Research Brief

Carbon dioxide concentrations in eutrophic lakes: undersaturation implies atmospheric uptake

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Abstract

Understanding concentrations and contributions of carbon dioxide (CO_2) in aquatic ecosystems is an important part of a comprehensive global carbon budget. Current dogma suggests that world lakes are important emitters of CO_2 to the atmosphere. We estimated the partial pressure of carbon dioxide (ρCO_2) in 131 agriculturally eutrophic lakes over a 7 year sampling period. Values of $\rho CO2$ in these lakes ranged from 0.1 to 40 392 μatm with a median of 322 μatm (n = 3049). In contrast to previous analyses of CO_2 in lakes, 60% of the eutrophic lake samples were undersaturated with CO_2. Correlation analysis implied that nutrient-driven primary production, reflected by high oxygen concentrations, drives CO_2 concentrations below atmospheric equilibrium. Multiple regression analysis showed several limnological and catchment characteristics that explained a statistically significant amount of variability in ρCO_2 (R^2 = 0.32). Important variables included chlorophyll *a* concentration and the ratio of total nitrogen to total phosphorus. Our estimated ρCO_2 values were significantly (p < 0.0001) lower than a previously published dataset of world lake ρCO_2 values derived primarily from oligotrophic–mesotrophic lakes. High-nutrient lakes, especially those that are small and rich in oxygen from primary production, could act as net atmospheric CO_2 uptake sites.

Key words: atmospheric flux, carbon cycling, carbon dioxide, eutrophication, lakes

Introduction

Understanding and addressing climate change is an important challenge (Houghton 2005). Quantifying rates and conversions in the global carbon (C) budget is an essential part of addressing (Karl and Trenberth 2003) and mitigating (Matthews and Caldeira 2008) global climate change. Recent research has indicated that continental waters routinely process C at significant rates (Cole et al. 2007, Downing 2009). Although inland waters comprise a small fraction of the earth's surface (~3%; Downing et al. 2006), they may play a major role in the global C cycle (Dean and Gorham 1998, Cole et al. 2007, Battin et al. 2008).

Agricultural eutrophication, one of the most significant current environmental problems (Dorioz and Ferhi 1994, Carpenter et al. 1998), will increase as the need for food, fiber, and fuel rises with global population. Increased agricultural eutrophication may amplify carbon processes, including sediment burial and primary production (Tranvik et al. 2009). Most research on carbon processing in continental waters has been performed in oligotrophic–mesotrophic systems (Cole et al. 1994, Duarte and Prairie 2005, Alin and Johnson 2007). Comparatively few studies, however, have sought to quantify rates in eutrophic and hypereutrophic systems (Duarte and Prairie 2005, Downing et al. 2008, Lazzarino et al. 2009). Although it has been hypothesized (e.g., Alin and Johnson 2007) that eutrophic lakes should have lower summer partial pressures of CO_2 than oligotrophic lakes due to high primary production, published summary studies on CO_2 saturation in eutrophic and hypereutrophic systems are rare (e.g., Lazzarino et al. 2009). Because of global eutrophication, it is important to understand the contribution of these types of systems to regional and global C cycles.

Previous studies have suggested the prevalence of CO_2

supersaturation in lakes worldwide (Cole et al. 1994, 2007, Kortelainen et al. 2006). Estimates indicate that ~90% of aquatic ecosystems studied emit CO_2 to the atmosphere (Kling et al. 1992, Cole et al. 1994, 2007) and that lakes are important global and regional CO_2 emitters. Eutrophication increases the conversion rate of inorganic carbon (free CO_2 and bicarbonate) to particulate organic matter, due to increased primary production (Smith 1979, Peters 1986); therefore, eutrophic and hypereutrophic systems could act as CO_2 uptake sites due to high phytoplankton productivity (Finlay et al. 2009, Lazzarino et al. 2009).

The objectives of this study were to (1) estimate the partial pressure of carbon dioxide (ρCO_2) in a large sample of agriculturally eutrophic lakes and impoundments, (2) determine how limnological, meteorological, biological, and physical characteristics of lakes and their catchments are related to summer levels of ρCO_2, and (3) compare our summer ρCO_2 values to previously published summer data on lakes and impoundments of varying size.

Study site

The 131 lakes and catchments used for this analysis (Table 1) are located in the midwestern United States (state of Iowa), one of the most intensive agricultural areas in the world (Rabalais et al. 1999).

Methods

Data were collected 3 times throughout the summer months (May–Aug) annually between 2000 and 2007. Surface mixed-zone composite water samples were collected from the deepest point of each lake.

