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Climate-dependent CO_2 emissions from lakes

Sarian Kosten,[1] Fábio Roland,[2] David M. L. Da Motta Marques,[3] Egbert H. Van Nes,[1]
Néstor Mazzeo,[4] Leonel da S. L. Sternberg,[5] Marten Scheffer,[1] and Jon J. Cole[6]

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[1] Inland waters, just as the world's oceans, play an important role in the global carbon cycle. While lakes and reservoirs typically emit CO_2, they also bury carbon in their sediment. The net CO_2 emission is largely the result of the decomposition or preservation of terrestrially supplied carbon. What regulates the balance between CO_2 emission and carbon burial is not known, but climate change and temperature have been hypothesized to influence both processes. We analyzed patterns in carbon dioxide partial pressure (pCO$_2$) in 83 shallow lakes over a large climatic gradient in South America and found a strong, positive correlation with temperature. The higher pCO$_2$ in warmer lakes may be caused by a higher, temperature-dependent mineralization of organic carbon. This pattern suggests that cool lakes may start to emit more CO_2 when they warm up because of climate change.

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1. Introduction

[2] The importance of the world's oceans in global carbon cycling is well known and their influence on atmospheric CO_2 concentrations is explicitly incorporated in climate change models [*Intergovernmental Panel on Climate Change* (*IPCC*), 2007]. So far, however, the role of inland waters has received less attention even though recent studies indicate that they play an important role in regulating carbon fluxes as well [*Cole et al.*, 2007; *Downing et al.*, 2008; *Duarte et al.*, 2008]. A significant part of the organic carbon initially sequestered as CO_2 by terrestrial ecosystems ends up in rivers and lakes. Only about half of this carbon is transported to the oceans [*Cole et al.*, 2007]. Much of the terrestrially produced carbon entering inland waters is buried in sediments or emitted as CO_2 to the atmosphere [*Cole et al.*, 2007]. In addition, primary production within inland waters represents a substantial carbon flux, especially in lakes with high concentrations of nutrients allowing high productivity [*Williamson et al.*, 2009]. This turns inland waters into carbon processing hot spots in terrestrial landscapes and despite the fact that inland waters occupy a relatively small fraction of the Earth's surface, they play an important role in the global carbon cycle by processing large amounts of terrestrially derived carbon [*Battin et al.*, 2009]. Depending on the balance between processes such as respiration, primary production, groundwater carbon inflow and calcite precipitation, these systems may be carbon sinks, or become supersaturated with CO_2 and act as CO_2 sources to the atmosphere [*Cole et al.*, 1994, 2000; *Duarte and Prairie*, 2005; *Sobek et al.*, 2005]. All these processes are likely sensitive to changes in temperature and hydrology.

[3] Very little is known about the overall effects of climatic change on the carbon cycling in inland waters. Temperature, for example, may affect carbon cycles in a direct way through its influence on aquatic respiration [*Sand-Jensen et al.*, 2007] and primary production [*Flanagan et al.*, 2003], which may be most evident when it coincides with an increase in nutrient loading [*Christoffersen et al.*, 2006]. A differential temperature dependence of respiration and photosynthesis may lead to a decrease in carbon fixation and an increase in carbon emission [*Lopez-Urrutia et al.*, 2006]. Altered precipitation regimes may influence lakes' metabolism as well. For instance through its effect on the hydraulic residence time, which can have several effects including altering carbon sedimentation and mineralization [*Algesten et al.*, 2004; *Curtis*, 1998]; changing terrestrial inputs of nutrients and organic matter, and possibly primary production as well [*Reynolds*, 1994; *Schallenberg and Burns*, 1997]. Temperature and precipitation also have an indirect effect on lake's carbon cycle through their influence on terrestrial carbon fixation and the subsequent carbon leaching to the lake [*Sobek et al.*, 2005].

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[1] Department of Aquatic Ecology and Water Quality Management, Wageningen University, Wageningen, Netherlands.

