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Lakes and reservoirs as regulators of carbon cycling and climate

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Abstract

We explore the role of lakes in carbon cycling and global climate, examine the mechanisms influencing carbon pools and transformations in lakes, and discuss how the metabolism of carbon in the inland waters is likely to change in response to climate. Furthermore, we project changes as global climate change in the abundance and spatial distribution of lakes in the biosphere, and we revise the estimate for the global extent of carbon transformation in inland waters. This synthesis demonstrates that the global annual emissions of carbon dioxide from inland waters to the atmosphere are similar in magnitude to the carbon dioxide uptake by the oceans and that the global burial of organic carbon in inland water sediments exceeds organic carbon sequestration on the ocean floor. The role of inland waters in global carbon cycling and climate forcing may be changed by human activities, including construction of impoundments, which accumulate large amounts of carbon in sediments and emit large amounts of methane to the atmosphere. Methane emissions are also expected from lakes on melting permafrost. The synthesis presented here indicates that (1) inland waters constitute a significant component of the global carbon cycle, (2) their contribution to this cycle has significantly changed as a result of human activities, and (3) they will continue to change in response to future climate change causing decreased as well as increased abundance of lakes as well as increases in the number of aquatic impoundments.

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Inland waters affect climate at the regional scale through exchange of heat and water with the atmosphere (Krinner 2003). In addition, they play a substantial role in the global carbon (C) cycle and thus potentially affect climate as well (Cole et al. 2007). The consumption and production of carbon dioxide, methane, and nitrous oxide by microorganisms influences the concentrations of these greenhouse gases (GHG) in the atmosphere and thereby affects the atmospheric heat budget. Despite the small fraction of the surface of the earth occupied by inland waters, they play a major role in the global C cycle (Dean and Gorham 1998; Cole et al. 2007; Battin et al. 2008). Important new analyses have shown that lakes are extremely active sites for transport, transformation, and storage of considerable amounts of carbon received from the terrestrial environment and therefore may have an effect that is disproportional to their spatial extent. Further, human alterations of the aquatic landscape, which occur directly through the construction of large hydroelectric reservoirs and innumerable farm ponds, will also contribute to and alter carbon balances. In addition, indirect effects will be experienced through loss of lakes in regions in which the climate is becoming drier.

The objectives of this manuscript are to describe the current role and to speculate about the future role of lakes in carbon cycling and climate; to suggest mechanisms that will alter their role as climate changes; to discuss how carbon metabolism in inland waters is likely to change in response to climate; and, finally, to suggest how these changes could be monitored and managed. We present a new analysis of how the extent and distribution of lakes will change geographically under projected changes in climate and hydrology. Finally, we revise the estimate for the extent of carbon transformations in inland waters, combining our new analysis for lakes and impoundments with results of a recent analysis for streams and rivers (Battin et al. 2008). We show that the carbon emissions from inland waters to the atmosphere are similar in magnitude to global terrestrial net ecosystem production and that the rate of burial of organic carbon in inland water sediments exceeds organic carbon sequestration on the ocean floor. Construction of impoundments, changing hydrology, and changing temperature will magnify the intensity of carbon cycling, increasing both burial and outgassing of carbon. Our analysis is focused on inland waters, including lakes and reservoirs, and for the global up-scaling of their role in the carbon cycle, we also include rivers and streams. The wetland part of the terrestrial–aquatic continuum plays an important role in the global C cycle but is not included in this analysis.

Current role of lakes in the global C cycle

Current abundance and size of lakes—Global integration of pools and transformations of carbon in lakes depend critically on estimates of their abundance and size distribution (Downing in press). Recent geographic information system and theoretical work (Lehner and Döll 2004; Downing et al. 2006) have shown that lake size and abundance distributions follow a power law probability distribution, that the coefficients of this equation are constant among regions, and that dry and moist regions of the Earth differ only in that drier regions have fewer lakes than moist regions. Furthermore, lakes and impoundments cover substantially more area (>3% of the continents) than hitherto believed (Downing et al. 2006).

Lakes as recipients of terrestrial carbon—Dissolved inorganic carbon and dissolved organic carbon (DIC and DOC, respectively) are the predominant carbon inputs to most lakes, followed by particulate organic carbon (POC) and particulate inorganic carbon. The relative importance of these inputs varies with lake location and hydrology (Fig. 1). There are latitudinal differences in the proportions of POC, DOC, and total inorganic carbon in global rivers (Meybeck 1993), which reflect climate, soil texture and geochemistry, and land use. In temperate regions and boreal forests in carbonate terrain, DIC is the dominate form of aquatic C (Finlay et al. 2009; Stets et al. 2009) due to high soil respiration, carbonate weathering, and groundwater flow (Fig. 1C–E). At higher northern latitudes, DIC may also dominate (Fig. 1A). In contrast, DOC dominates in the humid tropics and in noncarbonate boreal forest (Fig. 1B,F). The patterns depicted in Fig. 1, with losses and transformations of carbon during residence in inland waters, have been referred to as comprising an 'active freshwater pipe' (Cole et al. 2007).

Indigenous primary production of organic carbon in lakes—Primary production is strongly influenced by lake size, latitude, insolation, and nutrient availability. Of the 304 million lakes that Downing et al. (2006) estimated to occur globally, 277 million were in the smallest category (0.001–0.01 km^2), and the average lake size was only 0.012 km^2. Most lakes, therefore, are typically shallow with plenty of light and nutrients and therefore should be among the most productive systems on Earth (Wetzel 2001). Pace and Prairie (2005) estimated that the global gross primary production (GPP) of lakes is 0.65 Pg C yr^{-1}. This is likely an underestimate since it is based on an approximation of total lake area and does not emphasize the high production of small lakes, which are estimated to dominate globally (Downing et al. 2006). Considering the global GPP of 100–150 Pg C yr^{-1} (Randerson et al. 2002), it is clear that the global internal primary production of lakes represents only a minor fraction of global primary production, although very poorly constrained.

Mineralization and greenhouse gas emissions—Lakes can be sites of intense organic carbon (OC) mineralization. Sustained by allochthonous OC inputs, respiration dominates over primary production in most lakes (Del Giorgio and Peters 1993; Jansson et al. 2000; Duarte and Prairie 2005), resulting in CO_2 supersaturation (Sobek et al. 2005). The relative importance of sediment respiration is strongly affected by water column depth, and therefore the contribution of sediment respiration to total lake OC mineralization is moderate in some cases (Den Heyer and Kalff 1998; Algesten et al. 2005) but considerable in other cases (Pace and Prairie 2005; Kortelainen et al. 2006). It

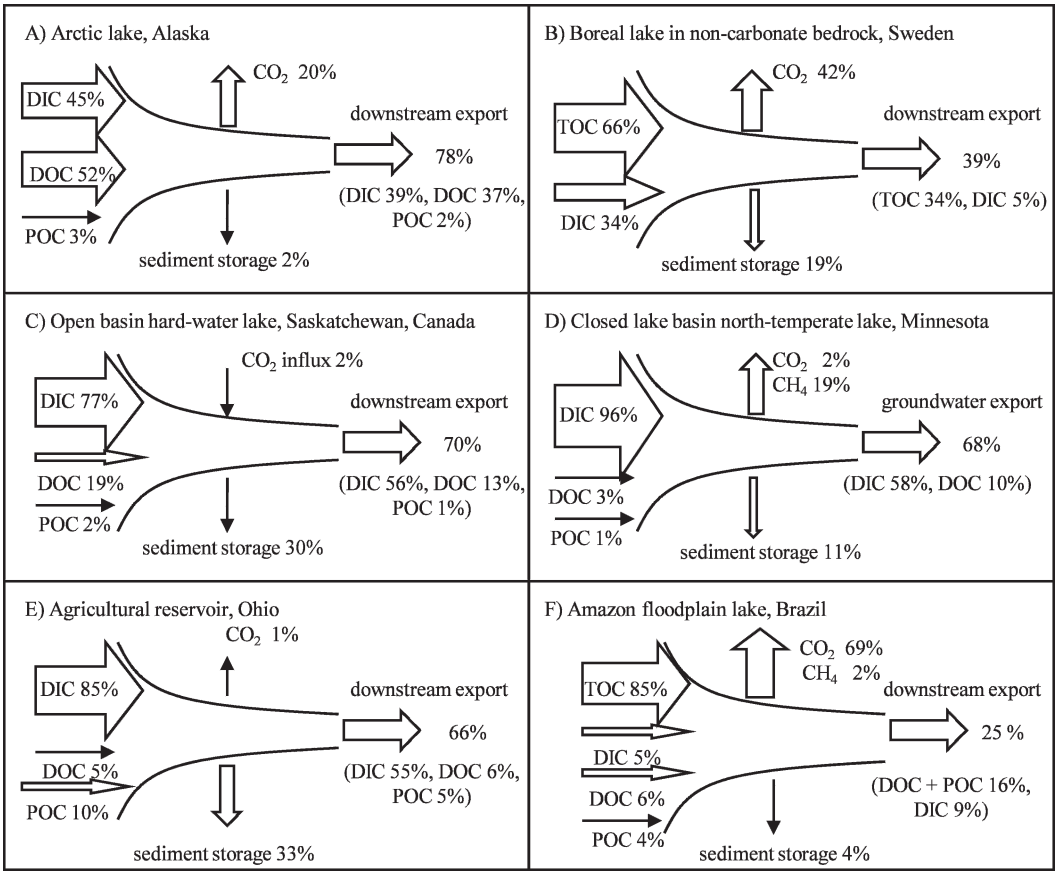

Fig. 1. Carbon budgets for diverse individual lakes, applying the 'active pipe' concept presented by Cole et al. (2007), depicting inland waters as a combined conduit and reactor for organic carbon, resulting in unidirectional flow from soils to sea and, at the same time, transformations and transport to the atmosphere and to sediment storage. Inputs of carbon can enter via upstream flow, groundwater inputs, atmospheric deposition, or fixation of atmospheric CO_2 by emergent macrophytes. Losses of carbon include inorganic and organic carbon sedimentation, CO_2 efflux to the atmosphere, and downstream flow via streams or groundwater. When possible, inputs and outputs were divided into dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and particulate organic carbon (POC). CH_4 emissions were measured in only (D) and (F) and have not been estimated for the other systems. Percentages represent proportions of total inputs and outputs accounted for by each carbon species. Ranges of error around estimates are not presented here but are considerable for several estimates (*see* References). These figures are thus considered to be best estimates based on current available data. (A) Summer carbon budget for Toolik Lake, on arctic tundra in Alaska, from Whalen and Cornwell (1985) and Kling et al. (1991, 2000). (B) Annual carbon budget for the Lake Frisksjön, in the boreal forest of Sweden, from Sobek et al. (2006). The total organic carbon (TOC) inputs arise primarily from both catchment export and macrophyte production in the littoral zone of the lake. (C) Summer carbon budget for Katepwa Lake, a polymictic, eutrophic, hard-water lake in the northern Great Plains, from Finlay et al. (2009, unpubl. data). Approximately half of the sediment storage is composed of precipitated $CaCO_3$. (D) Annual carbon budget for Williams Lake, Minnesota, a mesotrophic, dimictic, closed-lake basin, from Stets et al. (2009). (E) Summer carbon budget for a reservoir in an agricultural region in Ohio, from Knoll et al. (unpubl.). (F) Annual carbon budget for Lake Calado, a floodplain lake in the central Amazon Basin, from Lesack (1988) and Melack and Engle (in press). The separate TOC input represents macrophyte production and litterfall to the lake.

should be noted that since most lakes are small and shallow (Downing et al. 2006), much of the sediment is in contact with the upper mixed water layer rather than in cold hypolimnetic water, as in stratified lakes. This favors mineralization over burial, and CH_4 that is produced in shallow sediments largely escapes oxidation by methanotrophic bacteria and escape to the atmosphere (Bastviken et al. 2008).

