  predicted by the dual isotope flow (DIF) model with observed values for each lake. In the 12 compartments (Paul and Peter lakes) or 11 compartments (Peter + N&P; Tuesday Lake) are indicated by distinct symbols along with a 1:1 line. Least square regressions of predicted versus observed values were significant at  $p < 0.0001$  (see text).  
 × - DIC; ● - DOC; ▲ - Pelagic bacteria; ▼ - benthic algae; ▽ - macroinvertebrates; ■ - POC; □ - *Chaoborus*; ◆ - fish 1; ◇ - fish 2; ○ - fish3; ● - zooplankton.

Figure 4. Support of zooplankton, top panel, pelagic bacteria (middle panel) and benthic invertebrates (lower panel) by terrestrial sources (t-DOC, grey bar; t-POC, clear bar) and autochthonously produced C (“auto”, from either phytoplankton or periphyton, solid black bar).

Figure 5. Support of fishes by terrestrial sources. The bars are coded as in Figure 4 (t-DOC, grey bar; t-POC, clear bar; t-Prey, hatched bar; and autochthonously produced C (“auto”, solid black bar). The three groups of fishes modeled in each lake are indicated. Abbreviations are LMB = large mouth bass, YOY = young of year; 1+ - juvenile LMB.

Figure 1



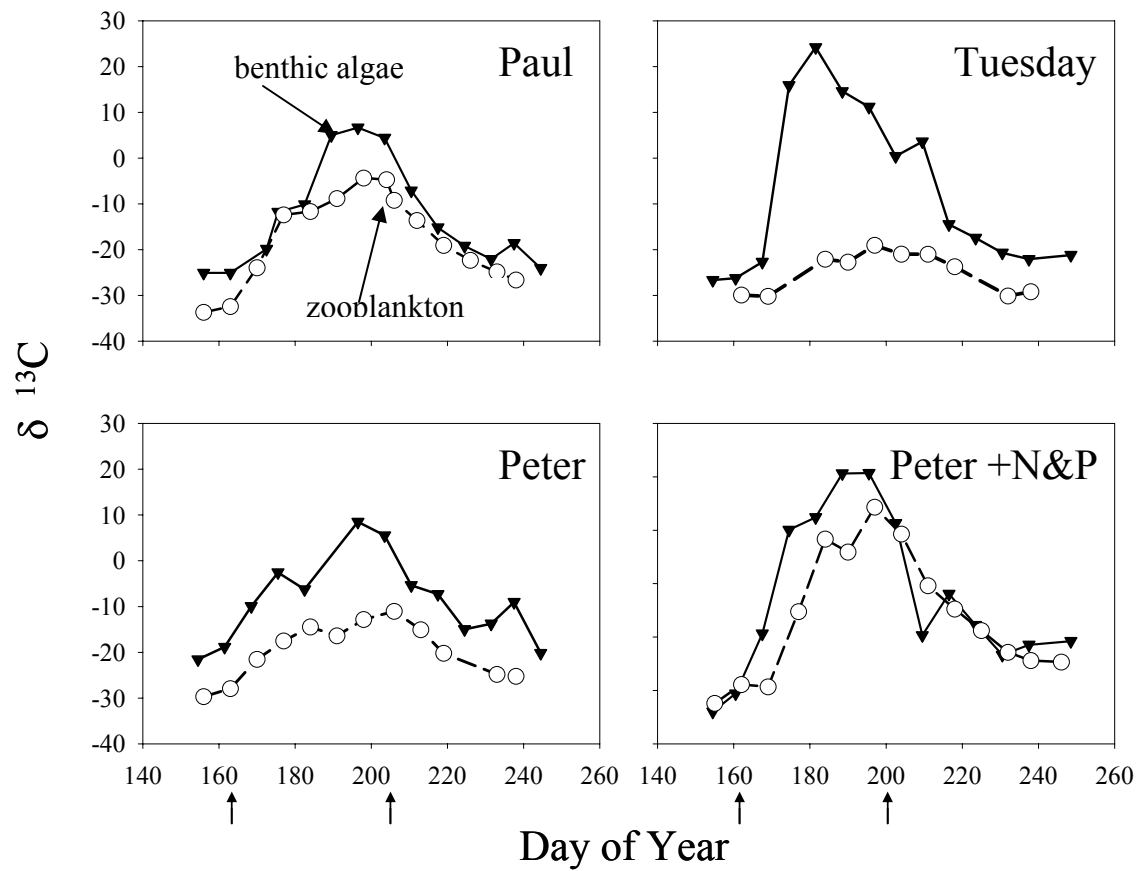


Figure 2

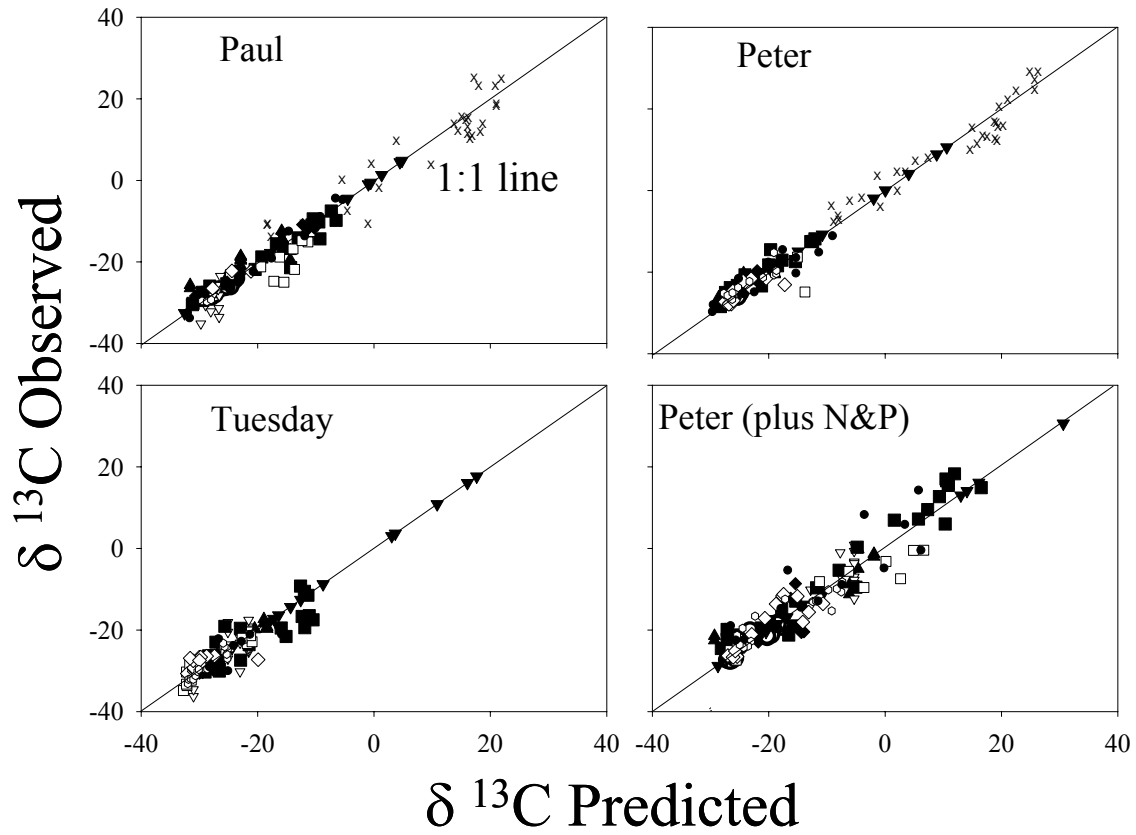
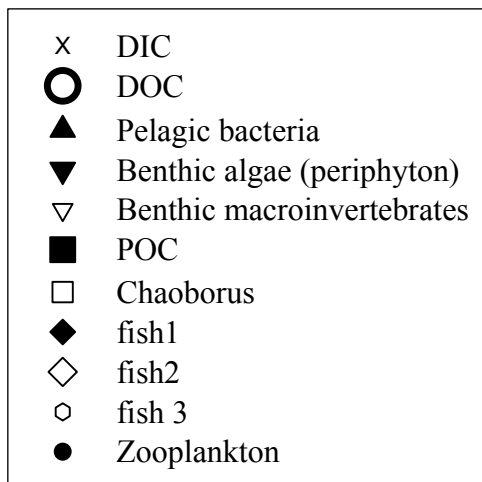


