JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 112, G02031, doi:10.1029/2006JG000200, 2007

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Carbon and water cycling in lake-rich landscapes: Landscape connections, lake hydrology, and biogeochemistry

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Received 18 March 2006; revised 19 December 2006; accepted 23 February 2007; published 21 June 2007.

[1] Lakes are low-lying connectors of uplands and wetlands, surface water and groundwater, and though they are often studied as independent ecosystems, they function within complex landscapes. One such highly connected region is the Northern Highland Lake District (NHLD), where more than 7000 lakes and their watersheds cycle water and carbon through mixed forests, wetlands, and groundwater systems. Using a new spatially explicit simulation framework representing these coupled cycles, the Lake, Uplands, Wetlands Integrator (LUWI) model, we address basic regional questions in a 72-lake simulation: (1) How do simulated water and carbon budgets compare with observations, and what are the implications for carbon stocks and fluxes? (2) How do the strength and spatial pattern of landscape connections vary among watersheds? (3) What is the role of interwatershed connections in lake carbon processing? Results closely coincide with observations at seasonal and annual scales and indicate that the connections among components and watersheds are critical to understanding the region. Carbon and water budgets vary widely, even among nearby lakes, and are not easily predictable using heuristics of lake or watershed size. Connections within and among watersheds exert a complex, varied influence on these processes: Whereas inorganic carbon budgets are strongly related to the number and nature of upstream connections, most organic lake carbon originates within the watershed surrounding each lake. This explicit incorporation of terrestrial and aquatic processes in surface and subsurface connection networks will aid our understanding of the relative roles of on-land, in-lake, and between-lake processes in this lake-rich region.

Citation: Cardille, J. A., S. R. Carpenter, M. T. Coe, J. A. Foley, P. C. Hanson, M. G. Turner, and J. A. Vano (2007), Carbon and water cycling in lake-rich landscapes: Landscape connections, lake hydrology, and biogeochemistry, *J. Geophys. Res.*, *112*, G02031, doi:10.1029/2006JG000200.

1. Introduction

[2] Understanding carbon and water cycling in lake-rich landscapes presents a fundamental challenge at the frontiers of ecosystem and landscape ecology. From an ecosystem perspective, the magnitude of stocks and fluxes to, within, and among uplands, wetlands, and lakes is an area of active research [*Strayer et al.*, 2003a], and a key frontier in the discipline [*Chapin et al.*, 2002; *Lovett et al.*, 2005]. From a landscape perspective, such strongly linked systems raise the question of quantifying the influence, function, and pattern of connections among elements and their influence on spatial variation across the region [*Reiners and Driese*, 2004; *Turner and Chapin*, 2005; *Wiens et al.*, 1985]. Analyses linking long-term, spatially extensive field data with conceptual models of mass flux through an integrated, spatially explicit framework provide an opportunity to make substantial progress toward understanding the relationship between pattern and process in coupled biogeochemical systems.

[3] One region inviting, and perhaps necessitating, this integrated perspective is the lake-rich Northern Highland Lake District (NHLD) of northern Wisconsin and the Upper Peninsula of Michigan [*Magnuson et al.*, 2006; *Peterson et al.*, 2003]. In this region, lakes, uplands, and wetlands interact in watersheds of varying size and shape, with aboveground and belowground connections influencing the movement of water [*Walker and Krabbenhoft*, 1998], nutrients [*Baines et al.*, 2000], and organisms [*Hrabik and Magnuson*, 1999; *Tonn et al.*, 1990]. The sandy glacial soils and gradually sloping land surface lead to groundwater being a significant water source for many lakes, influencing both biogeochemistry and biotic communities across the landscape [*Hrabik et al.*, 2005; *Krabbenhoft and Webster*,

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0148-0227/07/2006JG000200$09.00

1995; *Riera et al.*, 2000]. In lakes where groundwater is thought to be an important component of the water budget, there may be strong connections among sets of lakes and watersheds [*Anderson and Cheng*, 1993] that are challenging to observe [*Walker and Krabbenhoft*, 1998] with significant variations occurring horizontally [*Magnuson et al.*, 1998], vertically [*Schindler and Krabbenhoft*, 1998; *Walker et al.*, 2003], and temporally [*Webster et al.*, 2000]. The concept of landscape position [*Kratz et al.*, 1997], the result of an effort to understand major ecological drivers in the district, has proven to be a powerful tool for understanding both the long-term state of interconnected lakes in the NHLD as well as their varied biogeochemical and hydrologic responses to perturbations [*Anderson and Cheng*, 1993; *Carpenter et al.*, 2001; *Cole et al.*, 2000; *Soranno et al.*, 1999; *Webster et al.*, 2000]. However, the richly detailed knowledge of these intensively studied lakes has not been extended to the larger landscape of the entire NHLD, owing to lack of tools for addressing the complex hydrologic and biogeochemical connections among lakes and their watersheds at the regional scale.

[4] Despite challenges in representing integrated spatially explicit water/carbon budgets in large areas, much is known about the water and carbon balance in major ecosystem components: uplands, lakes, and groundwater pools of these ecosystems. These components include upland forests [*He et al.*, 2000], lakes [*Pace and Cole*, 2002], wetlands [*Elder et al.*, 2000; *Gergel et al.*, 1999], and groundwater pools [*Dripps et al.*, 2006]. Generally, hydrologically focused studies have centered on the substantial effects of a lake's groundwater collecting area [*Dripps et al.*, 2006; *Pint et al.*, 2003] and the relationship between lake area and watershed area [*Vassiljev*, 1997]. The sources, stocks and dynamics of carbon and other nutrients in lakes has been explored for multiple lakes [*Cole et al.*, 2002; *Elder et al.*, 2000; *Hanson et al.*, 2003; *Schindler and Krabbenhoft*, 1998] and extensive lake chains and regions [*Martin and Soranno*, 2006; *Soranno et al.*, 1999; *Xenopoulos et al.*, 2003]. Most recently, new GIS databases of morphometric and terrestrial factors have been used to marshal larger sets of factors to understand observed drivers of carbon concentration in lakes [*Elder et al.*, 2000; *Gergel et al.*, 1999], including models of spatially explicit movement of C within watersheds [*Canham et al.*, 2004]. However, a flexible, working framework is currently lacking for understanding both the magnitude and the spatial pattern of integrated water and carbon fluxes and how they interact to drive the state and behavior of linked sets of lakes.

[5] In regions such as the NHLD many of the carbon and water components are thought to be highly connected, but the extent to which the resulting watershed and lake budgets can be treated as essentially independent across a region, and the extent to which connections must be directly incorporated, is still unknown. Although measuring connection strengths and carbon and water fluxes can be done with substantial dedicated effort for a chain of lakes, it is likely to be prohibitively expensive for a landscape of dozens, hundreds, or thousands of lakes. As a result, quantifying the region-wide influence and patterns of connections among ecosystem components in this region remains a lingering question.

[6] To explore and better understand the importance of upstream and downstream connections for lateral fluxes among tightly coupled ecosystems, we developed a spatially explicit ecological numerical simulation model, LUWI (Lakes, Uplands, and Wetlands Integrator), for application to water and carbon processing in the Northern Highlands. Developed from a simpler prototype [*Cardille et al.*, 2004], the model simulates major stocks and flows of carbon and water in lakes and watersheds, using integrated simulations of terrestrial vegetation and lake carbon processing in a spatially explicit mass-movement framework. In this paper, following the general description of the model and its application in this region, we used LUWI to address the following questions about a groundwater-driven set of lakes in the Northern Highland Lake District: (1) How do simulated water and carbon budgets compare with observations, and what are the implications for carbon stocks and fluxes? (2) How do the strength and spatial pattern of landscape connections vary among watersheds? (3) What is the role of interwatershed connections in lake carbon processing?

2. Study Area

[7] The Northern Highland Lake District of northern Wisconsin and the Upper Peninsula of Michigan (Figure 1), is a 5000 km^2 region containing more than 7500 lakes [*Bureaus of Water Resources Management and of Fisheries Management*, 2001]. Lakes range in size from small ponds and bogs to lakes well over 1000 ha and have depths from 1 to more than 30 m. Lakes were formed during the retreat of the last glaciers some 12,000 years ago [*Martin*, 1965; *Peterson et al.*, 2003]. Deciduous and coniferous forests dominate the uplands, which comprise 62% of the surface area, and wetlands (25%) and lakes (13%) constitute the remainder. Lake density is higher near the center of the district; in Vilas County, the location of the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) Program [*Magnuson et al.*, 2006] (http://lter.limnology.wisc.edu), 15% of the surface area is open lake water.

[8] Data from three of the seven NTL-LTER study lakes were used extensively in this project. These lakes span much of the observed range of inorganic carbon concentrations in the region, but have low organic carbon concentrations relative to the range of other NTL-LTER lakes and lakes in the NHLD [*Magnuson et al.*, 2006]. The hydrologic and biogeochemical aspects of these lakes have been studied continuously since 1982 and form a long-term record suitable for comparison with the behavior of a steady state simulation model. The three lakes are: Crystal Lake, a small lake with little groundwater inflow, perched above the water table in typical years but a groundwater flow-through lake in wet years; Big Muskellunge Lake, a large deep lake with no permanent outflow stream in today's climate; and Allequash Lake, a drainage lake with a gauged outflow stream, surrounded by extensive wetlands and a spring input [*Magnuson et al.*, 2006].

[9] The analysis region for this study was the subregion of the NHLD estimated to be in the potential water-collecting area for Allequash Lake (Figure 1). We identified 72 watersheds (Figure 1) that could, in current or future climates, contribute to the hydrologic budget of Allequash

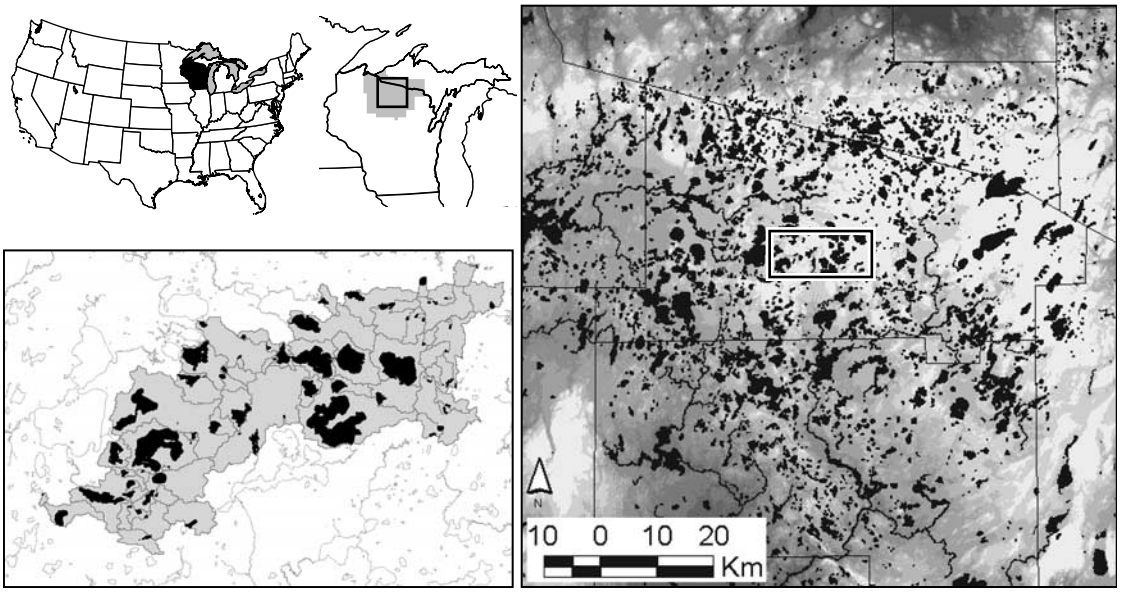

Figure 1. Location of Northern Highland Lake District in Wisconsin. Location of 72 study lakes within the larger 7500-lake landscape: lakes (black) and their estimated groundwater watersheds (gray).

Lake through surface or groundwater inputs. The watersheds included those for Crystal Lake and Big Muskellunge Lake. Three algorithms described below identify the potential stream connections, lake-to-groundwater connections, and groundwater flow paths that comprise the 72-watershed network.