OC in lakes is also mineralized via photochemical reactions (Salonen and Vähätalo 1994). However, direct photo-oxidation of OC to CO_2 accounted for less than 10% of dark respiration in the epilimnion of six boreal lakes (Granéli et al. 1996). Also, the partial pressure of CO_2 in the surface water of boreal lakes did not vary with ultraviolet irradiation levels (Sobek et al. 2003). Despite making a small contribution to the overall mineralization of OC in lakes, photochemical processes are critical to the decay of colored DOC in lakes (Molot and Dillon 1997). Although eutrophic lakes may be undersaturated, most of the lakes of the world are supersaturated in CO_2 and consequently emit CO_2 to the atmosphere (Sobek et al. 2005). Many studies indicate that the CO_2 emitted from lakes is mainly derived from in-lake respiration (Del Giorgio et al. 1999; Jansson et al. 2000), but the inflow of

CO_2-rich groundwater or surface water also contributes to lake CO_2 emission (Striegl and Michmerhuizen 1998). In lakes receiving very high DIC inputs (Fig. 1), the outgassing of CO_2 will largely depend on DIC inputs from the catchment, and in-lake metabolism will consequently play a minor role. Further, in saline, hard-water lakes, CO_2 emission is not driven by metabolism but rather by pH-related speciation of the DIC pool (Duarte et al. 2008). Cole et al. (1994) estimated that lakes emit about 0.14 Pg C yr^{-1} (as CO_2) to the atmosphere. This estimate included principally temperate lakes and a very few warm tropical lakes. Accounting for the greater emission of CO_2 from tropical lakes, compared to their temperate counterparts, may raise the above estimate by about 30% (H. Marotta unpubl.). Further, saline lakes, which, in spite of their large area (e.g., Caspian Sea, Aral Sea, Lake Chad), were not included in the work of Cole et al. (1994), contribute another 0.11–0.15 Pg C yr^{-1} to the atmosphere (Duarte et al. 2008). In total, global CO_2 emission from lakes could be as high as 0.53 Pg C yr^{-1}, taking into account the various lake types as well as recent estimates of the global area of lakes (Downing et al. 2006). Although this has previously been shown in regional studies of boreal and tropical forest landscapes (Richey et al. 2002; Algesten et al. 2004; Kortelainen et al. 2006), compared to the total export of carbon from the continents to the sea (roughly 0.9 Pg C yr^{-1}; Cole et al. 2007), CO_2 emission from lakes is likely to be an important term in the continental carbon balance (Fig. 1).

Anoxia in freshwater sediments contributes to high CH_4 emission on global (Bastviken et al. 2004*a*) and landscape (Christensen et al. 2007) scales. While CH_4 produced in hypolimnetic sediments is mostly oxidized to CO_2 by methanotrophic microbes (Striegl and Michmerhuizen 1998), production of CH_4 in epilimnetic sediments is the main driver of CH_4 emission from lakes (Bastviken et al. 2008). Apart from diffusion, CH_4 is also released from sediments via gas bubbles (ebullition). This process is the most important pathway of CH_4 emission from some lakes (Bastviken et al. 2004*a*), particularly shallow lakes with low hydrostatic pressure on the sediments. Vegetated lake littoral areas are 'hot spots' of CH_4 production, where CH_4 can escape via plant stems directly from the sediment into the atmosphere. Depending on the predominant plant species and sediment properties, increased water temperature and lake water level fluctuations may increase CH_4 production, and efflux can affect landscape C balances (Bergström et al. 2007).

In terms of overall C budgets, the emission of CH_4 from lakes is comparatively small (8–48 Tg C yr^{-1}; Bastviken et al. 2004*a*). CH_4 emission from lakes may represent 6–16% of total nonanthropogenic emissions, however, and is higher than methane emission from the ocean (Bastviken et al. 2004*a*). Further, if accounting for the 20-fold higher radiative forcing of CH_4, as compared to CO_2, and considering that several percent or more of the carbon is emitted from lakes as CH_4 rather than as CO_2 (Huttunen et al. 2003*b*), it is suggested that methane and carbon dioxide may be equally important links between lakes and the climate. The wide variation among CH_4 emission estimates in lakes illustrates, however, that CH_4 emission is not as well constrained as CO_2 emission. This is mainly due to the relative paucity of data compiled for methane (<100 lakes) compared to that compiled for CO_2 (>5000 lakes), but this variation is also connected to methodological limitations in the measurement of CH_4 ebullition as well as plant-mediated emissions from littoral vegetation. More field data and the emerging use of hydroacoustics to measure ebullition (Ostrovsky et al. 2008) will help to better constrain global estimates of CH_4 emission from lakes.

Lakes and reservoirs may act as sources or sinks of nitrous oxide (N_2O), a potent greenhouse gas that is produced via nitrification and denitrification. Lake morphometry may be an important predictor of emissions, since N_2O may be consumed in the hypolimnion, while shallow sediments contribute to N_2O emissions (Huttunen et al. 2003*a*; Wang et al. 2006). While relatively little research has addressed N_2O fluxes from lakes, current data indicate that lake and reservoir fluxes have similar areal rates to forests and wetlands but may be higher than those found in agricultural soils. Given the small areal extent of lakes, compared to those of forests, wetlands, and agriculture, it may be unlikely that lakes contribute a large fraction of global N_2O emissions (Mengis et al. 1997; Huttunen et al. 2004).

Burial and sedimentation of carbon in lakes—The significance of lake sediments in the global C cycle can be considered in terms of the carbon pool contained in lake sediments and the rate at which that pool is increasing. Cole et al. (2007) suggested that, because of their spatial extent and ability to preserve OC, lakes sequester large amounts of carbon in their sediments. Lake sediments have been estimated to contain 820 Pg of OC (Mulholland and Elwood 1982; Einsele et al. 2001; Cole et al. 2007). In addition to the considerable amount of OC stored in lake sediments, inorganic carbon can comprise a large share of the sediment mass in hard-water lakes with low sediment organic matter content. Therefore, even lakes with low organic matter content can store a large amount of C, and the global annual amount of OC buried in the sediments of natural lakes plus reservoirs exceeds that in ocean sediments by a factor of three (Dean and Gorham 1998).

Annual burial rates of OC and inorganic carbon tend to be highest in small, eutrophic lakes and impoundments (Downing et al. 2008). Sediment OC burial is high in lakes for several reasons: these lakes collect sediment from the watershed (von Wachenfeldt and Tranvik 2008), they retain sediments efficiently (they are often highly productive on an areal basis, generating autochthonous organic matter [Wetzel 2001]), and lake sediment oxygen concentrations are often low (Wetzel 2001). Furthermore, the recalcitrance of allochthonous organic matter permits efficient burial (von Wachenfeldt et al. 2008). As a result of the prevalence of small and shallow lakes on the global scale (Downing et al. 2006), most of the sediments in which OC resides are shallow sediments. How this affects burial is poorly understood. Mineralization is higher in shallow sediments (*see* above), but on the other hand, shallow sediment OC may be redistributed to deeper strata by sediment focusing,

through which it is subsequently buried (Benoy et al. 2007). The long-term average carbon burial rates in lakes are estimated to be between 4.5 and 14 g C m^{-2} yr^{-1} (Dean and Gorham 1998; Stallard 1998; Cole et al. 2007). If extrapolated, the range of global annual C storage rates is from 0.03 to 0.07 Pg C yr^{-1} (Dean and Gorham 1998; Einsele et al. 2001; Cole et al. 2007). An independent regional estimate for the Canadian boreal forest region indicates that this region alone could account for more than 10% (0.005–0.0085 Pg C yr^{-1}; Benoy et al. 2007) of our global estimate. These annual rates are similar to those seen for C burial in marine sediments (about 0.12 Pg yr^{-1}; Sarmiento and Sundquist 1992), although recent analyses indicate that burial rates in human-built impoundments and human-affected small lakes may be one to two orders of magnitude higher than those seen in natural lakes (average of 1000 g C m^{-2} yr^{-1}; Downing et al. 2008), with the highest values seen in small, eutrophic impoundments.

In view of increasing lake-water DOC concentrations in large regions (Tranvik and Jansson 2002; Monteith et al. 2007), it is important to note that DOC can be transformed to POC in the water column and can potentially be sequestered in lake sediments. Flocculation of DOC to POC is important in boreal lakes (von Wachenfeldt et al. 2008), where sedimentation of DOC may be of similar magnitude to the evasion of CO_2 to the atmosphere (von Wachenfeldt and Tranvik 2008). DOC flocculation and settling may affect sediment respiration and the potential for methanogenesis in the sediments of boreal, and possibly other, lakes.

Reservoir carbon dioxide and methane emission—Organic soils and plant biomass are flooded during river impoundment, which potentially contributes to large emissions of CO_2 and CH_4 to the atmosphere during the first years after flooding (Rudd et al. 1993; Kelly et al. 1997). As is the case with natural systems, greenhouse gases can be emitted via diffusion at the surface of the reservoir (CO_2 and CH_4), ebullition (bubble flux) in the reservoir (mainly for CH_4), diffusion through plant stems, and degassing downstream of the reservoir (mainly CH_4). In a study of boreal reservoirs flooded between 1991 and 2004, Tremblay et al. (2005) showed that emissions of GHG decline about 10 yr post-impoundment. Fluxes of GHG in boreal reservoirs were usually three to 10 times higher than those in natural lakes at their maximum, which occurs 2–5 yr after impoundment. In tropical impoundments, anoxic conditions can facilitate CH_4 production even 10 yr after impoundment (Abril et al. 2005).

One potentially important process for GHG emission from impoundments is the outgassing of GHG downstream of reservoirs, a process that bypasses the oxidation of methane that occurs in the water column as methane mixes up from the sediments and hypolimnion. Emissions downstream from tropical hydroelectric dams can be significant (Abril et al. 2005; Kemenes et al. 2007). As methane-rich water passes through turbines, hydrostatic pressure drops, and a large portion of the gas rapidly escapes to the atmosphere. For several years, the downstream degassing of methane from tropical hydroelectric reservoirs has been at the center of a debate (Rosa et al. 2004; Giles 2006) in which it has been argued that the greenhouse gas emission effects of some hydroelectric reservoirs can be greater than that of fossil fuel alternatives (Fearnside 1995, 2006).