Values for ρCO_2 were calculated for mixed-column samples using the same approach as others (e.g., Kling et al. 1992, Cole et al. 1994, Prairie et al. 2002). Equilibrium constants for various inorganic carbon species were determined from ionic strength (Butler 1992, Kling et al. 1992). Equilibrium constants for carbonic acid and bicarbonates were calculated from specific conductivity and temperature and derived from equations in Stumm and Morgan (1996). Alkalinity and pH were then used to calculate total inorganic carbon, and CO_2 was expressed as a partial pressure (ρCO_2) using Henry's constant, correcting for temperature, and using an altitude of 335 m a.s.l. (the mean altitude for the region studied; Mattson 1996). The potential areal net atmospheric flux (F_{atm}) of CO_2 (g C m^{-2}) across the air–water interface was calculated following Cole and Caraco (1998), assuming a partial pressure of CO_2 in the air of 370 µatm and normalizing wind speeds to a height of 10 m using the modified Witter and Chelton algorithm (Brown 1979). Where wind speed was not available for an individual

sampling event, a wind speed of 3 m s^{-1} was assumed (Cole and Caraco 1998). Net atmospheric exchange was calculated for the summer sampling period (123 d) to compare with previously published values because sampling occurred only during the summer months.

Composite mixed zone water samples were collected and analyzed for variables characterizing lakes at the time of sampling. Samples were analyzed for total phosphorus (TP; Murphy-Riley method with a persulfate digestion; APHA 1998), total nitrogen (TN), and NO_x (persulfate digestion with second derivative spectroscopy; Crumpton et al. 1992), ionized and unionized ammonia (phenate method; APHA 1998), dissolved organic carbon (DOC; Schimadzu TOC analyzer; AHPA 1998), and pH and total alkalinity (at 35 °C by electrode and titration to pH 4.5; APHA 1998).

Both chlorophyll *a* and phytoplankton biomass and diversity were estimated to characterize the amount and composition of phytoplankton present in each lake. Chlorophyll *a* was analyzed using the acetone extraction method (Jeffrey et al. 1997, APHA 1998). Phytoplankton samples were preserved with Lugol's solution and allowed to settle before biomass was estimated (Prescott 1931, Ward and Whipple 1959, Wehr and Sheath 2003).

Water column profiles of pH, water temperature, specific conductivity, turbidity, and dissolved oxygen (DO) were taken with a YSI 6600 Sonde. Meteorological data (air temperature, wind velocity and direction, barometric pressure, and altitude) were recorded using a Kestrel 2500 device. Secchi transparency (m) was measured following Wetzel and Likens (2000).

Analysis of geographic information systems (GIS; Gémesi 2007) provided land-use characteristics of watersheds calculated from a 2002 land use/land cover dataset, derived from 30 m LANDSAT imagery. Land uses were divided into 17 categories (http://www.gis.iastate.edu/data/; polygons, line features, raster datasets).

Correlation analysis was used to seek relationships between the calculated ρCO_2 and various meteorological, limnological, and catchment characteristics. Stepwise multiple linear regression was used to test the hypothesis that catchment land use, meteorological data, physical and biological characteristics of lakes, and nutrient concentrations were related to summer daytime ρCO_2. The most influential variables were sought via forward stepwise multiple linear regression (McGarigal et al. 2000) with a variable retention criterion of p = 0.01. Data were log transformed, when appropriate, to satisfy the assumptions of normality and homogeneity of variance before entering them into the model; ρCO_2 was also log transformed for this analysis. The slopes of some relationships were examined via LOWESS (f = 0.2; Cleveland and McGill 1985).

Results

The nutrient concentrations in the study lakes are in the upper half of those found worldwide (Table 1; Arbuckle and Downing 2001), making them among the most eutrophic. Chemical variables used to calculate ρCO_2 varied widely for our set of lakes, with pH from 6.5 to 10.6 and total alkalinity from 5 to 316 mg L^{-1} (Table 1).

Calculated ρCO_2 covered much of the range of those observed in lakes worldwide (Table 1; Cole et al. 1994, Lazzarino et al. 2009). The frequency distribution (Fig. 1) of ρCO_2 values for these lakes, however, showed a negatively skewed log normal distribution with a median of 322 µatm. Our ρCO_2 values were also significantly lower than those found in a large world dataset (Fig. 1; $t_{7954} = 16.8409$; $p < 0.0001$).

Many of the physical, nutrient, and biological measures obtained for this study were significantly correlated with log ρCO_2 (Table 1), although few independently had $|r| > 0.1$. Dissolved oxygen, chlorophyll a concentration, and TP concentration showed notable correlations with ρCO_2 (Figs. 1 and 2). Multiple regression analysis, however, found that ρCO_2 was correlated with several characteristics of lake environments (Table 2). Dissolved oxygen accounted for the most variation in log ρCO_2, followed by chlorophyll a concentration, TN:TP, DOC, and mean lake depth. Calculated CO_2 emission rates were also skewed left with the median falling below zero, indicating net atmospheric uptake (Fig. 3).

