A model of carbon evasion and sedimentation in temperate lakes

PAUL C. HANSON*, AMINA I. POLLARD*, DARREN L. BADE*, KATIE PREDICK†, STEPHEN R. CARPENTER* and JONATHAN A. FOLEY‡

*Center for Limnology, University of Wisconsin–Madison, 680 N. Park St., Madison, WI 53706-1492, USA, †Department of Zoology, University of Wisconsin–Madison, 430 Lincoln Dr, Madison, WI 53706, USA, ‡Center for Sustainability and the Global Environment (SAGE), Gaylord Nelson Institute for Environmental Studies, University of Wisconsin–Madison, 1710 University Ave., Madison, WI 53726, USA

Abstract

Lakes process terrigenous carbon. The carbon load processed by lakes may partially offset estimates made for terrestrial net ecosystem exchange (*NEE*). The balance within lakes between carbon burial and evasion to the atmosphere determines whether lakes are net sinks or net sources of atmospheric carbon. Here we develop a model to study processing of both autochthonous and allochthonous carbon sources in lakes. We run the model over gradients of dissolved organic carbon (*DOC*) and total phosphorus (*TP*) concentrations found in the Northern Highlands Lake District of Wisconsin. In our model, lakes processed between 5 and 28 g C m^{-2} (watershed) yr^{-1} derived from the watershed, which approximates one-tenth of *NEE* for similar terrestrial systems without lakes. Most lakes were net heterotrophic and had carbon evasion in excess of carbon burial, making them net sources of carbon to the atmosphere. Only lakes low in *DOC* and moderate to high in *TP* were net autotrophic and net sinks of carbon from the atmosphere.

Key words: carbon, flux, lake, landscape, metabolism, model, sedimentation

Received 8 September 2003; revised version received 31 December 2003 and accepted 14 January 2004

Introduction

North temperate lakes play an important role in processing organic carbon derived from the landscape as a whole. CO_2 supersaturation (Hope *et al.*, 1996; Striegl *et al.*, 2001; Sobek *et al.*, 2003) and net efflux of CO_2 from lakes to the atmosphere (Cole *et al.*, 1994; Riera *et al.*, 1999) suggest that most lakes vent terrigenous carbon to the atmosphere. Lakes act both as conduits of inorganic carbon to the atmosphere (Riera *et al.*, 1999; Hanson *et al.*, 2003) and as mineralization sites for terrigenous organic carbon (Hessen, 1992; del Giorgio *et al.*, 1999; Jansson *et al.*, 2000). Although the export of dissolved organic carbon (*DOC*) from terrestrial systems has been well documented (Mulholland, 2003), the view of lakes as 'hot spots' for carbon processing is tempered by uncertainties in the magnitude of the carbon load to lakes, the relative contributions of organic and inorganic carbon

Correspondence: Paul C. Hanson, tel. + 1 608 262 5953, fax + 1 608 265 2340, e-mail: pchanson@wisc.edu

forms to that load, and the influence of that load on key carbon cycling processes in lakes.

Understanding carbon cycling through lakes may reduce uncertainty in estimates of terrestrial net ecosystem exchange (*NEE*). For inverse modeling and biometric assessments, omission of processes such as carbon export through aquatic systems could result in biased estimates of carbon sequestration (Curtis *et al.*, 2002; Houghton, 2003). These systematic problems require independent data sources to identify and correct sources of error (Wilson & Baldocchi, 2001). Indeed, a direct comparison of eddy-covariance and ecological inventory estimates of carbon exchange in a midlatitude forest produced discrepancies of about 20% (Ehman *et al.*, 2002). In lake-rich landscapes, such as the Northern Highlands Lake District (NHLD) of Wisconsin, where lakes comprise 13% of the land surface (Peterson *et al.*, 2003), a significant amount of terrestrial carbon may be processed by the lakes. A first-order estimate can be obtained by comparing carbon efflux from lakes (e.g. 1–150 g C m^{-2} yr^{-1}) (Hanson, 2003) with *NEE* in forests (e.g. 70–350 g C m^{-2} yr^{-1}) (Curtis *et al.*,

2002). By changing net efflux from lakes to watershed areal units (i.e. lake area (LA) = 0.13 watershed area (WA) in the NHLD) and comparing the aforementioned ranges, lakes may mineralize and vent to the atmosphere from <1% to as much as 28% of the *NEE* from the landscapes in which they are embedded.

Understanding the role lakes play in processing landscape carbon requires quantifying the terrestrial loads as well as the in-lake processing of that carbon. *DOC* export via rivers and streams from terrestrial systems similar to those in northern Wisconsin range from about 1 to $10 \, \mathrm{g \, m^{-2} \, yr^{-1}}$ (Aitkenhead & McDowell, 2000). Streams clearly are an important source of *DOC* for many drainage lakes. Yet more than half of the lakes in Northern Wisconsin are seepage lakes (Eilers *et al.*, 1988), for which wetlands immediately surrounding the lake may be important *DOC* sources (Xenopoulos *et al.*, 2003). Although determining the carbon transport informs us of an important component of the lake carbon budget, our appraisal of its fate in lakes requires additional knowledge of lake biological and physicochemical processes. For example, terrigenous *DOC* can elevate lake respiration (*R*) (Cole *et al.*, 1994; Riera *et al.*, 1999; Hanson *et al.*, 2003) and suppress primary production (Jackson & Hecky, 1980; Jones, 1992; Carpenter *et al.*, 1998). However, the combined effects of carbon loading on lake metabolism, sedimentation, atmospheric flux, and long-term change remain largely unexplored.

How do terrestrial and aquatic sources of organic carbon interact to determine fates of organic carbon in a lake? The conceptual model needed to address this question is relatively simple. Figure 1 depicts an idealized lake situated in a forested landscape. Black arrows represent fluxes between systems, and the numbered labels adjacent to the arrows indicate the carbon forms. Following are descriptions of the numbered fluxes. (1) Positive net primary production (*NPP*) in terrestrial systems results in biomass accumulation. (2) Some of that biomass is mineralized and exported as dissolved inorganic carbon (*DIC*) in groundwater and surface water. (3) Additional biomass is leached through surface water as *DOC* or translocated as particulate organic carbon (*POC*). Carbon in the lake cycles through organic and inorganic forms (gray arrow). Primary producers fix *DIC* to *POC* and exude *DOC* in the process. The breakdown of *POC* produces *DIC* and *DOC*. Microbial respiration and photodegradation mineralize *DOC* to *DIC*. (4) A portion of the lake *POC* settles to the sediments. (5) *POC* in the sediments slowly mineralizes and releases *DIC* to the water column. (6) The CO_2 partial pressure gradient between the lake and the atmosphere drives net atmospheric flux (*NAF*) of *DIC*. (7) All forms of carbon are exported from the lake through surface flow. Although this system is rarely analyzed in an integrated way, many of the fluxes and transformations have been quantified (see Materials and methods for literature values).

In this study, we develop a process-based model of a simple landscape with an idealized north temperate lake that has gross biogeochemical characteristics of lakes found in the Upper Midwest of the USA. This
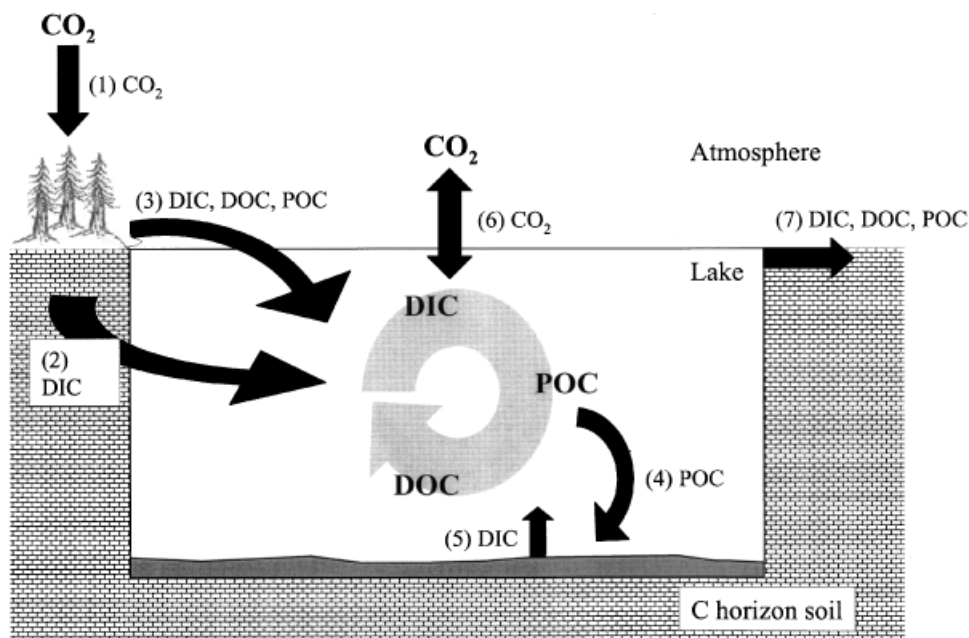

Fig. 1 A simplified diagram of carbon cycling through a landscape with one lake.

model accounts for internal lake carbon cycling, as well as carbon fluxes with terrestrial and atmosphere systems. We consider broad ranges in carbon loading and internal production in lakes, and explore model sensitivity to parameters. We identify areas of future research with implications for land use, spatial and temporal variability in carbon loading, and food web structures. Ultimately, we seek to understand the roles lakes play in processing terrestrial carbon and the implications for carbon flux to the atmosphere.