[2] Laboratory of Aquatic Ecology, Institute of Biology, Federal University of Juiz de Fora, Juiz de Fora, Brazil.

[3] Instituto de Pesquisas Hidráulicas, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

[4] Laboratorio de Ecología y rehabilitacíon de sistemas acuáticos, Facultad de Ciencias and CURE, Universidad de la República, Montevideo, Uruguay.

[5] Department of Biology, University of Miami, Coral Gables, Florida, USA.

[6] Cary Institute of Ecosystem Studies, Millbrook, New York, USA.

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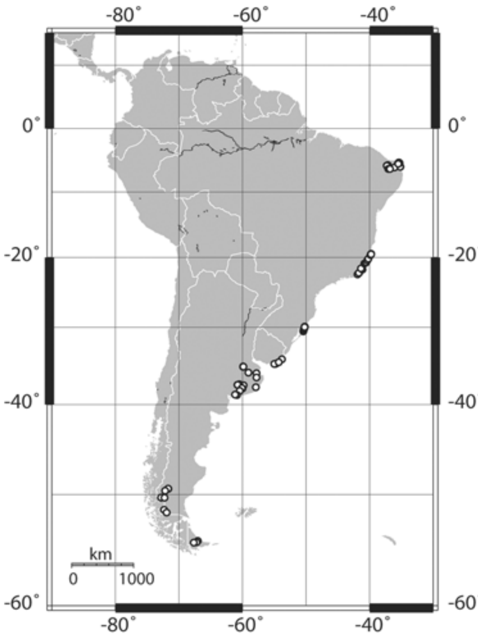

Figure 1. Location of the 82 South American lakes sampled.

[4] To explore the potential net effects of climate on carbon emissions from lakes, we sampled 82 comparable shallow lakes along a latitudinal gradient (5°–55°S) in South America (Figure 1) ranging in annual mean temperature from 4.0 to 27.6°C.

2. Methods

2.1. Site Description

[5] We sampled 82 lakes in the East of South America (Figure 1). Lakes were selected to resemble each other as much as possible morphologically, but to vary as much as possible in climate and, within climate regions, in trophic state. The lakes in our data set ranged from being oligotrophic to hypertrophic (Table 1). All lakes were shallow (maximum mean depth 4.5m) and relatively small (surface area ranged between 0.09 and 2.53 km^2) (Table 1). The climate conditions at the sampling sites varied considerably; the most northern lake sites had maximum monthly air temperature up to 28.7°C whereas at the most southern lake locations the maximum was only 8.2°C [*New et al.*, 2002]. At the time of sampling the lake water temperature ranged from approximately 10 to 30°C. In each climate region, lakes were selected to vary as much as possible in trophic state (Table 1 and *Kosten et al.* [2009a]).

2.2. Sampling

[6] Lakes South of 25°S were sampled once during summer, the lakes nearer to the equator were sampled during dry season between November 2004 and March 2006.

[7] We collected water samples along the whole water column with a 1.5 m long tube at 20 random points in each lake between 0930 and 1200 LT. Two liters of each of these depth-integrated samples were gathered in a 40 L bucket resulting in a depth and area integrated bulk sample. Filtration for various analyses in the laboratory was conducted directly after collection. Water and filters were then frozen until analysis. Sediment samples of the top 2 cm were taken in the center of the lake with a Kajak corer.

[8] Annual mean precipitation data were obtained from a high-resolution data set of surface climate over global land areas [*New et al.*, 2002].

2.3. Sample Analysis

[9] We determined the acid neutralizing capacity (ANC) titrimetrically using 0.05N HCl on unfiltered samples in the field directly after sampling. pH was determined also on unfiltered samples using a probe. Chlorophyll *a* (chl *a*) was extracted from filters (GF/C S&S) with 96% ethanol and absorbance was measured at 665 and 750 nm [*Nusch*, 1980]. For dissolved organic carbon, (DOC) analysis water was filtered through GF/F Whatman filters. DOC was determined by a Total Organic Carbon analyzer (Model 700, O.I.C International BV). As a measure for humic substances spectrophotometric light absorption at 380 nm was measured [*Buiteveld*, 1995] in filtered (0.45 μm S&S) water. The concentration of organic N and C in sediment was determined, after carbonate removal, using a CNS analyzer (NA-1500).