Figure 3



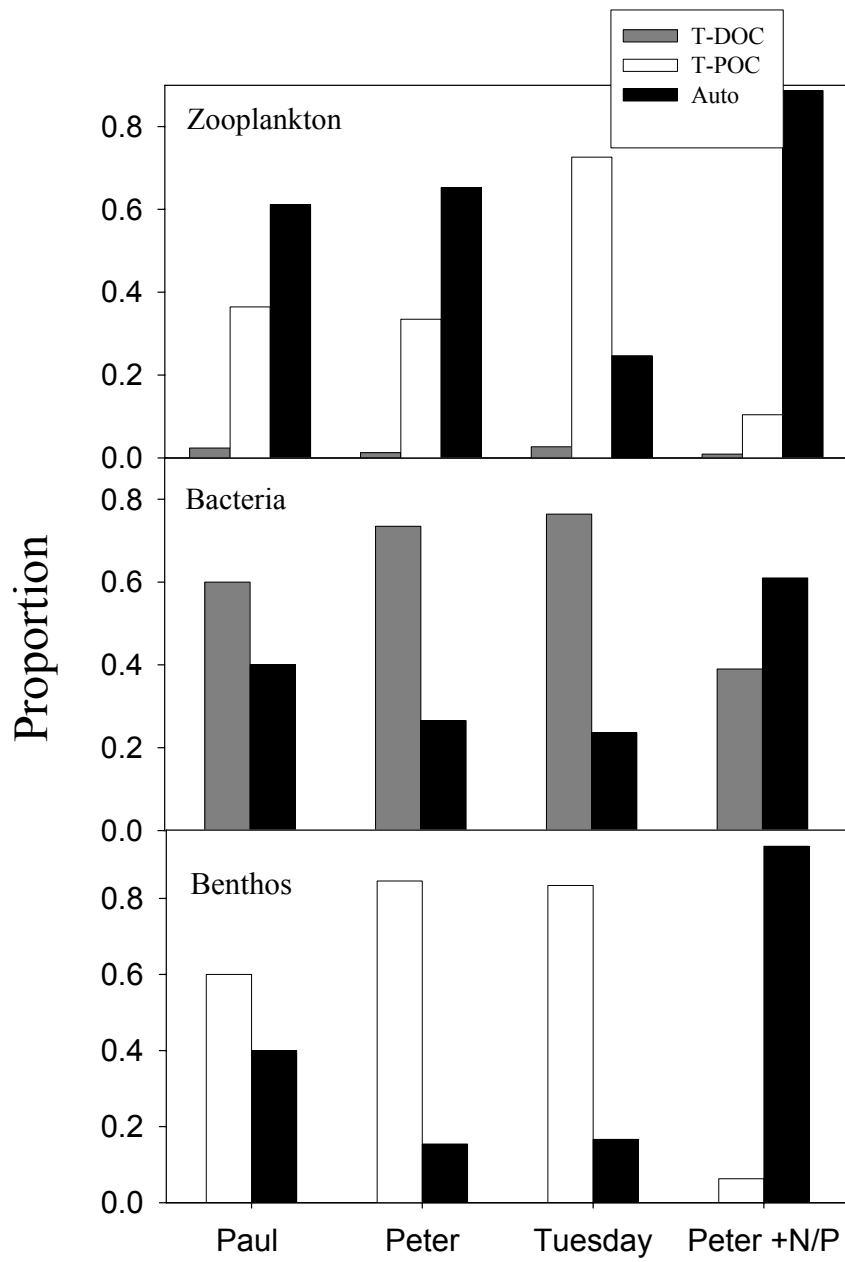


Figure 4

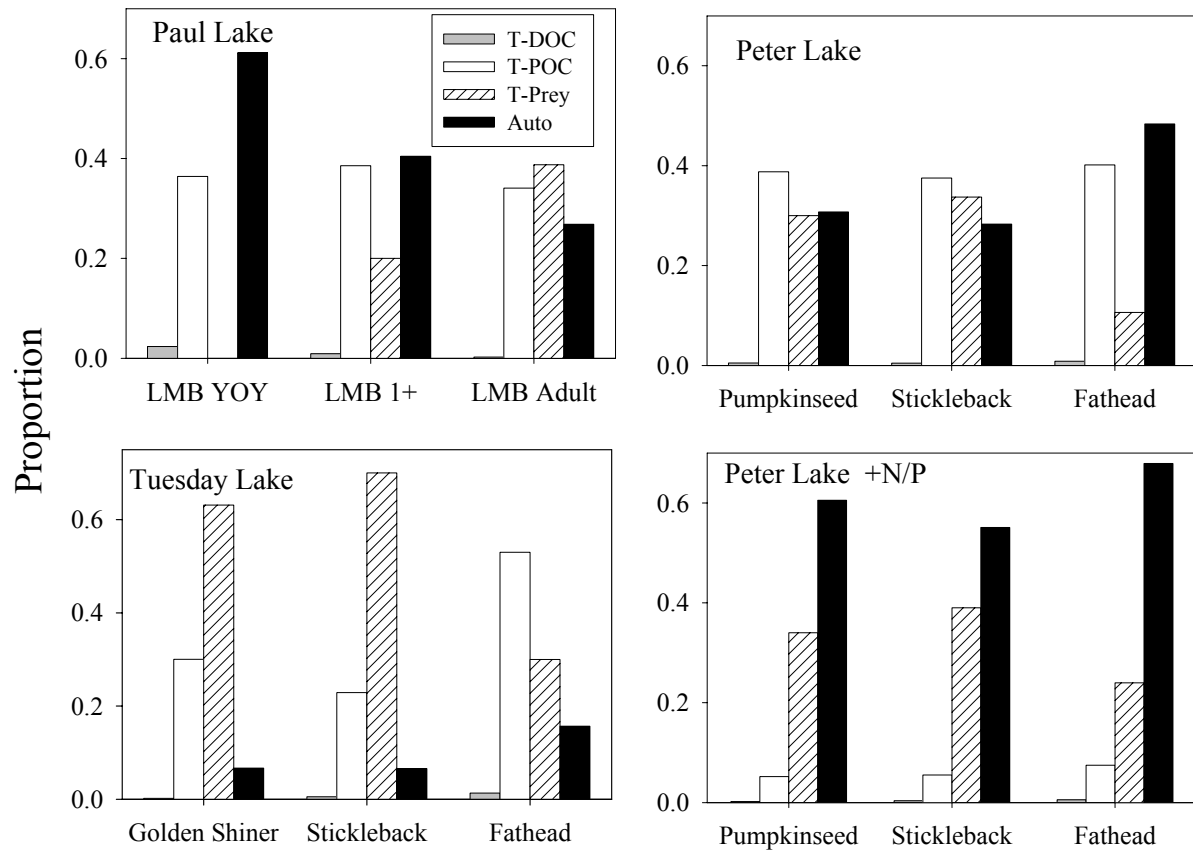


Figure 5

	Paul	Tuesday	Peter	Peter (+N&P)
Org C inputs				
GPP <sub>phyto</sub>	36.3	36.5	28.3	87.1
GPP <sub>benthic</sub>	9.5	0.6	5.6	15.5
<b>GPP<sub>tot</sub></b>	<b>45.9</b>	<b>37.2</b>	<b>34.1</b>	<b>102.6</b>
t-DOC	21.9	49.7	31.1	21.1
t-POC	4.7	15.8	6.2	4.7
t-prey	0.20	0.76	0.05	0.17
<b>t-Load<sub>tot</sub></b>	<b>27.7</b>	<b>66.3</b>	<b>38.0</b>	<b>34.6</b>
Respiratory				
R <sub>auto</sub>	9.7	4.7	6.9	13.3
Pelagic R <sub>h</sub>	23.4	16.0	20.2	43.2
Sediment R <sub>h</sub>	21.0	15.2	8.32	26.2
<b>R<sub>tot</sub></b>	<b>54.1</b>	<b>35.9</b>	<b>35.4</b>	<b>83.1</b>
Pelagic R <sub>h</sub> Sources				
Autochthonous	10.9	4.4	11.5	38.5
t-DOC	6.8	9.9	5.7	4.1
t-POC	5.5	0.8	2.6	0.4
t-Prey	0.20	0.76	0.05	0.17
Sediment R <sub>h</sub> Sources				
Autochthonous terrestrial	10.7	10.5	6.2	1.0

Table 1. Inputs and respiratory losses of organic C in the four experimental lakes. Values are mmol C m<sup>-2</sup>d<sup>-1</sup> and are derived from the DIF model, except for total gross primary production (GPP<sub>tot</sub>) and total system respiration (R<sub>tot</sub>) which were directly measured (see text and Appendix). The subscripts “phyto” and “benthic” for GPP refer to phytoplankton and benthic algae, respectively. t-Load<sub>tot</sub> is the total loading of terrestrial carbon from its three sources, terrestrial DOC (t-DOC), terrestrial particles (t-POC) and

terrestrial prey items (t-prey).  $R_{\text{auto}}$  is respiration by autotrophic organisms (sum of phytoplankton and periphyton respiration);  $R_h$ , respiration by heterotrophs (consumers). In the bottom two sections the sources of carbon respired by heterotrophs are partitioned. For pelagic heterotrophic R the figure shows C from primary production within the lake (AUTO), and that entering by the three terrestrial routes. The sources for benthic heterotrophic R can be partitioned only into AUTO and terrestrial. The fates of inputs not shown here include outflow and export to the hypolimnion. The DIF model also calculates these (see Appendix).