We use the model to address ecosystem questions that would be expensive to address by direct measurements in thousands of lakes on a landscape. What is the fate of terrigenous carbon in lakes? How does exogenous carbon loading alter key carbon cycling processes in lakes? At what carbon loads do lakes become net sources of carbon to the atmosphere? And how are these phenomena likely to be affected by other ecosystem drivers not explicitly included in the model, such as food webs?

Materials and methods

The biogeochemical characteristics of the modeled lake were consistent with lakes in the NHLD of northern Wisconsin. The watershed area (w) was $250 \times 10^4 \, \text{m}^2$, and the LA to WA ratio ($lw = 0.13$) was set to the open water ratio for the NHLD (Peterson et al., 2003). WA was used to scale areal rates of carbon loading and the water budget to the landscape. We did not explicitly account for land use or land cover, and we assumed that these lakes were located in carbonate-poor soils, based on the generally low carbonate alkalinity for lakes in this region (Eilers et al., 1988). We included sufficient detail in the water budget for estimating carbon loading and lake turnover rate. Our goal in this paper was a steady-state model driven by annual carbon loads, the data most commonly reported in the literature. Thus, annual loads were prorated to daily values. Lake total phosphorus (TP) concentrations were fixed at the beginning of any given model run. Because we consider the lake to be a homogeneous mixed reactor, we did not vary lake morphometry nor did we separate littoral and pelagic habitats. For simplicity, we assumed a cylindrical lake with mean depth (z) of 10 m in a circular watershed.

The model computes mass balances of carbon species at dynamic steady state (Fig. 2). We group carbon into three pools, DIC, DOC, and POC, resulting in the differential equations listed in Table 1. These were solved by an adaptive-step-size Runge–Kutta algorithm in modeling software (Matlab, v. 6.0, Mathsoft, Inc. 2000). The time-step is daily and all parameters and variables are described as daily values. All changes due
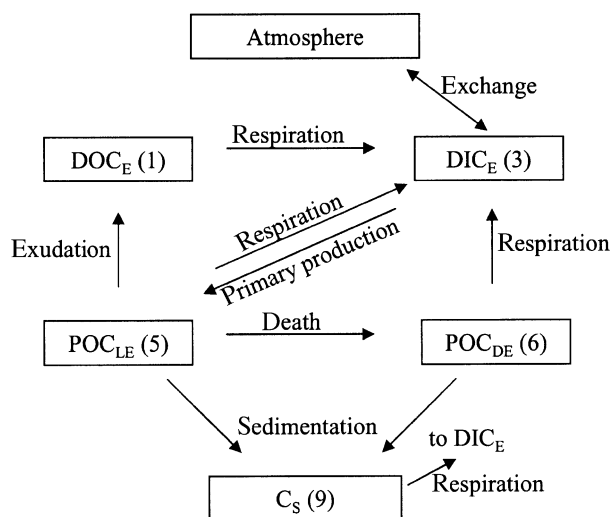

Fig. 2 A simplified schematic of the model, excluding loads and exports, during seasons when the water column is not stratified. Major carbon pools are boxes and conversions between pools are arrows. The equation numbers for pool changes are in parentheses and can be cross-referenced with Table 1.

to seasonality, such as water temperature, light, stratification and ice cover occur at discrete times. The model reaches annual dynamic equilibrium in less than 20 years, after which time we track pools and fluxes for 1 year. The model was run for 60 lakes that represented discrete points in TP and DOC gradients, as shown in Fig. 3 and as described below. Many parameters for this model were borrowed from the carbon cycling literature, in which it is important to distinguish between LA and WA (Table 2).

The number of days the lake was not covered in ice ($c = 224$ days) or was stratified ($h = 120$ days) was set to values typical of lakes in northern Wisconsin (NTL-LTER data set, http://lter.limnology.wisc.edu). We fixed water temperature at $4 \, ^\circ\text{C}$ during the winter, and $12 \, ^\circ\text{C}$ during spring and autumn. During summer stratification, we set the epilimnion to $20 \, ^\circ\text{C}$ and the hypolimnion to $12 \, ^\circ\text{C}$. The sediment temperature was set to the same value as the water immediately above it. Complete stratification occurred on the first day of the stratified period, and the thermocline depth (Zt) was set as a function of DOC concentration (Snucins & Gunn, 2000). Each stratum was assumed to be well mixed.

A water budget was created within the model to assess whether terrestrial loading rates gave reasonable values for ground- and surface-water carbon concentrations. The water input was modeled as precipitation (p) on the watershed and lake. Excess water, precipitation (p) – evapotranspiration (v), from the watershed was partitioned into groundwater (25%) and surface water (75%). Water was lost from the lake via

Table 1 Model differential equations and intermediate equations describing parameter implementation

Differential equations	No.
$\frac{dDOC_E}{dt} = DOC_{Gin} + DOC_{Qin} + DOC_{Pin} + GPP_{exudate} - R_{DOCE} - DOC_{Qout}$	(1)
$\frac{dDOC_H}{dt} = DOC_{Gin} + DOC_{Qin} - R_{DOCH} - DOC_{Qout}$	(2)
$\frac{dDIC_E}{dt} = DIC_{Gin} + DIC_{Qin} + DIC_{Pin} + R_A + R_{POCE} + R_{DOCE} + R_S$ $\quad - GPP - DIC_{Qout} - DIC_V - Flux_{atm}$	(3)
$\frac{dDIC_H}{dt} = DIC_{Gin} + DIC_{Qin} + DIC_{Pin} + R_{POCH} + R_{DOCH} + R_S - DIC_{Qout}$	(4)
$\frac{dPOC_{LE}}{dt} = GPP - R_A - GPP_{exudate} - Sed_{LE} - Death_{LE} - POC_{Qout}$	(5)
$\frac{dPOC_{DE}}{dt} = POC_{Qin} + Death_{LE} - R_{POCE} - Sed_{DE} - POC_{Qout}$	(6)
$\frac{dPOC_{LH}}{dt} = Sed_{LE} - Sed_{LH} - Death_{LH} - POC_{Qout}$	(7)
$\frac{dPOC_{DH}}{dt} = POC_{Qin} + Sed_{DE} + Death_{LH} - Sed_{DH} - R_{POCH} - POC_{Qout}$	(8)
$\frac{dC_S}{dt} = Sed_{DH} + Sed_{LH} - R_S$ (during stratified seasons) $\frac{dC_S}{dt} = Sed_{DE} + Sed_{LE} - R_S$ (during unstratified seasons)	(9)

Intermediate equations

$R_A = GPP \times ra$
$GPP_{exudate} = GPP \times a$
$R_{DOCE} = DOC_E \times eg$
$R_{DOCH} = DOC_H \times hg$
$R_{POCE} = POC_{DE} \times ef$
$R_{POCH} = POC_{DH} \times hf$
$R_S = C_S \times sf$
$Sed_{LE} = POC_{LE} \times 0.0188 \times (d/2)^2/z$
$Sed_{LH} = POC_{LH} \times 0.0188 \times (d/2)^2/z$
$Sed_{DE} = POC_{DE} \times 0.0188 \times (d/2)^2/z$
$Sed_{DH} = POC_{DH} \times 0.0188 \times (d/2)^2/z$
$Death_{LE} = POC_{LE} \times ed$
$Death_{LH} = POC_{LH} \times hd$

Subscript definitions are: G, groundwater; Q, surface water; P, precipitation; V, evaporation; E, epilimnion; H, hypolimnion; S, sediments; D, dead; and L, living.

evaporation, and outflow was calculated as inflow – evaporation, which assumed a steady-state lake volume. For carbon loading from surface and groundwater, we assumed that during stratification, both surface and groundwater carbon was distributed between the hypolimnion and epilimnion according to the ratio of the particular stratum volume to whole-lake volume.