[10] The δ^2H and $\delta^{18}O$ of the bulk lake water sample were determined in a Multiflow system connected to an Isoprime Mass Spectrometer (Thermo Electron, Waltham, Massachusetts, United States). All isotopic ratios are expressed in δ units relative to the Vienna mean standard ocean water, here as

$$\delta D \text{ or } \delta^{18}O = \left[\frac{R_{sample}}{R_{std}} - 1\right] \cdot 1000$$

in which R_{sample} and R_{std} are $^2H/H$ or $^{18}O/^{16}O$ ratios of the sample and standard, respectively. The precision of analysis is ±2.0‰ and ±0.1‰ for δ^2H and $\delta^{18}O$ values, respectively.

2.4. Calculations and Data Analysis

[11] The pCO_2 was calculated from the pH and the ANC, adjusting for temperature, ionic strength and air pressure [*Cole et al.*, 1994]. Subsequently, the results were expressed as undersaturated or supersaturated with CO_2 relative to the atmosphere (RS). We used the global average atmospheric CO_2 pressure for the year 2005 as a reference (P. Tans,

Table 1. General Data on the Lakes Sampled

	Range	Mean	Median
Area (km^2)	0.09–2.53	0.62	0.46
Mean depth (m)	0.50–4.50	1.80	1.60
Conductivity (μS cm^{-1})	38–4930	527	167
Total nitrogen (mg N L^{-1})	<0.10–25.80	1.80	0.40
Total phosphorus (mg P L^{-1})	0.02–9.14	0.27	0.10
PVI (%)[a]	0–81	11	1
Chlorophyll *a* (μg L^{-1})	0.6–2889.0	79.6	4.7
The extinction of light at λ = 380 nm, as a proxy for humic substances (m^{-1})	0.3–54.2	5.9	4.0
Total suspended solids (mg L^{-1})	2–663	43	9
Light attenuation coefficient (m^{-1})	0.50–43.60	4.60	2.50

[a] The percentage of the lake's volume filled with submerged vegetation.

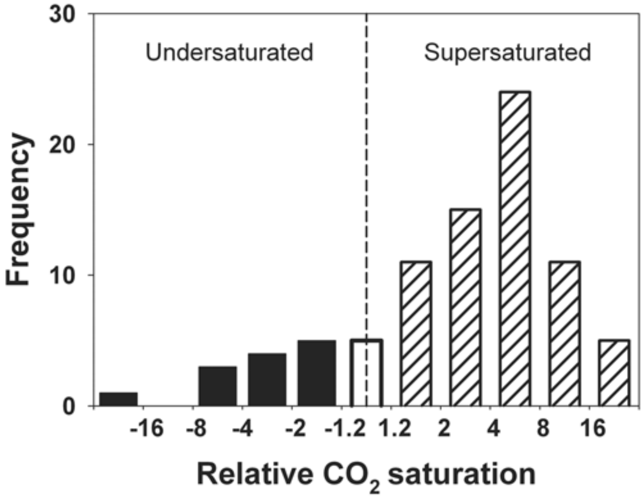

Figure 2. Frequency distribution of lakes undersaturated and supersaturated with CO_2 relative to the atmosphere. For undersaturation, the relative saturation (RS) = $-pCO_2$ (air)/pCO_2 (water); for supersaturation, RS = pCO_2 (water)/pCO_2 (air).