3. Model Structure and Data

[10] The LUWI model simulates water and carbon fluxes and pools for numerous connected watersheds. For all three components, the pools, fluxes, and network connections, are dynamic components of the model. The fundamental spatial unit of the model is a watershed, representing a spatially explicit estimate of the immediate groundwater capture zone for a given lake. (Methods for estimating watersheds are described in detail in the auxiliary material[1].) Therefore the spatial units vary in size depending on the estimated hydrologic contributing area for each lake. This watershed unit approach results in a substantially smaller number of modeled elements than a raster framework, permitting simulations covering spatial extents much larger than would be practical in a raster-based framework.

[11] In each watershed, three water pools (Lake, Groundwater, and Wetland) and two carbon pools (Lake OC, Lake IC) are represented, with stocks determined through a total of 18 fluxes into, within, and from watersheds (Figure 2). In the spatially explicit and dynamic framework, carbon processing within lakes and the strength of hydrologic connections among pools both within and among watersheds may change throughout a simulation depending on a number of factors, for example precipitation, evaporation, runoff and discharge, changing carbon stocks, and subsurface connections among watersheds. All stocks and fluxes are described below.

[1]Auxiliary materials are available in the HTML. doi:10.1029/2006JG000200.

3.1. Pools and Fluxes: Water

[12] Water pools and fluxes are represented at each time step for each watershed in the simulation (Figure 2). In a watershed, the Groundwater pool (of volume V_G, m^3) represents the saturated zone of the soil within a watershed, and may receive water via drainage through the soil column from uplands, and flow from upstream lakes, and other upstream groundwater pools. The Wetland pool (of volume V_T, m^3) is a coarse representation of the aggregate hydrologic processing within wetlands contained within the entirety of each watershed. Its balance derives from the groundwater flow in, inputs from and outputs to the atmosphere, and flow out to the lake. The Lake water pool (of volume V_L, m^3) is modeled as a dynamic balance between stream inflow and outflow, groundwater input and output, input from the wetland, and precipitation and evaporation on the lake.

3.1.1. To Watershed

[13] Water may enter a watershed in five ways (Figure 2 and Table 1). Precipitation on the lake (PL, m^3) and wetland (PT, m^3) are input terms provided by local climate records. They vary throughout the year, adding a volume proportional to the lake surface area (LA, m^2) and the wetland surface area (TA, m^2), respectively. Water may enter the groundwater pool of a watershed from one or more upstream lakes (LGI, m^3) or from upstream groundwater pools (GGI, m^3). Water may also arrive via streamflow (LLI, m^3) from one or more upstream watersheds.

3.1.2. Within Watershed

[14] Water may move within a watershed in five ways (Figure 2 and Table 1). Drainage from the terrestrial upland component, D (m^3), enters the Groundwater pool of a watershed. Surface runoff, RU (m^3), enters the lake directly from uplands. D and RU are input terms provided by the land surface model IBIS, formed as the residual from precipitation on the upland surface and evapotranspiration from modeled vegetation demand. Lakes can receive in-

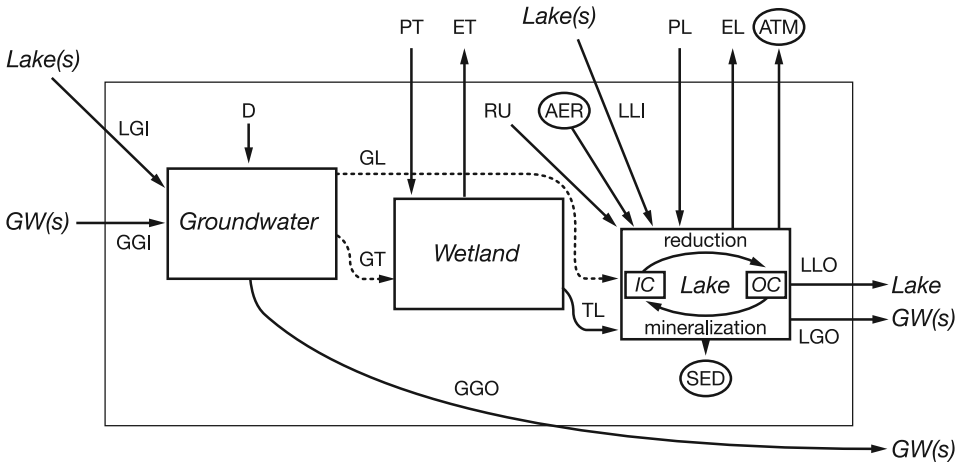

Figure 2. Conceptual graph of hydrologic and carbon fluxes and stocks. All hydrologic fluxes contain carbon except evaporation from the lake (EL) and wetland (EW). Carbon fluxes are water-borne except sedimentation (SED) and atmospheric exchange (ATM). Dynamic carbon stocks (IC, OC) are explicitly modeled in the lake as described in the text.

coming groundwater from their associated Groundwater pool via the GL (m^3) flux. Groundwater may enter the Wetland pool through the GT (m^3) flux. Water passing through the wetland enters the lake via the TL (m^3) flux.

3.1.3. From Watershed

[15] Water may leave a watershed in five ways (Figure 2 and Table 1). Water from the Groundwater pool may leave the watershed without passing through a Lake or Wetland, flowing instead to one or more downstream Groundwater pools (GGO, m^3). Flow may occur from a watershed's lake to the groundwater pool of one or more downstream watersheds (LGO, m^3). Streamflow may occur from a lake to one other lake (LLO, m^3). Two evaporative terms may remove water from a watershed: EL (m^3), evaporation from the lake surface, and ET (m^3), evaporation from the wetland. Both fluxes remove water from their respective pools in proportion to the pool's surface area and the evaporative demand from the modeled climate.

3.2. Pools and Fluxes: Carbon

[16] Carbon pools and fluxes are represented among and within watersheds at each time step. Two carbon pools are tracked within each lake: Inorganic Carbon (IC, g) and Organic Carbon (OC, g). All dissolved and particulate OC

Table 1. Fluxes of Water and Carbon in LUWI[a]

	Water, m^3			Carbon Concentration in Flux, g/m^3		
	Origin	Destination	Variable	IC[b]	OC[b]	Source[c]
Flows To watershed	precipitation	lake	PL	1.0	2.0	a
	precipitation	wetland	PT	1.0	2.0	a
	lake(s)	groundwater	LGI	lake conc	0.0	f
	groundwater(s)	groundwater	GGI	nm	nm	f
	lake(s)	lake	LLI	same as upstream lake	same as upstream lake	f
Flows within watershed	terrestrial	groundwater	D	nm	nm	na
	terrestrial	lake	RU	2.0	4.0	e
	groundwater	lake	GL	9.7	1.7	b
	groundwater	wetland	GT	nm	nm	f
	wetland	lake	TL	33.8	10.0	b
Flows from watershed	groundwater	groundwater(s)	GGO	nm	nm	f
	lake	groundwater(s)	LGO	lake conc	0.0	f
	lake	lake	LLO	same as upstream lake	same as upstream lake	f
Water-only exchanges with atmosphere	lake	atmosphere	EL	na	na	c
	wetland	atmosphere	EW	na	na	c
Carbon-only exchanges with atmosphere	lake	atmosphere	ATM	dynamic	-	f
	lake shore	lake	AET	-	7.8 g/m shoreline daily	d
Lake sedimentation	lake	sediment	SED	-	dynamic	f

[a]Here na means flux does not contain carbon and nm means that carbon in this flux is not explicitly modeled.

[b]Where concentrations are given for carbon species, the corresponding variable appears in the flux equations in description in the text. Examples: PLIC; LGOIC.

[c]Source notation: a, on the basis of pH of local precipitation and assumed low ANC in precipitation [*Willey et al.*, 2000], we calculated DIC of precipitation from carbonate equilibria [*Stumm and Morgan*, 1981]; b, by design of the conceptual model; c, evaporation amount from Sparkling Lake data (see text); d, fitted based on initial estimate of 4 g/day particulate organic carbon per meter of lake shoreline; e, Emily Stanley, personal communication, 2004; f, these values are modeled explicitly and vary dynamically through time in the simulation.

entering the lake is lumped into the OC pool. As with lake water stocks, carbon stocks in the lake may vary during the simulation according to lake inputs, lake outputs, and in-lake processing. Change in carbon content during groundwater flow is a quite complex phenomenon outside the scope of this model, and so carbon stocks are not explicitly tracked within the groundwater pools as well as in wetlands; instead, carbon concentrations in groundwater and the water leaving wetlands are treated as input terms with fixed values from observed data (Table 1). Reduction and mineralization are explicitly modeled in each lake, and reallocate carbon between the two pools at each time step as described below.

3.2.1. To Watershed

[17] Carbon contained in precipitation falling on the lake (PL) enters in fixed concentrations derived from observations (Table 1). Unlike other flows of carbon, the carbon concentration of incoming streamflow is not fixed, but is of the same concentration as the upstream lake from which it arrives.

3.2.2. Within Watershed

[18] AER (g) is the estimated aerial addition of carbon to the organic carbon pool of each lake from terrestrial sources within its watershed (including downed wood, pollen, insects, etc.). It was estimated to be 7.8 g/day per meter of lake shoreline, on the basis of model calibration runs for Crystal Lake. The area-normalized value (about 50 mg m^{-2} d^{-1} for Crystal Lake) is consistent with input rates of 35 to 104 mg m^{-2} d^{-1} measured in whole-lake experiments in the NHLD [*Carpenter et al.*, 2005].

3.2.3. From Watershed

[19] ATM (g), the net inorganic carbon flux between the lake and atmosphere, is a function of the concentration gradient between the lake and the atmosphere. Lake-to-groundwater flow (LGO) removes both water and IC from the upstream lake at its current concentration for transport to one or more downstream lakes. Streamflow (LLO) between lakes contains organic and inorganic carbon exported via streams at the concentrations of the upstream lake.

3.2.4. In-Lake Carbon Transformations

[20] In each lake, changes in concentrations of IC and OC result from loads, exports, and transformations of carbon and changes in lake water volume. Both surface and subsurface carbon loads are added to the existing lake IC and OC pools at each time step. Carbon export from the lake via groundwater and surface water is the product of the lake concentration and the export volume at each time step. Export from the water column also occurs through sedimentation (SED), which is the sum of two processes: a first-order decay of lake OC, for which the sedimentation rate coefficient is fit in the calibration process, and any flocculation of OC. The mass of OC that flocculates (C_{floc}, g) in each lake at each summer time step is calculated as

$$C_{floc} = \max(0, [OC] - (40 * ([OC])/(20 + [OC]) * V_L)).$$

This equation results in no flocculation for low-and medium-OC lakes (0–20 mg L^{-1}). For [OC] >20 mg L^{-1}, flocculation increases rapidly with increasing OC concentration. This limits the maximum OC concentration to 40 g m^{-3}, which is at the upper end of the range of concentrations found in lakes in this region [*Eilers et al.*, 1988].

[21] Atmospheric exchange of IC may be either toward or away from each lake at a given time step, depending on the CO_2 saturation condition of the lake at that time. The CO_2 fraction of the IC pool is calculated from an estimated value of lake acid neutralizing capacity (ANC) and the IC concentration of each lake [*Mook et al.*, 1974; *Zhang et al.*, 1995]. Atmospheric exchange, ATM, is calculated after *Cole and Caraco* [1998] as

$$ATM = k_{CO2} * (CO_{2water} - CO_{2atm})/Z_{mix},$$

where k_{CO2} (m d^{-1}) is calculated [*Wanninkhof et al.*, 1985] from an assumed value for k_{600} of 0.5 m d^{-1}. CO_{2water} is the mass (g) of CO_2 in the water and CO_{2atm} is the atmospheric equilibrium mass of CO_2 in the water, given the water temperature (see seasonality below) and the altitude of the NHLD. The mixed layer depth, Z_{mix}, varies seasonally and is detailed in the auxiliary material. Atmospheric exchange occurs only during ice-free seasons in the model.