The areal rate of *DOC* loading from the terrestrial system (DOC_Q) was varied from 2 to 20 g C m^{-2} WA yr^{-1} to represent export ranges from a variety of land covers (Mulholland, 2003). Lake *TP* concentration was varied from 5 to 100 µg L^{-1} to represent a broad range of productivity (Hanson *et al.*, 2003). *DIC* load from the terrestrial system through groundwater (DIC_G) was set to 3 g C m^{-2} WA yr^{-1} or 0.3 DOC_Q, whichever was larger. The minimum value ensured that groundwater

DIC concentrations were consistent with concentrations typical of the region (NTL-LTER data), and the higher values followed a relationship described by Dillon & Molot (1997). *DOC* and *POC* in groundwater were considered negligible, and *DIC* in fluvial input was set to 10 times atmospheric equilibrium (P. C. Hanson, unpublished data). Carbon outflow was the product of the daily epilimnetic concentrations of the carbon pools and the daily volumetric outflow of water. The parameter space for in-lake *DOC* and *TP* concentrations included combinations normally found in northern Wisconsin (Hanson *et al.*, 2003) (Fig. 3). We did not represent the relative frequency of occurrences of the combinations, but included six lakes for every 2 g C m^{-2} WA yr^{-1} increment in DOC_Q. Acid-neutralizing capacity (*ANC*) was set for each lake according to measured values from the data set used for *DOC* and
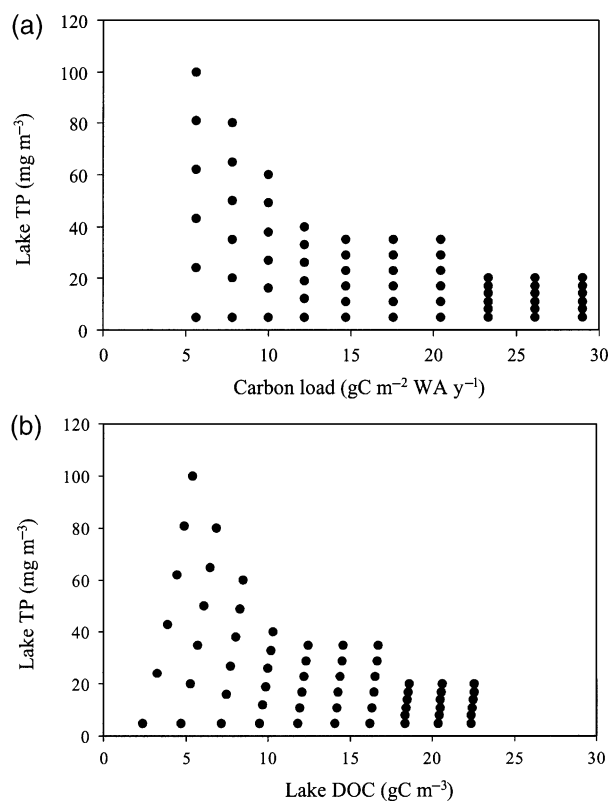
Fig. 3 The total carbon load (watershed area (WA) units) and total phosphorus (TP) concentration lake space used for simulations in this model. For each C load, six lakes spanning a TP gradient were simulated.

TP distributions. In general, ANC was directly related to TP and inversely related to DOC. To fill the complete DOC and TP space used in this model, ANC data were linearly interpolated between measured values. Maximum ANC ($1000\,\mu Eq\,L^{-1}$) was in the low DOC, high TP lake, and minimum ANC ($11\,\mu Eq\,L^{-1}$) was in the low TP, high DOC lake. pH and carbonate speciation (Stumm & Morgan, 1981) were calculated daily as a function of the dynamic DIC concentration and the fixed ANC.

Carbon is modeled within the lake in three pools – DOC, DIC and POC. Pools are separated according to strata, which include epilimnion and sediments for the entire year, plus the hypolimnion during summer stratification. During stratification, DIC and DOC do not pass between the hypolimnion and epilimnion, however, DIC fluxes to the atmosphere ($Flux_{atm}$) as a function of the concentration gradient and an assumed diffusion coefficient (k) (Cole et al., 2002). POC settles from the epilimnion, through the hypolimnion and into the sediments. DIC in the sediments is released to the stratum immediately above. Carbon is either converted between pools via gross primary production (GPP) and

R, or is lost from the active carbon pool in the lake due to sedimentation, NAF to the atmosphere, or export in lake outflow.

Primary production is assumed to occur only in the epilimnion. GPP in $mmol\,m^{-3}\,day^{-1}$ is calculated from an empirical relationship with TP, according to data from Hanson et al. (2003) as:

$$\ln GPP = 0.883\ln TP, \qquad (1)$$

where ln TP is the natural log of the TP concentration in $\mu g\,L^{-1}$. Total grams of production is the product of $e^{\ln GPP}$ in mass units and the epilimnion volume. GPP is returned to the DIC pool, exuded as DOC, or accumulated as POC, as follows. About 80% is quickly returned to DIC through autotrophic respiration, planktivory and mineralization of highly labile autotrophic products (ra). Rapid POC turnover (Cole et al., 2002) suggests that 85–90% of GPP may be respired in short order. Quay et al. (1986) suggest a lower range of 54–88%. A value of $0.80\,day^{-1}$ appears to be reasonable for ra, but we explore uncertainty in this parameter through sensitivity analysis. Three percent of GPP is exuded as refractory DOC (a). Literature-based estimates of extracellular release of DOC are around 10% of phytoplankton production (Baines & Pace, 1991). We assume that about one-third of this DOC is refractory, based on similar estimates from marine phytoplankton experiments (Biddanda & Benner, 1997). The impact of this assumption on the model is explored through sensitivity analysis of the a parameter. The remainder of GPP enters the POC pool. The rate ($ed = 0.03\,day^{-1}$) at which living POC (POC_L) in the epilimnion converts to dead POC (POC_D) was taken from Connolly & Coffin (1995). Conversion of POC_L to POC_D in the hypolimnion (hd) was assumed to be rapid, and all POC entering sediments was assumed to be dead. POC_L and POC_D sedimentation rate is calculated after Carpenter (1992), who used a modified Stoke's equation to model settling as a function of particle size (d). Particle size was estimated for combined pools of pico- and microplankton (Wetzel, 2001). Permanent burial in the sediments is a function of the sediment decay rate constant (sf) acting on accumulated sediments.

Whole-lake respiration is the sum of three first-order decay processes that occur independently of each other on a daily time-step. These rate constants represent fast, moderate and slow mineralization. The fast rate is conversion of GPP to DIC, which is ra as described above. The moderate rate is the mineralization of POC to DIC (ef for the epilimnion, hf for the hypolimnion, and sf for the sediments), which represents processes such as consumption and subsequent respiration of particles by higher orders in the food chain and mineralization of labile particulate substrates by

Table 2 Parameter values, state variables, drivers and their associated units as used in the model

Symbol	Name	Units	Value	Source
c	Ice-free days	day	224	NTL-LTER
h	Stratified days	day	120	NTL-LTER
w	Watershed area	m^2	250×10^4	*
lw	Lake area to watershed area ratio		0.13	Peterson *et al.* (2003)
z	Mean depth	m	10	*
v	Evapotranspiration	m day^{-1}	0.556/365	Webster *et al.* (2000)
p	Precipitation	m day^{-1}	0.831/365	Webster *et al.* (2000)
k	*NAF* piston velocity	m day^{-1}	0.5	Cole *et al.* (2002)
d	Diameter of particles	μm	5.0	Wetzel (2001)
t	Base temperature	°C	20	*
a	*GPP* that becomes exudate	Proportion	0.03	Biddanda & Benner (1997)
ra	*GPP* that is respired	Proportion	0.80	Quay *et al.* (1996); Cole *et al.* (2002)
ed	Death of algae rate constant (epi)	day^{-1}	0.03	Connolly & Coffin (1995)
ef	Conversion of *POC* to *DIC* (epi)	day^{-1}	0.05	*
eg	Conversion of *DOC* to *DIC* (epi)	day^{-1}	0.005	Houser (2001)
hd	Death of algae (hypo)	day^{-1}	0.90	*
hf	Conversion of *POC* to *DIC* (hypo)	day^{-1}	0.05	*
hg	Conversion of *DOC* to *DIC* (hypo)	day^{-1}	0.005	*
sf	Conversion of *POC* to *DIC* in sediments	day^{-1}	0.005	*
Lake state variables				
Zt	Thermocline depth	m		Snucins & Gunn (2000)
DIC	Dissolved inorganic carbon	g C m^{-2} LA		Output
DOC	Dissolved organic carbon	g C m^{-2} LA		Output
POC_D	Dead *POC*	g C m^{-2} LA		Output
POC_L	Living *POC*	g C m^{-2} LA		Output
NAF	Net atmospheric flux	g C m^{-2} LA		Output
S	Sediments	g C m^{-2} LA		Output
GPP	Gross primary production	g C m^{-2} LA day^{-1}		Hanson *et al.* (2003)
R	Respiration	g C m^{-2} LA day^{-1}		Output
Drivers				
TP	Total phosphorus	μg L^{-1}	5–100	Input
DOC_Q	*DOC* loading from surface water	g C m^{-2} WA yr^{-1}	2–16	Input
DIC_G	*DIC* loading from groundwater	g C m^{-2} WA yr^{-1}	$0.3\,DOC_Q$	Input
ANC	Acid-neutralizing capacity	μEq L^{-1}	1–1000	Input

The 'Source' column are parameter value references. Annual rates were converted to daily rates in the model by dividing by 365. Source fields that have asterisks are either inferred or derived from other sources, and are explained in the methods.
NAF, net atmospheric flux; *POC*, particulate organic carbon; *DIC*, dissolved inorganic carbon; WA, watershed area; LA, lake area.

microbes. Connolly & Coffin (1995) model *POC* mineralization, in part, as relatively rapid conversion (0.1–0.3 day^{-1}) of *POC* to labile *DOC*, which is then mineralized by bacteria. We chose to combine those two steps in our *POC* to *DIC* rate constants for the epilimnion and hypolimnion ($ef = hf = 0.05$ day^{-1}), because we assume that *DOC* in our model is relatively refractory. Cole *et al.* (2002) found *POC* turnover rates to be an order of magnitude faster than *DOC* turnover rates, further supporting our assumption. In this model, we assume that particles reaching the sediments are relatively refractory; thus, *sf* is an order of magnitude smaller than *ef* and *hf*. The third and slowest rate

constants are for the epilimnetic (*eg*) and hypolimnetic (*hg*) mineralization of recalcitrant *DOC* originating from loading and from primary production. In a study of north temperate lakes, Houser (2001) found the mean rate constant for *DOC* decay to be about 0.005 day^{-1}. Each respiration value, except *ra*, is adjusted for temperature using a form of the Arrhenius equation:

$$R_t = R_0 \times e^{(Q10 \times (\text{current temperature} - t)/10),} \qquad (2)$$

where t is the base temperature, R_0 is respiration unadjusted for temperature, Q_{10} is the temperature coefficient (assumed to be 2), and R_t is the temperature-adjusted respiration.