Trends in atmospheric carbon dioxide: Recent global CO_2, 2009, available at http://www.esrl.noaa.gov/gmd/ccgg/trends/#global). Lakes were classified as strongly CO_2 supersaturated (RS > 1.2); strongly undersaturated (RS < −1.2); or near saturation (−1.2 < RS < 1.2). The percentage of the lake's volume filled with submerged vegetation (PVI) was determined analogously to *Canfield et al.* [1984] (for details, see *Kosten et al.* [2009b]).

[12] As a proxy for the hydrological character of the lake we derived an inflow:evaporation ratio using δ^2H and $\delta^{18}O$ of the lake water. The derivation is based on the principle of light isotopes evaporating more quickly than heavy isotopes. The 'heavier' the lake water in comparison to the incoming water the more the lake water has been subject to evaporation. We calculated the inflow:evaporation ratio using the Gat-Bowser model [*Gat and Bowser*, 1991; *Rozanski et al.*, 2001]. The relative humidity input for the model was obtained from a global data set [*Bowen and Revenaugh*, 2003]. For the stable isotope composition of the inlet water we used the average composition of precipitation at the lake location as a proxy (extracted from map provided by G. J. Bowen (Waterisotopes.org, Purdue University, West Lafayette, 2003, available at http://wateriso.eas.purdue.edu/waterisotopes/pages/data_access/ArcGrids.html) on the basis of data from *Bowen and Revenaugh* [2003]). However, as the incoming water may have already been subject to evaporation in the watershed before it enters the lake, we may be overestimating the evaporation in the lake. The more the lake was subject to evaporation, for example due to a long hydraulic residence time, the smaller the inflow:evaporation ratio.

[13] Relations of pCO_2 versus climatological variables and local variables were first explored using simple linear regressions. The climatological variables included temperature, mean annual precipitation and the inlet:evaporation ratio. The local variables included PVI, chlorophyll *a* (chl *a*), the extinction of light at λ = 380 nm used as a proxy for humic substances (humic), dissolved organic carbon concentration (DOC), and two indicators for the relative influence of aquatic primary production and terrestrial carbon input: (1) the ratio between chlorophyll *a* and the extinction at λ = 380 nm (chl *a*: humic); and (2) the ratio between organic carbon and nitrogen in the sediment (C:N). A high chl *a*: humic ratio indicates that the primary production is relatively large compared to influence of terrestrial organic matter on the lake's metabolism. To the contrary, a high C:N ratio indicates a relatively strong terrestrial influence on the lake's metabolism, as the C:N ratio of terrestrial organic matter is generally higher than that of aquatic material [*Elser et al.*, 2000]. Next, we applied multiple linear regressions. The multiple linear regressions modeled pCO_2 using temperature and the variables explaining most of the variance in pCO_2 in the simple linear regressions. To enhance normality, both the dependent and the independent (except for temperature) variables were log transformed before analysis.

[14] All statistical analyses were performed using SPSS for Windows version 15.0 (SPSS, Chicago, Illinois, United States).

3. Results

[15] Only in a small fraction (6%) of the lakes, the carbon dioxide partial pressure (pCO_2) was within a range of ±20% from the equilibrium with the atmosphere (near saturation group). Most lakes (80%) were supersaturated (relative saturation > 1.2, Figure 2). The pCO_2 saturation increased with increasing temperature (Table 2). Temperature alone explained 13% (R^2) of the variance in pCO_2 (Table 2). Lakes with high abundances of primary producers (either phytoplankton or submerged macrophytes) generally have lower pCO_2's than expected based on temperature alone

Table 2. Simple Linear Regression Models Describing the Relationship of Lakes' Partial CO_2 Pressure and Different Climatological and Local Variables[a]