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## Appendix : Dual Isotope Flow Model

The Dual Isotope Flow (DIF) model calculates mass balances of total carbon and  $^{13}\text{C}$  in each of 12 compartments of a lake food web (Table A1). For each compartment the equations account for all inputs and outputs, to and from the epilimnion of the entire lake. The boundaries for the system are the atmosphere, the sediments, and water inputs and outputs through the lake perimeter.

A diagram for the C flows in the DIF model is presented in Figure A1. The coupled mass balances of all compartments are governed by 24 differential equations, one for total C ( $^{12}\text{C} + ^{13}\text{C}$ ) and one for  $^{13}\text{C}$  of each compartment. Although the model tracks both total carbon and  $^{13}\text{C}$  separately,  $^{13}\text{C}$  values in the more familiar  $\delta^{13}\text{C}$  units, to facilitate comparison with other studies. The lexicon for the model program written in Matlab is outlined in Table A2. The full set of 24 differential equations is presented in Table A3. Each term used in the model is defined in Table A4, along with a brief description of how the value was obtained and a citation where appropriate. Finally, Table A5 shows measurements of  $\delta^{13}\text{C}$  of representative terrestrial plants in the watersheds of the lakes.

The DIF model estimated carbon inputs, outputs, and flows among the compartments and calculates the proportion of carbon flow into each consumer compartment from internal primary production and terrestrial sources. Mass balance was maintained for both the entire ecosystem and each compartment. For most carbon pools, one flux was estimated by difference (Table A4). The model was further constrained by many fluxes that were measured or estimated from a combination of other measurements and literature values (Table A4).

The model predicts the time-dynamic values of  $^{13}\text{C}$  and total C in each compartment. These are converted to  $\delta^{13}\text{C}$  and compared to measurements of  $\delta^{13}\text{C}$  in each compartment. Values of fitted parameters were obtained by minimizing the sum of squared errors between measured and observed  $\delta^{13}\text{C}$  in the compartments, using all available  $\delta^{13}\text{C}$  measurements. Constrained least squares fits were computed using the FMINCON function of the Matlab Optimization Toolbox. Constraints were obtained from parameter definitions (e.g. by definition a particular parameter must be a positive real number), mass balance, or literature values.

The DIF model was solved using a program written in Matlab (versions 5.3 and 6.5) with a numerical method to account for the rapid dynamics of  $\text{DI}^{13}\text{C}$  relative to the  $^{13}\text{C}$  in other carbon pools. The 23 differential equations for compartments other than  $\text{DI}^{13}\text{C}$  were integrated using a fourth-order fixed-interval Runge-Kutta method (Press et al. 1989). The  $\text{DI}^{13}\text{C}$  equations were solved using calculus over time steps sufficiently short to assume that other compartments were constant. This enabled the model to fit accurately the dynamics of  $\text{DI}^{13}\text{C}$ , which were much faster than the other compartments due to daily additions and rapid exchange with the atmosphere. This procedure had no effect on the ability of the model to fit the time series in other compartments.

For both Tuesday Lake and Peter Lake +N&P,  $\text{DI}^{13}\text{C}$  dynamics were not simulated. In the former case fits with high  $R^2$  to observed  $\delta^{13}\text{C}$  of DIC could not be obtained. For the Tuesday addition, daily  $\text{DI}^{13}\text{C}$  values were interpolated from measurements and used as inputs to the DIF model to solve the other 23 differential equations. In nutrient-enriched Peter Lake, high pH and low  $\text{CO}_{2\text{aq}}$  created conditions in which chemically-enhanced diffusion of  $^{13}\text{C}$  with the atmosphere occurred (Wanninkhof

and Knox 1996) resulting in considerable uncertainty regarding isotope fractionation that occurs during chemically-enhanced diffusion (Bade and Cole, 2006). The DIF analysis for Peter Lake +N&P addition uses actual measured  $\text{DI}^{13}\text{C}$  values as input data. The lack of a true DIC compartment does not alter the estimates of allochthony or pathways. This omission does mean that the model has fewer observations to fit and thus the RSD's for the Tuesday and Peter simulations are based on slightly smaller N.

Model Sensitivity -The sensitivity of the DIF model to the values of key, fitted parameters was examined in several ways. The most critical of these examinations was a comparison of the estimates of allochthony in many compartments to estimates produced by two other independent models with entirely different structure. These comparisons are explained in Carpenter et al. 2005. In this Appendix, to show the sensitivity of the model to various parameters, the model for a single lake (Paul) is used. Shown in Table A6 are the effects of the values of five key parameters on the fit of the overall model, on the fit of two important components (particulate organic carbon and zooplankton), and on the estimate of zooplankton allochthony. Figure A2 shows the effect (both on total model fit and on the estimate of zooplankton allochthony) of simultaneously varying two of the parameters that make the most difference. These limited analyses of sensitivity demonstrate that the estimates of allochthony in these compartments are not very sensitive to modest changes in parameter values. However, the goodness of fit of the model to measurement decreases as parameters are moved away from the best-fit values. Similar sensitivity tests could be demonstrated for other parameters as well. Based on experience with this model and these experiments, the most temporally-variable or uncertain field measurements include the gas exchange coefficient, isotopic

fractionation by diverse producers, consumption rates of the entire fish population (mainly because of uncertainty in the population estimate), and temporal variability in the depth of the upper mixed layer. Future research using this approach should emphasize these field measurements where high variability seems to coincide with potentially high sensitivity.

Figure A1.

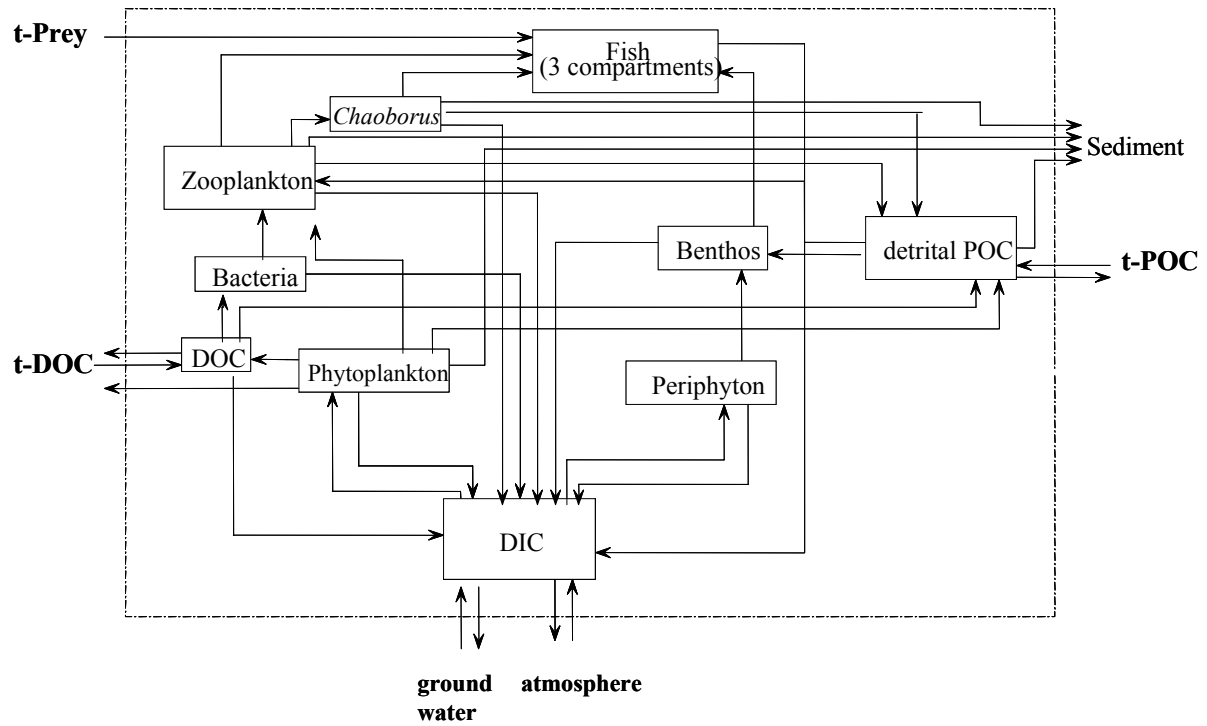


Figure A1. Schematic diagram of the DIF model to show the pathways of C movement. Carbon and  $^{13}\text{C}$  move between the 12 compartments shown, according to 24 differential equations (12 for total C [ $^{12}\text{C} + ^{13}\text{C}$ ]; 12 for  $^{13}\text{C}$ ). The equations, the definitions of variables and parameters and the method used to quantify them are given in Tables A1, A2, A3 and A4. The three types of terrestrial subsidies (terrestrial DOC, terrestrial POC and terrestrial prey items) are shown as t-DOC, t-POC and t-prey. The DIF model was used to quantify the importance of these terrestrial subsidies and in-lake primary production to the food web (modified from Carpenter et al. 2005)

Table A1. The 12 compartments used in the DIF model. In addition to the fluxes among these 12 compartments the model also uses fluxes across the ecosystem boundaries (inputs and outputs to and from the watershed, sedimentation, and gas exchange with the atmosphere).