Discussion

Our data suggest that many temperate zone eutrophic lakes are undersaturated with CO_2, at least during the summer, which differs from the results of many previous studies on temperate boreal lakes. This underscores the importance of quantifying CO_2 in diverse types of lakes for the inclusion of lakes in regional and global carbon

Table 1. Characteristics of 131 lakes analyzed from 2000 to 2007 for this study from an intensively agricultural region of the United States. Independent variables included in this table were all significantly correlated with log ρCO_2 ($p \leq 0.0005$). Variables marked * were log transformed and those marked † were candidate variables in a step-wise multiple regression (see Table 2).

| Independent variable	Median	Range	r-values
pH	8.6	6.4–10.6	−0.940
Dissolved oxygen (% saturation)†	108	3–322	−0.220
Alkalinity (mg L^{-1} of CaCO$_3$)	135	5–316	−0.170
Chlorophyll a (µg L^{-1})*†	25	<1–544	−0.091
Specific conductivity (µS cm^{-1} at 25ºC)	380	126 – 1360	+0.087
NH$_3$ (µ mol L^{-1})*	2.5	<1–124	+0.072
Water temperature (ºC)	24.8	12–34	−0.047
TN:TP (atomic)*†	22	<1–871	+0.040
Phytoplankton biomass (mg L^{-1})*†	25	<1–9656	−0.040
Catchment area less lake area (km^2)*	9	<1–31 080	+0.038
NO$_3$ (mg L^{-1})*	0.2	<0.01–19	+0.032
% Cyanobacteria of phytoplankton biomass	91	0–100	−0.032
Total Phosphorus (µg L^{-1})*†	73	4.6–776.5	−0.025
Lake volume (m^3)*	1.0×10^6	1.1×10^5–3.22×10^8	+0.023
Secchi transparency (m)*†	0.9	<0.1–9.5	+0.023
Lake area (m^2)*†	3.9×10^5	4.1×10^4–6.04×10^7	+0.021
Dissolved organic carbon (mg L^{-1})*†	7.6	<0.01–62.4	−0.017
Catchment area to lake area ratio*	22	<1–763	+0.016
Total Suspended Solids (mg L^{-1})*	11.8	<0.1–420	−0.012
Maximum lake depth (m)*	6.7	1.2–39.6	+0.008
Total Nitrogen (mg L^{-1})*†	1.5	0–20.6	+0.006
Mean lake depth (m)*†	2.8	0.9–11.5	+0.005
Effective breadth (m)*†	1203	136–6720	+0.004
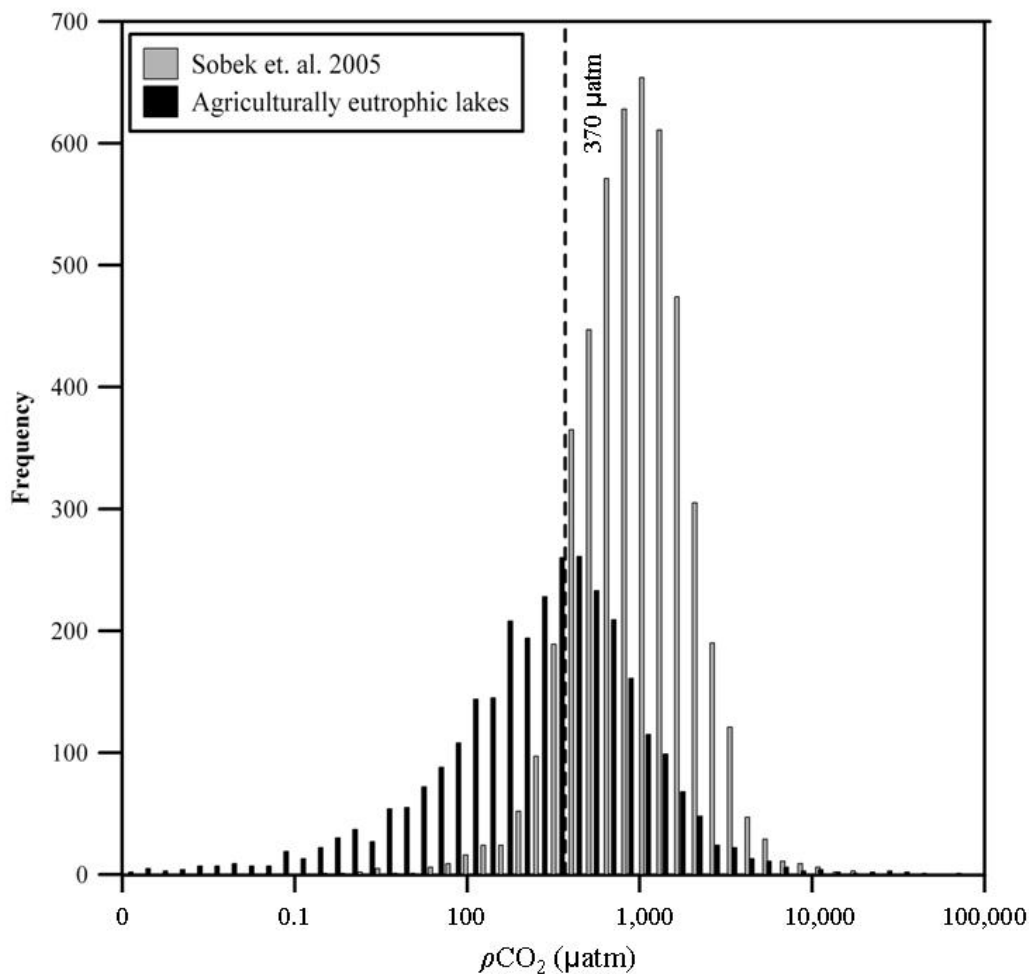
Fig. 1. Frequency distribution of estimated ρCO_2 values for agriculturally eutrophic lakes in our study from throughout the study period (dark grey; n = 3049) and a world dataset of lakes (light grey; n = 4902; Sobek et al. 2005).
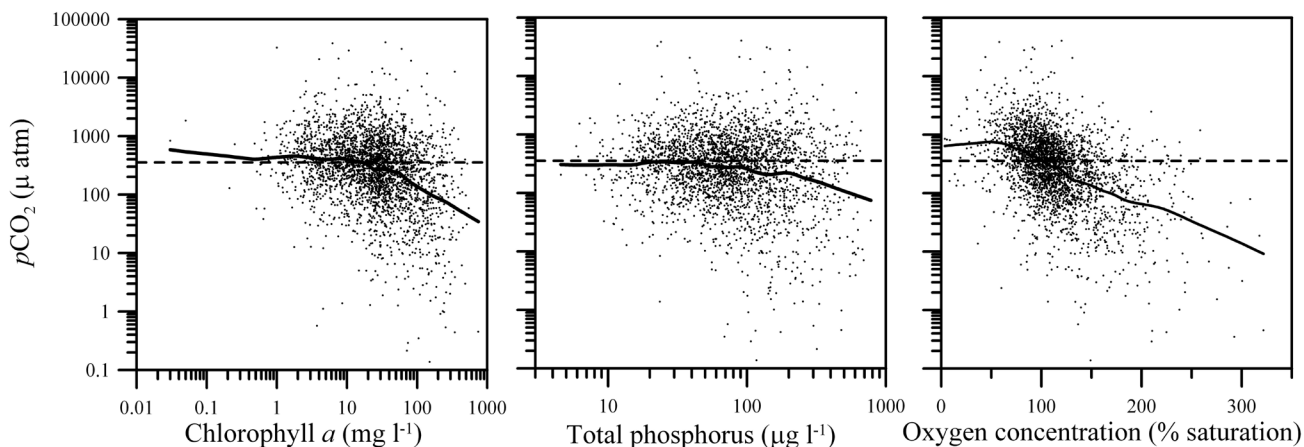