The role of hard-water and saline lakes in the global carbon budget—Hard-water and saline lakes comprise nearly half of the volume of all inland waters worldwide (Hammer 1986; Wetzel 2001) and have elevated DIC concentrations relative to soft-water systems. Together, these characteristics cause hard-water and saline lakes to contribute significantly to the global carbon budget (Duarte et al. 2008). The predominant mechanisms driving carbon processing in these lakes, however, is unclear. The high pH of these systems (Wetzel 2001) may lower CO_2 concentrations relative to HCO_3^- and CO_3^{2-}, and the high productivity of some of these lakes may further deplete dissolved CO_2, yet saline lakes are frequently observed to emit large quantities of CO_2 to the atmosphere (Duarte et al. 2008).

A highly resolved temporal analysis of six lakes in the northern Great Plains of Canada over the course of 14 yr showed high interannual variability of CO_2 flux driven by changes in pH (Finlay et al. 2009): when the pH exceeded 8.6, the lakes acted as carbon sponges, and when pH dropped below 8.6, the lakes outgassed CO_2. Similarly, Duarte et al. (2008) observed a pH dependence of CO_2 flux and concluded that the saline lakes in their study were acting as carbon sponges when pH exceeded 9.0. Many saline and hard waters have much higher concentrations of DIC relative to DOC (Wetzel 2001), indicating that factors regulating inorganic carbon, such as climate, watershed characteristics, or groundwater fluxes (Striegl and Michmerhuizen 1998), are more important than lake metabolic control of CO_2 flux.

Effects of food web structure and nutrient input on atmosphere–lake C flux—Nutrients and food web structure can interact to determine whether lakes and reservoirs are net sources or sinks for CO_2 by stimulating net production (Schindler et al. 1997) and increasing sedimentation rates (Flanagan et al. 2006). Suppression of small, zooplanktivorous fish by top predators allows zooplankton to thrive, suppressing phytoplankton. In contrast, a lack of top predators can increase phytoplankton abundance (D. E. Schindler et al. 1997). Food web interactions can also affect C flux through other mechanisms. For example, high-nutrient inputs and benthivorous fish can help maintain shallow lakes in a turbid state with high phytoplankton biomass, whereas a clear water state with abundant macrophytes and low phytoplankton may persist when nutrient loading and benthivorous fish biomass are low (Scheffer 1998). Understanding the effects of these food web interactions on C flux between lakes and the atmosphere and burial is especially important because climate warming, management, overfishing, and other stressors may shift lakes from one stable state to another (Allan et al. 2005; Ficke et al. 2007). In addition, land use change, nitrogen deposition, and the ongoing use of

fertilizers may continue to shift lakes and reservoirs toward the 'turbid state,' exacerbating the role of food web effects on C flux. The global role of these factors on the aquatic carbon cycle remains to be elucidated.

Improved quantification of the role of inland waters in the carbon cycle through remote sensing—Much of the above discussion is based on extrapolation of in situ measurements to regional and global scales. Remote sensing can provide more direct evidence of the global role of lakes in carbon cycling by allowing the accurate enumeration of total lake area, the documentation of changes in lake numbers and sizes over time, the estimation of DOC via remote sensing of colored DOM (CDOM), and the analysis of effects of changes in land cover on lake carbon content. The current estimate of global abundance and size distribution of lakes, ponds, and impoundments is based on the inter-regional similarity of the Pareto distribution (Downing et al. 2006). Cloud-free Landsat mosaics of most continental surfaces are available with about 15 m of spatial resolution, and synthetic aperture radar (SAR) data are available for many regions. SAR acquisitions are not influenced by cloud cover, and the signal is especially sensitive to water (Melack 2004). These data allow us to count nearly all lakes in the world, measure their surface area, and determine their size distribution. Landsat images with varying resolution are available for more than three decades, and SAR data are available for over a decade. Time series of these images make it possible to monitor changes in lake numbers and sizes. Lake DOC throughout the arctic, boreal, temperate, and tropical zones is dominated by CDOM, so monitoring DOC concentrations in lakes by remote sensing is possible if appropriate sensors are flown, using regional correlations between CDOM and DOC (Kutser et al. 2005*a*,*b*). Accordingly, remote sensing has the potential to provide large-scale estimates of the DOC pools of lakes.

Future role of lakes and impoundments in the global C cycle in response to climate change

Two fundamental ways in which the future role of lakes with regard to carbon cycling and climate will be changed are through (1) continuing alterations in the biogeochemical processes occurring in watersheds and within lakes and alterations in the occurrence and geographic distribution of lakes (e.g., by loss in regions where the climate will become dryer) and (2) the construction of new waterbodies. In Table 1 we present a synthesis of changes that will drive biogeochemical processes in lakes in the future.

Carbon, whether allochthonous or autochthonous, follows three major pathways in lakes and impoundments, with the relative importance of each determining whether the aquatic ecosystem is a source or sink of greenhouse gases (GHG; Fig. 2): (1) DOC and POC are transported from the water column to the sediment via flocculation of OC, incorporation into biological material, and sedimentation of particulate organic matter; (2) DOC and POC are degraded by photochemical and microbial processes (which leads to the eventual mineralization of OC to CH_4, CO, and CO_2); and (3) carbon compounds flow passively downstream to river, groundwater, and marine systems.

In order to gain a clearer understanding of how lakes regulate carbon flow within the context of climate change, we here explore how changes in climate and other anthropogenic forces alter the quantity and quality of carbon inputs from the watershed to lakes and how changes in climate affect the relative importance of each of the three carbon pathways (*see* above). It is important to assess how these three pathways can be managed and to understand both the strength and direction (positive or negative) of feedback in each. For example, DOC export from terrestrial environments is increasing across large regions (Monteith et al. 2007), although the underlying mechanisms need clarification. Understanding links and feedbacks among pathways of carbon processing and climate change or other anthropogenic influences is critical to understanding the role of freshwater systems to the global C cycle (Table 1).

Hydrology—Alterations in precipitation patterns with shifts in climate will likely affect the inputs of carbon to aquatic systems from the watershed. Most of these carbon inputs, including DIC, are ultimately derived from terrestrial primary production that has undergone various degrees of transformation. Thus, hydrological patterns affecting terrestrial primary production will also influence carbon loading to lakes. In some cases, increased drought has been associated with increased DOC inputs to lakes through the exposure of previously waterlogged peat to oxygen, thereby triggering microbial degradation and mobilization of DOC (Freeman et al. 2001). In contrast, other investigators indicate that drier climates yield lower concentrations of DOC in lakes as a result of increased water retention times in lakes and, hence, require more time for degradation processes to occur (D. W. Schindler et al. 1997). Wetter climates result in more export of DOC to lakes, and shorter water retention times allow less time for degradation and, hence, higher standing stocks of DOC in lakes (Hinton et al. 1997; Tranvik and Jansson 2002).

In addition, changes in land use and water management strategies modify lake and reservoir hydrology and DOC concentrations. Such changes will intensify as increases in the human population and food production require additional water diversion. Runoff is already significantly reduced in most populated regions (Gornitz et al. 1997; Vörösmarty and Sahagian 2000), resulting in longer residence time in many lakes and changes in the inputs to aquatic systems of DOC, POC, and DIC; nutrients; and acid and base ions. Likewise, reductions in atmospheric sulfur deposition have been linked to increases in DOC in lakes following their recovery from acidification (Evans et al. 2006; Monteith et al. 2007).

Vegetation and soil—Watershed changes in and redistribution of plant communities are clear consequences of global climate change (Williams et al. 2007). Modifications in temperature, nitrogen deposition, rainfall, and increased atmospheric CO_2 concentrations will affect the quantity

Table 1. Examples of carbon (C) processing and greenhouse gas (GHG) emissions by lakes and continental waters, including mechanisms, changes (Δ), monitoring, and management approaches. Letters in the first column refer to pathways indicated in Fig. 2.*

	Process controlling C cycling in lakes	C species affected	Example of change driving lake C inputs and processing	Potential change in DOC quantity	Potential change in DOC quality	Effect on GHG emission	Monitoring	Adaptation
A	ΔHydrology (e.g., timing and flux of water transporting DOC)	DOC, POC, and DIC	More summer storms driving flow paths through litter layer and wetlands	Increase during summer	More CDOM and some labile DOC in storm pulses	More CO_2 and CH_4	In situ sensors for CDOM and CO_2 at stream gauges	Local management of deforestation and livestock practices
A	ΔWater residence time	DOC, POC, and DIC	Prolonged (e.g., North American prairie lakes) or reduced (e.g., Fennoscandia) time for processing of C within lakes	With increasing residence time, increased loss by photo- and biodegradation	With increasing residence time, increasingly photobleached CDOM	Higher CO_2 emissions at high CDOM concentrations (i.e., at short residence times)	In situ sensors for CDOM and CO_2 at stream gauges	Local management of deforestation and livestock practices
B	ΔVegetation; CO_2 and temperature effects on plant species and litter production	DOC and POC	Increase in the structural, chemical complexity of plant tissue altering bioavailability and degradability	Increase, particularly in the fall with an increase in leaf litter	Increase in recalcitrant DOC	Change in CO_2 and CH_4 flux, more sedimentation	In situ sensors for CDOM and CO_2	Forest and land management
C	ΔAtmospheric deposition to terrestrial system, more nutrient flux from litter and soils	DOC and POC	More nitrate flux to lakes, driving phosphorus limitation and Δ in stoichiometry	More DON	Δ in C : N in DOM and humic DOC	More CO_2 and CH_4	In situ sensors for CDOM and CO_2	Increase in littoral wetlands in watersheds
D	ΔSeasonality of lake condition (e.g., ice-cover, flushing, stratification and temporal permanency)	DOC and POC	Increase in ice-free period, driving increase in summer phytoplankton and anoxia-driven methanogenesis in lake sediments	More DOC from algal growth, photolytic loss of DOC	Lower SUVA (<color) of humic DOC, more nonhumic DOC	More CO_2 and CH_4	In situ sensors for CDOM and CO_2; remote sensing	Global reduction in GHG
E	ΔAutochthonous production due to littoral vegetation, phytoplankton, or benthic algal mats	DOC and POC	Change in trophic structure as a result of loss of fish predators	More biolabile nonhumic DOC, increase in POC	Lower SUVA	Less CO_2 flux and increase in CH_4 from sediment	In situ sensors for CDOM and CO_2; remote sensing	Manage fishery
F	ΔMicrobial DOM degradation	DOC and DIC	Increase in water temperature, driving microbial degradation	Less DOC	Lower humic DOC and more nonhumic DOC	More CO_2 production in pelagic zone	In situ sensors for CDOM and CO_2; remote sensing	Global reduction in GHG
G	ΔPhotodecay caused by change in irradiance, water quality (pH, iron, and NO_3^-), and stratification	DOC and DIC	Increase in summer UV penetration due to photobleaching of CDOM during prolonged stratification	Less DOC	Lower DOC absorbance (UVA)	More CO_2 production in pelagic zone	In situ sensors for CDOM and CO_2	Reduce SO_4 and NO_3 deposition

Table 1. Continued.