<b>Number</b>	<b>Compartment</b>
1	Dissolved inorganic C
2	Dissolved organic C
3	Pelagic bacteria
4	Phytoplankton
5	Detrital pelagic particulate organic C
6	Benthic algae
7	Benthic invertebrates
8	Zooplankton
9	<i>Chaoborus</i>
10	Fish compartment 1 (see text)
11	Fish compartment 2 (see text)
12	Fish compartment 3 (see text)

Table A2. Lexicon used in the DIF Matlab code.

<b>Symbol</b>	<b>Explanation</b>
asn	assimilation by compartment n (dimensionless)
Cn	total consumption by compartment n ( $\text{mmol m}^{-2} \text{d}^{-1}$ )
Cn_m	total consumption of compartment m by compartment n ( $\text{mmol m}^{-2} \text{d}^{-1}$ )
cnm	donor-controlled consumption coefficient of compartment m by compartment n; $Cn\_m = cnm * Y(m,1)$
inn	input rate of compartment n ( $\text{mmol m}^{-2} \text{d}^{-1}$ )
outn	donor-controlled output coefficient of compartment n; output rate of compartment n in $\text{mmol m}^{-2} \text{d}^{-1} = outn * Y(n,1)$
pnm	proportion of diet of consumer n consisting of prey type m
Rn	total respiration of compartment n ( $\text{mmol m}^{-2} \text{d}^{-1}$ )
rn	respiration coefficient of compartment n; $Rn = rn * Y(n,1)$
Sedn	sedimentation coefficient of compartment n; sedimentation rate in $\text{mmol m}^{-2} \text{d}^{-1} = sedn * Y(n,1)$ .
Y(n,1)	Total carbon in compartment n
Y(n+12,1)	$^{13}\text{C}$ in compartment n

Table A3. Part I lists the equations for the mass balance of C; Part II lists the equations for the mass balance of  $^{13}\text{C}$ . Each equation calculates the instantaneous rate of change denoted by time index  $i$  of total C or  $^{13}\text{C}$  in the compartment. These rates are denoted  $dn$  for total C and  $dni$  for  $^{13}\text{C}$ , where  $n$  is compartment number 1 through 12. The equations retain their original Matlab formats. A brief description in words is given to guide the reader through the function of each mass balance. Table A4 gives a definition of each term used in each equation.

### **Part I. C mass equations.**

#### **Compartment 1 – Dissolved inorganic C.**

DIC enters and leaves in ground water or surface flow (in1, out1). The exchange with the atmosphere is controlled by the gas piston velocity ( $k$ ) and the concentration of aqueous  $\text{CO}_2$  relative to the atmosphere. Gross primary production (GPP) by both periphyton and phytoplankton removes  $\text{CO}_2$ ; respiration of all components of the ecosystem ( $R_{\text{tot}}$ ) adds  $\text{CO}_2$ .

$$d1 = -k(i) \cdot (\text{CO2aq}(i) - \text{satconc}(i)) - \text{GPP}(i) + R_{\text{tot}}(i) + \text{in1}(i) - \text{out1} \cdot Y(1,1);$$

#### **Compartment 2 – Dissolved organic C**

DOC enters and leaves in ground water or surface flow (in2, out2). It is consumed by bacteria (c32), produced by phytoplankton exudation (c24) and benthic algal exudation (c26). It is lost by photo-oxidation (photox) or conversion to particles by flocculation (c52).

$$d2 = +\text{in2}(i) - \text{out2} \cdot Y(2,1) - c32(i) \cdot Y(2,1) + c24(i) \cdot Y(4,1) + c26 \cdot Y(6,1) - \text{photox}(i) - c52 \cdot Y(2,1);$$

#### **Compartment 3 – Pelagic bacteria**

The outputs of bacterial biomass are respiration ( $r3$ ), grazing by zooplankton (c83), and outflow from the lake (out3). The input is bacterial consumption of DOC (c32).

$$d3 = +c32(i) \cdot Y(2,1) - r3(i) \cdot Y(3,1) - c83(i) \cdot Y(3,1) - \text{out3} \cdot Y(3,1);$$

#### **Compartment 4 – Phytoplankton**

Phytoplankton gain C from GPP in the water column which is expressed as the difference between total system GPP and benthic GPP (BfracGPP). Phytoplankton biomass is lost to exudation (c24), respiration ( $r4$ ), grazing by zooplankton (c84), sedimentation as live cells (physed), conversion to detritus (c54), or outflow from the lake.

$$d4 = + (1 - B_{\text{fracGPP}}(i)) \cdot \text{GPP}(i) - c24(i) \cdot Y(4,1) - r4(i) \cdot Y(4,1) - c54(i) \cdot Y(4,1) - c84(i) \cdot Y(4,1) - \text{physed}(i) \cdot Y(4,1) - \text{out4} \cdot Y(4,1);$$

### Compartment 5 – Detrital POC.

dPOC comes from both terrestrial (in5) and lake sources. Lake sources include zooplankton feces that are not directly sedimented and *Chaoborus* feces that are not directly sedimented. For example, the contribution to dPOC of zooplankton feces derived from phytoplankton is  $(1 - \text{fecesed}) \cdot (1 - \text{as8}) \cdot c84(i) \cdot Y(4,1)$  where  $1 - \text{as8}$  is the proportion of phytoplankton that are consumed but not assimilated, and  $1 - \text{fecesed}$  is the proportion of zooplankton feces that does not sediment immediately. Additional sources of DPOC include phytoplankton that die (c54) and DOC that flocculates (c52). dPOC is lost to sedimentation (sed5), outflow (out5) and consumption by zooplankton.

$$d5 = + \text{in5}(i) + (1 - \text{fecesed}) \cdot (1 - \text{as8}) \cdot c83(i) \cdot Y(3,1) + (1 - \text{fecesed}) \cdot (1 - \text{as8}) \cdot c84(i) \cdot Y(4,1) + (1 - \text{fecesed}) \cdot (1 - \text{as8}) \cdot c85(i) \cdot Y(5,1) + (1 - \text{fecesed}) \cdot (1 - \text{as9}) \cdot c98(i) \cdot Y(8,1) + c54(i) \cdot Y(4,1) - \text{sed5}(i) \cdot Y(5,1) - \text{out5} \cdot Y(5,1) - c85(i) \cdot Y(5,1) + c52 \cdot Y(2,1);$$

### Compartment 6 – Benthic algae (periphyton)

Benthic algae gain C from benthic primary production (see Compartment 4). Losses are respiration (r6), grazing by benthic invertebrates (c76), leaching of DOC (c26), and transfer of dead benthic algae to sediments (accum6).

$$d6 = + B_{\text{fracGPP}}(i) \cdot \text{GPP}(i) - r6(i) \cdot Y(6,1) - c76(i) \cdot Y(6,1) - c26 \cdot Y(6,1) - \text{accum6}(i) \cdot Y(6,1);$$

### Compartment 7 – Benthic invertebrates

Benthic invertebrates gain C by consuming periphyton (c76) and detritus on sediments. Benthic invertebrate biomass is lost to respiration (r7) and to consumption by fish (c10\_7, c11\_7, c12\_7).

$$d7 = + c76(i) \cdot \text{as7} \cdot Y(6,1) + (1 - p76) \cdot C7 \cdot \text{as7} - r7 \cdot Y(7,1) - c10\_7(i) \cdot Y(7,1) - c11\_7(i) \cdot Y(7,1) - c12\_7(i) \cdot Y(7,1);$$

### Compartment 8 – Zooplankton

Zooplankton gain C by grazing on bacteria (c83), phytoplankton (c84), and detrital POC (c85). Zooplankton biomass is lost to respiration (r8) and to consumption by *Chaoborus* (c98), and the three fish compartments (c10\_8; c11\_8; c12\_8).

$$d8 = + \text{as8} \cdot c83(i) \cdot Y(3,1) + \text{as8} \cdot c84(i) \cdot Y(4,1) + \text{as8} \cdot c85(i) \cdot Y(5,1) - r8 \cdot Y(8,1) - c98(i) \cdot Y(8,1) - c10\_8(i) \cdot Y(8,1) - c11\_8(i) \cdot Y(8,1) - c12\_8(i) \cdot Y(8,1) - \text{zoopsed}(i);$$

c84 is calculated as:

$$c84 = p84 * C8 / X4$$

where

$$p84 = WPHYT * X4 / (wbact * X3 + wphyt * X4 + wdpoc * X5)$$

It is assumed that bacteria and dpoc were consumed in proportion to their abundance, and therefore set wbact and wdpoc equal to 1. The model fits WPHYT to the observed  $^{13}C$  time series, thereby adjusting the proportion of phytoplankton in the diet using the observed labeling of the grazers. Analogous equations were used to compute p83, c83, p85 and c85.