		Regression Statistics		
Model	Log(pCO_2) =	F_1	R^2	n
1	$2.08^{(<0.001)} + 0.04^{(0.001)}$ temperature	12.13	0.13	82
2	$-0.17^{(0.877)} + 1.08^{(0.005)}$ log(total annual precipitation)	8.37	0.08	82
3	$2.55^{(<0.001)} + 0.98^{(<0.001)}$ log(inflow:evaporation)[b]	21.87	0.24	70
4	$3.33^{(<0.001)} - 0.30^{(<0.001)}$ log(chl *a*)	18.14	0.19	82
5	$3.15^{(<0.001)} - 0.18^{(0.047)}$ log(PVI)[c]	4.06	0.05	82
6	$3.10^{(<0.001)} - 0.08^{(0.548)}$ log(humic)[d]	0.36	0.01	82
7	$3.50^{(<0.001)} - 0.42^{(0.010)}$ log(DOC)	6.96	0.08	82
8	$3.20^{(<0.001)} - 0.36^{(0.001)}$ log(chl *a*: humic)[e]	21.63	0.21	82
9	$0.70^{(0.103)} + 2.27^{(0.001)}$ log(C:N)[f]	32.45	0.30	79

[a] The *p* value of the parameters are presented between brackets.

[b] Inflow:evaporation ratio.

[c] The percentage of the lake's volume filled with submerged vegetation (PVI) was augmented with 1% to avoid zero's.

[d] The extinction of light at λ = 380 nm is used as a proxy for humic substances.

[e] Chlorophyll *a* concentration:extinction at λ = 380 nm ratio.

[f] Organic carbon: total nitrogen ratio in the top sediment.

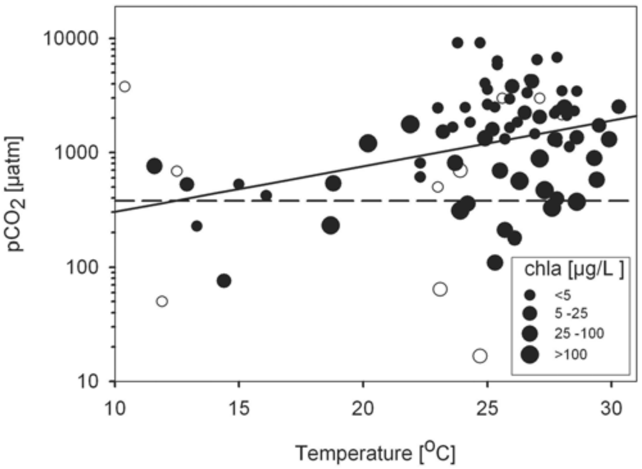

Figure 3. Partial CO_2 pressure (pCO_2) in lakes along a water temperature gradient in South America. Lakes differed in trophic status (size of symbols indicate chlorophyll *a* concentrations; open symbols represent lakes with substantial growth of submerged vegetation (>25% of the lake volume is filled with vegetation)). Continuous line represents the regression line between pCO_2 and the water temperature measured in the lakes. Lakes depicted below the dashed line are undersaturated in pCO_2 relative to the atmosphere.

(Figure 3, see also negative parameters in the models 4 and 5 in Table 2), whereas lakes with low abundances of primary producers generally fall above the pCO_2 temperature regression line.

[16] In the simple linear regressions pCO_2 was best explained by the inflow:evaporation ratio ($R^2 = 0.24$, model 3 in Table 2), the ratio between algal biomass (expressed as chl *a*) and the light extinction $\lambda = 380$ nm (used as a proxy for humic substances) ($R^2 = 0.21$, model 8 in Table 2), and the C:N ratio in the sediment ($R^2 = 0.30$, model 9 in Table 2). Lakes with a high inflow:evaporation ratio had relatively high pCO_2's compared to lakes with a low inflow:evaporation ratio. Furthermore, in lakes with a relatively strong terrestrial influence (i.e., a low chl *a*: humic ratio or a high C:N ratio), the pCO_2 tended to be high as well.

[17] The pCO_2 could significantly be explained by a combination of temperature and the before mentioned variables, increasing the degree of explanation (adjusted R^2) of pCO_2 (Table 3). At similar inflow:evaporation ratios, the cooler lakes had a lower pCO_2 than the warmer lakes (Table 3, Figure 4a). In the same way, the warm lakes generally had a higher pCO_2 than the cooler lakes at similar chl *a*: humic ratios (Table 3, Figure 4b).