[22] Transformation of carbon in a lake occurs through reduction and oxidation acting on the IC and OC pools. Reduction, which converts IC to OC, occurs in the mixed layer only during the ice-free season in the model. It is calculated as the product of gross primary production (GPP), calculated from the estimated value of total phosphorus concentration (TP), and the reduction coefficient, which is assumed to be 0.2 [*Hanson et al.*, 2004]. The reduction coefficient determines the proportion of GPP that remains in the OC pool, with the remainder of GPP reverting to the IC pool. Oxidation is calculated as a first-order decay of the OC pool from the entire lake, with the decay coefficient (oxidation coefficient) fit during the model calibration process. Both reduction and oxidation are adjusted for temperature according to the Arrhenius equation (e.g., for oxidation),

$$Ox_t = Ox_0 \times 2^{((\text{Current Temperature} - \text{BaseT})/10)},$$

where BaseT = 20 is the base temperature, Ox_0 is oxidation unadjusted for temperature, and Ox_t is the temperature-adjusted oxidation.

3.3. Driving Data

[23] A wealth of existing and new driving data was used to explore the ability of the model to capture major features of today's hydrology and carbon processing in the NHLD. Designed for application over the entire NHLD, the model required the estimation of key properties of lakes, watersheds, and the explicit connections among them. Detailed hydrologic, carbon, and morphometric properties of all but a few of the 7500+ lakes of the Northern Highland Lake District are virtually unknown. This necessitated the development of a large amount of new information across the region, extrapolating when possible from lakes and watersheds having well-understood properties. In all but the LTER lakes, only lake area and lake and land elevation were known a priori; lake connection information was interpreted for the NHLD from these data sources. These and other driving data are described below.

3.3.1. Lake Area, Volume, and Depth

[24] We used the Wisconsin Department of Natural Resources lake coverage [*Bureaus of Water Resources*

Management and of Fisheries Management, 2001], as the basis for the location and area of each lake in the NHLD. Because the actual lake volume and depth are unknown for nearly all lakes, we digitized 53 bathymetric maps of the most commonly studied lakes in the NHLD in order to develop a relationship to estimate the standard lake volume (SV, m^3) and depth on the basis of the observed surface area. Across a wide range of lake sizes, the relationship between lake surface area (LA, m^2) and standard volume (computed in a GIS using standard techniques for gridded data) was highly significant: $SV = 1.04 * (LA)^{1.11}$ ($R^2 = 0.94$, n = 53). Because of the tight relationship, we used this equation to estimate lake volume for 69 of the 72 lakes in the simulation. The heavily studied Crystal Lake, Big Muskellunge Lake, and Allequash Lake were part of the digitized bathymetric data set, and we used the volume and mean depth estimates from the bathymetric map rather than the equation for those three lakes.

3.3.2. Lake and Watershed Elevation

[25] We used the National Elevation Data set [*Gesch et al.*, 2002], produced from topographic maps and having 30-m pixels with highly precise and internally consistent elevation values. Elevation values across the NHLD were used to estimate watershed boundaries, mean watershed elevations, lake elevations, and relative elevation differences between modeled components as described below.

3.3.3. Watershed Boundaries

[26] Groundwater flow boundaries can differ from those of surface flow [*Dripps et al.*, 2006; *Pint et al.*, 2003], yet for all but a handful of well-studied lakes in the NHLD, neither the groundwater nor surface watershed boundaries are known. Using elevation data and lake locations, we delineated watershed boundaries for each of the 72 lakes of the study by traversing uphill from each lake using standard GIS techniques. Although this approach delineated surface flow boundaries, we reasoned that in the absence of specific groundwater watershed information across the NHLD, surface watershed boundaries could be used to capture the contributing area for the hydrologic and carbon budgets of the region. These immediate watershed areas represent the basic model calculation units and range from 0.2 ha to 1550 ha (Figure 1).

3.3.4. Terrestrial Vegetation Model

[27] We estimated monthly values of surface runoff (R) and drainage to groundwater (D) using the land-surface model IBIS [*Kucharik et al.*, 2000]. The model is driven with daily weather data, and initialized with vegetation information (i.e., vegetation type, leaf area index) and soil information (i.e., texture and physical properties) as described below. IBIS has been used to investigate biophysical, ecological, and hydrologic processes at local, regional, and global scales [*Donner et al.*, 2004; *Foley et al.*, 1996; *Kucharik et al.*, 2000; *Lenters et al.*, 2000; *Twine et al.*, 2004], and has been extensively evaluated across the Northern Highlands [*Dripps et al.*, 2006; *Vano et al.*, 2006].

3.3.5. Terrestrial Vegetation

[28] Land cover within each watershed was estimated from the WISCLAND land cover classification [*Wisconsin Department of Natural Resources*, 1998]; the region's current vegetation is dominated by temperate forest, comprising mixtures of deciduous and coniferous plants. Uplands were modeled as the Mixed Forest type in IBIS, which has been shown to represent aspects of the hydrology well in this region [*Dripps et al.*, 2006]. The surface area of wetlands varied in proportion and amount in each watershed, and was estimated using the total of all the wetland categories in the WISCLAND land cover classification.

3.3.6. Soil

[29] Soil was represented with multiple layers that varied with depth. For each layer the model simulates the unique temperature, volumetric water content, and ice content at each time step. For this study, the first 0.05 m of soil was designated to be an organic layer, with properties outlined by *El Maayar et al.* [2001]. Because differences among soil texture in this region do not drive hydrologic variability [*Vano et al.*, 2006], the soil type for depths between 0.05 to 1.5 m was designated as sandy loam, containing the physical and hydrological characteristics including sand, silt, and clay fractions, wilting point, and field capacity outlined by *Campbell and Norman* [1998]. This soil profile is representative of the soils within the study region based on soil information for the *Soil Survey Staff* [1994] soil data set.

3.3.7. Climate

[30] We ran IBIS using daily input derived from the CRU05 Climate Data set [*New et al.*, 2000] and the NCEP Climate Data set [*Kalnay et al.*, 1996; *Kistler et al.*, 2001], as outlined by *Vano et al.* [2006]. Precipitation data from the Minocqua Dam weather station, located at 44.88°N, 89.07°W (National Climate Data Center Cooperative Observer Program (NCDC-COOP), National Water Service, 2005, available online at: http://www.coop.nws.noaa.gov) were used to represent the local rainfall found in the Allequash watershed. The model was run from 1948 to 2000, with simulated results extracted to coincide with stream gauge measurements from 1992 to 2000. Lake evaporation rates were derived using the energy budget method from Sparkling Lake, located near the Allequash watershed [*Lenters et al.*, 2005] from 1989 to 1998.

3.3.8. Phosphorus and ANC

[31] Total phosphorus concentration (TP) and acid neutralizing capacity (ANC) were estimated for each lake and held fixed during the simulation. The values were estimated from linear regressions with lake area and perimeter, based on data obtained from a regional lake survey conducted in 2004 [*Hanson et al.*, 2007]. To avoid calculation errors in the carbonate equilibria, any ANC values that would have been calculated as negative by the regression were set to 1 μEq L^{-1}.

3.3.9. Lake Seasonality

[32] The year was divided into four seasons for lake carbon processing, based on mean ice coverage and thermal stratification data from the NTL-LTER: winter (days 0–110 and 330–365), spring and fall mixis (days 111–139 and 271–329, respectively), and summer (days 140–270). For winter, water temperature was set to 4°C, and the lakes were assumed to be ice covered. For both spring and fall mixis, water temperature was set to 12°C and the mixed layer depth was equal to the mean depth. For summer, lake temperature was set to 20°C.

[33] Summer mixed layer depth Z_{mix} in each lake was calculated dynamically in each lake as a function of its daily organic carbon concentration. Dissolved organic carbon influences stratification in small lakes (<500 ha) by chang-

Table 2. Landscape-Derived Parameters Computed for Within- and Among-Watershed Fluxes

Flux	kf[a]	Distance[b]	Flow Width[c]	Elevation Differenced[d]	P1[e]	P2[e]
GGI, GGO	1.00E − 05	dist (W1, W2)	shared perim (W1, W2)	elevW1 − elevW2	1	1
GL	7.70E + 02	dist (W1, L1)	perim (L1)	elevW1 − elevL1	1	1
GT	1.29E + 02	dist (W1, L1)	perim (T1)	elevW1 − elevL1	1	1
LGI, LGO	2.24E + 02	dist (W1, W2)	shared perim (W1, W2)	elevW1 − elevW2	1	1
LLI, LLO	1.10E + 06	dist (L1, L2)	1.0	elevL1 − elevL2	0.5	0.67
TL	1.84E + 01	5.0	perim (L1)	0.005	0.5	0.67

[a]Here kf denotes the fixed flow rate coefficient for each flow (m^2/s), different for each of the five flows, but spatially unvarying across the study area. Read 1.00E − 05 as 1.00×10^5.

[b]W1 and W2 denote upstream watershed and downstream adjacent watershed; dist is distance between two stocks (e.g., dist (W1, W2) is the straight-line distance between the centroids of Watershed 1 and Watershed 2).

[c]Here perim is perimeter of the polygon representing the lake, wetland, or estimated groundwater watershed. Wetlands were assumed to be circular, with area calculation described in separate section. Watershed delineation is described in a separate section, with perimeter calculated in GIS. Lake perimeter is from GIS coverage.

[d]Here elev is elevation of centroid of lake or watershed. Slope of wetland-lake flow is estimated to be 0.001, the order of magnitude of slopes between sets of lakes in the NHLD.

[e]P1 and P2 are described in text.

ing lake optical properties that control lake energy budgets [*Snucins and Gunn*, 2000], and more than 95% of lakes in the NHLD are smaller than 500 ha [*Hanson et al.*, 2007]. To calibrate the relationship between OC concentration and summer mixed depth for the NHLD, we computed a regression ($R2 = 0.72$, $p < 0.0001$) between the two using data from a survey of lakes covering a wide range in OC in the NHLD [*Hanson et al.*, 2003], with the mixed layer depth calculated as

$$\ln(\text{Zmix}) = -0.739 * \ln([\text{OC}]) + 2.698,$$

where ln([OC]) is the natural log of OC concentration in units of mg L^{-1}.

3.4. Connections Within and Among Watersheds

[34] In the groundwater-dominated NHLD, connections among watersheds may be both above and below ground. We based our estimates of belowground connections on the idea that the network of connections across a large area could be determined using the elevation differences and the distances between lakes and their immediate watersheds. Although greatly simplified [see *Walker et al.*, 2003; *Walker and Krabbenhoft*, 1998], this allowed integrated water and carbon routing and transformation through a web of lake connections to be tested against observed data.

[35] Lake polygon centroid coordinates were used for lake locations, and the elevation from the DEM was used as its characteristic elevation. The watershed centroid and the mean elevation of the entire area enclosed by the watershed were used as the location and elevation of the groundwater pool. The modeled location and elevation of each lake's associated wetland are described below. Using a variety of standard GIS techniques, the set of potential aboveground and belowground connections was specified for each watershed as described below.

3.4.1. Within-Watershed Connections

[36] In each watershed, elevation differences, flow widths, and effective distances were calculated for the GL, GT, and TL fluxes (Figure 1 and Table 2, with greater detail provided in the auxiliary material). For groundwater to wetland (GT) flow the wetland was modeled as having the same elevation and location as its lake, with flow width proportional to the perimeter of the wetland (Table 2), and estimated wetland perimeter as that of a circular wetland covering the same area as that derived from the land cover classification for each watershed. For wetland to lake (TL) flow the wetland was arbitrarily chosen to be located 5 m from the lake and 0.005 m above it (on the basis of the characteristic slope of the region), with a width proportional to the GIS-determined perimeter of the lake. Groundwater to lake (GL) flow in a watershed was based on the difference in elevations of the groundwater pool and the lake and the distance between them, with the characteristic width equal to the perimeter of the lake.