### **Compartment 9 *Chaoborus***

*Chaoborus* grow by consuming zooplankton (c98). *Chaoborus* biomass is lost by respiration (r9) and consumption by the three types of fish (c10\_9; c11\_9; c12\_9).

$$d9 = + as9 * c98(i) * Y(8,1) - r9 * Y(9,1) - c10\_9(i) * Y(9,1) - c11\_9(i) * Y(9,1) - c12\_9(i) * Y(9,1) - chaobsed(i);$$

### **Compartments 10, 11, 12: 3 categories of fish (see main text)**

In each case fish biomass is lost to its own respiration (r10, r11, r12) and to consumption by piscivorous fish where relevant (e.g. c12\_10). Fish gain carbon by consuming terrestrial prey items (e.g. C12\_T), *Chaoborus* (e.g. c10\_9), zooplankton (e.g. c10\_8) and other fish compartments. Depending on the particular lake and fish species, some transfers may be set to zero. Each fish has a characteristic assimilation efficiency (e.g. as10).

$$d10 = + as10 * c10\_7(i) * Y(7,1) + as10 * c10\_8(i) * Y(8,1) + as10 * c10\_9(i) * Y(9,1) + as10 * C10\_T(i) - r10(i) * Y(10,1) - c11\_10(i) * Y(10,1) - c12\_10(i) * Y(10,1);$$

$$d11 = + as11 * c11\_7(i) * Y(7,1) + as11 * c11\_8(i) * Y(8,1) + as11 * c11\_9(i) * Y(9,1) + as11 * c11\_10(i) * Y(10,1) + as11 * C11\_T(i) - r11(i) * Y(11,1);$$

$$d12 = + as12 * c12\_7(i) * Y(7,1) + as12 * c12\_8(i) * Y(8,1) + as12 * c12\_9(i) * Y(9,1) + as12 * c12\_10(i) * Y(10,1) + as12 * C12\_T(i) - r12(i) * Y(12,1);$$

### **Part II. Equations for $^{13}C$**

The equations for  $^{13}C$  are more complicated than those for total C, because the  $^{13}C$  equations must account for the different proportions of  $^{13}C$  in each compartment. For

example, the respiration of bacteria (r3) returns DIC of different  $^{13}\text{C}$  than does that of zooplankton (r7).

The  $^{13}\text{C}$  equations are presented below, noting any differences from the total C equations presented in Part I. The parts of the equation that are straightforward extensions of Part I are not annotated.

### Compartment 1 DI $^{13}\text{C}$

The exchange of  $^{13}\text{C}$ - $\text{CO}_2$  between lake and atmosphere depends on the gas piston velocity (k) and the difference in partial pressure of  $^{13}\text{C}$ - $\text{CO}_2$  in the water and the atmosphere. Note that atmospheric exchange for  $^{13}\text{C}$  and  $^{12}\text{C}$  are independent of each other. Note also that the  $^{13}\text{C}$  content of many pools changes instantaneously and is updated regularly as all 24 equations are solved simultaneously. Photosynthetic fractionation is applied using 'f13\_4' and 'f13\_6' for phytoplankton and benthic algae (periphyton) respectively. The terms "p13(compartment)" such as "p13bact" refer to the model-predicted values of the proportion of  $^{13}\text{C}$  to C in that compartment. The fitted model parameters are arrived at by minimizing the SSE of a least squares regression of predicted versus directly measured  $^{13}\text{C}$  in these compartments.

$$\begin{aligned}
 d1i = & -k(i) * ((\text{CO2aq}(i) * p13\text{co2}) - (\text{satconc}(i) * \text{Patm})) \\
 & - (1 - \text{BfracGPP}(i)) * \text{GPP}(i) * f13\_4 * p13\text{co2} \\
 & - \text{BfracGPP}(i) * \text{GPP}(i) * f13\_6 * p13\text{co2} \\
 & - \text{out1} * Y(1,1) * p13\text{dic} \\
 & + \text{in1}(i) * P_{\text{gw}} \\
 & + r3(i) * Y(3,1) * p13\text{bact} \\
 & + r4(i) * Y(4,1) * p13\text{phyt} \\
 & + r6(i) * Y(6,1) * p13\text{peri} \\
 & + r7 * Y(7,1) * p13\text{bugs} \\
 & + r8 * Y(8,1) * p13\text{zoop} \\
 & + r9 * Y(9,1) * p13\text{chaob} \\
 & + R10(i) * p13\text{fish10} \\
 & + R11(i) * p13\text{fish11} \\
 & + R12(i) * p13\text{fish12} \\
 & + \text{photox}(i) * p13\text{doc} \\
 & + \text{sedresp}(i) * P_{\text{sed}};
 \end{aligned}$$

**Compartment 2 DO  $^{13}\text{C}$ .** pX3\_auto is the proportion of C used by bacteria (compartment 3) that is of autotrophic origin (Table A4). Pter is the proportion of  $^{13}\text{C}$  in terrestrial inputs. (Table A4)

$$\begin{aligned}
 d2i = & + \text{in2}(i) * P_{\text{ter}} + c24(i) * Y(4,1) * p13\text{phyt} \\
 & + c26 * Y(6,1) * p13\text{peri} \\
 & - \text{out2} * Y(2,1) * p13\text{doc} \\
 & - pX3\_auto * c32(i) * Y(2,1) * ((Y(4,1) * c24(i)) / (Y(4,1) * c24(i)))
 \end{aligned}$$

+ Y(6,1).\*c26)).\*p13phyt  
 - pX3\_auto.\*c32(i).\*Y(2,1).\*((Y(6,1).\*c26)./(Y(4,1).\*c24(i)  
 + Y(6,1).\*c26)).\*p13peri  
 - (1-pX3\_auto).\*c32(i).\*Y(2,1).\*Pter  
 - photox(i).\*p13doc  
 - c52.\*Y(2,1).\*p13doc;

### Compartment 3 Pelagic bacterial <sup>13</sup>C.

For bacteria (and all other consumers) the DIF model assigns the <sup>13</sup>C of biomass to the <sup>13</sup>C of respiration.

d3i= + pX3\_auto.\*c32(i).\*Y(2,1).\*((Y(4,1).\*c24(i)./(Y(4,1).\*c24(i)...  
 + Y(6,1).\*c26)).\*p13phyt  
 + pX3\_auto.\*c32(i).\*Y(2,1).\*((Y(6,1).\*c26)./(Y(4,1).\*c24(i)...  
 + Y(6,1).\*c26)).\*p13peri  
  
 + (1-pX3\_auto).\*c32(i).\*Y(2,1).\*Pter  
 - r3(i).\*Y(3,1).\*p13bact  
 - c83(i).\*Y(3,1).\*p13bact  
 - out3.\*Y(3,1).\*p13bact;

### Compartment 4 -Phytoplankton <sup>13</sup>C

d4i= + (1-BfracGPP(i)).\*GPP(i).\*f13\_4.\*p13co2  
 - c24(i).\*Y(4,1).\*p13phyt  
 - r4(i).\*Y(4,1).\*p13phyt  
 - c54(i).\*Y(4,1).\*p13phyt  
 - c84(i).\*Y(4,1).\*p13phyt  
 - physed(i).\*Y(4,1).\*p13phyt  
 - out4.\*Y(4,1).\*p13phyt;

### Compartment 5.- Detrital PO <sup>13</sup>C

Because dPOC has multiple possible sources the DIF model must keep track of the unique proportion of <sup>13</sup>C in each source. Because material egested by zooplankton that does not sediment (1-fecesead) has the <sup>13</sup>C value of the material consumed (bacteria, phytoplankton, dPOC, or zooplankton), these sources are considered separately.

d5i= + in5(i).\*Pter  
 + (1-fecesead).\*(1-as8).\*c83(i).\*Y(3,1).\*p13bact.  
 + (1-fecesead).\*(1-as8).\*c84(i).\*Y(4,1).\*p13phyt.  
 + (1-fecesead).\*(1-as8).\*c85(i).\*Y(5,1).\*p13dpoc.  
 + (1-fecesead).\*(1-as9).\*c98(i).\*Y(8,1).\*p13zoop  
 + c54(i).\*Y(4,1).\*p13phyt