Fig. 2. Relationships between partial pressure of CO_2 (ρCO_2) and selected variables most strongly correlated to it (see Table 1). The dashed line on all panels represents ρCO_2 at atmospheric equilibrium (370 µatm). Solid lines are LOWESS fits of the data (Cleveland 1981, Cleveland and McGill 1985). The Lowess f value was set to 0.2, and LOWESS smoothing was performed on the logarithms of ρCO_2.

budgets. Only 40% of the eutrophic lakes we studied were supersaturated with CO_2, whereas 87% of the 1835 lakes in the Cole et al. (1994) study were found to be supersaturated with CO_2. Lazzarino et al. (2009) also observed 87% of all Florida lakes supersaturated with CO_2 at the time of sampling. Sobek et al. (2003) found that all but one of the 33 boreal lakes they studied was supersaturated with CO_2.

Our study lakes had ρCO_2 values significantly lower than those of the rest of the world's lakes analyzed in the recent literature (Fig. 2). The median ρCO_2 value of 323 μatm was substantially below atmospheric equilibrium. Agriculturally eutrophic lakes seem to be less saturated than other world lakes and may be absorbing CO_2 from the atmosphere more frequently than degassing during summer months, as compared to the dataset compiled by Sobek et al. (2005) for ice-free freshwater natural lakes.

The involvement of high primary production in creating patterns of CO_2 concentrations and evasion is apparent from significant correlations with chlorophyll a and TP (Fig. 2). LOWESS fits showed that CO_2 decreased below atmospheric equilibrium at chlorophyll a levels of 10–20 μg L^{-1}, approximately the range at which noticeable phytoplankton blooms become apparent in lakes (Bachmann and Jones 1974). Although the majority of our samples showed a negative correlation between CO_2 and chlorophyll a concentration, some lakes showed CO_2 supersaturation in lakes with high chlorophyll, likely due to the frequently high respiration rates found in eutrophic waters. Further, LOWESS fits indicate that CO_2 decreased below atmospheric equilibrium at TP concentrations of around 30–60 μg L^{-1} (Fig. 2), near the level of nutrient enrichment, implying passage from mesotrophy to eutrophy (Kalff 2002). Values of ρCO_2 also showed a notable reciprocal relationship with DO (Table 1; Fig. 2), which was expected because CO_2 uptake by primary producers can evolve substantial DO. In lakes that are undersaturated with DO, LOWESS fits suggest median ρCO_2 is oversaturated, implying atmospheric evasion (Fig. 2). A number of lakes were supersaturated with both oxygen (O_2) and CO_2, likely due to wind mixing of surface waters near the time of sampling.