Model calibration and sensitivity analysis

The model was calibrated to three relatively conservative lake indices – concentrations of *DIC*, *DOC* and *POC*. We calibrated the model to summer conditions reported in Hanson *et al.* (2003) for epilimnetic *DIC* and *DOC* concentrations. We calibrated hypolimnetic values, as well as autumn, winter and spring conditions for the above variables to data from the NTL-LTER data set. Water budgets were adjusted so that a given lake's mean residence time in years equaled its average mean depth in meters (Michaels, 1995).

We expected our dynamic carbon pools to fall within measured ranges for the region (Table 3). Although there is more uncertainty in measured values of *GPP* and *R* than of carbon pools, we expected our model to approximate literature values for *GPP* and *R* as well. We expected our values for sedimentation and *NAF* to fall within the range found in the literature. Most importantly, we compared *NAF* with the accumulation of carbon in the sediment pool (*S*) in our model to determine the extent to which terrigenous carbon is buried in the sediments or fluxed to the atmosphere.

Sensitivity analysis was performed on the model by assessing the magnitude of change in state variables in response to changes in parameter values. The default simulation against which all others were compared had parameter values set according to Table 2, and driver variables set as follows: $TP = 15\,\mu g\,L^{-1}$, $DOCQ = 4\,g\,m^{-2}\,yr^{-1}$, and $ANC = 200\,\mu Eq\,L^{-1}$. These *TP* and *ANC* values, as well as the resulting lake *DOC* concentration, typify low to moderately productive lakes for the region, and produce *NAF* and *S* of the same magnitude in this model. To test model sensitivity, we increased the value by 10% for a given parameter while keeping the remaining parameters at their default values, and recorded the change in *NAF* and *S*. We repeated this procedure for each parameter, thus running 19 simulations. The model was considered sensitive to a parameter if the change in *NAF* or *S* exceeded 10% of the value in the default simulation.

Results

We varied total carbon loads from about 4 to $26\,g\,C\,m^{-2}\,WA\,yr^{-1}$, which resulted in mean lake *DOC* concentrations ranging from about 2 to $20\,mg\,L^{-1}$. Lakes with low *DOC* concentrations had received the lowest ratio of organic carbon to inorganic carbon in the loads (*OC:IC*). Over the first four loads, *OC:IC* increased from 0.75 to 2.85 and stabilized at about 3.17 thereafter. This model behavior resulted from our algorithm for *DIC* load as a function of *DOC* load, coupled with the high *DIC* concentration in surface waters.

The model showed expected annual carbon cycling dynamics with respect to *DIC*, *DOC* and *POC* concentrations across a range of *DOC* loads and *TP* concentrations. Annual dynamics for an oligotrophic lake are depicted in Fig. 4. During the stratified season, there was a slight drawdown of epilimnetic *DOC* ($\sim$1 mg L^{-1}), and a slight increase in hypolimnetic *DOC* ($\sim$0.1 mg L^{-1}). From autumn through spring, there was an increase in *DOC*, due to temperature-suppressed ecosystem respiration (*R*). Epilimnetic *DIC* remained relatively low during the stratified season ($\sim$1.5 mg L^{-1}), whereas hypolimnetic *DIC* increased slightly (to $\sim$3 mg L^{-1}). During spring and autumn, *DIC* fell in response to the concurrent processes of primary production and temperature suppressed respiration. *POC* remained low ($\sim$0.3 mg L^{-1}) year round, but with moderate net increases during the spring and fall. Although most lakes followed expected patterns in carbon concentrations, high *DOC* lakes showed unusually high annual variation in epilimnetic *DOC*. For example, *DOC* drawdown in our model was about 11 mg L^{-1} in a lake with mean annual *DOC* $\sim$25 mg L^{-1}, whereas the epilimnetic drawdown in *DOC* from a similar lake in our calibration data set was only 6.5 mg L^{-1}. Mean annual surface water carbon concentrations matched our expectations, with the exception of *DOC* and *POC* in the mesotrophic lake being slightly high. Table 3 shows mean annual surface water values

Table 3 Mean annual surface water concentrations for four representative lake types

Lake type	TP	DOC		DIC		POC	
		Cal	Sim	Cal	Sim	Cal	Sim
Oligotrophic	5	1.4–3.9	2.4	0.2–11.5	0.8	0.1–0.5	0.3
Mesotrophic	35	3.6–5.3	5.7	7.0–11.2	8.6	0.1–0.7	0.9
Eutrophic	100	2.8–10.5	5.4	9.0–13.0	9.3	0.1–4.7	2.5
Dystrophic	17	8.8–21.8	20.6	0.1–1.2	0.7	0.1–0.9	0.2

Columns are calibration values (Cal) and simulation results (Sim) for the selected lake types. Total phosphorus (*TP*) is in $\mu g\,L^{-1}$, and dissolved organic carbon (*DOC*), dissolved inorganic carbon (*DIC*) and particulate organic carbon (*POC*) are in $mg\,L^{-1}$.
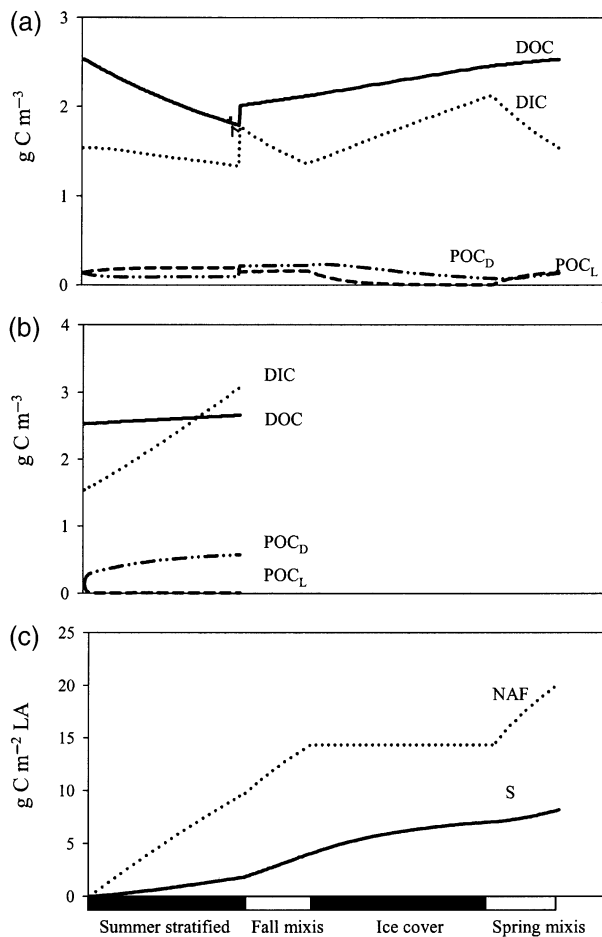
Fig. 4 Annual dynamics of carbon pools in a lake with total phosphorus $(TP) = 5\,\mu g\,L^{-1}$ and dissolved organic carbon $(DOC) = 3\,mg\,L^{-1}$. Panels show time series of (a) epilimnetic carbon pools, (b) hypolimnetic carbon pools, and (c) sediments (S) and net atmospheric flux (NAF) in lake area (LA) units. S and NAF are cumulative.

for lake carbon concentrations from our simulations for typical categories of lakes.