3.4.2. Between-Watershed Connections

[37] Since any lake in the model, given the right inputs, might overflow its banks to form a stream, we determined a web of potential stream connections for each lake. To estimate these lake-to-lake connections (LLI, LLO), for each lake we determined a single downstream lake for streamflow using the DEM and a standard GIS sink-filling technique, and parameterized the Manning equation with a characteristic stream width of 1 m (Table 2). For lake-to-groundwater connections (LGI, LGO), we used the set of watershed mean elevations and between-watershed adjacencies to determine, for each watershed, the number of immediately adjacent downstream groundwater pools to which water could flow from each lake (Table 2). We used the same web of connections to estimate the directions, elevation differences, and distances governing groundwater-to-groundwater flux (GGI, GGO); for GG and LG fluxes the characteristic flow width was the length of the shared perimeter between the watersheds (Table 2). Flux distances and elevation differences varied substantially across the landscape (Figure 1), though surprisingly, the slopes (elevation difference: lateral distance) of many of these connections were very near 1/1000, suggesting a characteristic downstream gradient throughout the study area. With a model focus on the area upstream of Allequash Lake, the resulting web of LL, LG, and GG connections indicated that, given the right simulated conditions, 71 upstream watersheds could potentially contribute water to Allequash Lake through surface and subsurface connections; these formed the boundaries of the study area and the set of modeled lakes. An additional ring of connections to all adjacent downhill watersheds was also computed, so that the watersheds at the edge of the study area transported only

the appropriate amount of water and carbon toward Allequash Lake. The remainder of the water and carbon in those watersheds was removed from the modeled Allequash system. The model run included these 47 attached watersheds, although their budgets and behavior were outside of the study region and thus were not included in the analysis.

3.5. Calibration and Testing Data

[38] Model calibration and evaluation employed the few observable characteristics of water flow and carbon processing available across large areas: hydrologic type, streamflow measurements, and carbon concentration measurements.

3.5.1. Hydrologic Type

[39] The DNR records for many NHLD lakes included information about the ''hydrologic type,'' a variable representing whether or not a given lake had a permanent stream flowing from it. In practice, however, this simple binary classification was not always clear: the hydrologic type value for many of the 72 lakes disagreed among the Eastern Lakes Survey [*Eilers et al.*, 1988], data collected by Birge and Juday in the early to mid 20th century, and 1:24,000 topographic maps of lakes in the region. We used a preponderance of the evidence as the ground truth value for the hydrologic type of each lake, used for calibration and model evaluation.

3.5.2. Stream Gauges

[40] The North Temperate Lakes Water, Energy, and Biogeochemical Budgets (NTL-WEBB) of the U.S. Geological Survey monitors stream gauges throughout the Trout Lake basin [*Elder et al.*, 1992; *Walker and Bullen*, 2000]. We used 9-year monthly average gauge measurements from Allequash Creek (modeled as LLO flow from Allequash Lake) and Allequash Springs (modeled as GT flow in the Allequash watershed) from the period of 1992–2000 to calibrate the magnitude and timing of modeled water flows within the model.

3.5.3. Carbon Concentration Observations

[41] To test the behavior of the carbon model in the absence of potentially complicating interwatershed links, the lake carbon model was calibrated separately. After runs to annual dynamic equilibrium in IC and OC, the equilibrium values were compared with mean monthly values from carbon observations between 1985 and 2002. Four NTL-LTER lakes (Crystal Lake, Big Muskellunge Lake, Allequash Lake, Trout Bog) were chosen as calibration points to cover large gradients in IC (range of $\sim$0.5–$\sim$12 g m^{-3}) and OC (range of $\sim$1–$\sim$20 g m^{-3}).

4. Model Simulation and Analysis

[42] Using a daily time step, the carbon and water inputs, and the connection network, the simulation was run for 50 years, at which point all pools and fluxes were in steady state among all lakes and watersheds. At monthly and yearly timescales, we extracted both carbon and water data for the 72 simulated watersheds and determined the model's success in simulating these processes at multiple spatial and temporal scales. To assess the broad-scale hydrologic predictions, we assessed the simulated hydrologic balance across the 72 lakes. Model performance for carbon processing was verified by comparing annual and monthly carbon concentrations and water outputs in Crystal, Big Muskellunge, and Allequash lakes to observations. After verifying model performance, we used the results to address our driving questions.

[43] To explore the variation in water and carbon budgets across the landscape (question 1), we extracted the annual budgets for each of the 72 lakes, and normalized budget elements using the flow volumes of each lake determine the proportion of the input and output budgets represented by each flux. We then arranged these budgets according to increasing watershed area. We expected that this landscape-scale factor would allow us to isolate the part of water and carbon budgets that was not driven by connections among watersheds, but instead correlated with morphometric factors.

[44] To quantify the strength of upstream and downstream connections in the modeled landscape (question 2), we analyzed the water and carbon budgets according to the source (in the case of water) and destination (for carbon) in the budget of each lake. Because the functional behaviors of connections in LUWI can vary with water level and are thus dynamic throughout a simulation, the impacts of these connections may vary spatially and can affect water and carbon cycles differently. We combined the fluxes comprising the water input budget for each lake according to three broad categories of possible sources: (1) water originating in the lake's watershed (Drainage from uplands D, Wetland Precipitation PT, Surface Runoff R); (2) water originating in an upstream watershed, reaching the lake via either Streamflow (LLI) or after first entering the groundwater pool from upstream watersheds (LGI, GGI); and (3) Precipitation directly on the lake surface (PL). As we did for the hydrologic budget, we grouped components of the carbon budget to quantify the strength of connections in determining, for each lake, the balance among each of three fates of lake carbon: (1) transport farther downstream via groundwater (LGO) or streamflow (LLO); (2) sedimentation (SED); or (3) flux to the atmosphere (ATM) (Figure 2).

[45] To address the role of lakes in carbon and water budgets at the landscape scale (question 3), assessing only the net carbon flux from the lake's surface would tell an incomplete story. In a setting where a lake may readily transport carbon downstream to become sediment in or be vented from lakes lower in the landscape, the fate of carbon can be distinguished along two related axes. First, as places where carbon is converted between organic and inorganic forms, a lake may favor the conversion of carbon toward either the IC pool (which we term ''mineralizer lakes'') or the OC pool (''reducer lakes''). Second, we assessed the balance among the potential sources of IC in a lake. For lakes in which the IC production from mineralized OC within the lake was less than the IC load from outside the lake, we labeled those lakes ''conveyors'' of IC from outside the lake's borders to the atmosphere. In other lakes, IC production from mineralization exceeded IC load from without; we labeled those ''reactor'' lakes.

5. Model Results

5.1. Question 1: How do Simulated Water and Carbon Budgets Vary, Match Observations, and Affect Carbon Stocks and Fluxes?

5.1.1. Model Performance and Behavior

[46] Our modeled results for annual averages and seasonal dynamics for carbon (Figure 3) and water (Figure 4)

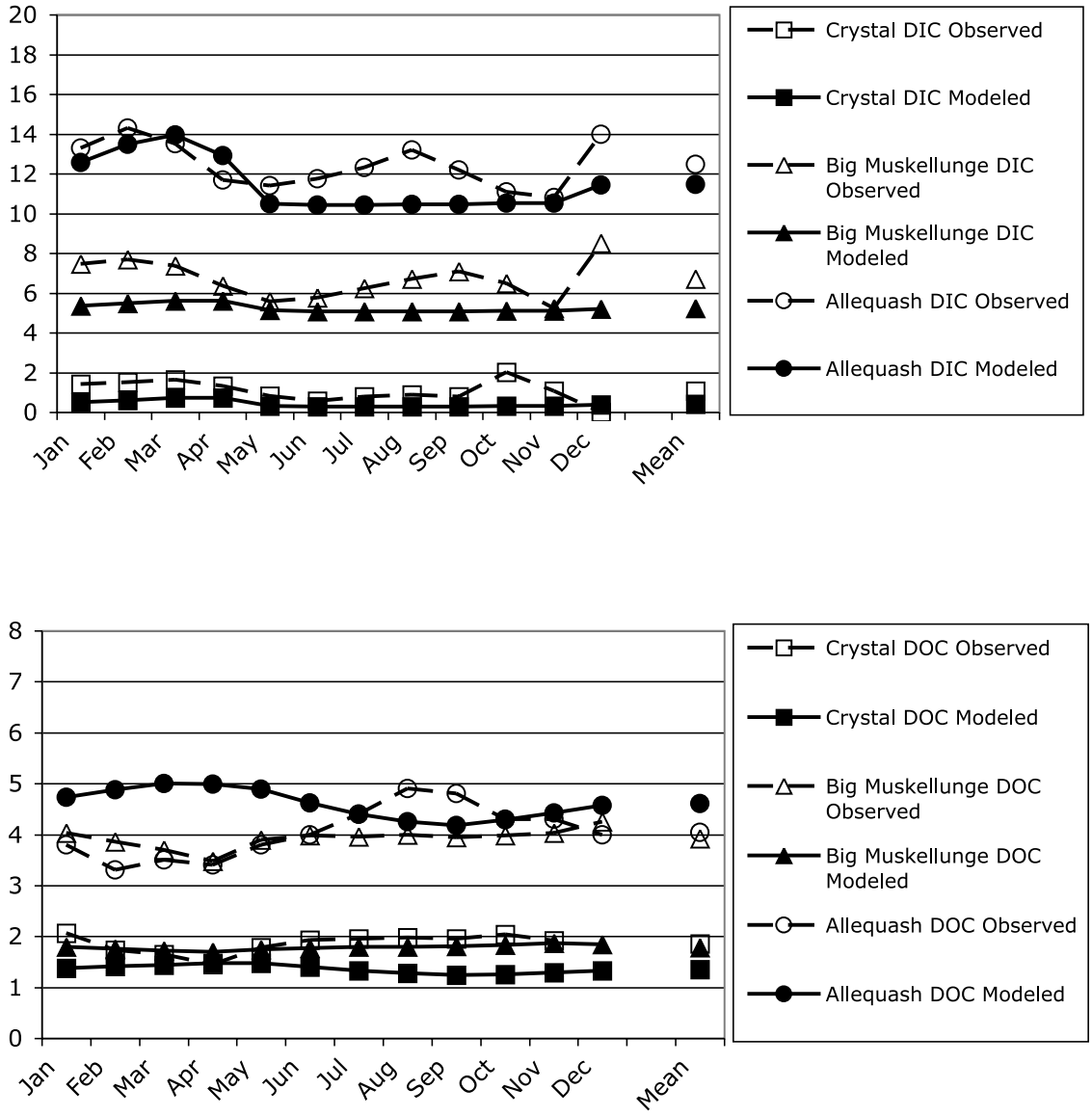

Figure 3. (top) IC and (bottom) OC modeled and observed seasonal concentrations in Crystal, Big Muskellunge, and Allequash lakes.

generally matched observations in our three test lakes: Crystal, Big Muskellunge, and Allequash. Simulations of annual and seasonal concentrations of IC agreed well with observations in these lakes (Figure 3). IC seasonal variability was dampened relative to observed values, and annual means (Figure 3, right) were somewhat lower in modeled lakes than observations.

[47] Results for organic carbon were more mixed. The modeled annual concentrations of OC agreed well with observations, particularly for Crystal and Big Muskellunge lakes, which have lower OC concentrations. The annual means of modeled OC in the three lakes were ranked correctly, with the mean modeled OC for Big Muskellunge providing the biggest problem for the model. However, despite the good annual agreement, the modeled seasonal changes in OC concentration were nearly opposite of what was observed for these three lakes. This may be largely due to a too-simple assumption for aerial inputs of carbon, in which aerial carbon was applied evenly to the lake's surface throughout the year. This approach would seem to have limited the model result in two ways. First, the even application of aerial carbon misses the large pulse of carbon

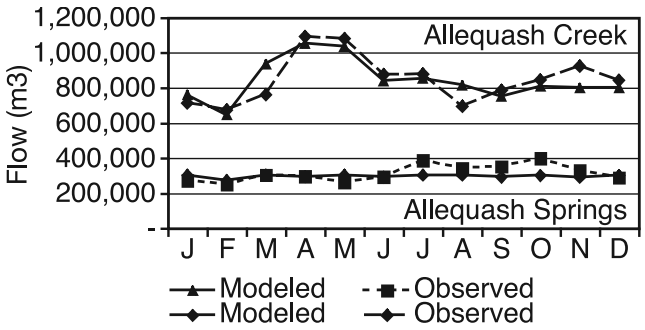

Figure 4. Monthly flows from Allequash Creek and Allequash Springs, modeled and observed.