	Process controlling C cycling in lakes	C species affected	Example of change driving lake C inputs and processing	Potential change in DOC quantity	Potential change in DOC quality	Effect on GHG emission	Monitoring	Adaptation
H	ΔSedimentation caused by Δ salinity, pH, cations	DOC and POC	Drought-caused increase in salinity enhancing DOC flocculation	Less DOC	Lower SUVA	Less CO_2 flux	Sensor	Manage draw-down through water markets

* DOC, dissolved organic carbon; POC, particulate organic carbon; DIC, dissolved inorganic carbon; CDOM, colored dissolved organic matter; DON, dissolved organic nitrogen; DOM, dissolved organic matter; C : N, carbon : nitrogen; SUVA = specific ultraviolet absorbance; UV, ultraviolet.

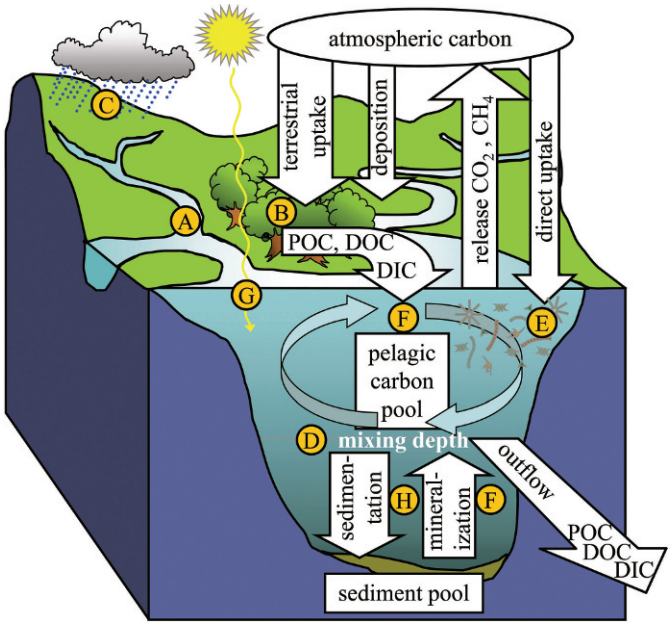

Fig. 2. Schematic diagram showing pathways of carbon cycling mediated by lakes and other continental waters. The letters correspond to rows in Table 1.

and quality of OC produced in the watershed (Canham et al. 2004; Sobek et al. 2007). Higher temperatures induce alterations in forest tree species (Petit et al. 2008), replacement of forest ecosystems with grassland-dominated ecosystems (Anderson 1991), upward shifts of alpine plants (Walther et al. 2005), and primary succession in newly deglaciated landscapes (Engstrom et al. 2000). Changes in plant species influence litter fall and humus accumulation in forest ecosystems (Kalbitz et al. 2000). Increases in watershed net primary production are likely to result in higher DOC concentrations, bacterial production, bacterial respiration, and emission of CO_2 to the atmosphere in subarctic lakes (Jansson et al. 2008). Warming-induced decomposition of soil organic matter, especially in arctic and subarctic soils (Anderson 1991), will result in greater transport of allochthonous DOC to lakes that previously received low inputs (e.g., alpine lakes, or those resulting from glacial retreat) as well as altered DOC quality (e.g., replacement of herbs with less productive shrubs) (Shaver et al. 2000).

The direct effects of increased CO_2 on vegetation and DOC quality may be particularly pronounced. At present, atmospheric CO_2 is nearly 35% higher than preindustrial levels and is increasing (IPCC 2007). Elevated CO_2 conditions lead to increased carbon fixation, subsequently increasing the concentration of carbohydrates and phenolic compounds (e.g., lignin and condensed tannins) in plant tissues (Tuchman et al. 2002). Overflow of carbon to secondary structural and defense compounds leads to higher C : nitrogen ratios and reduced bioavailability. Shifts in peatland plant species composition under elevated CO_2 concentrations and air temperatures boost DOC export (Fenner et al. 2007).

The carbon flow from watersheds to lakes may also be modified by the cumulative effects of atmospheric nutrient

deposition in the watershed and could have important effects on carbon flow to lakes. Nitrogen saturation resulting from wet and dry deposition from agricultural or industrial processes will increase exchange of nitrogen from plants to soil, the storage of OC in terrestrial ecosystems, and soil acidification (Vitousek et al. 1997; Fenn et al. 1998). For example, DOC release from peat increases upon fertilization from atmospheric nitrogen deposition (Bragazza et al. 2006).

Seasonality—At high latitudes, changes in snow cover and permafrost have led to increases in DOC and nitrogen in nearby lakes and impoundments (Baron et al. 1994; Zimov et al. 2006). Changes in the duration of ice and snow cover modify the carbon flow from the watershed through effects on both runoff and vegetation. The length of the main growing and runoff season, as defined by annual mean air temperatures and amplitudes, is a good predictor for DOC concentrations, both on temporal and spatial scales (Weyhenmeyer and Karlsson 2009). Sobek et al. (2007) found that global lake DOC concentrations are better explained by altitude than by annual mean air temperatures, which may be explained by lower DOC at higher altitudes as a result of steep topography and thin soils. Annual temperature amplitude may contribute to this pattern, although this possibility is not resolved in the global data set of Sobek et al. (2007), which relied on a global temperature database with limited resolution.

DOC mineralization and DIC release are also linked to seasonal changes in ice cover and lake stratification. Changes in lake mixing regimes, resulting from increased temperature or modified hydrology, may create stronger and prolonged stratification in lakes, resulting in oxygen deficiency, lowering of DOC mineralization rates (*see* below), and a reduction in annual primary productivity (O'Reilly et al. 2003). The resulting increase in stability of the hypolimnion and the creation of prolonged anoxia also favor DOC mineralization to methane (Bastviken et al. 2004*a*).

Autochthonous primary production—Sources of autochthonous DOC include extracellular release by phytoplankton, release by grazers, and lysis of plankton. A large fraction of this DOC is consumed and respired rapidly by microbial activity, while a smaller, more refractory fraction accumulates and is degraded over longer timescales (Stedmon and Markager 2005). Increases in nutrient input, from either watershed or airshed processes, may increase the autochthonous production of DOC and the relative importance of autochthonous DOC compared to that of allochthonous DOC. With decreasing allochthony, the evasion of CO_2 to the atmosphere is expected to decrease (Jansson et al. 2008).

Microbial degradation—Changes in the quality and quantity of DOC available in aquatic ecosystems may have direct consequences on lake productivity. Increasing allochthonous DOC inflow benefits organisms that can directly utilize it and may cause a shift from a phytoplankton-dominated system to bacterioplankton-dominated system (Jansson et al. 2000).

Oxygen is often deficient in lakes. The primary attack on organic matter via oxygenases and reactive oxygen species is an important step in the mineralization of OC and is restricted to oxygenated environments (Zehnder and Svensson 1986). While autochthonous OC is mineralized at similar rates under both oxic and anoxic conditions, the mineralization of allochthonous OC is suppressed under anoxic conditions (Hulthe et al. 1998; Bastviken et al. 2004*b*) because allochthonous OC is rich in aliphatic polymers, triterpenes, lignin, and humic matter, which are resistant to anaerobic degradation (Zehnder and Svensson 1986). Accordingly, even the OC of very old sediments can be readily degraded by aerobic bacteria under oxic conditions (Moodley et al. 2005).

Anoxia in hypolimnia and sediments therefore has two major carbon cycling effects: methanogenesis is stimulated, and the mineralization of allochthonous OC is suppressed. Accordingly, Huttunen et al. (2006) found that the diffusive flux of methane from lake sediments to the water column was negatively related to the oxygen penetration depth. Climate change is likely to affect the mixing conditions of lakes (King et al. 1997). Longer and stronger stratification periods will result in decreased hypolimnetic oxygen concentrations (Jankowski et al. 2006), thereby shortening the oxygen exposure time of sediment OC. Given the strong dependence of OC burial efficiency on oxygen exposure time, it is likely that climate change will enhance OC sequestration and hamper OC mineralization in sediments. With prolonged periods of anoxia, a larger share of the total OC mineralization will occur as methanogenesis. Depending on the extent of methane oxidation in the water column, which in turn primarily depends on water depth, increased methanogenesis may result in enhanced methane emission from lakes. Given that the radiative forcing of CH_4 is about 20-fold higher than that of CO_2, it takes only a very small increase in methane emission to offset the positive feedback of OC sequestration to increased anoxia due to climate change.

Photodegradation—The chromophoric (colored) fraction of aquatic CDOM absorbs light and is subject to photochemical reactions upon exposure to solar radiation. These photochemical reactions modify the chemical properties and biological availability of CDOM (Molot and Dillon 1997; Bertilsson and Tranvik 2000). Exposure of CDOM to solar irradiance can also result in direct photolysis to CO_2 (Granéli et al. 1996). Climate-related increases in the stability of lake stratification lead to increasingly photodegraded epilimnetic CDOM and protection of hypolimnetic CDOM from sunlight. The integrated outcome of these two alterations is unclear.

Sedimentation—The relative concentrations of particulate and dissolved organic matter present in lake water and in sediments will be influenced by flocculation and sedimentation. Increases in salinity due to longer retention time or lower runoff will increase flocculation and absorption of DOC on $CaCO_3$ particles in hard-water lakes (Mulholland 1981). Such processes may increase sedimentation of refractory or highly photobleached DOC.

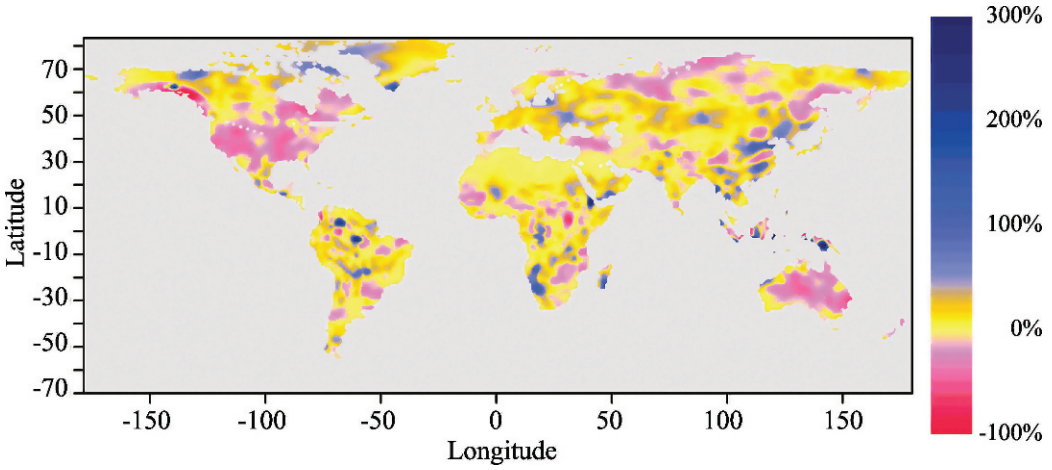

Fig. 3. Projected directions of future change in lake abundance. These projections are expressed as percentage changes from 2009 to 2050 in the areal extent and numerical abundance of lakes, given conservative IPCC climate change scenario B1 (IPCC 2007) and the historical relationship between lake abundance and runoff derived from empirical analyses (Downing et al. 2006).