4. Discussion

[18] The small fraction of lakes that is in equilibrium with the atmosphere indicates that most lakes were either sinks or sources to the atmosphere (Figure 2). As in surveys in other parts of the world [*Cole et al.*, 1994; *Sobek et al.*, 2003], most lakes were supersaturated, indicating that these lakes are net sources of CO_2 to the atmosphere. In fact, pCO_2 tends to be lowest in summer [*Kelly et al.*, 2001] or dry season [*Richey et al.*, 2002] precisely when our samples were taken. Therefore the annual average relative saturation per lake is likely even higher than we report here.

[19] The ratio between phytoplankton biomass and the light extinction at $\lambda = 380$ nm explained 21% (R^2) of the variation in pCO_2 (Table 2). Most likely this is because the light extinction at this wavelength, which we used as a proxy for the level of humic substances can be used as an indicator for terrestrial carbon input. When the terrestrial carbon is mineralized this may lead to a net CO_2 production. Phytoplankton, on the other hand, takes up CO_2 during photosynthesis, reducing CO_2 concentrations in the water. The higher the density of phytoplankton compared to the level of humic substances, the lower the pCO_2 tends to be. Besides phytoplankton, submerged vegetation may contribute substantially to the primary production in shallow lakes thereby lowering the pCO_2. Indeed, the pCO_2 is systematically lower in lakes with high abundances of submerged vegetation (Table 2 and Figure 3).

[20] In other lake data sets, pCO_2 was found to be positively correlated to DOC concentrations [*Prairie et al.*, 2002; *Sobek et al.*, 2003, 2005]. Although our lakes had a wide range in extinction at $\lambda = 380$ nm (used as a proxy for humic substances) and dissolved organic carbon (0.3–54.2 m^{-1} and 1.7–86 mg C L^{-1}, respectively), we did not find a significant relation between pCO_2 and the light extinction, and the explained variance in pCO_2 by DOC was low ($R^2 = 0.08$, Table 2). Our lakes, however, also covered a wide range in productivity and as pCO_2 is influenced by primary production and respiration simultaneously, the chlorophyll *a*:

Table 3. Multiple Linear Regression Models Describing the Relationship of Lakes' Partial CO_2 Pressure, Temperature, and Local Environmental Variables[a]

Coefficients[b]					Regression Statistics		
Intercept	Temperature	Inflow:evaporation	Chl *a*: humic	C:N		R^2_{adj}	n
$1.93^{(<0.001)}$	$0.03^{(0.035)}$	$0.99^{(<0.001)}$			$F_2 = 13.84$	0.27	70
$2.20^{(<0.001)}$	$0.04^{(<0.001)}$		$-0.37^{(<0.001)}$		$F_2 = 21.48$	0.34	82
$2.17^{(<0.0001)}$	$0.03^{(0.023)}$	$0.67^{(0.005)}$	$-0.23^{(0.011)}$		$F_3 = 12.29$	0.33	70
$-0.03^{(0.94)}$	$0.04^{(<0.001)}$			$2.15^{(<0.001)}$	$F_2 = 25.93$	0.39	79
$0.48^{(0.36)}$	$0.03^{(0.020)}$	$0.54^{(0.015)}$		$1.62^{(0.001)}$	$F_3 = 12.6$	0.35	67

[a] In the lower part we used the ratio between organic carbon and nitrogen in the sediment (C:N) instead of the chl *a*:humic ratio as an indicator for the relative influence of terrestrial and aquatic organic matter. Only significant models are shown. The *p* value of the parameters is presented between brackets. For explanation of the variables, see Table 2.

[b] All variables (except of temperature) were log transformed before analysis.