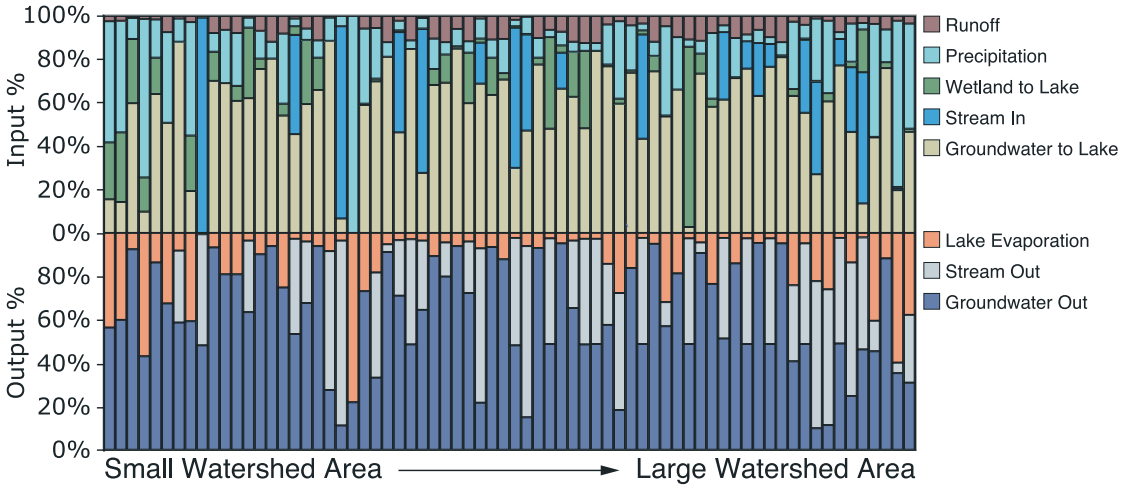

Figure 5. Modeled annual water budgets in today's climate, ordered along a gradient of increasing watershed area. Each column represents one of the 72 lakes modeled in this study, ordered in increasing watershed area. (top) Water inputs vary substantially among lakes, with groundwater flow into the lake the dominant input for most. (bottom) Output budgets vary with evaporation from the lake surface most important for small and large watersheds. The importance of streamflow to lake water budgets is not closely correlated with watershed area.

as a result of autumn leaf fall. We expect that a more seasonally unbalanced carbon input would have changed the shape of the OC concentration curve to align much better with observations, and model calibration would have brought the modeled and observed values close together. Second, aerial carbon was applied in the model only at the lake perimeter. This fails to account for aerial carbon falling on a lake's surrounding catchment, in particular its wetlands. We expect that had aerial carbon been applied to wetlands, we would have seen a pulse of that carbon enter a lake from its wetland. This would have affected the pulse of carbon especially strongly for Allequash, which was surrounded by substantial upstream wetlands, than for the other two lakes, which were not. For these two reasons, a more detailed algorithm for aerial carbon will likely appear in future model versions.

[48] The two surface flows predicted from this simulation agreed well with the two gauged surface flows (Figure 4). We accurately captured surface water flow in Allequash Springs, the surface flow that enters Allequash Lake, though flow variability in the later months of the year was somewhat different from observed values. Allequash Creek, the surface flow draining Allequash Lake, was very well represented at both annual and monthly timescales (Figure 4).

[49] Predictions across all 72 lakes of hydrologic type, the most basic characteristic of lake hydrologic behavior,

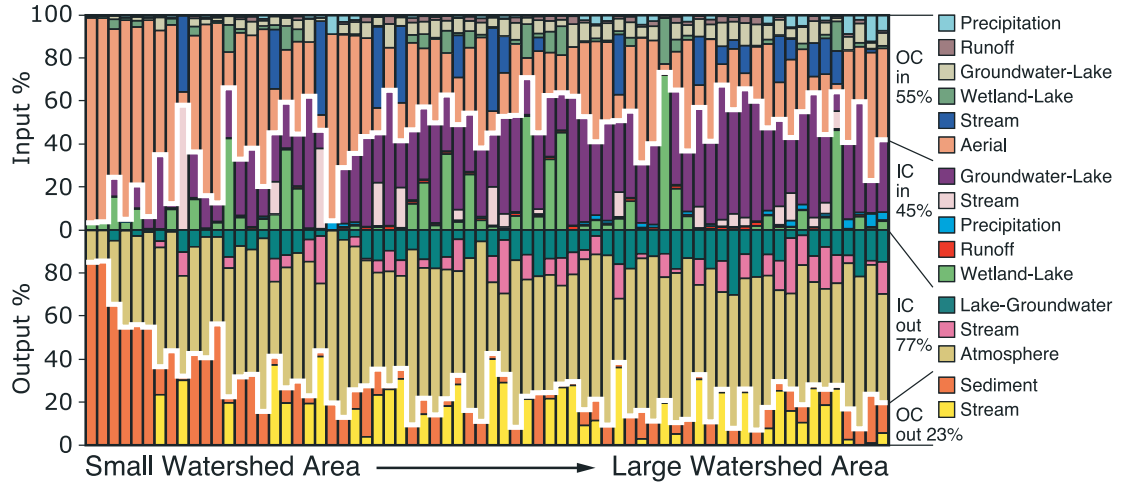

Figure 6. Modeled annual carbon budgets in today's climate, ordered along a gradient of watershed area. Input and output budget components, showing a decreasing importance of aerial inputs (part of OC In) as carbon inputs in larger watersheds, and an increasing importance of groundwater-to-lake IC inputs (part of IC In) in larger watersheds. The largest output budget term for most lakes was export to the atmosphere (part of IC Out), with sedimentation (part of OC out) most important in small watersheds. White lines separate organic and inorganic inputs and outputs.

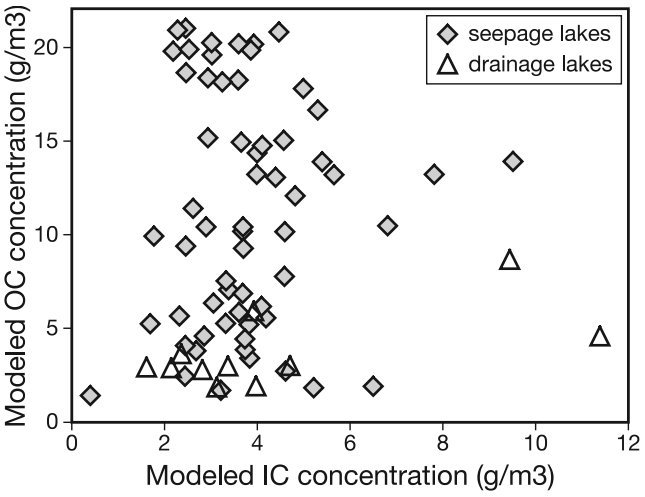

Figure 7. Modeled concentrations of IC and OC at steady state. Shaded diamonds, modeled values for seepage lakes; open triangles, modeled values for drainage lakes.

agreed well with observations. The proportion of surface outflow to each lake's modeled water budget was distinctly bimodal; using a cutoff of 50% of a lake's water budget, 15 lakes were classified as drainage and 57 as seepage. Of 11 true drainage lakes, 9 were classified correctly; of 61 true seepage lakes, 55 were classified correctly. The resulting confusion matrix of predicted and observed values revealed that the model simulated hydrologic lake type with a Tau_p value of 0.66, indicating a fit considerably better than what would be expected owing to chance [*Ma and Redmond*, 1995].

5.1.2. Water Budget Variation

[50] The simulation appropriately modeled the set of lakes as primarily groundwater-driven, with additional inputs and outputs playing substantial roles in the hydrologic budget of some lakes (Figure 5). Simulated water budgets varied substantially by lake, and were not strongly related to watershed size. Across all 72 lakes, the mean contributions of hydrologic sources to lake water budgets were: groundwater 55%; streams 11%; wetlands 9%; overland flow 6%; and precipitation 18%. The mean hydrologic outputs from the 72 lakes were: groundwater 61%; streams 25%; evaporation 14%, and variation around both input and output mean values was high. There were no clear trends in the relative importance of the five lake inputs and three lake outputs when watersheds were arranged along a gradient of increasing size (Figure 5), suggesting that a complex interaction of lake size, watershed size, precipitation timing and amount, wetland volume, and connection direction and strength interact to determine individual lake water budgets.

5.1.3. Carbon Budget Variation

[51] Lake carbon budgets varied greatly across the landscape (Figure 6). Unlike the hydrologic budgets, variation in carbon budgets among lakes was more clearly associated with watershed area. In particular, OC inputs of leaves, pollen, and insects (modeled as proportional to lake perimeters) dominated the inputs of lakes with small watersheds. Additionally, these small watersheds appear more likely than those with larger watersheds to convert a high percentage of particulate organic carbon inputs to sediment. In larger watersheds IC inputs (primarily through groundwater inflow) more evenly balanced those from OC (Figure 6). For all but the smallest watersheds, IC flux to the atmosphere was the single largest output term, with all lakes being sources of carbon to the atmosphere. Modeled input carbon budgets were more evenly balanced between IC and OC than carbon outputs. Across the 72 lakes, the mean inputs of total carbon were 45% IC and 55% OC. In contrast, the mean outputs were 77% IC and 23% OC (Figure 6). The model suggests rapid cycling of carbon from the water column within these lakes; with sedimentation included as an export, the steady state residence time of carbon in lake water was less than a year for all but a few modeled lakes.

[52] Simulated lake concentrations of OC and IC (Figure 7) suggested a complex relationship between the responses of OC and IC to water and carbon inputs from within the watershed, from precipitation, and from upstream watersheds. Lakes clustered by hydrologic type along these carbon gradients, with drainage lakes having much lower OC than many seepage lakes. OC in seepage lakes exhibits much more variability than drainage lakes, with a range that fully encompasses that for drainage lakes.

[53] Modeled carbon export from terrestrial systems to lakes ranges from 13–1032 gC m^{-2} LA yr^{-1} (mean of 70 gC m^{-2} LA yr^{-1}, or 15 gC m^{-2} yr^{-1} in land area). Carbon export from terrestrial systems in the literature derives mainly from stream measurements, with typical values ranging from about 1 to 10 gC m^{-2} WA yr^{-1} in watersheds similar to those in northern Wisconsin [*Aitkenhead and McDowell*, 2000]. Not every lake in our study had active stream connections, but for those that did, the mean loading in land area units by streams ($\sim$7.8 gC m^{-2} yr^{-1}) was well within literature values.

5.2. Question 2: How do the Strength and Spatial Pattern of Landscape Connections Vary Among Watersheds?

[54] LUWI simulates a wide variety of biogeochemical processes for each lake, and a large number of them may be strongly influenced by both upstream and downstream connections among watersheds. For example, carbon flux from a given wetland to its associated lake during a simulation is influenced by the volume of water in the wetland, which is influenced by the flow from groundwater to the wetland, which in turn may be driven by the groundwater pools and lakes of upstream watersheds. This effect may well differ among watersheds and vary according to a complex set of characteristics of the lake, upland, and wetland of each. In this section we describe the role of adjacent connections on carbon and water budgets, summarized for the entire 72-lake landscape. For water, we illustrate the dependence of annual budgets on upstream watersheds; for carbon, we partition the annual estimated carbon budgets of each lake among three potential destinations, among them the transport to downstream watersheds.