We compared modeled results for lake GPP, R, and net ecosystem production (NEP) with estimates from another study. Figure 5 compares metabolism over a gradient in DOC, where the direct measurements were made using data sondes (Hanson *et al.*, 2003). The model results for GPP agreed well with direct measurements (Fig. 5a). The results for R (Fig. 5b) and NEP (Fig. 5c) occupied roughly the same lake space as literature values, but diverged somewhat at higher DOC concentrations. The high DOC lakes from the literature are surrounded by bog mats, in which the interstitial waters have extremely high DIC concentrations (Kratz TK, unpublished data). This DIC may be transported to the lake at a rate high enough to artificially elevate R as measured by sondes (Hanson *et al.*, 2003). Figure 6
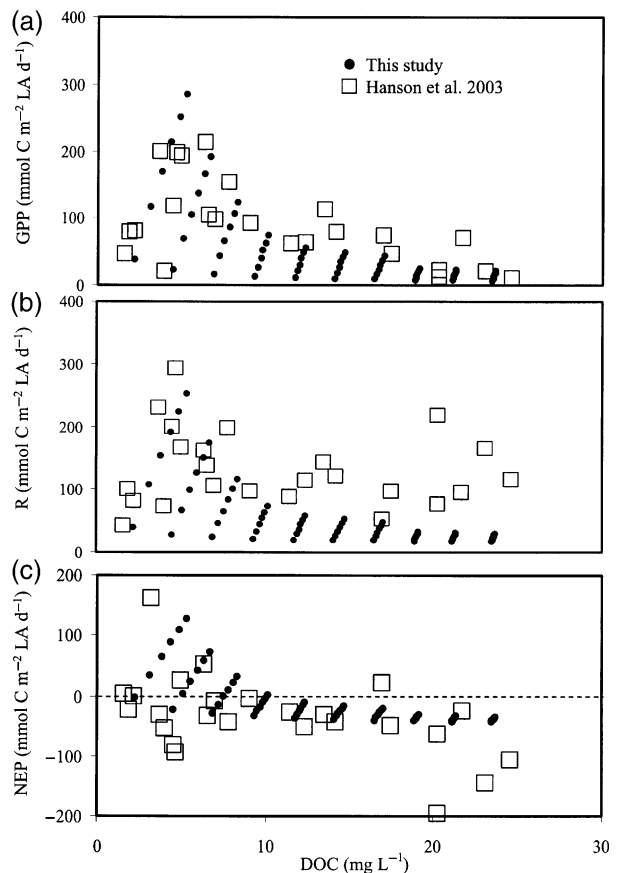

Fig. 5 Simulation results, as well as data from Hanson *et al.* (2003), are plotted against dissolved organic carbon (DOC). Areal lake metabolism is represented by plots of (a) gross primary production (GPP), (b) R, and (c) net ecosystem production (NEP). Figure legend is in panel a.

compares model results and literature values over a TP gradient. Once again, model results for GPP agreed well with direct measurements (Fig. 6a), but model results for R were consistently lower than direct measurements (Fig. 6b). For NEP, model results were directly related with TP, but direct measurements showed considerable scatter at TP concentrations below $40\,\mu g\,L^{-1}$.

Sedimentation, NAF and metabolism

The influence of terrestrial carbon on the lake carbon budget was a function of the carbon load as well as the lake TP concentration. We gauged the contributions of autochthonous and allochthonous carbon sources to the lake carbon cycle by plotting carbon accumulation in the sediment pool (S) and NAF against the ratio of GPP to total (inorganic + organic) carbon loading from the watershed (C_{load}) (Fig. 7). As $GPP:C_{load}$ increased, S increased and NAF decreased. At low $GPP:C_{load}$, NAF
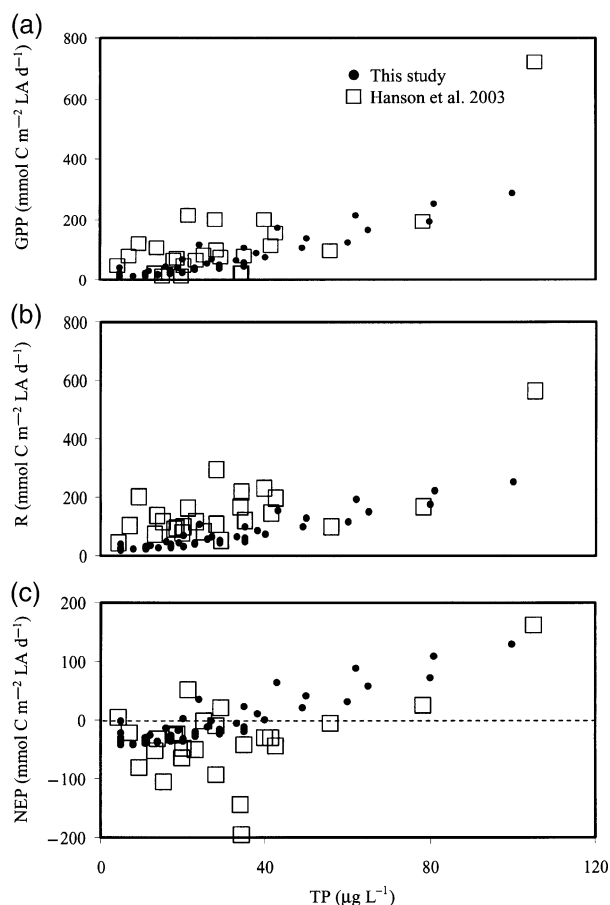
Fig. 6 Simulation results, as well as data from Hanson *et al.* (2003), are plotted against total phosphorus (*TP*). Areal lake metabolism is represented by plots of (a) gross primary production (*GPP*), (B) *R*, and (C) net ecosystem production (*NEP*). Figure legend is in panel a.
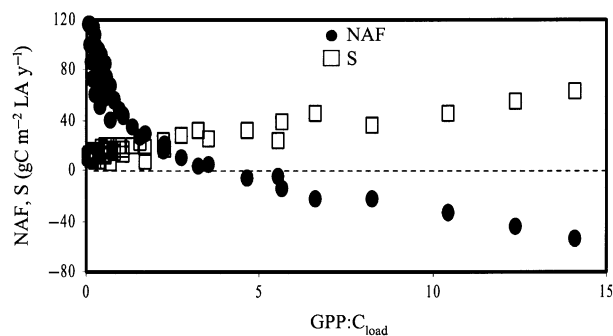

Fig. 7 Net atmospheric flux (*NAF*) and *S* as a function of the ratio of internal production (gross primary production (*GPP*)) to total carbon load (C_{load}).

was greater than *S*, and lakes were net sources of carbon to the atmosphere. When $GPP : C_{load}$ exceeded 2.5, *S* exceeded *NAF* and lakes became net sinks of atmospheric carbon.

Calculating the balance between contrasting ecosystem processes can provide convenient metrics for classifying net trophic level and fluxes in lakes. Net ecosystem production ($NEP = GPP - R$) describes the metabolic balance of the aquatic system, such that negative *NEP* equals heterotrophy and positive *NEP* equals autotrophy. Heterotrophy implies that an external source of organic carbon is fueling *R* in excess of *GPP*. Net carbon flux ($Flux_{net} = NAF - S$) describes the lake as a net source (positive (+)$Flux_{net}$) of carbon to the atmosphere or a net sink (negative (−)$Flux_{net}$) of carbon from the atmosphere.

NEP and $Flux_{net}$ showed similar but opposite responses over *TP* and C_{load} gradients. As C_{load} increased, *NEP* decreased (Fig. 5c) and $Flux_{net}$ increased

(Fig. 8a). Above C_{load} load of $10 \, g \, m^{-2} \, WA \, yr^{-1}$, almost all lakes had negative *NEP* and positive $Flux_{net}$, regardless of *TP* concentration. Below C_{load} of $10 \, g \, m^{-2} \, WA \, yr^{-1}$, results were mixed. About one-fourth of the lakes showed heterotrophy and positive $Flux_{net}$, whereas others showed the opposite trend. Those lakes with positive *NEP* and negative $Flux_{net}$ were highest in *TP*. As *TP* concentration increased, *NEP* increased (Fig. 6c) and $Flux_{net}$ decreased (Fig. 8b). When *TP* was above $35 \, \mu g \, L^{-1}$, lakes had positive *NEP* and negative $Flux_{net}$, but at or below $35 \, \mu g \, L^{-1}$; only three lakes with moderately high *TP* and low *DOC* showed this balance. $Flux_{net}$ and *NEP* were inversely related (Fig. 9).

Model sensitivity analysis

Model sensitivity to parameter changes was indicated by changes in *NAF* and *S* from their values calculated under default conditions ($22.7 \, gC \, m^{-2} \, LA \, yr^{-1}$ for *NAF* and $13.7 \, gC \, m^{-2} \, LA \, yr^{-1}$ for *S*). The model was slightly sensitive to changes in five parameters. A 10% increase in ice-free days (*c*) led to a 10.2% increase in *S*. Increasing LA to WA ratio (*lw*), precipitation (*p*), and base temperature (*t*) led to decreases in *NAF* of 15.4%, 15.9%, and 12.8%, respectively. Increasing evapotranspiration (*v*) increased *NAF* by 12%. The model was very sensitive to *ra*, the term that represents rapid mineralization of *GPP* products. An increase of 10% in *ra* led to a 41.6% decrease in *S* and a 26.4% increase in *NAF*.