The net rate of flocculation will also be modified by changes in particle concentration, pH, and temperature (Lick et al. 1992).

Management and monitoring of effects of climate change on inland water carbon cycling—Climate-related changes to either the watershed inflows or DOC, POC, and DIC or the relative strength of the three major in-lake pathways (sedimentation, mineralization, and downstream transport) will induce a complex response in the carbon pool. As indicated in Table 1, the factors controlling the quality and quantity of carbon inputs to lakes (e.g., hydrology, vegetation, atmospheric deposition, seasonality) are linked to in-lake processes (e.g., autochthonous production, microbial degradation, photochemical decay, sedimentation). As the relative strength of the major carbon pathways changes, the success of management strategies will be affected as well. Adaptive management strategies will help to address the uncertainty and variability inherent in climate change (Clark 2002; Petts et al. 2006). Long-term monitoring (e.g., the deployment of sensors that measure CDOM and CO_2) will indicate changes in carbon inflow and pathways and will allow for appropriate modifications to watershed and lake management (Adrian et al. 2009).

Anthropogenic change in occurrence of inland waters and its consequences

In addition to biogeochemical changes in lakes and impoundments, the other fundamental ways in which the future role of lakes with regard to carbon cycling and climate will be changed are through (1) alterations in the occurrence and geographic distribution of natural lakes and (2) the construction of new waterbodies. Remote sensing can be used in the future to enumerate total lake area and to study temporal changes in lake numbers and sizes.

Changing size and distribution of lakes as a result of altered runoff—In the future, as runoff declines in moist regions, the lake-size distribution will be truncated at the upper end, and large waterbodies with complex topography may be dissected into smaller ones. In regions in which runoff will increase, many small waterbodies will be formed, and small lakes will coalesce into large ones. In all geographic regions, the size distribution will be dominated by small lakes (Downing et al. 2006). Using an empirical regression relating the numerical density of lakes to the size of lakes and local runoff (Downing et al. 2006), we projected future changes in global natural lake abundance (Figs. 3, 4). Projected local runoff for 2009 and 2050 was derived using the conservative B1 scenario (IPCC 2007) generated by the Community Climate System Model (CCSM) of the National Center for Atmospheric Research. The CCSM is a fully coupled atmospheric–ocean global circulation model and is one of the main models used in the IPCC's Fourth Assessment Report (IPCC 2007). Changes in projected lake abundance by 2050 are expressed as percentages of 2009 abundance in Fig. 3. This approach does not consider land slope or regional hypsometry but does reflect relative rates of change in lake abundance and moisture if conservative climate change scenarios are realized. Climate models, climate change scenarios, and lake distribution models are all subject to variable uncertainty. Rates of change in lake area at various latitudes were projected using this same approach (Fig. 4). These projections represent a new equilibrium state for lakes and are not adjusted for the length of time it takes for an existing lake to decline (as a result of large storage) or for a new lake to become established.

These results indicate that the distribution of lakes will change regionally (Fig. 3). However, the total global area of natural lakes will not be altered appreciably by 2050 (Fig. 4). Still, much of the Earth will experience declines in lake abundance, although these will be balanced by some large increases in localized areas with increased runoff. In general, much of the North American continent is projected to see substantial declines, as is Western Europe, much of Asia, Australia, and New Zealand. South America and Africa will likely see increases and decreases with high

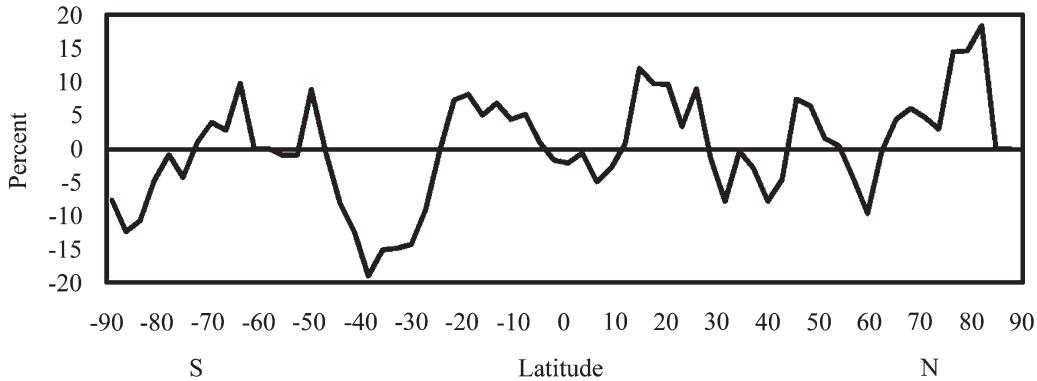

Fig. 4. Latitudinal distribution of change in lake area projected from the data on large lakes (Lehner and Döll 2004), corrected for the abundance of small lakes according to Downing et al. (2006), and rates of change projected as explained in the legend of Fig. 3.

heterogeneity. Several circumpolar areas will have increased lake abundance, provided the thawed soils can retain lake basins.

Changing abundance of inland waters as a result of construction of impoundments—So much water is retained behind dams that global sea level rise has been reduced by 0.55 mm yr^{-1} over the past 50 yr (Chao et al. 2008). Estimates of the total area of reservoirs vary (St. Louis et al. 2000; Shiklomanov and Rodda 2003; Lehner and Döll 2004), but it is clear that their area is substantial compared to that of natural lakes (Downing et al. 2006). As water demands for agriculture, domestic use, and hydroelectric generation increase, large impoundments and agricultural ponds will likely increase in area at a rate of about 1–2% per year (Downing et al. 2006). This means that impoundment surface areas worldwide will increase from about 400,000 km^2 to nearly 1 million km^2 by 2050, or by about a one-quarter measure of the natural lake area (4.2 million km^2), subject to the limitations imposed by land scarcity and available runoff. Given the high burial rates and methane emissions reported for these systems, this increase in impoundment surface area is likely a very important *global* change in the freshwater carbon transformations. The net effect of impoundments on the carbon cycle depends on the type of habitats being inundated. Possibly wetlands comprise a substantial fraction of inundated areas, resulting in the loss of areas with high potential emissions of CH_4 and also high carbon burial.

The sediments of reservoirs have been estimated to accumulate 0.16–0.2 Pg of OC annually (Mulholland and Elwood 1982; Dean and Gorham 1998), substantially more than is buried in natural lakes, and this amount is still likely underestimated (Cole et al. 2007). In addition, inventories of dams and major impoundments have typically missed small, low-tech agricultural ponds. Small agricultural impoundments occupy >75,000 km^2 globally (Downing et al. 2006), so they may bury an additional amount of OC at an average rate of around 0.15 Pg of OC each year. This is an amount similar to that buried by all larger impoundments and represents one third the carbon delivered to the ocean annually by the rivers of the world (Degens et al. 1991; Stallard 1998). Considering the world's moderate-sized impoundments (0.01–100 km^2), modern measurements of carbon deposition imply that they bury carbon at a rate of 0.6 Pg yr^{-1}, which is four times the carbon buried by the oceans annually and much greater than the amount estimated in past studies (Mulholland and Elwood 1982; Dean and Gorham 1998). St. Louis et al. (2000) estimated that world artificial reservoirs could emit 0.07 Pg CH_4 yr^{-1}, 90% of the emissions occurring in the tropics. As a comparison, Bastviken et al. (2004*a*) calculated the global emissions from lakes to be 0.008–0.048 Pg CH_4 yr^{-1}. Obviously, the emissions from reservoirs, in particular in the tropics, are a factor in the global methane budget, one that is at least equally important to the emissions from natural lakes (although as yet poorly constrained) but most likely to increase with the growing number of impoundments.

Regional changes in inland water occurrence and carbon cycling

Changing climate and runoff as well as impoundment construction are expected to change the role of inland waters in different ways in different geographic regions. Below we give examples of climatic and geographic zones in which major changes are anticipated with regard to carbon cycling and climate effects (Table 2).

Arctic regions—Carbon storage in high-latitude peatlands is estimated to represent one third or more of the global soil carbon pool (Post et al. 1982; Zimov et al. 2006). With the melting of permafrost and the formation of thaw ponds and lakes, this pool will become available for increased microbial and photochemical transformations, especially under the increased runoff scenario predicted for arctic and subarctic regions (IPCC 2007; Fig. 3). Larger emissions of CO_2 and CH_4 are expected, especially where thermokarst erosion and ponding is occurring (Walter et al. 2006). The persistence of this aquatic state apparently varies substantially between regions of varying geomorphology (Smith et al. 2005). Part of this eroded carbon and peat is also expected to reach the ocean in the future. Consequently, essentially all fluxes of the freshwater 'pipe' (i.e., Fig. 1) in polar (mostly Arctic) regions will accelerate, primarily driven by increased mobilization of OC from peat and increased precipitation.

Table 2. Examples of changes in carbon processing by lakes by 2050. Projections combine information on known mechanisms of carbon processing in lakes with projected changes in lake abundance, climate, and human perturbations (*see* text).

Region	Projected runoff change	Important perturbations	Effect on lake carbon processing
Polar	Increased runoff	Permafrost loss; increased temperature	Increased CO_2; increased CH_4; decreased burial; increased export
Boreal	Increased runoff	Increased temperature; increased dams; increased abundance of beavers	Increased CO_2; increased CH_4; increased burial; increased export
Temperate	Decreased runoff	Increased eutrophication; droughts	Increased CH_4; increased burial; decreased export
Tropics	Increased runoff	Increased dams	Increased CH_4; increased CO_2; increased burial; decreased export

Boreal regions—Important perturbations to the aquatic transport and processing in boreal regions are likely to comprise increased abundance of lakes fueled by increased precipitation and increased impoundment. Some of the anticipated increased impoundment in the Northern Hemisphere may occur from beaver activity, as beaver habitat is expected to increase (Allen 1983). As is the case in the Arctic, the inputs from terrestrial systems should increase as a result of increased precipitation, resulting in higher DOC concentrations (Tranvik and Jansson 2002) and intensification of sedimentation, mineralization, and outgassing of carbon. Accordingly, precipitation and CO_2 outgassing evasion from the 37 largest lakes in Finland (>100 km^2) were closely related (Rantakari and Kortelainen 2005). Simultaneously, increased runoff will result in shorter water residence time in lakes and, hence, in a smaller fraction of the imported OC being processed before further transport downstream to the sea.