Multiple regression analysis explained 33% of the variance in ρCO_2 (Table 2). Dissolved oxygen explained the most variance in the model, showing that ρCO_2 was drawn down as O_2 concentrations increased. The reciprocal relationship between CO_2 and O_2 has also been documented in boreal lakes (Kortelainen et al. 2006). In the boreal region, however, this relationship is presumably due to the degradation of organic matter rather than high primary production. Intense primary production apparently can draw down CO_2 to levels below atmospheric equilibrium. Lakes that are net undersaturated with CO_2, like many of the lakes in this study, may be net-autotrophic because CO_2 is drawn in and sequestered within the lake. Although the reciprocal relationship between O_2 and CO_2 is not causal, it does indicate the importance of photosynthesis and respiration in eutrophic summer surface waters.

Multiple regression (Table 2) also indicated chlorophyll a concentration is an important variable accounting for variation in ρCO_2. Chlorophyll is a frequently used surrogate of primary production in lakes. Increased chlorophyll, resulting in high primary production, indicated elevated photosynthesis in the water column. High rates of photosynthesis may draw down CO_2 as phytoplankton absorb CO_2, disequilibrating the alkalinity buffering reactions during the daylight hours. Primary production is likely the driving biological force behind the variability in ρCO_2 levels we observed.

The ratio of TN to TP was positively related to ρCO_2 in our lakes. In-lake nutrient ratios are largely driven by land use in agricultural watersheds (Arbuckle and Downing

Table 2. Multiple regression analyses of variation in ρCO_2 related to several limnological variables. Partial t-values indicate the size of statistical effects of the independent variables when all other variables are considered. The forward stepwise regression analysis of ρCO_2 had an adjusted $R^2 = 0.32$, F = 108.6, p <0.0001, and number of samples = 1735. For this regression, independent variables with * were log transformed before entering into the model. ρCO_2 was also log transformed for this analysis.

Independent variable	Regression coefficient	Partial t	p
Intercept	3.18	26.81	<0.0001
TN:TP*	0.0299	9.96	<0.0001
Lake size (m^2)*	0.2944	5.68	<0.0001
Mean lake depth (m)*	−0.2592	−4.49	<0.0001
Effective breadth (m)*	−0.3073	−5.04	<0.0001
Dissolved organic carbon (mg L^{-1})*	−0.1775	−5.59	<0.0001
Chlorophyll a concentration (μg L^{-1})*	−0.1605	−6.12	<0.0001
Dissolved oxygen (% saturation)	−0.0075	−21.11	<0.0001

2001). The ratio TN:TP is driven by the fraction of the watershed under row-crop versus land uses where large amounts of manure are deposited or applied (Arbuckle and Downing 2001). Our results suggest that lakes with low N:P, presumably via pastureland and manure application in the watershed, have lower amounts of ρCO_2 and are therefore likely to be atmospheric uptake sites. A tendency of low CO_2 concentrations in eutrophic lakes to persist across seasons potentially has major implications for global carbon cycling because watersheds are receiving increasingly large amendments of manure, either as fertilizer or simple land disposal (Sharpley et al. 1998), although full annual CO_2 and sediment data are needed to understand the full implications of increased fertilization on carbon cycling.

Other studies have shown positive correlations between DOC or color (a variable often tied to DOC) and ρCO_2 (Reche and Pace 2002, Hope et al. 2004, Lazzarino et al. 2009). Our study lakes, however, implied a negative correlation between DOC and ρCO_2 and accounted for only a small portion of the total variance explained (Table 2). In other lakes, DOC has been observed as being derived from the watershed and photooxidized to CO_2 in the lake, resulting in a negative relationship between the 2 variables. In eutrophic lakes, however, we suspect that DOC is phytoplankton-derived and is not photooxidized due to limited light penetration. The flux of DOC from particulate (algal) to dissolved forms is likely high relative to the breakdown rate of particulate DOC during the summer daytime. Thus, the DOC pool increases with productivity. It is also possible that high levels of primary production are masking the possible influence of DOC on CO_2 within our study lakes.