Discussion

Lakes process terrestrial carbon

Our results suggest that lakes can process and vent to the atmosphere a significant proportion of carbon fixed in terrestrial systems. In our model, terrestrial carbon export was about $5–28 \, gC \, m^{-2} \, WA \, yr^{-1}$. As much as

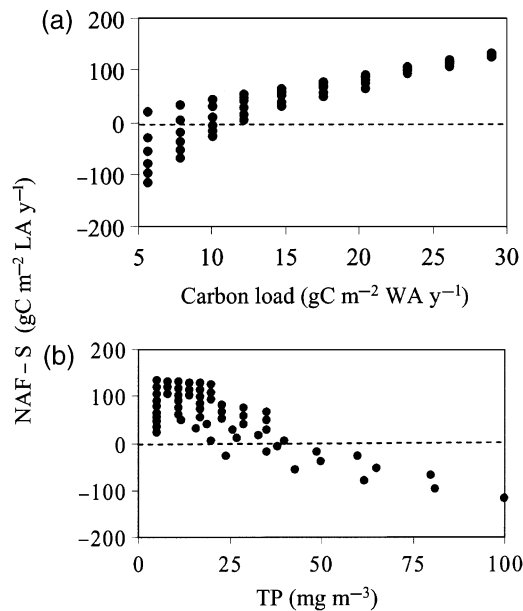**Fig. 8** The difference between net atmospheric flux (*NAF*) and accumulation of carbon in the sediment pool (*S*) (*NAF−S*) as a function of C loading and total phosphorus (*TP*) concentration. (a) *NAF−Sed* is directly related with carbon loading and (b) inversely related with *TP* loading. Most lakes had *NAF* in excess of *S*.
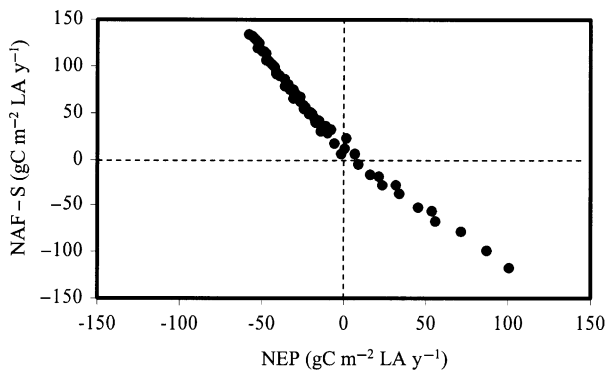

Fig. 9 Net atmospheric flux (*NAF*) minus accumulation of carbon in the sediment pool (*S*) (*NAF−S*) is inversely related to net ecosystem production (*NEP*).

60% of that carbon was returned to the atmosphere. By comparing lake *NAF* with *NEE* estimates for northern hardwood forests ($160 \, gC \, m^{-2} \, yr^{-1}$) (Barford *et al.*, 2001), we find that a single lake in a watershed may process and vent as much as 3–9% of terrestrial *NEE*. Much of the remaining terrigenous carbon was exported from the lake as *DOC* and *POC*. Because most of the exported C is in a form that will not be sedimented, we speculate that it, too, may be destined for mineralization and vented to the atmosphere. By combining *NAF* and export numbers, we raise the percentage of

terrigenous carbon fluxed to the atmosphere to as much as 90% of the carbon load. This flux equates to 3–14% of terrestrial *NEE*. The upper end of this range is of the same magnitude as error associated with eddy-covariance estimates of terrestrial *NEE* (Baldocchi, 2003), as well as disturbance effects on terrestrial *NEP*, such as nitrogen deposition, climate change, and CO_2 fertilization (Chen *et al.*, 2000).

The influence of autochthonous and allochthonous carbon on lake carbon cycling

Terrigenous sources can contribute as much as *GPP* to lake carbon pools. Though direct measurements of loads and aquatic ecosystem production are difficult to make in real ecosystems, estimates exist. Biddanda & Cotner (2002) found that allochthonous contributions to Lake Michigan were as much as 0.1 *GPP*, which would be equivalent to our *GPP*:C_{load} result of 10 (Fig. 7). Based on our model, oligotrophic and mesotrophic lakes have much lower *GPP*:C_{load} ratios of about 0.7 and 3, depending on *TP* concentration. Our lower estimates may reflect shorter water residence times in our lakes, which are an order of magnitude lower than that of Lake Michigan. The contribution of allochthonous carbon to lake metabolism also can be evaluated in terms of its subsidy to aquatic ecosystem *R*. Cole *et al.* (2002) found that 52% of *R* was supported by allochthonous *DOC*. A lake of similar nutrient concentrations in our model showed that allochthonous C subsidized at least 40% of *R*. Though all *DOC* in our model was pooled, making it impossible to determine which source was mineralized vs. exported, we can only balance *R* in excess of *GPP* through mineralization of allochthonous sources. In high C_{load} lakes, allochthonous C may subsidize as much as 85% of *R*.

Carbon loading influenced lake productivity through its effects on *DOC* concentration. In our model, shading did not limit light, and volumetric productivity was the same for all lakes of a given *TP* concentration. It was the effect of *DOC* on thermocline depth that indirectly limited productivity. As *DOC* concentration increased, thermocline depth decreased, and the biologically active volume of the lake decreased. Given two morphometrically equivalent lakes, one with a *DOC* concentration of $3 \, mg \, L^{-1}$ would have nearly five times the phototrophic volume of a lake with $25 \, mg \, L^{-1}$ of *DOC*.

Lakes often are categorized by trophic status, which is associated with *TP* and *DOC* concentrations (Kalff, 2002). In Fig. 10, we display the carbon budgets of four selected lake types from our model: oligotrophic (low *TP*, low *DOC*), eutrophic (high *TP*, low *DOC*), mesotrophic (moderate *TP*, low *DOC*) and dystrophic (low-to-moderate *TP*, high *DOC*). The oligotrophic lake had

NAF in excess of S. Its carbon load ($43\,g\,C\,m^{-2}\,LA\,yr^{-1}$) was similar to estimates for Mirror Lake (as high as $40\,g\,C\,m^{-2}\,LA\,yr^{-1}$) (Likens, 1985), as well as Canadian shield lakes (1–$52\,g\,C\,m^{-2}\,LA\,yr^{-1}$) (Dillon & Molot, 1997). The modeled S values ($7\,g\,C\,m^{-2}\,LA\,yr^{-1}$) also were similar to those for Mirror Lake (less than $12\,g\,C\,m^{-2}\,LA\,yr^{-1}$) (Cole et al., 1989). NAF in the oligotrophic lake ($28\,g\,C\,m^{-2}\,LA\,yr^{-1}$) was higher than a value of 13.8 estimated by Riera et al. (1999) for an oligotrophic lake in the same region. The eutrophic lake had the strongest NAF into the lake, and it also had the highest S. The eutrophic and mesotrophic lakes had S exceeding NAF. The dystrophic lake was qualitatively different from the others in that its load was roughly four times that of the others. Such a high load could represent carbon export from abundant surrounding wetlands, which can contribute as much as $500\,g\,C\,m^{-2}\,LA\,yr^{-1}$ (Kortelainen, 1993; del Giorgio & Peters, 1994). The high load to the dystrophic lake forces NAF to exceed S by a great margin, even though S was moderate ($17\,g\,C\,m^{-2}\,LA\,yr^{-1}$) and comparable with that of a similar lake ($18\,g\,C\,m^{-2}\,LA\,yr^{-1}$) (Jonsson et al., 2001). NAF in the modeled dystrophic lake ($141\,g\,C\,m^{-2}\,LA\,yr^{-1}$) was somewhat higher than a value estimated for a dystrophic lake in the same

region ($120\,g\,C\,m^{-2}\,LA\,yr^{-1}$) (Riera et al., 1999). Sedimentation values for all four lakes lie within reported estimates for organic carbon burial in temperate lakes (5–$72\,g\,C\,m^{-2}\,LA\,yr^{-1}$) (Dean & Gorham, 1998).

Most lakes were heterotrophic on an annual basis, and only under low DOC and moderate-to-high TP were lakes autotrophic. This result is consistent with previous work describing heterotrophy as the dominant condition in north temperate lakes during stratified periods (del Giorgio & Peters, 1994; Hanson et al., 2003; but see also Carignan et al., 2000). We also found that when DOC concentration in lakes exceeded $8\,mg\,L^{-1}$ (DOC loading of about $8\,g\,m^{-2}\,WA\,yr^{-1}$), lakes were consistently heterotrophic, but below that DOC concentration the trophic statuses varied, depending on the DOC and TP concentrations (Fig. 5c). In some ways, it was not surprising that this result was consistent with those of Hanson et al. (2003), because the GPP relationship in this study was derived empirically from TP and GPP data in theirs. However, the mechanisms for respiration were different between the two studies. Measured R was estimated from changes in gas concentration, whereas we modeled R as first-order decay rates from multiple carbon pools. The influence of DOC concentration on NEP has been reported in
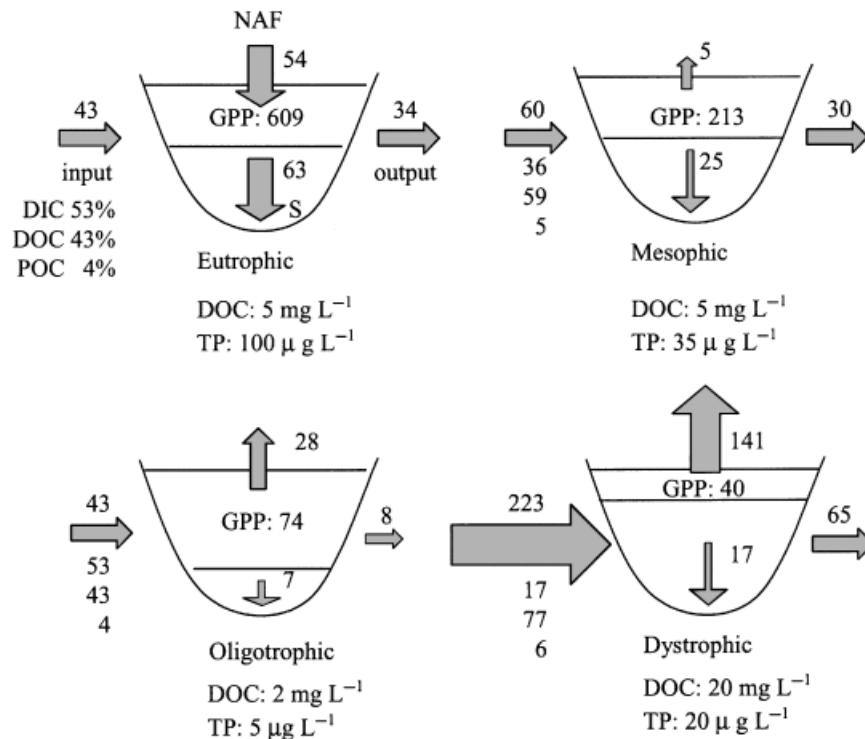