**Compartment 6.-Benthic algal <sup>13</sup>C**

$$\begin{aligned}
 d6i = & + (\text{BfracGPP}(i) \cdot \text{GPP}(i) \cdot f_{13\_6} \cdot p_{13co2}) \\
 & - r6(i) \cdot Y(6,1) \cdot p_{13peri} \\
 & - c76(i) \cdot Y(6,1) \cdot p_{13peri} \\
 & - c26 \cdot Y(6,1) \cdot p_{13peri} \\
 & - \text{accum6}(i) \cdot Y(6,1) \cdot p_{13peri};
 \end{aligned}$$

**Compartment 7 - Benthic invertebrate <sup>13</sup>C**

$$\begin{aligned}
 d7i = & + as7 \cdot c76(i) \cdot Y(6,1) \cdot p_{13peri} \\
 & + as7 \cdot C7(i) \cdot (1-p76) \cdot Pter... \\
 & - r7 \cdot Y(7,1) \cdot p_{13bugs...} \\
 & - c10\_7(i) \cdot Y(7,1) \cdot p_{13bugs} \\
 & - c11\_7(i) \cdot Y(7,1) \cdot p_{13bugs} \\
 & - c12\_7(i) \cdot Y(7,1) \cdot p_{13bugs};
 \end{aligned}$$

**Compartment 8 - Zooplankton <sup>13</sup>C**

$$\begin{aligned}
 d8i = & + as8 \cdot c83(i) \cdot Y(3,1) \cdot p_{13bac} \\
 & + as8 \cdot c84(i) \cdot Y(4,1) \cdot p_{13phyt} \\
 & + as8 \cdot c85(i) \cdot Y(5,1) \cdot p_{13dpoc} \\
 & - r8 \cdot Y(8,1) \cdot p_{13zoop} \\
 & - c98(i) \cdot Y(8,1) \cdot p_{13zoop} \\
 & - c10\_8(i) \cdot Y(8,1) \cdot p_{13zoop} \\
 & - c11\_8(i) \cdot Y(8,1) \cdot p_{13zoop} \\
 & - c12\_8(i) \cdot Y(8,1) \cdot p_{13zoop};
 \end{aligned}$$

**Compartment 9 - *Chaoborus* <sup>13</sup>C**

$$\begin{aligned}
 d9i = & + as9 \cdot c98(i) \cdot Y(8,1) \cdot p_{13zoop} \\
 & - r9 \cdot Y(9,1) \cdot p_{13chaob} \\
 & - c10\_9(i) \cdot Y(9,1) \cdot p_{13chaob} \\
 & - c11\_9(i) \cdot Y(9,1) \cdot p_{13chaob} \\
 & - c12\_9(i) \cdot Y(9,1) \cdot p_{13chaob};
 \end{aligned}$$

**Compartments 10,11, 12 - Fish <sup>13</sup>C**

$$\begin{aligned}
 d10i = & + as10 \cdot c10\_7(i) \cdot Y(7,1) \cdot p_{13bugs} \\
 & + as10 \cdot c10\_8(i) \cdot Y(8,1) \cdot p_{13zoop} \\
 & + as10 \cdot c10\_9(i) \cdot Y(9,1) \cdot p_{13chaob} \\
 & + as10 \cdot C10\_T(i) \cdot Pter \\
 & - r10(i) \cdot Y(10,1) \cdot p_{13fish10} \\
 & - c11\_10(i) \cdot Y(10,1) \cdot p_{13fish10} \\
 & - c12\_10(i) \cdot Y(10,1) \cdot p_{13fish10};
 \end{aligned}$$

$$\begin{aligned}d11i= & + as11.*c11\_7(i).*Y(7,1).*p13bugs \\ & + as11.*c11\_8(i).*Y(8,1).*p13zoop \\ & + as11.*c11\_9(i).*Y(9,1).*p13chaob \\ & + as11.*c11\_10(i).*Y(10,1).*p13fish10 \\ & + as11.*C11\_T(i).*Pter \\ & - r11(i).*Y(11,1).*p13fish11;\end{aligned}$$

$$\begin{aligned}d12i= & + as12.*c12\_7(i).*Y(7,1).*p13bugs \\ & + as12.*c12\_8(i).*Y(8,1).*p13zoop \\ & + as12.*c12\_9(i).*Y(9,1).*p13chaob \\ & + as12.*c12\_10(i).*Y(10,1).*p13fish10 \\ & + as12.*C12\_T(i).*Pter \\ & - r12(i).*Y(12,1).*p13fish12;\end{aligned}$$

Table A4A. Parameters and variables used in the Dual Isotope Flow Model. For each parameter or variable from the DIF model equations (Table A3), this table presents a brief explanation, the approach to estimating the numerical value, the method, and a reference where applicable. Values of the parameters and variables are given in Table A4B.

<b>Parameter or Variable</b>	<b>Explanation</b>	<b>Approach</b>	<b>Comment</b>	<b>Reference</b>
accum6	Death rate of benthic algae, assumed added to sediment surface	Mass balance was used to estimate accum6 + R6. R6 assumed to be 80% of the total.		
as10, as11, as12	Assimilation coefficients for each species of fish	Fish Bioenergetics Model		Hanson et al. 1997
as7	Assimilation coefficient for benthic macro invertebrates	Literature		Blumenshine et al. 1997
as8	Assimilation coefficient for zooplankton	Fitted		Lampert 1987
as9	Assimilation coefficient for <i>Chaoborus</i>	Fitted		Ramcharan et al. 2001
BfracGPP	Proportion of GPP that is benthic	Estimated from lake morphometry and in-lake measurement		Vadeboncoeur et al. 2001
C10_T C11_T C12_T	Consumption of terrestrial prey items by each fish compartment	Measured and calculated from bioenergetics model	Bioenergetics model and fish diet data	Hanson et al. 1997, Hodgson and Kitchell 1987; Hodgson and Hansen 2005
c10_7 c11_7 c12_7	Consumption coefficient of macroinvertebrates by each fish compartment	Measured and calculated from bioenergetics model	Bioenergetics model and fish diet data	ibid.

c10_8 c11_8 c12_8	Consumption coefficient of zooplankton by each fish compartment	Measured and calculated from bioenergetics model	Bioenergetics model and fish diet data	ibid.
c10_9 c11_9 c12_9	Consumption coefficient of <i>Chaoborus</i> by each fish compartment	Measured and calculated from bioenergetics model	Bioenergetics model and fish diet data	ibid.
c11_10	Consumption coefficient of YOY bass by adult and in Paul Lake	Measured and calculated from bioenergetics model	Bioenergetics model and fish diet data	ibid.
c24	Coefficient of DOC release by phytoplankton	Fitted		Baines and Pace (1991)
c26	Coefficient of DOC release by benthic algae	Assumed to be 0 to the water column		
c32	Coefficient of DOC consumption by bacteria	Mass balance		
c52	Flocculation of DOC to dPOC	Fitted		
c54	Coefficient for conversion of live phytoplankton to dPOC	Mass balance		
C7	Total consumption by benthic macroinvertebrates	Mass Balance		
C8	Total zooplankton consumption	Mass balance		
c83	Coefficient for consumption of bacteria by zooplankton	Calculated from C8, p83 and bacterial total C		
c84	Coefficient for consumption of phytoplankton by zooplankton	Calculated from C8, p84 and phytoplankton total C		

c85	Coefficient for Consumption of dPOC by zooplankton	Calculated from C8, p85 and dPOC		
c98	Coefficient for consumption of zooplankton by <i>Chaoborus</i>	Calculated from C9 and zooplankton total C		
CO <sub>2</sub> Aq	Aqueous [CO <sub>2</sub> ]	Measured	Water pCO <sub>2</sub>	Cole et al 2000
f13_4	Isotopic fractionation in phytoplankton photosynthesis	Fitted	Corroborated by fits of time series models and direct field measurements	Carpenter et al. 2005, Bade et al. (2006)
f13_6	Isotopic fractionation in benthic algal photosynthesis	Fitted	Corroborated by fits of time series models	Carpenter et al. 2005
feced	Proportion of zooplankton and <i>Chaoborus</i> feces that sediment directly	Fitted		
GPP	Gross primary production (whole system)	Measured	Continuous O <sub>2</sub> and temperature (sondes)	Cole et al. 2000, Hanson et al. 2003
in1	Inflow of DIC	Mass balance		
in2	Inflow of DOC	Mass balance		
in5	Input of terrestrial POC	Fitted	Corroborated by fits of time series models	Carpenter et al. 2005
k	Gas piston velocity	Calculated from k <sub>600</sub> , temperature and Schmidt number		Wanninkhof et al. 1985
k <sub>600</sub>	Gas piston velocity	Measured	SF <sub>6</sub>	Cole and Caraco 98, Bade and Cole 2006