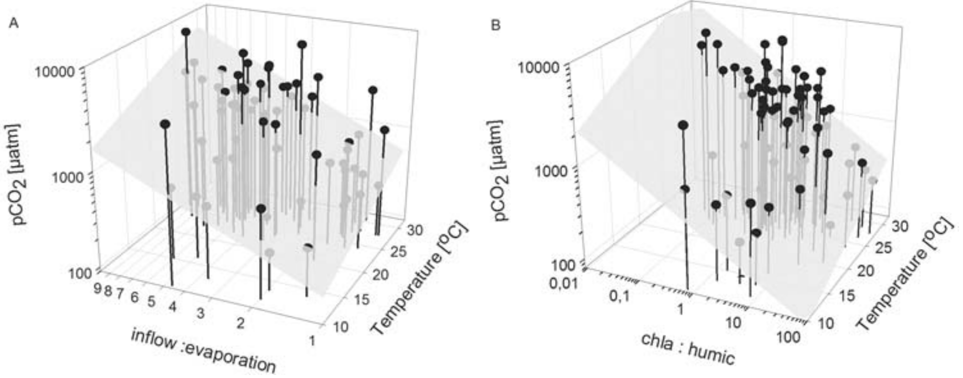

Figure 4. Partial CO_2 pressure (pCO_2) in South American lakes over a temperature gradient and a gradient of (a) a ratio between inflow and evaporation and (b) a ratio between algal biomass (expressed as chlorophyll *a*) and the extinction of light at $\lambda = 380$ nm, as a proxy for humic substances. The transparent planes indicate the multiple linear regression models. Grey points have a lower and black points have a higher pCO_2 than expected on the basis of the models.

humic substances ratio may therefore be most informative. A relatively constant primary production in comparison to the variation in DOC in the other data sets may explain the overruling influence of DOC on the pCO_2 in those earlier studies. The strong correlation between DOC and chlorophyll *a* in our data set ($R^2 = 0.48$, $p < 0.001$) might indicate that in eutrophic lakes, much of the DOC is algal derived which may explain the negative correlation between pCO_2 and DOC (Table 2).

[21] Our data furthermore suggest that hydrological characteristics of the lake, i.e., the ratio between inflow and evaporation, strongly affects the pCO_2 (Table 2). In part this may reflect a temperature effect. Evaporation plays an important role in the energy budget of the lake and strong evaporation cools down the lake [*Lenters et al.*, 2005]. Hydrology, however, also affects the input of terrestrial carbon to the lake. Indeed, pCO_2 was generally high in lakes where the volume of incoming water from the watershed was large in comparison to the volume that had evaporated. The importance of lakes' hydrology is in line with results from studies in other parts of the world [*Algesten et al.*, 2004]. Although the pCO_2 may be influenced by the inflow of CO_2 rich groundwater as well [*Striegl and Michmerhuizen*, 1998], a dominant role of the terrestrial input in our lakes is suggested by the fact that 21% of the variance in pCO_2 could be explained by the chlorophyll *a*: humic substances ratio.

[22] As an alternative indicator of the relative importance of terrestrial input, we analyzed the ratio between organic carbon and nitrogen in the sediment, a high C:N ratio indicating a relatively strong terrestrial influence on the lake's metabolism. Indeed we found this indicator to explain a comparable part (30%) of the variance in pCO_2 levels as the inflow:evaporation ratio (Table 2). Adding the ratios chlorophyll *a*: humic substances or C:N to regression models explaining pCO_2 levels from the hydrology indicator did not add to the explanatory power (Table 3), suggesting that the hydrology might affect the carbon balance largely through its relative effects on allochthonous carbon input and in-lake primary productivity.