5.2.1. Water: Upstream Connections

[55] The hydrologic importance of upstream watershed connections varied greatly among lakes, with an average lake receiving 32% of its water budget via upstream connections, 48% from water falling in its watershed, and 19% from direct precipitation on the lake (Figure 8, inset). The influence of upstream hydrologic connections differed sub-

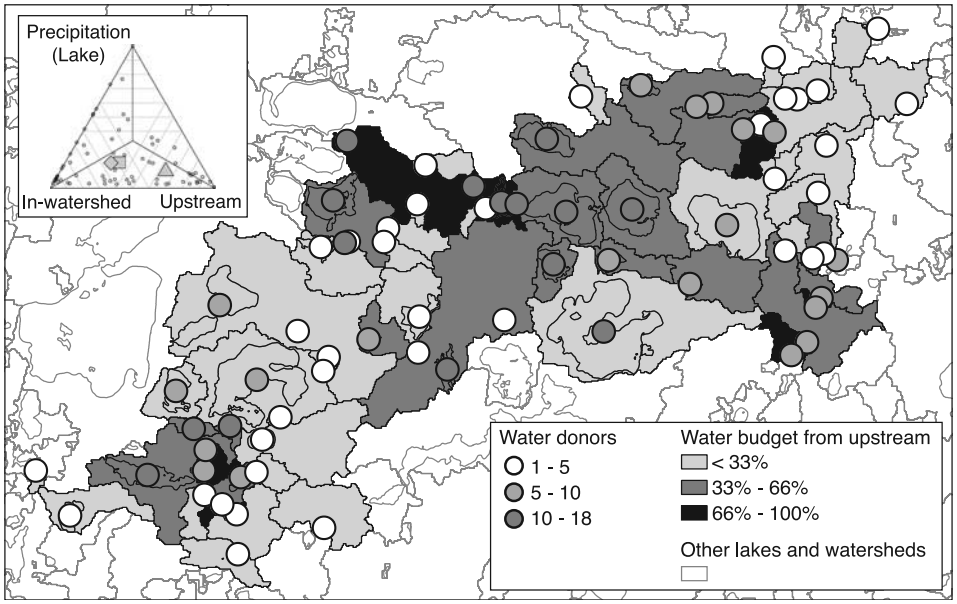

Figure 8. Spatial variation of the importance of upstream connections to lake water budgets. Light polygons show watersheds with a small influence of upstream connections; dark polygons show highly connected watersheds. Circles indicate the number of upstream watersheds implicated in providing 95% of each lake's water budget in today's climate. All water in the model originates in precipitation. Top inset shows the balance in each lake among initial sources of that precipitation: lake, in-watershed, and via connections from upstream watersheds. Shaded diamond, average source values for seepage lakes; shaded triangle, average source values for drainage lakes; shaded square, average source values for all lakes.

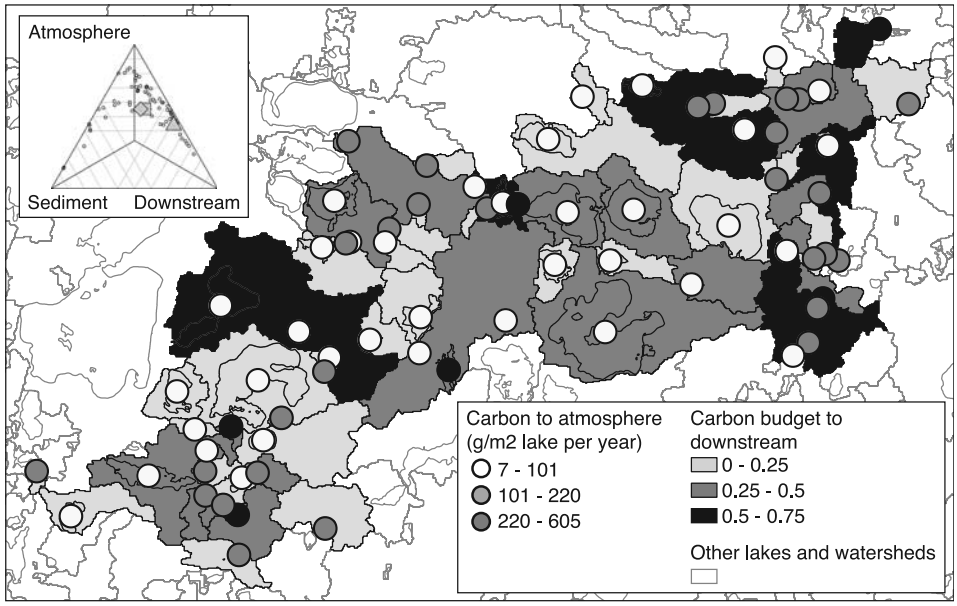

Figure 9. Modeled spatial variation of carbon budgets showing the strength of downstream connections in lake carbon budgets and atmospheric flux in the region. Light polygons show watersheds exporting a relatively small proportion of carbon to downstream watersheds. Dark polygons show watersheds with lake carbon budgets more strongly connected to downstream watersheds, through streamflow or lake to groundwater flow. Circles indicate the amount of carbon fluxed to the atmosphere per unit lake area. Inset shows the proportion of each lake's carbon budget transported to each of three destinations: atmosphere, sediment, and downstream watersheds via connections.

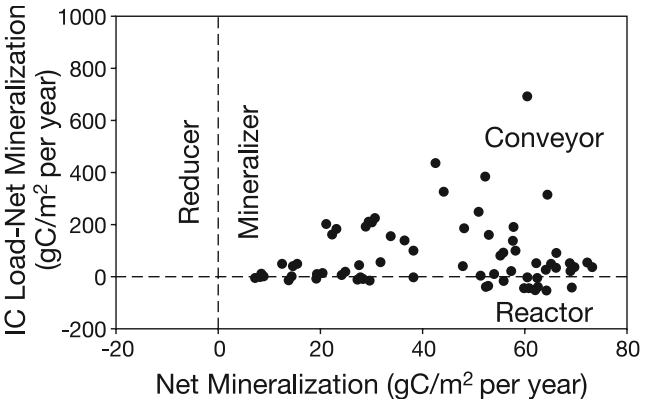

Figure 10. Net mineralization and reduction in a lake related to the conveyor/reactor status of inorganic carbon. Net mineralization is the difference between gross mineralization and reduction.

stantially between lakes modeled as seepage and those modeled as drainage. Among those with lake type correctly classified, the typical seepage lake received 27% of its budget from upstream connections. In contrast, drainage lakes were modeled as having much stronger upstream links, with 63% of their water budgets, on average, coming from upstream (Figure 8, inset).

[56] The spatial pattern of the importance of upstream hydrologic connections suggested spatial clustering of some aspects of lake water budgets (Figure 8). Lake water budgets that relied little on upstream connections (light-colored watersheds, for example in the southern part of the study area) were clustered together on the landscape, suggesting that this part of the region is made up of contiguous but relatively isolated watersheds. Similarly, clustering of lakes with budgets relying more strongly on upstream connections (for example, the dark band of watersheds in the upper middle of the study area) suggested connected chains of watersheds with active surface connections. A second measure of connectivity, the number of lakes that contributed significantly to a given lake's water budget, showed evident clustering as well (Figure 8, circles). Lakes that receive water from a large number of other lakes appear close to one another in the landscape, and lakes that receive water from only a few other lakes appear close to one another. These two measures of upstream hydrologic connectivity were related for many watersheds but not entirely coincident: For example, Allequash Lake, with its dark circle on a light background, was connected to a large number (9) of upstream lakes relative to the proportion of its budget (30%) that arrived from upstream.

5.2.2. Carbon: Downstream Connections

[57] Simulated regional carbon budgets show that 58% of lake carbon is vented to the atmosphere, 15% is deposited in sediments, and 27% is exported downstream to lower lying watersheds (Figure 9, inset). As with water processing, drainage lakes behave differently from seepage lakes. On average, drainage lakes route 50% of their carbon budget to downstream watersheds as IC and OC within streamflow and flow to groundwater, while seepage lakes are similar to the regional average.

[58] There was clear spatial clustering of aspects of lake carbon budgets (Figure 9). Some lakes were strongly connected to downstream neighbors by carbon export along tightly connected lake chains. In particular, lakes that were highest in the landscape (in the eastern part of the study area) exported much of their carbon to downstream watersheds. These same lakes had high atmosphere exchange. Lakes whose carbon budgets were the most isolated from downstream watersheds were also clustered, and vented less carbon to the atmosphere per unit area than the strongly connected lakes nearby.

5.3. Question 3: What is the Role of Interwatershed Connections in Lake Carbon Processing?

[59] In watersheds with a rich set of connections, single-lake estimates of carbon flux do not adequately describe the potentially complex relationship between carbon transport among lakes, its residence time in lakes and watersheds, and the role of in-lake mineralization and reduction. Along one of the two axes of landscape-scale lake carbon processing, all lakes were mineralizer lakes, with a mean net mineralization rate of ~50% of the OC load (Figure 10). Net mineralization requires that allochthony exceed autochthony, indicating that lakes in this study are net heterotrophic. Along the second lake carbon processing axis, most lakes were conveyor lakes, with IC loading exceeding net mineralization of OC. The mineralization of OC and the conveyance of IC to the atmosphere and downstream are both processes contributing to the predominance of CO_2 supersaturation in lakes [*Hanson et al.*, 2004]. Although all lakes were mineralization sites of terrigenous C, these results suggest that for most lakes IC loading is more important than OC mineralization as a contributor to efflux of CO_2 from lakes to the atmosphere.

[60] On average, upstream watershed connections provided a small portion (~12%) of each lake's organic carbon budget (Figure 11, top). Within-watershed sources such as wetland to lake flow, in-lake primary production, and aerial inputs of wood, leaves, and other organic matter dominated most OC budgets. With relatively few lakes connected by streams in the study area, lakes with large upstream OC connections tended to be those whose water budgets were strongly tied to a large number of upstream watersheds (Figure 5). Upstream watersheds contributed more extensively to inorganic carbon budgets, supplying about 23% of the IC in each lake from outside the watershed (Figure 11, bottom). The characteristics of lakes having high upstream IC inputs were less easily identified than those with high OC upstream connections, perhaps because of the many pathways of IC to a lake.

6. Discussion

[61] The routing and transformation of both water and carbon in lakes depends on a combination of both internal and external factors including lake size, lake shape, watershed attributes, and upstream and downstream connections. Even in intensively studied lake districts, it is a challenge to extrapolate from relatively few lakes and watersheds to dynamics at a regional scale. Given the lack of precise, long-term information for most lakes of the NHLD, the

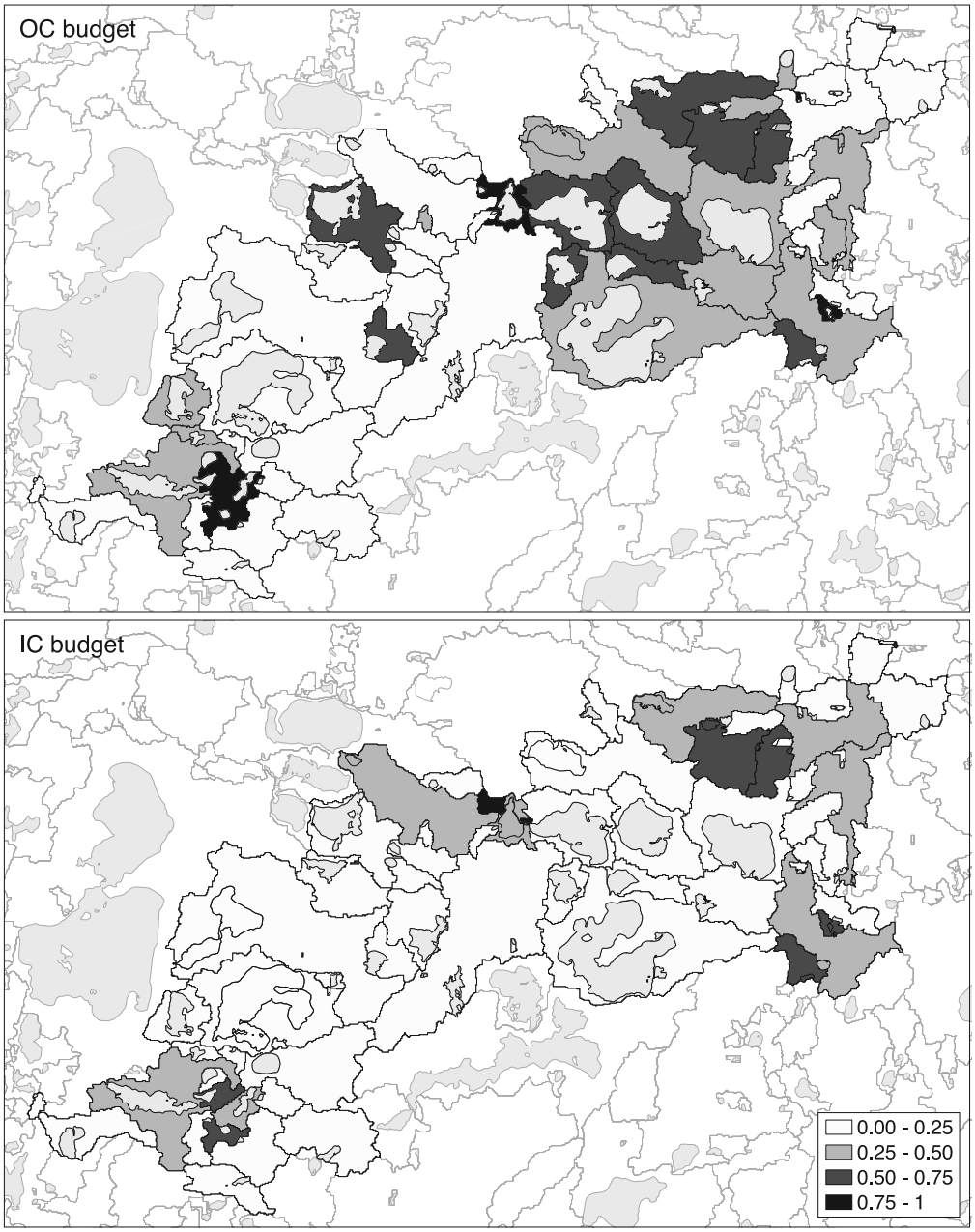

Figure 11. Proportion of IC and OC lake budgets derived from upstream sources. Role of upstream watersheds in organic carbon budget (above) and inorganic carbon budget (below) for each simulated lake. Inorganic and organic carbon, though closely related via in-lake chemistry, do not respond equally strongly to landscape position. A small proportion of lakes have organic carbon budgets strongly tied to upstream watersheds (top: dark watersheds); inorganic carbon budgets in these lakes are more strongly related to upstream watersheds (bottom: dark watersheds). This seems primarily driven by the modes of input of these two carbon types: Organic carbon lake budgets are dominated by inputs from wetlands and lake perimeters, whereas inorganic inputs are more evenly allocated among multiple inputs in today's climate. See also Figure 6.

