Spatial and temporal dynamics of pCO₂ and CO₂ flux in tropical Lake Malawi

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Abstract

Numerous studies have documented CO₂ dynamics in temperate lakes, but few such studies have been conducted on tropical lakes. Spatial and seasonal variation of air and water pCO₂, along with supporting limnological and meteorological variables, were measured aboard a vessel of opportunity along the north–south axis of Lake Malawi. These measurements were used to estimate annual net lake-atmosphere CO₂ flux and infer mechanisms regulating it. Surface pCO₂ and CO₂ flux varied significantly with season and location. Temporally, the lake was CO₂-undersaturated during the rainy season and the mixing season, and supersaturated at the onset of the mixing season and during the hot, stratified season. Concurrent measurements of lake temperature, weather conditions, phytoplankton biomass, and seston δ¹³C suggest that periods of net CO₂ flux into the lake correspond with higher phytoplankton growth rates resulting from internal nutrient loading in the mixing season and allochthonous nutrient inputs in the rainy season. Unlike the rest of the lake, the southernmost region of the lake was usually CO₂ supersaturated even though phytoplankton productivity is highest in this region. While the upwelling of hypolimnetic water at the southern end of the lake is a major source of nutrients that drive phytoplankton photosynthesis and CO₂ uptake, the CO₂ introduced in upwelled water appears to overwhelm photosynthetic capacity locally, especially at the onset of the mixing season. Lake Malawi appears to be a net CO₂ sink with an annual whole-lake CO₂ flux of $-2.17 \pm 0.25 \times 10^{10}$ mol C yr$^{-1}$ and a mean daily CO₂ flux of $-2.05 \pm 0.27$ mmol C m$^{-2}$ d$^{-1}$. A comparison of deep-water C : P ratios with epilimnetic seston C : P ratios suggests that P is recycled more efficiently than C in the lake’s anoxic hypolimnion, and so P vertical mixing creates a carbon deficit that is met by flux from the atmosphere into the lake.

Inland lakes play a vital role in the global carbon cycle (Tranvik et al. 2009), serving both as sinks for organic carbon, and as atmospheric sources/sinks of CO₂ (Mulholland and Elwood 1982; Dean and Gorham 1998; Cole et al. 2007; Tranvik et al. 2009). These aquatic systems actively process terrestrial carbon, emitting large amounts of CO₂ to the atmosphere (Dean and Gorham 1998; Cole et al. 2007; Tranvik et al. 2009; Deemer et al. 2016) while also accumulating organic carbon in their sediments (Mulholland and Elwood 1982). Numerous studies (Cole et al. 1994, 2000; del Giorgio et al. 1997; Duarte and Prairie 2005; Alin and Johnson 2007) suggest that most lakes are net sources of CO₂ to the atmosphere, in which case allochthonous contributions to respiration in these lakes exceed net autochthonous C fixation (Kling et al. 1991; Cole et al. 1994, 2000; Sobek et al. 2005; Bellido et al. 2009). That phosphorus and dissolved organic carbon (DOC) concentrations are key drivers of metabolism in many lakes has been widely documented (del Giorgio and Peters 1994; Cole et al. 2000; Hanson et al. 2003). Phosphorus promotes CO₂ uptake by phytoplankton while DOC promotes microbial respiration. The relative importance of these processes can vary temporally, depending on external loads, temperature, solar radiation, and internal dynamics, which are controlled in part by vertical mixing (Sobek et al. 2005; Roehm et al. 2009; Lapierre and del Giorgio 2012).