Temperate regions—The most significant climate change affecting the function of temperate lakes in the global C cycle in the next several decades will be decreased runoff, which will most likely result in (1) reduced total lake abundance, (2) reductions in large lakes as a result of fragmentation, and (3) decreases in the areal extent of lakes. Prairie lakes in North America and Eurasia may become increasingly endorheic, resulting in evapoconcentration of dissolved substances, including DOC. Hence, the frequency of lakes with high conductivity and high concentrations of recalcitrant DOC with very low color because of extensive photobleaching (Waiser and Robarts 2000) will increase. Concomitant with projected alterations in lake abundance and size in temperate zones is a predicted increase in eutrophication and drought, resulting from growing requirements for biofuels and foods and their associated fertilizer and water demands. The additive effect of decreased lake size and increased primary production should yield an amplification in OC burial as a result of the increased autochthonous production and preservation (Cotner and Biddanda 2002; Downing et al. 2008). Further, increased production, duration of stratification, and sedimentation should generate increased prevalence of hypolimnetic anoxia and, accordingly, CH_4 production. Although increased temperatures and longer residence times caused by decreased runoff will accelerate microbial respiration and photochemical degradation of OC, the combined effects of increased autochthonous production and increased OC burial efficiency due to increased anoxia should offset increased CO_2 production.

Tropics—The most important changes in the tropics are likely to be increased abundance of lakes as a result of increased water impoundment. Higher temperatures in the tropics should favor bacterial metabolism, and, thus, a larger fraction of incoming OC should be respired. Increased temperatures should amplify anoxia and stimulate methane production as well. Because methane is a potent greenhouse gas, the impoundment of water in the tropics may be an important positive feedback process in the regulation of climate change.

Revising the active pipe model: the mass transfer of carbon through inland waters and its contribution to the global C cycle

The current focus on the role of terrestrial DOC in lake functioning has been referred to as 'carbocentric limnology' (Prairie 2008). This view was perhaps anticipated many years ago by some of the pioneers of limnology ("Kennt man die Eigenfarbe eines Sees, so kennt man auch seine übrigen Eigenschaften"—"if you know the color of a lake, you also know its other characteristics"; Thienemann 1925) and is an integral part of the wider study of the global C cycle and climate change. According to Cole et al. (2007), the processing of allochthonous carbon in lakes results in a global annual burial of 0.23 Pg and emission of 0.75 Pg C. In a separate study of lakes in Canada's boreal biome (Benoy et al. 2007) the estimated ratio of burial to emission is similar (5.0–8.5 Tg buried to 3.3–5.8 Tg evaded). The synthesis in this paper indicates that, considering that lakes have a greater spatial extent (Downing et al. 2006) and that saline lakes emit more substantial carbon to the atmosphere (Duarte et al. 2008) than hitherto known, lakes alone may emit as much as 0.53 Pg C yr^{-1} as CO_2 (0.11 Pg C yr^{-1} indicated by Cole et al. [2007]). Interestingly, Battin et al. (2008) assessed the global net heterotrophy of riverine networks (and by implication net emission of mineralized carbon), including streams, rivers, and estuaries, but without considering lakes and impoundments. For rivers and estuaries they arrive at numbers similar to those

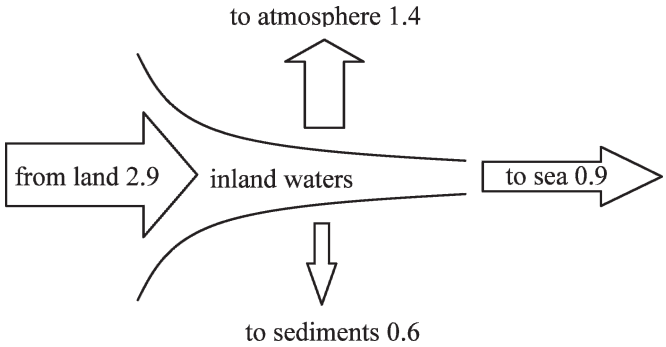

Fig. 5. Revision of the 'active pipe' hypothesis advanced by Cole et al. (2007). Revised values are explained in the text and represent annual transport of carbon (Pg, 10^{15} g).

reported by Cole et al. (2007), but for streams, which were not analyzed by Cole et al. (2007), they add another 0.32 Pg C yr^{-1}. This number is based on in-stream heterotrophy and does not take into account release of CO_2 imported as DIC from soils and groundwater. Hence, the total current emissions from inland waters, adding streams and a revised number for lakes to the budget of Cole et al. (2007), may be as high as 1.4 Pg C yr^{-1}. Similarly, the carbon burial in sediments, considering larger lake area estimates and revised numbers for the burial in small impoundments, may amount to 0.6 Pg C yr^{-1} (Fig. 5).

Given the annual transport of 0.9 Pg C to the ocean, and given the loss from inland waters via outgassing and burial (a total of 2 Pg), the total amount of OC imported to inland waters from the terrestrial environment must be on the order of 2.9 Pg yr^{-1}. The outgassing of CO_2 in the inland waters corresponds largely to respiration of terrestrial OC, directly in the aquatic environment or in soils followed by export to inland waters as DIC. The annual loss of 2 Pg is similar to the total global net ecosystem production (about 2 Pg C yr^{-1}; Randerson et al. 2002). For comparison, the annual emissions of carbon from inland waters, previously not considered in global C budgets, constitute a number (1.4 Pg) of the same order of magnitude as fossil fuel combustion, carbon emissions caused by deforestation, and carbon uptake by the oceans (6.4 Pg, 1.6 Pg, and 2.6 Pg, respectively; Burgermeister [2007]; likewise for carbon burial in inland waters [0.6 Pg]).

Given the large amounts of carbon being processed, improved quantification of these fluxes is crucial to understanding of the global C cycle and climate system. In addition, as also pointed out by Benoy et al. (2007), better knowledge of the mechanisms regulating degradation and preservation of OC in inland waters is essential to assessing the ultimate net effect of carbon processing in these systems. For example, increased burial of OC in inland waters represents a net sequestration of carbon only if it would not have been sequestered in the terrestrial habitats that exported the carbon and if the carbon would not have been otherwise sequestered downstream in the sea. Likewise, increased evasion of CO_2 to the atmosphere as a result of enhanced mineralization in lakes where the DOC concentration has been increased is not a new source of CO_2 to the atmosphere unless the same OC would have escaped mineralization if kept in soils or if transported to the ocean.

The mass of methane emission is of minor importance for the carbon mass transfer and hence is not included in the calculations above. As a result of its 20 times higher greenhouse warming potential (GWP) compared to CO_2, however, it is of great interest. The contribution from lakes (8–48 Tg yr^{-1}; Bastviken et al. 2004*a*) in combination with the likely emissions from large impoundments (70 Tg yr^{-1}; St. Louis et al. 2000) and an expected high but unknown amount of emission from the globally abundant small impoundments such as farm ponds (Downing et al. 2008) points to emissions from inland waters that are on the order of 100 Tg yr^{-1} or more. This is roughly an addition of 20% to the previously estimated global emissions (410–660 Tg CH_4 yr^{-1}, including 92–232 Tg from wetlands, but without specifically considering lakes and reservoirs; Wuebbles and Hayhoe 2002). This also places CO_2 and CH_4 from inland waters roughly equal in terms of GWP. Considering that impoundments are increasing worldwide, the substantial contribution of impoundments, including tropical hydroelectric reservoirs, will increase substantially.

It is clear from this synthesis that lakes, impoundments, and other inland waters (1) constitute a significant component of the global C cycle, (2) have changed in their contribution, significantly as a result of human activities, and (3) will continue to change in the future in response to climate change coupled with increases in the small and large impoundments. These changes include sequestration in sediments and emissions to the atmosphere as well as altered transport to the sea. Strong feedback effects on the climate system from inland waters are expected from increased methane emissions with continuing permafrost thaw and with continued construction of impoundments; in both cases, the result will be enhanced emissions of methane. Lakes are active, changing, and important regulators of the carbon cycle and global climate.

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References

Abril, G., and others. 2005. Carbon dioxide and methane emissions and the carbon budget of a 10-year old tropical reservoir (Petit Saut, French Guiana). Glob. Biogeochem. Cycles **19:** GB4007, doi: 10.1029/2005GB002457.

ADRIAN, R., AND OTHERS. 2009. Lakes as sentinels of climate change. Limnol. Oceanogr. **54:** 2283–2297.

ALGESTEN, G., S. SOBEK, A. K. BERGSTRÖM, A. ÅGREN, L. J. TRANVIK, AND M. JANSSON. 2004. Role of lakes for organic carbon cycling in the boreal zone. Glob. Change Biol. **10:** 141–147.

———, ———, ———, A. JONSSON, L. TRANVIK, AND M. JANSSON. 2005. Contribution of sediment respiration to summer CO_2 emission from low productive boreal and subarctic lakes. Microb. Ecol. **50:** 529–535.

ALLAN, J. D., R. ABELL, Z. HOGAN, C. REVENGA, B. W. TAYLOR, R. L. WELCOMME, AND K. WINEMILLER. 2005. Overfishing of inland waters. Bioscience **55:** 1041–1051.

ALLEN, A. W. 1983. Habitat suitability index models: Beaver. U.S. Fish and Wildlife Service. Report No. FWS/OBS-82/10.30 [revised].

ANDERSON, J. M. 1991. The effects of climate change on decomposition processes in grassland and coniferous forests. Ecol. Appl. **1:** 326–347.

BARON, J. S., D. S. OJIMA, E. A. HOLLAND, AND W. J. PARTON. 1994. Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest—implications for aquatic systems. Biogeochemistry **27:** 61–82.

BASTVIKEN, D., J. J. COLE, M. PACE, AND L. TRANVIK. 2004*a*. Methane emissions from lakes: Dependence of lake characteristics, two regional assessments, and a global estimate. Glob. Biogeochem. Cycles **18:** GB4009, doi: 10.1029/2004GB002238.

———, ———, M. L. PACE, AND M. C. V. DE BOGERT. 2008. Fates of methane from different lake habitats: Connecting whole-lake budgets and CH_4 emissions. J. Geophys. Res. Biogeosci. **113:** G02024, doi: 10.1029/2007JG000608.

———, L. PERSSON, G. ODHAM, AND L. TRANVIK. 2004*b*. Degradation of dissolved organic matter in oxic and anoxic lake water. Limnol. Oceanogr. **49:** 109–116.

BATTIN, T. J., AND OTHERS. 2008. Biophysical controls on organic carbon fluxes in fluvial networks. Nat. Geosci. **1:** 95–100.

BENOY, G., K. CASH, E. MCCAULEY, AND F. WRONA. 2007. Carbon dynamics in lakes of the boreal forest under a changing climate. Environ. Rev. **15:** 175–189.

BERGSTRÖM, I., S. MÄKELÄ, P. KANKAALA, AND P. KORTELAINEN. 2007. Methane efflux from littoral vegetation stands of southern boreal lakes: An upscaled regional estimate. Atmos. Environ. **41:** 339–351.

BERTILSSON, S., AND L. TRANVIK. 2000. Photochemical transformation of dissolved organic matter in lakes. Limnol. Oceanogr. **45:** 753–762.

BRAGAZZA, L., AND OTHERS. 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. Proc. Natl. Acad. Sci. USA **103:** 19386–19389.