LUWI simulation model provides a valuable tool for hypothesizing about and understanding this region.

[62] In this study, the LUWI model linked a set of simplified carbon processing and water routing models with modeled terrestrial outputs, and results closely coincide with much of what is known about carbon and water across multiple spatial and temporal scales. The simulation correctly models many basic attributes of the region, beginning with its character as a groundwater-driven region with few permanent stream outlets. The simulation also closely matches observations for lake hydrologic type, the most basic characteristic of lake hydrologic behavior, in nearly all study lakes and adequately predicts seasonal and annual carbon and water fluxes for the three highly studied test

lakes. Corroboration success indicates that the simulation and its inputs are an acceptable representation of this lake-rich region.

[63] These results clearly indicate that the connectivity among lakes and watersheds should not be ignored when assessing the carbon and water budgets of lakes in this region. On average, lakes receive about a third of their water budget from upstream watersheds, enough to allow them to persist (in seepage lakes) and to cause some to overflow into streams (in drainage lakes). However, this connectivity varies dramatically across lakes for carbon and hydrologic processes, dominating the inputs and driving the outputs of some lakes while doing little to affect processing in others. The effect of connections on carbon budgets is less direct than for water, but also evident: nearly 30% of the carbon reaching a typical lake is subsequently transported downstream. The fate of carbon in a particular lake is due, in part, to its active hydrologic connections: carbon trapped in a seepage lake is more likely to be mineralized or sedimented, whereas a drainage lake may carry a substantial amount of carbon downstream. However, the geographic proximity of lakes is not necessarily indicative of their hydrologic connectivity; some nearby lakes are effectively isolated watersheds, whereas other more distant lakes are connected.

[64] The strength and effects of both surface and subsurface connections should be thought of as dynamic, rather than static. This functional connectivity in a given climate may vary substantially from the potential connectivity estimated by elevation-based algorithms. In a wetter or flashier setting, for example, greater streamflow may carry more carbon between lakes, changing the spatial pattern or amount of sedimentation and atmospheric flux, and strengthening the signal of upstream lakes with respect to in-watershed inputs. Some potential connections may be employed only in wet climates; conversely, the functional importance of other connections may grow or shrink in drier settings. We also expect that the land cover within a watershed is likely to play some role in the hydrology [*Vano et al.*, 2006] and thus affect the carbon processing of the lakes of the region. Analyzing the sensitivity of the biogeochemical processes in this landscape to drivers of land cover and climate is among the next immediate goals of this work.

[65] Budgets of both water and carbon were surprisingly variable among lakes, considering their proximity, connections, and similar shape and setting. The simplest distinction among lakes, the hydrologic characteristic of being either seepage or drainage, was useful in our analyses, yet not sufficient to explain the differences among budgets and behavior. Water budgets, for example, among lakes were more similar than the seepage/drainage distinction would suggest, with several stream flows comprising between 40% and 60% of the water output budget. The similarity between some seepage and drainage lakes extended to carbon processing as well (Figure 9), with many lakes categorized as ''seepage'' but transporting some of their carbon via intermittent streamflow in addition to lake-to-groundwater flow. The carbon results suggest a second axis of lake classification, based on carbon processing and related to watershed size (Figure 6) or atmospheric flux (Figure 10).

[66] Including the full carbon budget in lakes allows us to discriminate between lake trophic status and the role that lakes play in storing or exporting carbon [*Lovett et al.*, 2006]. Lakes in our study are foci of OC mineralization, venting a substantial portion of the derived IC to the atmosphere (Figure 10). These results also indicate that terrestrial IC sources account for a substantial portion of the IC effluxed to the atmosphere from lakes (i.e., lakes as ''conduits''). The terrestrial IC, if unaccounted in lake studies, can be mistakenly attributed to in-lake mineralization of OC. We were also surprised at the magnitudes of aerial inputs of OC that were required to sustain OC concentrations, even the relatively low OC concentration of isolated Crystal Lake. With lake trophic status defined as the balance between in-lake mineralization of OC and in-lake production of OC, this study suggested that many lakes are both sources of carbon to the atmosphere and net heterotrophic.

[67] Determining the level of spatial and temporal complexity to represent in a model is a perennial challenge that is exacerbated when representing large regions. The system we have modeled is spatially complex, with interacting elements that are heterogeneous, exhibit nonlinear dynamics and directional interactions, producing spatially explicit response variables [*Strayer et al.*, 2003b]. Although the model successfully represented key carbon and water stocks and fluxes in the known lakes of the study area, it is still a highly simplified simulation of lake and watershed processing. Simplifications not directly modeled include ice cover, ice scour, substrate differences along flow paths, lake hydrodynamics, effects of varying lake shapes, food webs, behavior of carbon along stream paths, and anaerobic sediment processes. These simplifications are not intended to minimize the importance of these factors and processes, but rather to construct a model with as few parameters as practicable that gives understandable and testable results across a large area. Because the model has few parameters, the complex spatial and temporal carbon and water budgets can be more readily understood as the consequence of modeling decisions. The ways in which the model fails are as informative as the ways it succeeds, and suggest ways in which the model might be improved, whether through increased detail, differing assumptions, or different parameterization. Further investigations into the conditions in which these assumptions most strongly affect lake carbon and water cycling will provide an interesting area for future research.

[68] For these reasons, formal validation of the model is currently outside our scope of interest. The spirit in which we undertook this work was not to produce a model that closely fit the data, but rather to sharpen hypotheses of the regional function of the aquatic/terrestrial landscape. By ignoring some of the details known for highly studied LTER lakes, we developed a model that is driven with only that data available for all lakes, producing a model with which we can make interesting hypotheses about lakes for which we know almost nothing. Nevertheless, we expect to undertake a model validation exercise when this model is extended to the much larger 7000-lake landscape, using a large amount of data gathered from different sources. These include the decades of occasional observations from different agencies all over the larger NHLD region, as well as the product of our own 170-lake survey of randomly selected lakes from the full NHLD region.

[69] The LUWI model provides a framework for ecosystem analysis in space across gradients in lake size and

watershed area, simultaneously deriving the dynamic landscape positions of a large web of lakes that may be connected along multiple sets of pathways. Through the use of an aquatic-terrestrial model simulating both water and carbon dynamics in an extensive, hydrologically complex landscape, this study provides the ability to make and test new hypotheses about the integrated biogeochemical functioning of the ecosystems of the NHLD. Though based on decades of studies in the field, the patterns shown here could not be investigated without a simulation model. By using a lake's watershed as the organizing ecological unit, we found that questions of the regional-scale function of hundreds or thousands of lakes are tractable and readily suggest new avenues of study. We can now ask new questions about, for example, the potential behavior of lake-rich regions under regional perturbations such as climate change or local pressures such as land use change. In addition to such scenarios of regional futures, this approach may also be used as a way to decide among hypotheses about the set of connections among watersheds, confronting the resulting model run with observed data. Similarly, this framework might be used to hypothesize differences in groundwater carbon concentrations across landscapes and to estimate the effect of the uncertainty of this or other similar simplifications. The LUWI framework is designed to distinguish the watershed-specific behavior among lakes and watersheds varying in morphometry, watershed characteristics, wetland size, initial condition, and upstream and downstream connections. This explicit incorporation of terrestrial and aquatic processes in surface and subsurface connection networks will aid our understanding of the relative roles of on-land, in-lake, and between-lake processes in this lake-rich region.

Notation

AER aerial addition of carbon to the organic carbon pool, g.
ANC acid neutralizing capacity, μEq L^{-1}.
ATM net inorganic carbon flux between the lake and atmosphere, positive away from the lake, g.
C_{floc} flocculation mass of carbon to sediment, g.
D drainage to groundwater from terrestrial uplands, m^3.
EL evaporation from the lake surface, m^3.
ET evaporation from the wetland, m^3.
GGI groundwater-to-groundwater input from one or more upstream groundwater pools, m^3.
GGO groundwater-to-groundwater output to one or more downstream groundwater pools, m^3.
GL groundwater-to-lake input from a watershed groundwater pool, m^3.
GT groundwater-to-wetland input from a watershed's groundwater pool, m^3.
IC inorganic carbon in a lake, g.
LA lake surface area, m^2.
LGI lake-to-groundwater input from one or more upstream lakes, m^3.
LGO lake-to-groundwater out to one or more downstream lakes, m^3.
LLI lake-to-lake input from one or more upstream lakes, m^3.
LLO lake-to-lake output to one downstream lakes, m^3.
OC organic carbon in a lake, g.
PL lake precipitation, m^3.
PT wetland precipitation, m^3.
RU surface runoff to lake from terrestrial uplands, m^3.
SED sedimentation, g.
SV standard volume of a lake, the volume on which the head for LGO and LLO fluxes are based, m^3.
TA wetland surface area, m^2.
TL wetland-to-lake input from a watershed's wetland pool, m^3.
TP total phosphorus concentration, g/m^3.
V_G dynamic groundwater volume, m^3.
V_L dynamic lake volume, m^3.
V_T dynamic wetland volume, m^3.
Z_{mix} summer mixed layer depth in a lake, m.

[70] **Acknowledgments.** We thank the Andrew W. Mellon Foundation and NSF for their generous support. We also thank three anonymous reviewers and the Associate Editor for their excellent, detailed suggestions that greatly improved the manuscript. Researchers at Northern Temperate Lakes Long-term Ecological Research site and the USGS WEBB project have developed many of the concepts modeled here, in addition to providing the decades of biogeochemical and hydrological data making possible the assessment of these results. Tim Kratz of NTL-LTER and Randy Hunt of the USGS provided valuable feedback in the early stages of this project, in addition to advancing many of the broader concepts explored here. Bill Feeny of the UW-Madison Zoology Department produced novel figures of complex water and carbon budgets. A dedicated team of University of Wisconsin undergraduates developed analysis tools, performed calibration studies, organized decades of biogeochemical data, and digitized and analyzed lake maps during the entirety of this project. They consistently demonstrated a generosity of spirit and a willingness to submit to quite substantial time pressure, often working very late nights and weekends: For this we thank Sean Cornelius, Tjahjono Tjandra, Aubrey Barnard, and Jim Coloso. Without them and the others mentioned here, this project would most certainly not have been possible.

References

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

Anderson, M. P., and X. X. Cheng (1993), Long-term and short-term transience in a groundwater lake system in Wisconsin, USA, *J. Hydrol.*, *145*, 1–18.

Baines, S. B., et al. (2000), Synchronous behavior of temperature, calcium, and chlorophyll in lakes of northern Wisconsin, *Ecology*, *81*, 815–825.