Partial effects of physical characteristics of the study lakes also explained significant variance in ρCO_2 (Table 2). Deep lakes seem to have higher ρCO_2, possibly because shallow lakes have more sediment influence on the water column by continually mixing nutrients and organic carbon and driving up primary production, thereby decreasing ρCO_2. Accounting for the influence of lake depth, lakes with large surface areas and those with large fetches also had relatively low ρCO_2, possibly because lakes with large surface areas lakes have a greater potential for degassing, thus allowing more rapid equilibration of ρCO_2 with the atmosphere.

Much of the literature suggests that lakes are net heterotrophic, meaning that most carbon consumed in them is imported from the catchment and either buried in the sediments or exported to the atmosphere as CO_2 (del Giorgio et al. 1997, 1999). Overall, our correlation results (Table 1) indicate that lakes with high concentrations of chlorophyll *a* and DOC, and those that have a low N:P ratio, are likely to have low partial pressures of CO_2 and may be regionally important sites for atmospheric CO_2 uptake.

Although we were unable to evaluate potential CO_2 fluxes for the entire year, we followed the common approach of approximating summer flux rates from punctual measures (Fig. 3; e.g., Kelly et al. 2001, Lazzarino et al. 2009). Like others, we sampled during the daytime when photosynthesis is high. Diel and seasonal CO_2 studies in eutrophic systems are still needed to better understand CO_2 flux linked to photosynthesis and respiration. The efflux rates we estimate in these lakes seem much lower than those found elsewhere, affirming the possibility that many eutrophic lakes act as atmospheric CO_2 uptake sites (Table 3). Algesten et al. (2004) estimated flux using relationships between DOC and CO_2 in a subset of lakes then extrapolating to many lakes in northern and central Sweden. Kortelainen et al.
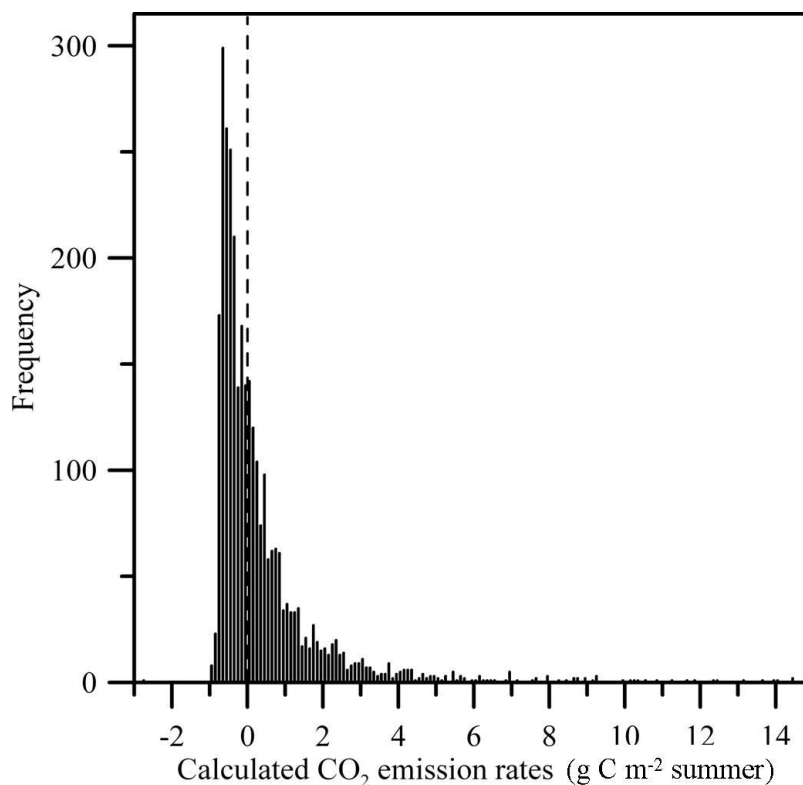

Fig. 3. Calculated carbon evasion rates for our study lakes (n = 131) over multiple years. The dashed line indicates atmospheric equilibrium (median = –0.1). Values were calculated for each sampling event and reflect summer evasion (May–Aug; 123 days).

Table 3. Calculated areal carbon emission rates for different groups of lakes. Rates from our study are estimated using 3 summer ρCO_2 readings, wind measurements at time of sampling, and surface areas of each lake studied. All data are expressed as arithmetic averages or ranges when given, except those from our study. All studies included daytime measurements. Our data were highly skewed, so the median value is reported instead of the mean because it more accurately reflects the distribution of our data.