BURGERMEISTER, J. 2007. Missing carbon mystery: Case solved? Nat. Rep. **3:** 36–37.

CANHAM, C. D., AND OTHERS. 2004. A spatially explicit watershed-scale analysis of dissolved organic carbon in Adirondack lakes. Ecol. Appl. **14:** 839–854.

CHAO, B. F., Y. H. WU, AND Y. S. LI. 2008. Impact of artificial reservoir water impoundment on global sea level. Science **320:** 212–214.

CHRISTENSEN, T. R., AND OTHERS. 2007. A catchment-scale carbon and greenhouse gas budget of a subarctic landscape. Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. **365:** 1643–1656.

CLARK, M. J. 2002. Dealing with uncertainty: Adaptive approaches to sustainable river management. Aquat. Conserv. Mar. Freshw. Ecosyst. **12:** 347–363.

COLE, J. J., N. F. CARACO, G. W. KLING, AND T. K. KRATZ. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science **265:** 1568–1570.

———, AND OTHERS. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems **10:** 171–184.

COTNER, J. B., AND B. A. BIDDANDA. 2002. Small players, large role: Microbial influence on biogeochemical processes in pelagic aquatic ecosystems. Ecosystems **5:** 105–121.

DEAN, W. E., AND E. GORHAM. 1998. Magnitude and significance of carbon burial in lakes, reservoirs, and peatlands. Geology **26:** 535–538.

DEGENS, E. T., S. KEMPE, AND J. E. RICHEY. 1991. Summary: Biogeochemistry of major world rivers, p. 323–347. *In* E. T. Degens, S. Kempe and J. E. Richey [eds.], Biogeochemistry of major world rivers. Wiley.

DEL GIORGIO, P. A., J. J. COLE, N. F. CARACO, AND R. H. PETERS. 1999. Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. Ecology **80:** 1422–1431.

———, AND R. H. PETERS. 1993. Balance between phytoplankton production and plankton respiration in lakes. Can. J. Fish. Aquat. Sci. **50:** 282–289.

DEN HEYER, C., AND J. KALFF. 1998. Organic matter mineralization rates in sediments: A within- and among-lake study. Limnol. Oceanogr. **43:** 695–705.

DOWNING, J. A. In press. Global limnology: Up-scaling aquatic services and processes to the planet earth. Verh. Int. Ver. Limnol.

———, AND OTHERS. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol. Oceanogr. **51:** 2388–2397.

———, AND ———. 2008. Sediment organic carbon burial in agriculturally eutrophic impoundments over the last century. Glob. Biogeochem. Cycles **22:** GB1018, doi: 10.1029/2006GB002854.

DUARTE, C. M., AND Y. T. PRAIRIE. 2005. Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems **8:** 862–870.

———, ———, C. MONTES, J. J. COLE, R. G. STRIEGL, J. MELACK, AND J. A. DOWNING. 2008. CO_2 emissions from saline lakes: A global estimate of a surprisingly large flux. J. Geophys. Res. **113:** G04041, doi: 10.129/2007JG000637.

EINSELE, G., J. YAN, AND M. HINDERER. 2001. Atmospheric carbon burial in modern lake basins and its significance for the global carbon budget. Glob. Planet. Change **30:** 167–195.

ENGSTROM, D. R., S. C. FRITZ, J. E. ALMENDINGER, AND S. JUGGINS. 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. Nature **408:** 161–166.

EVANS, C. D., P. J. CHAPMAN, J. M. CLARK, D. T. MONTEITH, AND M. S. CRESSER. 2006. Alternative explanations for rising dissolved organic carbon export from organic soils. Glob. Change Biol. **12:** 2044–2053.

FEARNSIDE, P. 2006. Greenhouse gas emissions from hydroelectric dams: Reply to Rosa et al. Clim. Change **75:** 103–109.

FEARNSIDE, P. M. 1995. Hydroelectric dams in the Brazilian Amazon as sources of greenhouse gases. Environ. Conserv. **22:** 7–19.

FENN, M. E., AND OTHERS. 1998. Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. Ecol. Appl. **8:** 706–733.

FENNER, N., C. FREEMAN, M. A. LOCK, H. HARMENS, B. REYNOLDS, AND T. SPARKS. 2007. Interactions between elevated CO_2 and warming could amplify DOC exports from peatland catchments. Environ. Sci. Technol. **41:** 3146–3152.

FICKE, A. D., C. A. MYRICK, AND L. J. HANSEN. 2007. Potential impacts of global climate change on freshwater fisheries. Rev. Fish Biol. Fish. **17:** 581–613.

FINLAY, K., P. LEAVITT, B. WISSEL, AND Y. T. PRAIRIE. 2009. Regulation of spatial and temporal variability of carbon flux in six hard-water lakes of the northern Great Plains. Limnol. Oceanogr. **54:** 2553–2564.

FLANAGAN, K. M., E. MCCAULEY, AND F. WRONA. 2006. Freshwater food webs control carbon dioxide saturation through sedimentation. Glob. Change Biol. **12:** 644–651.

FREEMAN, C., N. OSTLE, AND H. KANG. 2001. An enzymic 'latch' on a global carbon store—a shortage of oxygen locks up carbon in peatlands by restraining a single enzyme. Nature **409:** 149.

GILES, J. 2006. Methane quashes green credentials of hydropower. Nature **444:** 524–525.

GORNITZ, V., C. ROSENZWEIG, AND D. HILLEL. 1997. Effects of anthropogenic intervention in the land hydrologic cycle on global sea level rise. Glob. Planet. Change **14:** 147–161.

GRANÉLI, W., M. J. LINDELL, AND L. J. TRANVIK. 1996. Photo-oxidative production of dissolved inorganic carbon in lakes of different humic content. Limnol. Oceanogr. **41:** 698–706.

HAMMER, U. T. 1986. Saline lake ecosystems of the world. Dr W. Junk Publishers.

HINTON, M. J., S. L. SCHIFF, AND M. C. ENGLISH. 1997. The significance of storms for the concentration and export of dissolved organic carbon from two Precambrian Shield catchments. Biogeochemistry **36:** 67–88.

HULTHE, G., S. HULTH, AND P. O. J. HALL. 1998. Effect of oxygen on degradation rate of refractory and labile organic matter in continental margin sediments. Geochim. Cosmochim. Acta **62:** 1319–1328.

HUTTUNEN, J. T., T. HAMMAR, P. MANNINEN, K. SERVOMAA, AND P. J. MARTIKAINEN. 2004. Potential springtime greenhouse gas emissions from a small southern boreal Lake Keihasjarvi (Finland). Boreal Environ. Res. **9:** 421–427.

———, S. JUUTINEN, J. ALM, T. LARMOLA, T. HAMMAR, J. SILVOLA, AND P. J. MARTIKAINEN. 2003*a.* Nitrous oxide flux to the atmosphere from the littoral zone of a boreal lake. J. Geophys. Res. Atmos. **108:** 4421, doi: 10.1029/2002JD002989.

———, T. S. VAISANEN, S. K. HELLSTEN, AND P. J. MARTIKAINEN. 2006. Methane fluxes at the sediment–water interface in some boreal lakes and reservoirs. Boreal Environ. Res. **11:** 27–34.

———, AND OTHERS. 2003*b.* Fluxes of methane, carbon dioxide and nitrous oxide in boreal lakes and potential anthropogenic effects on the aquatic greenhouse gas emissions. Chemosphere **52:** 609–621.

INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE (IPCC). 2007. Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller [eds.], Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

JANKOWSKI, T., D. M. LIVINGSTONE, H. BUHRER, R. FORSTER, AND P. NIEDERHAUSER. 2006. Consequences of the 2003 European heat wave for lake temperature profiles, thermal stability, and hypolimnetic oxygen depletion: Implications for a warmer world. Limnol. Oceanogr. **51:** 815–819.

JANSSON, M., A.-K. BERGSTRÖM, P. BLOMQVIST, AND S. DRAKARE. 2000. Allochthonous organic carbon and phytoplankton/bacterioplankton production relationship in lakes. Ecology **81:** 3250–3255.

———, T. HICKLER, A. JONSSON, AND J. KARLSSON. 2008. Links between terrestrial primary production and bacterial production and respiration in lakes in a climate gradient in subarctic Sweden. Ecosystems **11:** 367–376.

KALBITZ, K., S. SOLINGER, J. H. PARK, B. MICHALZIK, AND E. MATZNER. 2000. Controls on the dynamics of dissolved organic matter in soils: A review. Soil Sci. **165:** 277–304.

KELLY, C. A., AND OTHERS. 1997. Increases in fluxes of greenhouse gases and methyl mercury following flooding of an experimental reservoir. Environ. Sci. Technol. **31:** 1334–1344.

KEMENES, A., B. R. FORSBERG, AND J. M. MELACK. 2007. Methane release below a tropical hydroelectric dam. Geophys. Res. Lett. **34:** L12809, doi: 10.1029/2007GL029479.

KING, J. R., B. J. SHUTER, AND A. P. ZIMMERMAN. 1997. The response of the thermal stratification of south bay (Lake Huron) to climatic variability. Can. J. Fish. Aquat. Sci. **54:** 1873–1882.

KLING, G. W., G. W. KIPPHUT, AND M. C. MILLER. 1991. Arctic lakes and streams as gas conduits to the atmosphere: Implications for tundra carbon budgets. Science **251:** 298–301.

———, ———, M. M. MILLER, AND W. J. O'BRIEN. 2000. Integration of lakes and streams in a landscape perspective: The importance of material processing on spatial patterns and temporal coherence. Freshw. Biol. **43:** 477–497.

KORTELAINEN, P., AND OTHERS. 2006. Sediment respiration and lake trophic state are important predictors of large CO_2 evasion from small boreal lakes. Glob. Change Biol. **12:** 1554–1567.

KRINNER, G. 2003. Impact of lakes and wetlands on boreal climate. J. Geophys. Res. Atmos. **108:** 4520, doi: 10.1029/2002JD002597.

KUTSER, T., D. C. PIERSON, K. Y. KALLIO, A. REINART, AND S. SOBEK. 2005*a.* Mapping lake CDOM by satellite remote sensing. Remote Sens. Environ. **94:** 535–540.

———, D. PIERSON, L. TRANVIK, A. REINART, S. SOBEK, AND K. KALLIO. 2005*b.* Using satellite remote sensing to estimate the colored dissolved organic matter absorption coefficient in lakes. Ecosystems **8:** 709–720.

LEHNER, B., AND P. DÖLL. 2004. Development and validation of a global database of lakes, reservoirs and wetlands. J. Hydrol. **296:** 1–22.

LESACK, L. F. W. 1988. Mass balance of nutrients, major solutes, and water in an Amazon floodplain lake and biogeochemical implications for the Amazon basin. Ph.D. thesis. Univ. of California.

LICK, W., J. LICK, AND C. K. ZIEGLER. 1992. Flocculation and its effect on the vertical transport of fine-grained sediments. Hydrobiologia **235:** 1–16.