Fig. 10 Carbon loading (input), accumulation of carbon in the sediment pool (S), net atmospheric flux (NAF) and output (as labeled in the upper left lake) from four lakes representing the classical categories of lake trophic status. Units for the values adjacent to arrows are $gC\,m^{-2}\,LA\,yr^{-1}$. Dissolved organic carbon (DOC) and total phosphorus (TP) concentrations are mean annual values. Numbers below the input arrows are the relative percentages of the different carbon species in the input.

other research as well. Prairie *et al.* (2002) suggest that as *DOC* concentration exceeds about $6\,mg\,L^{-1}$, lakes become net heterotrophic.

Lakes as net sinks or net sources of carbon

The combined influences of *TP* concentration and carbon load on *NAF* and *S* are highlighted in Fig. 11. Using the results of the simulations for each carbon load, we determined the *TP* concentration at which *NAF* equaled *S* and plotted it as the solid line. We performed a similar calculation for *R* and *GPP* and plotted it as the dashed line. Filled circles representing lakes in this study were plotted on the graph according to their assumed carbon loads and *TP* concentrations. About 75% of the lake space in this study was in the regions of heterotrophy and net sources of carbon to the atmosphere. Only those lakes low in carbon load and moderate-to-high in *TP* fell into the autotrophic and net sink regions. Although our model did not address the frequency distribution of lake *DOC* and *TP* concentrations, many of the lakes in this region of Wisconsin are oligotrophic, or similar in nutrient concentrations to those lakes in the lower left corner of the figure. Because these lakes are close to the trophic threshold line, we felt the model warranted closer inspection of the most influential parameter at these nutrient concentrations. The following analysis investigates the positions of those lines as a function of *ra*, the proportion of *GPP* respired quickly.

The value of *ra* influenced the amount of lake space that fell into the heterotrophic and net source classifica-

tions. When *ra* was set to 0.88, about 90% of the total lake space was heterotrophic and the threshold for lakes with the least carbon load rose to about $22\,\mu g\,TP\,L^{-1}$. When *ra* was 0.72, about 65% of the total lake space was heterotrophic and the autotrophic threshold for oligotrophic lakes dropped to about $5\,\mu g\,TP\,L^{-1}$. Only by reducing *ra* to values below about 0.7 could we force the autotrophic threshold below $5\,\mu g\,TP\,L^{-1}$ for the lowest *DOC* lakes. However, when *ra* was this low, carbon burial in lakes with $TP > 80\,\mu g\,L^{-1}$ was well above $100\,gC\,m^{-2}\,LA\,yr^{-1}$, which exceeded literature values for eutrophic lakes (Rea *et al.*, 1981). The mechanism by which changes in *ra* propagate through the model is by the inverse relationship of *ra* with POC_L, which could also be thought of as algal biomass. The uncertainty in *ra* may reflect scatter in relationships between *TP* and algal biomass in real systems. Although the range in summer epilimnetic POC_L in our model falls within reported algal biomass values for lakes with similar *TP* concentrations (Wetzel, 2001), algal biomass in real lakes can be influenced by factors other than *TP*, including aquatic food webs. Experiments on lakes have demonstrated that food webs can alter primary productivity, which in turn can alter carbon *NAF* with the atmosphere (Schindler *et al.*, 1997). The abundance of zooplankton can either increase or decrease C flux out of the mix layer, depending on plankton concentrations (Sarnelle, 1999).

A simple approach to evaluating the effect of consumers on *NAF* and *S* in this model is to adjust
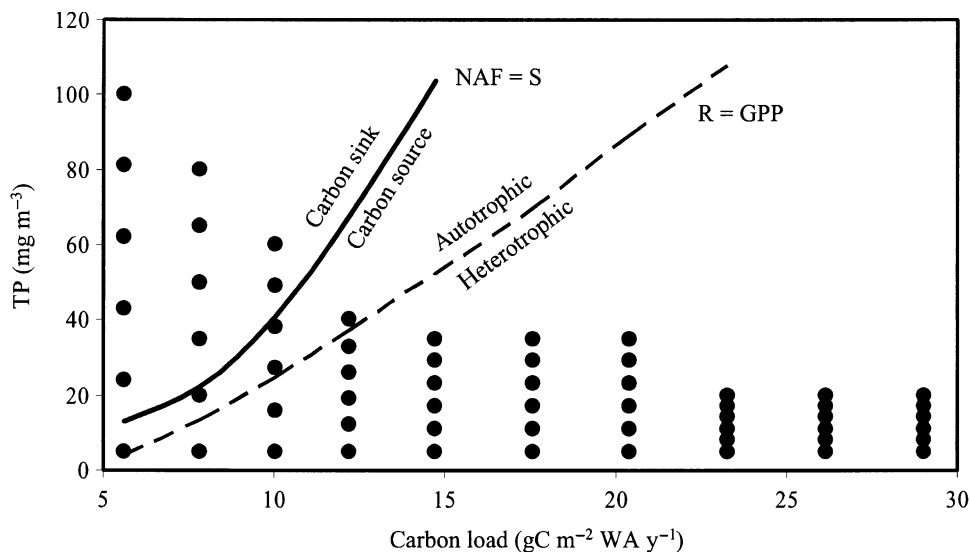

Fig. 11 Lakes from the simulation are plotted in a lake space with gradients of total C loading and total phosphorus (*TP*) concentration. The dashed line represents the dissolved organic carbon (*DOC*) and *TP* combinations that produce net ecosystem production (*NEP*) of zero (gross primary production (*GPP*) = *R*). Lakes above this line are autotrophic, and lakes below are heterotrophic. The solid line represents *DOC* and *TP* combinations in which *S* equals net atmospheric flux (*NAF*). Lakes above this line are net sinks of atmospheric carbon and lakes below this line are net sources of atmospheric carbon.

the parameter (*ed*) that converts POC_L to POC_D. If we assume that consumers ingest POC_L and excrete POC_D, which is subject to sedimentation and bacterial respiration, then the effect of consumers on the system is analogous to that of *ed*. Evaluating the model's sensitivity to consumers was accomplished by evaluating its sensitivity to changes in *ed*. A decrease in *S* of 10% required a doubling of *ed*. To increase *NAF* by 10%, *ed* was increased 18-fold. The greater sensitivity of *S* to *ed* may be the result of excluding consumer respiration in this analysis. Although adding the consumer pool would allow for partitioning between consumer excretion and respiration, the simplicity of the present model seems justified by its lack of sensitivity to *ed*.

Conclusions

This model of a lake in a landscape is perhaps the simplest representation that could be used to address our questions about the contributions of lakes to processing, sequestration, and atmospheric flux of carbon. Despite its simplicity, the patterns predicted by the model are consistent with the available literature and our field measurements. It is somewhat surprising that a steady-state model was generally consistent with measurements of dynamic ecosystem processes. Nevertheless, further modeling and empirical work on temporal change in carbon processing is needed to determine the conditions under which steady-state assumptions may be important, and understand the patterns of change in carbon processing over time.

The model suggests that carbon processing by lakes is significant and worthy of exploration as an important component of carbon processing on landscapes rich in lakes. What spatial patterns of carbon processing emerge from the topographic, hydrologic, and biotic heterogeneity of real landscapes? How does the variable morphometry of real lakes affect the magnitude of *NAF* and carbon sequestration? As landscapes become drier or wetter over long-time scales, how do changes in lake dimensions affect carbon processing, CO_2 flux, and carbon sequestration at the landscape scale? These are among the questions that suggest the need for modeling and observational approaches that address landscapes and the lakes they contain in integrated ways.