Group	Calculated areal carbon emission rates	Time period for emission rate report	Source
Our 131 study lakes	-0.1 g C m^{-2}	Summer (123 days)	This study
Finnish lakes	42 g C m^{-2}	Annual	Kortelainen et al. (2006)
Large lakes of the world	62 g C m^{-2}	Annual	Alin and Johnson (2007)
Florida lakes	328 g C m^{-2}	Annual	Lazzarino et al. (2009)
Saline lakes	3.6–4.6 g C m^{-2}	Daily	Duarte et al. (2008)

(2006) sampled 177 lakes 4 times throughout the year and extrapolated these to estimate annual flux rates. Alin and Johnson (2007) gathered previously published ρCO_2 and wind speed data to estimate yearly flux rates. Duarte et al. (2008) assembled published ρCO_2 values and used a gas exchange coefficient of 0.8 m d^{-1} and a wind velocity of 3 m s^{-1} to estimate yearly flux rates. Lazzarino et al. (2009) used summer CO_2 values and averaged wind speeds to estimate yearly flux rates. Our median flux was negative, meaning that over half our lakes were not CO_2 saturated (Table 3). Many published studies performed on less nutrient-rich ecosystems have shown that some are continuously supersaturated with CO_2, although summer saturation in oligotrophic systems may decline when production is high.

Acknowledgements

References

Algesten G, Sobek S, Bergstrom AK, Agren A, Tranvik LJ, Jansson M. 2004. Role of lakes for organic carbon cycling in the boreal zone. Glob Change Biol. 10(1):141-147.

Alin SR, Johnson TC. 2007. Carbon cycling in large lakes of the world: A synthesis of production, burial, and lake-atmosphere exchange estimates. Glob Biogeochem Cy. 21(3):GB3002.

[APHA] American Public Health Association. 1998. Standard methods for the examination of water and wastewater, 20th ed. Washington (DC): American Public Health Association.

Arbuckle KE, Downing JA. 2001. The influence of watershed land use on lake N:P in a predominantly agricultural landscape. Limnol Oceanogr. 46(4):970-975.

Bachmann RW, Jones JR. 1974. Phosphorus inputs and algal bloom in lakes. Iowa State J Res. 49(1):155-160.

Battin TJ, Kaplan LA, Findlay S, Hopkinson CS, Marti E, Packman AI, Newbold JD, Sabater F. 2008. Biophysical controls on organic carbon fluxes in fluvial networks. Nat Geosci. 1(2):95-100.

Brown GS. 1979. Estimation of surface wind speeds using satellite-borne radar measurements at normal incidence. J Geophys Res. 84(8):3974-3978.

Butler JN. 1992. Carbon dioxide equilibrium and their applications. Chelsea (MI): Lewis.

Carpenter SR, Caraco NF, Correll DL, Howarth RW, Sharpley AN, Smith VH. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol Appl. 8(3):559-568.

Cleveland WS, McGill R. 1985. Graphical perception and graphical methods for analyzing scientific-data. Science. 229(4716):828-833.

Cole JJ, Caraco NF, Kling GW, Kratz TK. 1994. Carbon-dioxide super-saturation in the surface waters of lakes. Science. 265(5178):1568-1570.

Cole JJ, Caraco NF. 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF6. Limnol Oceanogr. 43(4):647-656.

Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG. Duarte CM, Kortelainen P, Downing JA, et al. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems. 10(1):171-184.

Crumpton WG, Isenhart TM, Mitchell PD. 1992. Nitrate and organic N analyses with 2nd-derivative spectroscopy. Limnol Oceanogr. 37(4):907-913.

Dean WE, Gorham E. 1998. Magnitude and significance of carbon burial in lakes, reservoirs, and peatlands. Geology. 26(6):535-538.

del Giorgio PA, Cole JJ, Caraco NF, Peters RH. 1999. Linking

planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. Ecology. 80(4):1422-1431.

del Giorgio PA, Cole JJ, Cimbleris A. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. Nature. 385(6612):148-151.

Dorioz JM, Ferhi A. 1994. Nonpoint pollution and management of agricultural areas: phosphorus and nitrogen transfer in an agricultural watershed. Water Res. 28(2):395-410.

Downing JA. 2009. Global limnology: Up-scaling aquatic services and processes to planet Earth. Verh Internat Verein Limnol. 30(8):1149-1166.

Downing JA, Cole JJ, Middelburg JJ, Striegl RG, Duarte CM, Kortelainen P, Prairie YT, Laube KA. 2008. Sediment organic carbon burial in agriculturally eutrophic impoundments over the last century. Global Biogeochem Cy. 22(1):GB1018.

Downing JA, Prairie YT, Cole JJ, Duarte CM, Tranvik LJ, Striegl RG, McDowell WH, Kortelainen P, Caraco NF, Melack J, et al. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol Oceanogr. 51(5):2388-2397.

Duarte CM, Prairie YT, Montes T, Cole JJ, Striegl R, Melack J, Downing JA. 2008. CO_2 emissions from saline lakes: A global estimate of surprisingly large flux. J Geophys Res. 113:G04041.

Duarte CM, Prairie YT. 2005. Prevalence of heterotrophy and atmospheric CO_2 emissions from aquatic ecosystems. Ecosystems. 8(7):862-870.

Finlay K, Levitt B, Wissel B, Prairie YT. 2009. Regulation of spatial and temporal variability of carbon flux in six hard-water lakes of the northern great plains. Limnol Oceanogr. 53(6):2553-2564.