out1	Outflow of DIC	Measured	Measured [DIC]; measured water residence time	Stainton 1973; Cole and Pace 1998
out2	Outflow of DOC	Measured	Measured [DOC]; measured water residence time	Shimadzu 5050 TOC Analyzer, Cole and Pace 1998
out3	Outflow of bacteria	Measured	Measured bacteria biomass; measured water residence time	Pace and Cole 1996; Cole and Pace 1998
out4	Phytoplankton loss in outflow	Measured	Chlorophyll-a, Water residence time	Holm-Hansen and Reimann 1978
out5	Outflow of dPOC	Calculated from [dPOC] and water residence time		Cole and Pace 1998
p13_CO2	Proportion of $^{13}\text{C}$ in aqueous $\text{CO}_2$	from $^{13}\text{C}$ -DIC (below)	Carbon species and isotopes proportions calculated from pH, temp.	Bade et al. 2004, Mook et al. 1974
p13bact	Proportion of $^{13}\text{C}$ in pelagic bacteria	Model prediction	Measured by dialysis regrowth	Kritzberg et al 2004, 2005
p13bugs	Proportion of $^{13}\text{C}$ in benthic macroinvertebrates	Model prediction	Measured directly	Carpenter et al. (2005)
p13Cdoc	Proportion of $^{13}\text{C}$ in DOC	Model prediction	Measured directly	Bade et al. 2006
p13Cfish10,(and 11,12)	Proportion of $^{13}\text{C}$ in the three fish in each lake	Model prediction	Measured directly	
p13chaob	Proportion of $^{13}\text{C}$ in <i>Chaoborus</i>	Model prediction	Measured directly	Carpenter et al. 2005; Bade 2004

p13dic	Proportion of $^{13}\text{C}$ in DIC	Model prediction (Paul, Peter). Measured directly (Tuesday, Peter +N&P)	Measured directly	Bade et al. 2004; Pace et al. 2004
p13peri	Proportion of $^{13}\text{C}$ in benthic algae	Measured as regrowth in situ on tiles, collections of natural material		Pace et al. 2004; Carpenter et al. 2005
p13phyt	Proportion of $^{13}\text{C}$ in phytoplankton	Model prediction. Calculated from fl3_4, p13_CO2	Measured directly on physically separated phytoplankton and by models	Bade 2004; Bade et al. 2006; Pace et al. 2004.
p13zoop	Proportion of $^{13}\text{C}$ in zooplankton	Model prediction	Measured directly	Cole et al. 2002; Pace et al. 2004
p83	Proportion of bacteria in zooplankton consumption	Grazing not accounted for by phytoplankton (1-p84) was divided among bacteria and DPOC in proportion to their biomass		
p84	Proportion of phytoplankton in zooplankton diet	Fitted		
p85	Proportion dPOC in zooplankton diet	Grazing not accounted for by phytoplankton (1-p84) was divided among bacteria and DPOC in proportion to their biomass		
Patm_13C	Proportion of $^{13}\text{C}$ in atmospheric $\text{CO}_2$	Literature		Peterson and Fry 1987
Pgw	Proportion of $^{13}\text{C}$ in inflowing DIC	Measured		
photox	DOC photo-oxidation	Fitted	Estimated from literature for comparison	Graneli et al. 1996
physed	Sedimentation loss of live phytoplankton	Fitted		

Psed	Proportion of $^{13}\text{C}$ in sedimenting organic C	Calculated from the components of sedimentation (physed, fecesed, sed5) and the proportions of $^{13}\text{C}$ in each		
Pter	Proportion of $^{13}\text{C}$ in terrestrial inputs	Measured $\delta^{13}\text{C}$ of 10 species of terrestrial plants in watershed (Table A5 below)		
pX3_auto	Proportion of bacterial consumption accounted for by consumption of DOC released by phytoplankton	Fitted		
r10,r11,r12	Respiration for each species of fish	Fish Bioenergetics Model	Hanson et al. 1997	
r3	Respiration of pelagic bacteria	Measured	From bacterial production, growth efficiency, and dark bottle respiration	Pace and Cole 2000; Kritzberg et al. 2004
r4	Phytoplankton respiration	Measured	Dark bottle respiration, chlorophyll-a, and r3.	Pace and Cole 2000
r6	Respiration of benthic algae	Mass balance was used to estimate $\text{accum6} + \text{R6}$ . R6 assumed to be 80% of the total.		
r7	Respiration by macroinvertebrates	Assumed to be $0.03 \text{ d}^{-1}$		
r8	Zooplankton respiration	Fitted	Lynch et al 1986	
r9	<i>Chaoborus</i> respiration	Fitted	Giguère 1980; Bade 2004.	

R <sub>tot</sub>	Whole ecosystem Respiration	Measured	Continuous O <sub>2</sub> and temperature (sondes)	Cole et al. 2000, Hanson et al. 2003
Satconc	CO <sub>2</sub> Aq at atmos equilibrium	Measured	Air pCO <sub>2</sub>	Cole et al. 1994
sed5	Sedimentation of dPOC	Calculated from mass balance of dPOC		
WPHYT	Electivity coefficient for zooplankton grazing on phytoplankton	fitted		

Table A4B. Values of parameters and variables used in the Dual Isotope Flow Model. Each parameter or variable is defined in Table A4A. Units- “Prop.” means a proportion or dimensionless value; otherwise actual units are shown. Values are either single values for a given lake “single” or the mean of daily values used in the model (“mean”). The values of the time-dynamic model predictions of  $^{13}\text{C}$  in each compartment are not given in this Table. See text Figures 2 and 3.

<b>Parameter or Variable</b>	<b>Units</b>	<b>Single or mean of daily</b>	<b>Paul</b>	<b>Peter</b>	<b>Tuesday</b>	<b>Peter +N&amp;P</b>
accum6	prop.	mean	0.079	0.179	0.66	
as10, as11, as12	prop.	single	0.9	0.9	0.9	0.9
as7	prop.	single	0.7	0.7	0.6	0.7
as8	prop.	single	0.8	0.9	0.9	0.9
as9	prop.	single	0.8	0.8	0.9	0.5
BfracGPP	prop.	mean	0.21	0.17	0.18	0.15
C10_T	mmol C	mean	0.0045	0.055	0.64	0.025
C11_T	$\text{m}^{-2}\text{d}^{-1}$		0.22	0.0026	0.139	0.084
C12_T			0	0.017	0.051	0.085
c10_7	prop.	mean	0.009	0.0028	0.0069	0.0017
c11_7			0.28	0.0001	0.00045	0.0025
c12_7			0.023	0.0017	0.0077	0.0021
c10_8	prop.	mean	0.023	0.0017	0	0.0017
c11_8			0.0045	0.00004	0.0022	0.00002
c12_8			0.0057	0.001	0.002	0.00006
c10_9		mean	0.0004	0	0.0049	0
c11_9	prop.		0.00006	0	0.0014	0.058
c12_9			0.0007	0.026	0.0048	0.12

c11_10	prop.	note: c11 is never piscivorous	0	0	0	0
c24	prop.	mean	0.41	0.37	0.23	0.19
c26	prop.	mean	0	0	0.002	0
c32	prop.	mean	0.017	0.014	0.018	0.037
c52	prop.	mean	0.02	0.025	0.03	0.001
c54	prop.	mean	0.78	0.13	0.87	0.34
C7	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	6.56	0.48	0.67	2.25
C8	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	10.9	8.14	1.29	14.1
c83	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.13	0.053	0.015	0.072
c84	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.19	0.21	0.0063	0.047
c85	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.13	0.053	0.015	0.072
c98	prop.	mean	0.12	0.001	0.07	0.006
CO <sub>2</sub> Aq	μM	mean	27.4	54.8	47.0	2.6
f13_4	per mil	single	12.0	15.6	14.2	-2.5
f13_6	per mil	single	12.9	10.9	2	-2.5
fecesed	prop.	single	0.80	0.76	0.95	0.05
GPP	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	45.9	34.1	37.1	102.6
in1	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	-1.4	18.1	17.2	6.3

in2	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	21.9	31.1	49.7	21.2
in5	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	5.6	6.2	15.8	4.7
k	m d <sup>-1</sup>	mean	0.43	0.43	0.43	not used
k <sub>600</sub>	m d <sup>-1</sup>	single	0.4	0.4	0.4	0.4
out1	d <sup>-1</sup>	single	0.0025	0.0025	0.0025	0.0025
out2	d <sup>-1</sup>	single	0.0025	0.0025	0.0025	0.0025
out3	d <sup>-1</sup>	single	0.0025	0.0025	0.0025	0.0025
out4	d <sup>-1</sup>	single	0.0025	0.0025	0.0025	0.0025
out5	d <sup>-1</sup>	single	0.0025	0.0025	0.0025	0.0025
p13_CO2		Model prediction	see text Figs 2,3			
p13bact		Model prediction	see text Figs.2,3			
p13bugs		Model prediction	see text Figs.2,3			
p13Cdoc		Model prediction	see text Figs.2,3			
p13Cfish10 ,(and 11,12)		Model prediction	see text Figs. 2,3			
p13chaob		Model prediction	see text Figs. 2,3			
p13dic		Model prediction	see text Figs.2,3			
p13peri		Model prediction	see text Figs. 2,3			