Acknowledgements

References

Aitkenhead JA, McDowell WH (2000) Soil C : N ratio as a predictor of annual riverine DOC flux at local and global scales. *Global Biogeochemical Cycles*, **14**, 127–138.

Baines SB, Pace ML (1991) The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. *Limnology and Oceanography*, **36**, 1078–1090.

Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present, and future. *Global Change Biology*, **9**, 479–492.

Barford CC, Wofsy SC, Goulden ML et al. (2001) Factors controlling long- and short-term sequestration of atmospheric CO_2 in a mid-latitude forest. *Science*, **294**, 1688–1690.

Biddanda BA, Benner R (1997) Carbon, nitrogen, and carbohydrate fluxes during the production of particulate and dissolved organic matter by marine phytoplankton. *Limnology and Oceanography*, **42**, 506–518.

Biddanda BA, Cotner JB (2002) Love handles in aquatic ecosystems: the role of dissolved organic carbon drawdown, resuspended sediments, and terrigenous inputs in the carbon balance of Lake Michigan. *Ecosystems*, **5**, 431–445.

Carignan R, Dolors P, Vis C (2000) Planktonic production and respiration in oligotrophic Shield lakes. *Limnology and Oceanography*, **45**, 189–199.

Carpenter SR (1992) Destabilization of planktonic ecosystems and blooms of blue-green algae. In: *Food Web Management, a Case Study of Lake Mendota* (ed. Kitchell JF), pp. 461–481. Springer-Verlag, Inc, New York.

Carpenter SR, Cole JJ, Kitchell JF et al. (1998) Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. *Limnology and Oceanography*, **43**, 73–80.

Chen J, Chen W, Liu J et al. (2000) Annual carbon balance of Canada's forests during 1895–1996. *Global Biogeochemical Cycles*, **14**, 839–849.

Cole JJ, Caraco NF, Kling GW et al. (1994) Carbon dioxide supersaturation in the surface waters of lakes. *Science*, **265**, 1568–1570.

Cole JJ, Caraco NF, Strayer CL et al. (1989) A detailed organic carbon budget as an ecosystem-level calibration of bacterial respiration in an oligotrophic lake during midsummer. *Limnology and Oceanography*, **34**, 286–296.

Cole JJ, Carpenter SR, Kitchell JF et al. (2002) Pathways of organic carbon utilization in small lakes: results from a whole-lake ^{13}C addition and coupled model. *Limnology and Oceanography*, **47**, 1664–1676.

Connolly JP, Coffin RB (1995) Model of carbon cycling in planktonic food webs. *Journal of Environmental Engineering – ASCE*, **121**, 682–690.

Curtis PS, Hanson PJ, Bolstad P et al. (2002) Biometric and eddy covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology*, **113**, 3–19.

Dean WE, Gorham E (1998) Magnitude and significance of carbon burial in lakes, reservoirs, and peatlands. *Geology*, **26**, 535–538.

del Giorgio PA, Cole JJ, Caraco NF *et al.* (1999) Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. *Ecology,* 80, 1422–1431.

del Giorgio PA, Peters RH (1994) Patterns in planktonic P : R ratios in lakes: influence of lake trophy and dissolved organic carbon. *Limnology and Oceanography,* 39, 772–787.

Dillon PJ, Molot LA (1997) Dissolved organic and inorganic carbon mass balances in central Ontario lakes. *Biogeochemistry,* 36, 29–42.

Ehman JL, Schmid HP, Grimmond CSB *et al.* (2002) An initial intercomparison of micrometeorological and ecological inventory estimates of carbon exchange in a mid-latitude deciduous forest. *Global Change Biology,* 8, 575–589.

Eilers JM, Brakke DF, Landers DH (1988) Chemical and physical characteristics of lakes in the Upper Midwest, United States. *Environmental Science & Technology,* 22, 164–172.

Hanson PC (2003) *Metabolism in the surface waters of north temperate lakes.* PhD thesis, University of Wisconsin.

Hanson PC, Bade DL, Carpenter SR *et al.* (2003) Lake metabolism: relationships with dissolved organic carbon and phosphorus. *Limnology and Oceanography,* 48, 1112–1119.

Hessen DO (1992) Dissolved organic carbon in a humic lake: effects on bacterial production and respiration. *Hydrobiologia,* 229, 115–123.

Hope D, Kratz TK, Riera JL (1996) Relationship between pCO_2 and dissolved organic carbon in northern Wisconsin lakes. *Journal of Environmental Quality,* 25, 1442–1445.

Houghton RA (2003) Why are estimates of the terrestrial carbon balance so different? *Global Change Biology,* 9, 500–509.

Houser JN (2001) *Dissolved organic carbon in lakes: Effects on thermal structure, primary production, and hypolimnetic metabolism.* PhD thesis, University of Wisconsin.

Jackson TA, Hecky RE (1980) Depression of primary productivity by humic matter in lake and reservoir waters of the boreal forest zone. *Canadian Journal of Fisheries and Aquatic Sciences,* 37, 2300–2317.

Jansson M, Bergstrom AK, Blomqvist P *et al.* (2000) Allochthonous organic carbon and phytoplankton/bacterioplankton production relationships in lakes. *Ecology,* 81, 3250–3255.

Jones RI (1992) The influence of humic substances on lacustrine planktonic food chains. *Hydrobiologia,* 229, 73–91.

Jonsson A, Meili M, Bergstrom AB *et al.* (2001) Whole-lake mineralization of allochthonous and autochthonous organic carbon in a large hume lake (Ortrasket, N. Sweden). *Limnology and Oceanography,* 46, 1691–1700.

Kalff J (2002) *Limnology.* Prentice-Hall, Inc, Upper Saddle River.

Kortelainen P (1993) Content of total organic carbon in Finnish lakes and its relationship to catchment characteristics. *Canadian Journal of Fisheries and Aquatic Sciences,* 50, 1477–1483.

Likens GE (1985) *An Ecosystem Approach to Aquatic Ecology: Mirror Lake and its Environment.* Springer, Berlin.

Michaels SS (1995) *Regional analysis of lakes, groundwaters, and precipitation, Northern Wisconsin: a stable isotope study.* MS thesis, University of Wisconsin.

Mulholland PJ (2003) Large-scale patterns in dissolved organic carbon concentration, flux, and sources. In: *Aquatic Ecosystems: Interactivity of Dissolved Organic Matter* (eds Stuart EG, Findlay G, Sinsabaugh RL), pp. 139–159. Elsevier Science, USA.

Peterson GD, Beard TD, Beisner BE *et al.* (2003) Assessing future ecosystem services: a case study of the Northern Highlands Lake District, Wisconsin. *Conservation Ecology,* 7, 1 [online] URL: http://www.consecol.org/vol7/iss3/art1.

Prairie YT, Bird DF, Cole JJ (2002) The summer metabolic balance in the epilimnion of southeastern Quebec lakes. *Limnology and Oceanography,* 47, 316–321.

Quay PD, Emerson SR, Quay BM *et al.* (1996) The carbon cycle for Lake Washington – a stable isotope study. *Limnology and Oceanography,* 31, 596–611.

Rea DK, Wen RM, Meyers PA (1981) Sedimentary processes in the Great Lakes. *Reviews of Geophysics and Space Physics,* 19, 635–648.

Riera JL, Schindler JE, Kratz TK (1999) Seasonal dynamics of carbon dioxide and methane in two clear-water lakes and two bog lakes in northern Wisconsin, U.S.A. *Canadian Journal of Fisheries and Aquatic Science,* 56, 265–274.

Sarnelle O (1999) Zooplankton effects on vertical particulate flux: Testable models and experimental results. *Limnology and Oceanography,* 44, 357–370.

Schindler DE, Carpenter SR, Cole JJ *et al.* (1997) Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science,* 277, 248–251.

Snucins E, Gunn J (2000) Interannual variation in the thermal structure of clear and colored lakes. *Limnology and Oceanography,* 45, 1639–1646.

Sobek SGA, Bergstrom A, Jansson M *et al.* (2003) The catchment and climate regulation of pCO_2 in boreal lakes. *Global Change Biology,* 9, 630–641.

Striegl RB, Kortenainen RBP, Chanton JP *et al.* (2001) Carbon dioxide partial pressure and 13C content of north temperate and boreal lakes at spring ice melt. *Limnology and Oceanography,* 46, 941–945.

Stumm W, Morgan JJ (1981) *Aquatic Chemistry,* 2nd edn. John Wiley and Sons, Toronto.

Webster KE, Soranno PA, Baines SB *et al.* (2000) Structuring features of lake districts: landscape controls on lake chemical responses to drought. *Freshwater Biology,* 43, 449–515.

Wetzel RG (2001) *Limnology,* 3rd edn. Academic Press, San Diego.

Wilson KB, Baldocchi DD (2001) Comparing independent estimates of carbon dioxide exchange over five years at a deciduous forest in the southern United States. *Journal of Geophysical Research-Atmospheres,* 106, 34167–34178.

Xenopoulos MA, Lodge DM, Frentress J *et al.* (2003) Regional comparisons of watershed determinants of dissolved organic carbon in temperate lakes from the Upper Great Lakes region and selected regions globally. *Limnology and Oceanography,* 48, 2321–2334.