Gémesi Z. 2007. Plumbing agricultural landscapes for water quality improvement: coexistance of intensive agriculture and good water quality. [master's thesis], [Ames (IA)]: Iowa State University.

Hope D, Palmer SM, Billett MF, Dawson JJC. 2004. Variations in dissolved CO_2 and CH_4 in a first-order stream and catchment: an investigation of soil-stream linkages. Hydrol Process. 18(17):3255-3275.

Houghton J. 2005. Global warming. Rep Prog Phys. 68:1343-1403.

Jeffrey SW, Mantoura RFC, Wright SW. 1997. Phytoplankton pigments in oceanography: Guidelines to modern methods. New York (NY): UNESCO Publishing.

Kalff J. 2002. Limnology: Inland water ecosystems. Upper Saddle River (NJ): Prentice-Hall.

Karl TR, Trenberth KE. 2003. Modern global climate change. Science. 302(5651):1719-1723.

Kelly CA, Fee E, Ramlal PS, Rudd JWM, Hesslein RH, Anema C, Schindler EU. 2001. Natural variability of carbon dioxide and net epilimnetic production in the surface waters of boreal lakes of different sizes. Limnol Oceanogr. 46(5):1054-1064.

Kling GW, Kipphut GW, Miller MC. 1992. The flux of CO_2 and CH_4 from lakes and rivers in arctic Alaska. Hydrobiologia. 240(1):23-36.

Kortelainen P, Rantakari M, Huttunen JT, Mattsson T, Alm J, Juutinen S, Larmola T, Silvola J, Martikainen PJ. 2006. Sediment respiration

and lake trophic state are important predictors of large CO_2 evasion from small boreal lakes. Glob Change Biol. 12(8):1554-1567.

Lazzarino JK, Bachmann RW, Hoyer MV, Canfield DE. 2009. Carbon dioxide supersaturation in Florida lakes. Hydrobiologia. 627(1):169-180.

Matthews HD, Caldeira K. 2008. Stabilizing climate requires near-zero emissions. Geophys Res Lett. 35(4):LO4705.

Mattson MT. 1996. MacMillian color atlas of the states. Upper Saddle River (NJ): Prentice Hall International.

McGarigal K, Cushman A, Stafford S. 2000. Multivariate statistics for wildlife and ecology research. New York (NY): Springer.

Peters RH. 1986. The role of prediction in limnology. Limnol Oceanogr. 31(5):1143-1156.

Prairie YT, Bird DF, Cole JJ. 2002. The summer metabolic balance in the epilimnion of southeastern Quebec lakes. Limnol Oceanogr. 47(1):316-321.

Prescott GW. 1931. Iowa algae: Univeristy of Iowa studies in natural history. Iowa City (IA): University of Iowa.

Rabalais NN, Downing JA, Baker JL, Diaz RJ, Prato T, Zimmerman R. 1999. Gulf of Mexico hypoxia: Land and sea interactions. Task force report No. 134, Council for Agricultural Science and Technology, Ames (IA).

Reche I, Pace ML. 2002. Linking dynamics of dissolved organic carbon in a forested lake with environmental factors. Biogeochemistry. 61(1):21-36.

Sharpley A, Meisinger JJ, Breeuwsma A, Sims JT, Daniel T. 1998. Impacts of animal manure management on ground and surface water quality. In: Hatfield J, Stewart B, editors. Animal waste utilization: effective use of manure as a soil resource. Ann Arbor (MI): Ann Arbor Press. p.173-242.

Smith VH. 1979. Nutrient dependence of primary productivity in lakes. Limnol Oceanogr. 24(6):1051-1064.

Sobek S, Algesten G, Bergstrom AK, Jansson M, Tranvik LJ. 2003. The catchment and climate regulation of $p CO_2$ in boreal lakes. Glob Change Biol. 9(4):630-641.

Sobek S, Tranvik LJ, Cole JJ. 2005. Temperature independence of carbon dioxide supersaturation in global lakes. Global Biogeochem Cy. 19:GB2003. doi:10.1029/2004GB002264.

Stumm W, Morgan JJ. 1996. Aquatic chemistry: Chemical equilibria and rates in natural waters. New York (NY): Wiley Interscience.

Tranvik L, Downing JA, Cotner JB, Lioselle SA, Striegl RG, Ballatore TJ, Dillon P, Finlay K, Fortino K, Knoll LB, et al. 2009. Lakes and impoundments as regulators of carbon cycling and climate. Limnol Oceanogr. 6(2):2298-2314.

Ward HB, Whipple GC. 1959. Freshwater Biology. New York (NY): Wiley Interscience.

Wehr JD, Sheath RGE. 2003. Freshwater Algae of North America: ecology and classification. London (UK): Academic Press.

Wetzel RG, Likens GE. 2000. Limnological analyses, 3rd ed. New York (NY): Springer-Verlag.