[23] For the lakes in our data set cooler lakes generally had a lower pCO_2 than warmer lakes (Table 3); the coldest lakes in our data set generally being carbon sinks and the warmer lakes in our data set being carbon sources (Figure 3). To filter out the effects of idiosyncratic differences in terrestrial inputs and productivity among lakes we looked at relationships between pCO_2 and the main indicators of these processes along the temperature gradient (Table 3, Figure 4). This again suggested a significant influence of temperature on the pCO_2. At similar inflow:evaporation ratios, or similar chlorophyll *a*: humic ratios the warmer lakes had a higher pCO_2 than the cooler lakes (Table 3, Figure 4). The logarithm of the pCO_2 in lakes with a water temperature of 30°C was 0.3 to 0.4 units higher than in lakes with a water temperature of 20°C (see temperature regression coefficients Table 3), suggesting an approximate 2–2.5 times increase in pCO_2 per 10°C in comparable lakes.

[24] Although the pCO_2 is not a direct measure of the carbon flux in lakes, it is the most important factor influencing this flux [*Sobek et al.*, 2005]. Therefore, our findings indicate a substantial influence of climate on CO_2 efflux from lakes. The apparent effect of hydrology on the pCO_2 in lakes suggested by our results implies that future changes in evaporation [*Roderick and Farquhar*, 2002] and precipitation regimes [*IPCC*, 2007] may have a strong impact on lake carbon emissions. In addition there is a clear relationship between pCO_2 and temperature. Although clearly correlations do not give insight in causal relationships, various mechanisms could contribute to such a temperature effect. In addition to the direct effect of temperature on the CO_2 flux (gasses dissolve better in colder than in warmer water), there is possibly an increase in net heterotrophy with temperature. Rates of respiration tend to increase stronger than production with temperature [*Biddanda and Cotner*, 2002; *Lopez-Urrutia et al.*, 2006; *Rivkin and Legendre*, 2001; *Sand-Jensen et al.*, 2007]. Importantly, the relatively strong

increase of respiration with temperature [*Acuña et al.*, 2008] implies that warm lakes might metabolize a substantially larger portion of the terrestrial organic matter influx than cooler ones [*Biddanda and Cotner*, 2002; *Jansson et al.*, 2008]. Primary production, on the other hand, may be limited by other factors than temperature (e.g., nutrients or light) this may prevent primary production from 'keeping up' with respiration when temperature increases.

5. Final Remarks

[25] Most likely, rising global temperatures will promote increased atmospheric greenhouse gas concentrations [*Cox and Jones*, 2008]. In fact, estimates based on ancient climate variation suggest that this effect may be quite large [*Scheffer et al.*, 2006]. Future climate prognosis often neglect the feedback effect of temperature on greenhouse gas fluxes as our knowledge of the processes involved is insufficient leading to large uncertainties [*Jones et al.*, 2006]. Our results suggest that warm inland waters emit more CO_2 than comparable cooler lakes. Carbon emission from cool lakes may therefore increase with climate warming. While this positive feedback mechanism has negative consequences from a climate change perspective, the sensitivity of the carbon balance of lakes to in-lake productivity and hydrology also suggests that a better understanding of the regulating mechanisms might give opportunities for managers to design climate friendlier management strategies of these hot spots of carbon channeling.

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J. J. Cole, Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA.

D. M. L. Da Motta Marques, Instituto de Pesquisas Hidráulicas, Universidade Federal do Rio Grande do Sul, Porto Alegre RS 91501-970, Brazil.

S. Kosten, M. Scheffer, and E. H. Van Nes, Department of Aquatic Ecology and Water Quality Management, Wageningen University, PO Box 47, NL-6700 AA Wageningen, Netherlands. (sarian.kosten@wur.nl)

N. Mazzeo, Laboratorio de Ecología y rehabilitacíon de sistemas acuáticos, Facultad de Ciencias and CURE, Universidad de la República, Iguá 4225, CP 11400 Montevideo, Uruguay.

F. Roland, Laboratory of Aquatic Ecology, Institute of Biology, Federal University of Juiz de Fora, Juiz de Fora MG 36.036-900, Brazil.

L. da S. L. Sternberg, Department of Biology, University of Miami, Coral Gables, FL 33124, USA.