p13phyt		Model prediction	see text Figs. 2,3			
p13zoop		Model prediction	see text Figs.2,3			
p83	prop.	mean	0.039	0.017	0.035	0.023
p84	prop.	mean	0.38	0.64	0.105	0.43
p85	prop.	mean	0.58	0.34	0.86	0.55
Patm 13C	prop.	single	0.0011035			
Pgw	prop.	single	0.011	0.011	0.011	0.011
photox	d <sup>-1</sup>	mean	1.08	1.42	0.36	0.083
physed	d <sup>-1</sup>	mean	0.39	0.34	0.67	0.099
Psed	prop.	single	0.011	0.0109	0.0109	0.0109
Pter	prop.	single	0.0108	0.0108	0.0108	0.0108
pX3 auto	prop.	single	0.4	0.27	0.24	0.61
r10	mmol C	mean	0.19	0.029	0.062	0.031
r11	m <sup>-2</sup> d <sup>-1</sup>		0.0039	0.067	0.067	0.067
r12			0.001	0.04	0.04	0.004
r3	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	3.52	4.85	6.10	7.49
r4	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.13	0.13	0.094	0.051
r6	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.32	0.12	0.07	0.16
r7	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.18	0.01	0.01	0.08
r8	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.07	0.16	0.03	0.08
r9	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.05	0.03	0.03	0.05

R <sub>tot</sub>	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	54.1	35.4	35.9	83.1
Satconc	μM	mean	13.3	13.2	13.1	13.1
sed5	mmol C m <sup>-2</sup> d <sup>-1</sup>	mean	0.59	0.57	0.77	0.65
WPHYT	proportion	single	1.5	4	0.4	0.7

Table A5. Measured  $\delta^{13}\text{C}$  of terrestrial plants collected near the shores of the study lakes. The proportion of  $^{13}\text{C}$  in terrestrial plants (Pter) was taken as the average of these measurements of dominant species in the watersheds of the lakes.

Plant Species	$\delta^{13}\text{C}$
Balsam fir, <i>Abies balsamea</i>	-31.9
Sugar maple, <i>Acer saccharum</i>	-30.9
Red maple, <i>Acer rubrum</i>	-29.8
Tamarack, <i>Larix laricina</i>	-29.1
White spruce, <i>Picea glauca</i>	-28.7
Leatherleaf, <i>Chamaedaphne calyculata</i>	-28.2
Ginseng, <i>Panax quinquefolius</i>	-31.9
<i>Sphagnum</i> spp.	-27.7
Cottongrass, <i>Eriophorum spissum</i>	-27.3
Bog rosemary, <i>Andromeda glaucophylla</i>	-26.6

Table A6. Model sensitivity to changes in parameter values. Shown for the Paul Lake model are the effects of varying the values of several key parameters to the residual standard deviation of the model (RSD model) and the RSD of two compartments, POC and zooplankton (zoop). Shown also is the effect on the estimate of zooplankton allochthony. For each parameter the best fit value used in the model is indicated in the row labeled “nominal”. The smaller the RSD, the better the fit between modeled and observed  $^{13}\text{C}$ . Definitions of these parameters are given in Table A4A and an graphical example of varying the values of two parameters simultaneous is shown in Fig A2.  $c84 = C8 * w\text{phyt} / (w\text{phyt} + w\text{bact} + w\text{dpoc})$ .

Parameter	test value	RSD model	RSD POC	RSD Zoop	Zoop alloch
shift_4	6	4.5	0.77	0.77	0.38
<b>nominal</b>	<b>12</b>	3.9	0.56	0.42	0.38
	10	4.0	0.61	0.51	0.38
	15	4.1	0.51	0.91	0.38
	20	4.9	0.67	0.57	0.38
	25	6.1	0.91	0.91	0.38
WPHYT	0.5	3.9	0.64	0.51	0.42
	0.8	3.9	0.61	0.45	0.43
	1.0	3.9	0.59	0.43	0.42
<b>nominal</b>	<b>1.5</b>	3.9	0.56	0.42	0.38
	1.8	4.0	0.55	0.43	0.36
	2.0	4.0	0.54	0.44	0.34
	2.4	4.1	0.53	0.48	0.32
in5_mg	0	4.3	0.86	0.67	0.34
	30	4.1	0.69	0.51	0.36
<b>nominal</b>	<b>67</b>	3.9	0.56	0.42	0.38
	90	3.9	0.52	0.41	0.39
	120	3.9	0.51	0.44	0.40
	150	3.9	0.52	0.5	0.41
as8	0.2	6.6	3.9	2.1	0.62
	0.4	4.1	0.60	0.96	0.46
	0.6	4.0	0.55	0.51	0.4
<b>nominal</b>	<b>0.8</b>	3.9	0.56	0.42	0.38
	0.9	3.9	0.57	0.42	0.37

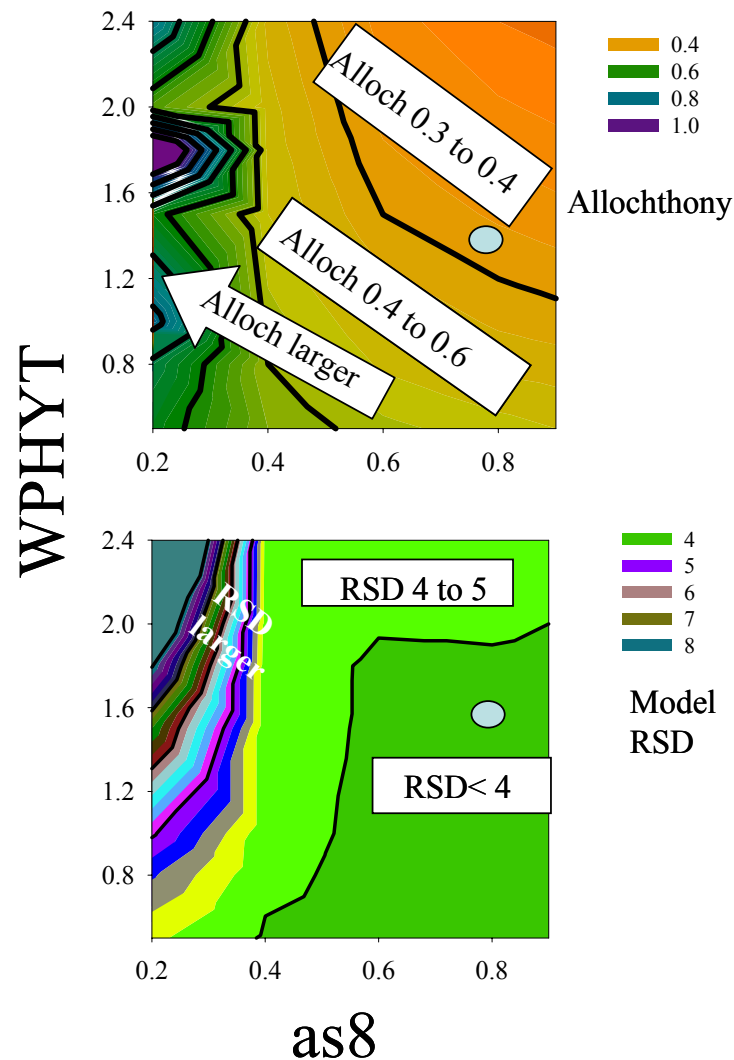


Figure A2. Graphical representation of model sensitivity to parameter values for the Paul Lake model. The upper panel show the effect of varying as8 (zooplankton assimilation efficient) and WPHYT (electivity coefficient for zooplankton consumption of phytoplankton) on modeled allochthony in zooplankton. The lower panel shows the effect on the residual standard deviation (RSD) of the model. Higher values of RSD mean poorer fit to data. For both panels the best fit (“nominal”) solutions for these parameters is shown with a blue circle. The best fit values of both parameters are obtained in the model by minimizing the variance between observed and measured  $^{13}\text{C}$  in all compartments of the model (see Methods). The exercise shows is that zooplankton allochthony is not very sensitive to relatively large changes in these parameters. As long as as8 is between about 0.4 and 0.9 (which is about the literature range) zooplankton allochthony is between about 40 and 60%. Even larger changes in as8 do not lower the estimate of allochthony, but low values of as8, near 0.2 lead to higher estimates in allochthony. When as8 is lower than 0.2 the model fails to arrive at acceptable fits. Similarly, unless as8 is low changes in WPHYT simply move allochthony within the 0.4 to 0.6 range. The exercise also shows that the model fits best (has lowest RSD) in the neighborhood of the nominal values of as8 and WPHYT and that moving either or both away from these values reduces the goodness of fit. The model fits very poorly, for example at low values of as8 and very high values of WPHYT.

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