Bureaus of Water Resources Management and of Fisheries Management (2001), Wisconsin Lakes, report, 180 pp., Madison, Wis.

Campbell, G. S., and J. M. Norman (1998), *An Introduction to Environmental Biophysics*, 286 pp., Springer, New York.

Canham, C. D., et al. (2004), A spatially explicit watershed-scale analysis of dissolved organic carbon in Adirondack lakes, *Ecol. Appl.*, *14*, 839–854.

Cardille, J. A., et al. (2004), Impacts of climate variation and catchment area on water balance and lake hydrologic type in groundwater-dominated systems: A generic lake model, *Earth Interact.*, *8*, 1–24.

Carpenter, S. R., et al. (2001), Trophic cascades, nutrients, and lake productivity: Whole-lake experiments, *Ecol. Monogr.*, *71*, 163–186.

Carpenter, S. R., et al. (2005), Ecosystem subsidies: Terrestrial support of aquatic food webs from C-13 addition to contrasting lakes, *Ecology*, *86*, 2737–2750.

Chapin, F. S., et al. (2002), *Principles of Terrestrial Ecosystem Ecology*, 436 pp., Springer, New York.

Cole, J. J., and N. F. Caraco (1998), Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF6, *Limnol. Oceanogr.*, *43*, 647–656.

Cole, J. J., et al. (2000), Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations, *Limnol. Oceanogr.*, *45*, 1718–1730.

Cole, J. J., et al. (2002), Pathways of organic carbon utilization in small lakes: Results from a whole-lake C-13 addition and coupled model, *Limnol. Oceanogr.*, *47*, 1664–1675.

Donner, S. D., et al. (2004), Impact of changing land use practices on nitrate export by the Mississippi River, *Global Biogeochem. Cycles*, *18*, GB1028, doi:10.1029/2003GB002093.

Dripps, W. R., et al. (2006), Estimating recharge rates with analytic element models and parameter estimation, *Ground Water*, *44*, 47–55.

Eilers, J. M., et al. (1988), Chemical and physical characteristics of lakes in the Upper Midwest, United States, *Environ. Sci. Technol.*, *22*, 164–172.

Elder, J. F., et al. (1992), Water, energy, and biogeochemical budgets (WEBB) program: Data availability and research at the Northern Temperate Lakes site, Wisconsin, report, 15 pp., U. S. Geol. Surv., Madison, Wis.

Elder, J. F., et al. (2000), Sources and yields of dissolved carbon in northern Wisconsin stream catchments with differing amounts of peatland, *Wetlands*, *20*, 113–125.

El Maayar, M., et al. (2001), Validation of the Integrated Biosphere Simulator over Canadian deciduous and coniferous boreal forest stands, *J. Geophys. Res.*, *106*, 14,339–14,355.

Foley, J. A., et al. (1996), An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, *Global Biogeochem. Cycles*, *10*, 603–628.

Gergel, S. E., et al. (1999), Dissolved organic carbon as an indicator of the scale of watershed influence on lakes and rivers, *Ecol. Appl.*, *9*, 1377–1390.

Gesch, D., et al. (2002), The National Elevation Dataset, *Photogramm. Eng. Remote Sens.*, *68*, 5–11.

Hanson, P. C., et al. (2003), Lake metabolism: Relationships with dissolved organic carbon and phosphorus, *Limnol. Oceanogr.*, *48*, 1112–1119.

Hanson, P. C., et al. (2004), A model of carbon evasion and sedimentation in temperate lakes, *Global Change Biol.*, *10*, 1285–1298.

Hanson, P. C., S. R. Carpenter, J. A. Cardille, M. T. Coe, and L. A. Winslow (2007), Small lakes dominate a random sample of regional lake characteristics, *Freshwater Biol.*, doi:10.1111/j.1365-2427.2007.01730.x, in press.

He, H. S., et al. (2000), GIS interpolations of witness tree records (1839–1866) for northern Wisconsin at multiple scales, *J. Biogeogr.*, *27*, 1031–1042.

Hrabik, T. R., and J. Magnuson (1999), Simulated dispersal of exotic rainbow smelt (Osmerus mordax) in a northern Wisconsin lake district and implications for management, *Can. J. Fish. Aquat. Sci.*, *56*, 35–42.

Hrabik, T. R., et al. (2005), Landscape-scale variation in taxonomic diversity in four groups of aquatic organisms: The influence of physical, chemical, and biological properties, *Ecosystems*, *8*, 301–317.

Kalnay, E., et al. (1996), The NCEP/NCAR 40-year reanalysis project, *Bull. Am. Meteorol. Soc.*, *77*, 437–471.

Kistler, R., et al. (2001), The NCEP-NCAR 50-year reanalysis: Monthly means CD-ROM and documentation, *Bull. Am. Meteorol. Soc.*, *82*, 247–267.

Krabbenhoft, D. P., and K. E. Webster (1995), Transient hydrogeological controls on the chemistry of a seepage lake, *Water Resour. Res.*, *31*, 2295–2305.

Kratz, T. K., et al. (1997), The influence of landscape position on lakes in northern Wisconsin, *Freshwater Biol.*, *37*, 209–217.

Kucharik, C. J., et al. (2000), Testing the performance of a dynamic global ecosystem model: Water balance, carbon balance, and vegetation structure, *Global Biogeochem. Cycles*, *14*, 795–825.

Lenters, J. D., et al. (2000), Surface water balance of the continental United States, 1963–1995: Regional evaluation of a terrestrial biosphere model and the NCEP/NCAR reanalysis, *J. Geophys. Res.*, *105*, 22,393–22,425.

Lenters, J. D., et al. (2005), Effects of climate variability on lake evaporation: Results from a long-term energy budget study of Sparkling Lake, northern Wisconsin (USA), *J. Hydrol.*, *308*, 168–195.

Lovett, G. M., et al. (Eds.) (2005), *Ecosystem Function in Heterogeneous Landscapes*, 489 pp., Springer, New York.

Lovett, G., et al. (2006), Is net ecosystem production equal to ecosystem carbon accumulation?, *Ecosystems*, *9*, 152–155.

Ma, Z. K., and R. L. Redmond (1995), Tau coefficients for accuracy assessment of classification of remote-sensing data, *Photogramm. Eng. Remote Sens.*, *61*, 435–439.

Magnuson, J. J., et al. (1998), Isolation vs. extinction in the assembly of fishes in small northern lakes, *Ecology*, *79*, 2941–2956.

Magnuson, J. J., et al. (2006), *Long-Term Dynamics of Lakes in the Landscape: Long-Term Ecological Research on North Temperate Lakes*, 400 pp., Oxford Univ. Press, New York.

Martin, L. (1965), *The Physical Geography of Wisconsin*, 3rd ed., 608 pp., Univ. of Wis. Press, Madison.

Martin, S., and P. A. Soranno (2006), Lake landscape position: Relationships to hydrologic connectivity and landscape features, *Limnol. Oceanogr.*, *51*, 801–814.

Mook, W. G., et al. (1974), Carbon isotope fractionation between dissolved bicarbonate and gaseous carbon dioxide, *Earth Planet. Sci. Lett.*, *22*, 169–176.

New, M., et al. (2000), Representing twentieth-century space-time climate variability. Part II: Development of 1901–96 monthly grids of terrestrial surface climate, *J. Clim.*, *13*, 2217–2238.

Pace, M. L., and J. J. Cole (2002), Synchronous variation of dissolved organic carbon and color in lakes, *Limnol. Oceanogr.*, *47*, 333–342.

Peterson, G. D., et al. (2003), Assessing future ecosystem services: A case study of the Northern Highland Lake District, Wisconsin, *Conserv. Ecol.*, *7*(3): 1. [online] URL: http://www.consecol.org/vol7/iss3/art1/.

Pint, C. N., et al. (2003), Flow path delineation and ground water age, Allequash Basin, Wisconsin, *Ground Water*, *41*, 895–902.

Reiners, W. A., and K. L. Driese (2004), *Transport Processes in Nature: Propagation of Ecological Influences Through Environmental Space*, 302 pp., Cambridge Univ. Press, New York.

Riera, J. L., et al. (2000), A geomorphic template for the analysis of lake districts applied to the Northern Highland Lake District, Wisconsin, USA, *Freshwater Biol.*, *43*, 301–318.

Schindler, J. E., and D. P. Krabbenhoft (1998), The hyporheic zone as a source of dissolved organic carbon and carbon gases to a temperate forested stream, *Biogeochemistry*, *43*, 157–174.

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

Soil Survey Staff (1994), General Soil Map (STATSGO), http://soildatamart.nrcs.usda.gov, Nat. Resour. Conserv. Serv., U.S. Dep. of Agric., Fort Worth, Texas.

Soranno, P. A., et al. (1999), Spatial variation among lakes within landscapes: Ecological organization along lake chains, *Ecosystems*, *2*, 395–410.

Strayer, D. L., et al. (2003a), Effects of land cover on stream ecosystems: Roles of empirical models and scaling issues, *Ecosystems*, *6*, 407–423.

Strayer, D. L., et al. (2003b), What kind of spatial and temporal details are required in models of heterogeneous systems?, *Oikos*, *102*, 654–662.

Stumm, W., and J. J. Morgan (1981), *Aquatic Chemistry: An Introduction Emphasizing Chemical Equilibria in Natural Waters*, 2nd ed., 780 pp., John Wiley, Hoboken, N. J.

Tonn, W. M., et al. (1990), Intercontinental comparison of small-lake fish assemblages—The balance between local and regional processes, *Am. Nat.*, *136*, 345–375.

Turner, M. G., and F. S. I. Chapin (2005), Causes and consequences of spatial heterogeneity in ecosystem function, in *Ecosystem Function in Heterogeneous Landscapes*, edited by G. M. Lovett et al., pp. 9–30, Springer, New York.

Twine, T. E., et al. (2004), Effects of land cover change on the energy and water balance of the Mississippi River basin, *J. Hydrometeorol.*, *5*, 640–655.

Vano, J. A., J. A. Foley, C. J. Kucharik, and M. T. Coe (2006), Evaluating the seasonal and interannual variations in water balance in northern Wisconsin using a land surface model, *J. Geophys. Res.*, *111*, G02025, doi:10.1029/2005JG000112.

Vassiljev, J. (1997), Simulating the palaeorecord of northern European lakes using a coupled lake-catchment model, thesis, 19 pp., Lund Univ., Lund, Sweden.

Walker, J. F., , and T. D. Bullen (Ed.) (2000), Trout Lake, Wisconsin: A Water, Energy, and Biogeochemical Budgets Program site, U. S. Dep. of the Inter., U. S. Geol. Surv., Reston, Va.

Walker, J. F., and D. P. Krabbenhoft (1998), Groundwater and surface-water interactions in riparian and lake-dominated systems, in *Isotope Tracers in Catchment Hydrology*, edited by C. Kendall and J. J. McDonnell, pp. 467–488, Elsevier, New York.

Walker, J. F., et al. (2003), Variability of isotope and major ion chemistry in the Allequash basin, Wisconsin, *Ground Water*, *41*, 883–894.

Wanninkhof, R., et al. (1985), Gas exchange wind speed relationship measured with sulfur hexafluoride on a lake, *Science*, *227*, 1224–1226.

Webster, K. E., et al. (2000), Structuring features of lake districts: Landscape controls on lake chemical responses to drought, *Freshwater Biol.*, *43*, 499–515.

Wiens, J., et al. (1985), Boundary dynamics—A conceptual framework for studying landscape ecosystems, *Oikos*, *45*, 421–427.

Willey, J. D., et al. (2000), Rainwater dissolved organic carbon: Concentrations and global flux, *Global Biogeochem. Cycles*, *14*, 139–148.

Wisconsin Department of Natural Resources (1998), Wisconsin Land Cover Image–Level 2 (WISCLAND), report, Madison. (Available at http://www.dnr.state.wi.us/maps/gis/datalandcover.html)

Xenopoulos, M. A., 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, *Limnol. Oceanogr.*, *48*, 2321–2334.

Zhang, J., et al. (1995), Carbon-isotope fractionation during gas-water exchange and dissolution of CO_2, *Geochim. Cosmochim. Acta*, *59*, 107–114.

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