MELACK, J., AND D. L. ENGLE. In press. An organic carbon budget for an Amazon floodplain lake. Verh. Int. Ver. Limnol.

MELACK, J. M. 2004. Remote sensing of tropical wetlands, p. 319–343. *In* S. Ustin [ed.], Manual of remote sensing, 3rd ed., v. 4. Remote sensing for natural resources management and environmental monitoring. Wiley.

MENGIS, M., R. GACHTER, AND B. WEHRLI. 1997. Sources and sinks of nitrous oxide (N_2O) in deep lakes. Biogeochemistry **38:** 281–301.

MEYBECK, M. 1993. Riverine transport of atmospheric carbon—sources, global typology and budget. Water Air Soil Pollut. **70:** 443–463.

MOLOT, L. A., AND P. J. DILLON. 1997. Photolytic regulation of dissolved organic carbon in northern lakes. Glob. Biogeochem. Cycles **11:** 357–365.

MONTEITH, D. T., AND OTHERS. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature **450:** 537–540.

MOODLEY, L., J. J. MIDDELBURG, P. M. J. HERMAN, K. SOETAERT, AND G. J. DE LANGE. 2005. Oxygenation and organic-matter preservation in marine sediments: Direct experimental evidence from ancient organic carbon-rich deposits. Geology **33:** 889–892.

MULHOLLAND, P. J. 1981. Formation of particulate organic carbon in water from a southeastern swamp-stream. Limnol. Oceanogr. **26:** 790–795.

———, AND J. W. ELWOOD. 1982. The role of lake and reservoir sediments as sinks in the perturbated global carbon-cycle. Tellus **34:** 490–499.

O'REILLY, C. M., S. R. ALIN, P. D. PLISNIER, A. S. COHEN, AND B. A. MCKEE. 2003. Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. Nature **424:** 766–768.

OSTROVSKY, I., D. F. MCGINNIS, L. LAPIDUS, AND W. ECKERT. 2008. Quantifying gas ebullition with echosounder: The role of methane transport by bubbles in a medium-sized lake. Limnol. Oceanogr. Methods **6:** 105–118.

PACE, M. L., AND Y. T. PRAIRIE. 2005. Respiration in lakes, p. 103–122. *In* P. A. del Giorgio and P. J. L. B. Williams [eds.], Respiration in aquatic ecosystems. Oxford Univ. Press.

PETIT, R. J., F. S. HU, AND C. W. DICK. 2008. Forests of the past: A window to future changes. Science **320:** 1450–1452.

PETTS, G. E., J. NESTLER, AND R. KENNEDY. 2006. Advancing science for water resources management. Hydrobiologia **565:** 277–288.

POST, W. M., W. R. EMANUEL, P. J. ZINKE, AND A. G. STANGENBERGER. 1982. Soil carbon pools and world life zones. Nature **298:** 156–159.

PRAIRIE, Y. T. 2008. Carbocentric limnology: Looking back, looking forward. Can. J. Fish. Aquat. Sci. **65:** 543–548.

RANDERSON, J. T., F. S. CHAPIN, J. W. HARDEN, J. C. NEFF, AND M. E. HARMON. 2002. Net ecosystem production: A comprehensive measure of net carbon accumulation by ecosystems. Ecol. Appl. **12:** 937–947.

RANTAKARI, M., AND P. KORTELAINEN. 2005. Interannual variation and climatic regulation of the CO_2 emission from large boreal lakes. Glob. Change Biol. **11:** 1368–1380.

RICHEY, J. E., J. M. MELACK, A. K. AUFDENKAMPE, V. M. BALLESTER, AND L. L. HESS. 2002. Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO_2. Nature **416:** 617–620.

ROSA, L. P., M. A. DOS SANTOS, B. MATVIENKO, E. O. DOS SANTOS, AND E. SIKAR. 2004. Greenhouse gas emissions from hydroelectric reservoirs in tropical regions. Clim. Change **66:** 9–21.

RUDD, J. W. M., R. HARRIS, C. A. KELLY, AND R. E. HECKY. 1993. Are hydroelectric reservoirs significant sources of greenhouse gases? AMBIO **22:** 246–248.

ST. LOUIS, V. L., C. A. KELLY, E. DUCHEMIN, J. W. M. RUDD, AND D. M. ROSENBERG. 2000. Reservoir surfaces as sources of greenhouse gases to the atmosphere: A global estimate. Bioscience **50:** 766–775.

SALONEN, K., AND A. VÄHÄTALO. 1994. Photochemical mineralization of dissolved organic-matter in Lake Skjervatjern. Environ. Int. **20:** 307–312.

SARMIENTO, J. L., AND E. T. SUNDQUIST. 1992. Revised budget for the oceanic uptake of anthropogenic carbon dioxide. Nature **356:** 589–593.

SCHEFFER, M. 1998. Ecology of shallow lakes. Chapman and Hall.

SCHINDLER, D. E., S. R. CARPENTER, J. J. COLE, J. F. KITCHELL, AND M. L. PACE. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. Science **277:** 248–251.

SCHINDLER, D. W., P. J. CURTIS, S. E. BAYLEY, B. R. PARKER, K. G. BEATY, AND M. P. STAINTON. 1997. Climate-induced changes in the dissolved organic carbon budgets of boreal lakes. Biogeochemistry **36:** 9–28.

SHAVER, G. R., AND OTHERS. 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. Bioscience **50:** 871–882.

SHIKLOMANOV, I. A., AND J. C. RODDA. 2003. World water resources at the beginning of the twenty-first century. Cambridge Univ. Press.

SMITH, L. C., Y. SHENG, G. M. MACDONALD, AND L. D. HINZMAN. 2005. Disappearing arctic lakes. Science **308:** 1429.

SOBEK, S., G. ALGESTEN, A.-K. BERGSTRÖM, M. JANSSON, AND L. J. TRANVIK. 2003. The catchment and climate regulation of pCO_2 in boreal lakes. Glob. Change Biol. **9:** 630–641.

———, B. SÖDERBÄCK, S. KARLSSON, E. ANDERSSON, AND A. K. BRUNBERG. 2006. A carbon budget of a small humic lake: An example of the importance of lakes for organic matter cycling in boreal catchments. AMBIO **35:** 469–475.

———, L. J. TRANVIK, AND J. J. COLE. 2005. Temperature independence of carbon dioxide supersaturation in global lakes. Glob. Biogeochem. Cycles **19:** GB2003, doi: 10.1029/2004GB002264.

———, ———, Y. T. PRAIRIE, P. KORTELAINEN, AND J. J. COLE. 2007. Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. Limnol. Oceanogr. **52:** 1208–1219.

STALLARD, R. F. 1998. Terrestrial sedimentation and the carbon cycle: Coupling weathering and erosion to carbon burial. Glob. Biogeochem. Cycles **12:** 231–257.

STEDMON, C. A., AND S. MARKAGER. 2005. Tracing the production and degradation of autochthonous fractions of dissolved organic matter by fluorescence analysis. Limnol. Oceanogr. **50:** 1415–1426.

STETS, E. G., R. G. STRIEGL, G. R. AIKEN, D. O. ROSENBERRY, AND T. C. WINTER. 2009. Hydrologic support of carbon dioxide flux revealed by whole-lake carbon budgets. J. Geophys. Res. Biogeosci. **114:** G01008, doi: 10.1029/2008JG000783.

STRIEGL, R. G., AND C. M. MICHMERHUIZEN. 1998. Hydrologic influence on methane and carbon dioxide dynamics at two north-central Minnesota lakes. Limnol. Oceanogr. **43:** 1519–1529.

THIENEMANN, A. 1925. Inland waters of central Europe. E. Schweizbart'sche Verlagsbuchshandlung. [Written in German].

TRANVIK, L. J., AND M. JANSSON. 2002. Climate change—terrestrial export of organic carbon. Nature **415:** 861–862.

TREMBLAY, A., L. VARFALVY, C. ROEHM, AND M. GARNEU. 2005. Greenhouse gas emissions—fluxes and processes. Springer-Verlag.

TUCHMAN, N. C., R. G. WETZEL, S. T. RIER, K. A. WAHTERA, AND J. A. TEERI. 2002. Elevated atmospheric CO_2 lowers leaf litter nutritional quality for stream ecosystem food webs. Glob. Change Biol. **8:** 163–170.

VITOUSEK, P. M., AND OTHERS. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. Ecol. Appl. **7:** 737–750.

VON WACHENFELDT, E., S. SOBEK, D. BASTVIKEN, AND L. J. TRANVIK. 2008. Linking allochthonous dissolved organic matter and boreal lake sediment carbon sequestration: The role of light-mediated flocculation. Limnol. Oceanogr. **53:** 2416–2426.

———, AND L. J. TRANVIK. 2008. Sedimentation in boreal lakes—the role of flocculation of allochthonous dissolved organic matter in the water column. Ecosystems **11:** 803–814.

VÖRÖSMARTY, C. J., AND D. SAHAGIAN. 2000. Anthropogenic disturbance of the terrestrial water cycle. Bioscience **50:** 753–765.

WAISER, M. J., AND R. D. ROBARTS. 2000. Changes in composition and reactivity of allochthonous DOM in a prairie saline lake. Limnol. Oceanogr. **45:** 763–774.

Walter, K. M., S. A. Zimov, J. P. Chanton, D. Verbyla, and F. S. Chapin. 2006. Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. Nature **443:** 71–75.

Walther, G. R., S. Berger, and M. T. Sykes. 2005. An ecological 'footprint' of climate change. Proc. R. Soc. B Biol. Sci. **272:** 1427–1432.

Wang, H. J., W. D. Wang, C. Q. Yin, Y. C. Wang, and J. W. Lu. 2006. Littoral zones as the "hotspots" of nitrous oxide (N_2O) emission in a hyper-eutrophic lake in China. Atmos. Environ. **40:** 5522–5527.

Wetzel, R. G. 2001. Limnology, 3rd ed. Academic Press.

Weyhenmeyer, G. A., and J. Karlsson. 2009. Nonlinear response of dissolved organic carbon concentrations in boreal lakes to increasing temperatures. Limnol. Oceanogr **54:** 2513–2519.

Whalen, S. C., and J. C. Cornwell. 1985. Nitrogen, phosphorus, and organic-carbon cycling in an Arctic lake. Can. J. Fish. Aquat. Sci. **42:** 797–808.

Williams, A. L., K. E. Wills, J. K. Janes, J. K. V. Schoor, P. C. D. Newton, and M. J. Hovenden. 2007. Warming and free-air CO_2 enrichment alter demographics in four co-occurring grassland species. New Phytol. **176:** 365–374.

Wuebbles, D. J., and K. Hayhoe. 2002. Atmospheric methane and global change. Earth Sci. Rev. **57:** 177–210.

Zehnder, A. J. B., and B. H. Svensson. 1986. Life without oxygen—what can and what cannot. Experientia **42:** 1197–1205.

Zimov, S. A., E. A. G. Schuur, and F. S. Chapin. 2006. Permafrost and the global carbon budget. Science **312:** 1612–1613.

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