Our current understanding of carbon dynamics in lakes is based to a large extent on studies conducted in small to medium size temperate lakes (Hope et al. 1996; Kelly et al. 2001; Roehm et al. 2009; Kortelainen et al. 2013). While air–water CO₂ fluxes have been reported for a number of small tropical lakes and reservoirs (DeSontro et al. 2018), these systems are under-represented in global budgets, and virtually no direct measurements have been made for large tropical systems (Raymond et al. 2013). There is evidence that small tropical lakes and reservoirs tend to be CO₂-supersaturated (Raymond et al. 2013), like many temperate lakes (Cole et al. 1994). However, the mechanisms that regulate CO₂ dynamics in large, tropical lakes may be different considering...
their unique features. For example, two of the African Great Lakes, Tanganyika and Malawi, are old (several million years), deep, and meromictic. Long hydraulic residence times and slow vertical mixing result in significant differences in water chemistry relative to most large, temperate lakes (Bootsma and Hecky 2003; Katsev et al. 2017), such as high concentrations of dissolved nutrients and CO₂ as well as anoxia in their hypolimnia. Anoxic conditions may inhibit the recycling of organic carbon while accelerating the recycling of phosphorus (Nürnberg 1984; Benitez-Nelson et al. 2007; Sobek et al. 2009), which may affect the balance between community respiration and carbon fixation. Lake Malawi also has relatively low concentrations of DOC, ranging between 20 and 140 \( \mu \text{mol L}^{-1} \) (Ramlal et al. 2003), which might be expected to result in low surface pCO₂ (Jonsson et al. 2003, 2008; Sobek et al. 2005; Lapierre and del Giorgio 2012).

To address the dearth of information on pCO₂ dynamics and driving mechanisms in large, tropical systems, we conducted 12 whole-lake surveys of surface pCO₂ and other physical and chemical variables over an annual cycle on Lake Malawi. Our research was guided by the following hypotheses: (1) surface pCO₂ varies seasonally according to previously observed temporal patterns of phytoplankton productivity; (2) selective recycling of P relative to C below the epilimnion promotes net CO₂ uptake from the atmosphere; (3) CO₂ flux from the atmosphere to the lake is greatest in the southern part of the lake, where upwelling of nutrient-rich water promotes high phytoplankton biomass and photosynthetic rates.

Materials and methods

Lake Malawi lies between latitudes 9°30'S and 14°30'S and longitudes 33°30'E and 35°30'E (Fig. 1) at the southern end of the East African Rift valley. The lake is one of the world’s oldest (5–10 million years old), largest (29,500 km²), and deepest (max. 700 m) (Bootsma and Hecky 2003). The physical characteristics of Lake Malawi have been described by others (Bootsma and Hecky 1993; Cohen et al. 1993; Vollmer et al. 2002). The open waters of the lake are nutrient poor (concentrations of soluble reactive phosphorus [SRP] and dissolved inorganic nitrogen are less than 0.1 \( \mu \text{mol L}^{-1} \)), but ammonium and SRP concentrations increase with depth, reaching concentrations of 25 \( \mu \text{mol L}^{-1} \) and 4 \( \mu \text{mol L}^{-1} \), respectively, in the anoxic hypolimnion below 200 m (Bootsma and Hecky 1993; Wüest et al. 1996). Regional climatological conditions are divided into three distinct seasons: the hot, wet season (December–April); the cool, dry season (May–September); and the hot, stratified season (October–November). The cool, dry season is characterized by relatively low air temperature (20–22°C), accompanied by low surface-water temperatures and strong southeast trade winds. During the hot, stratified season, wind speeds decline and air temperatures increase, resulting in lake surface temperatures as high as 29°C and stronger, shallower stratification.

The open waters of Lake Malawi have low chlorophyll a (Chl a) with a mean of < 1 \( \mu \text{g L}^{-1} \). However the lake’s southern end displays higher Chl a concentrations with a mean of > 2 \( \mu \text{g L}^{-1} \) and concentrations > 7 \( \mu \text{g L}^{-1} \) in the cool, dry season when vertical mixing and upwelling introduce nutrient-rich deep water to this region (Patterson and Kachinjika 1995). In addition, phytoplankton photosynthetic rates in the southern end of the lake are relatively high, exceeding 1 g C m⁻² d⁻¹ (Degnbol and Mapila 1982; Bootsma 1993b). Phytoplankton photosynthesis varies seasonally, with high rates observed during the cool, mixing season and rainy season, and low rates in the hot, stratified season (Bootsma 1993a; Patterson and Kachinjika 1995). Hence, there is reason to expect that lake-atmosphere CO₂ flux also varies temporally and spatially.

A lake-wide sampling program on Lake Malawi aboard the passenger ferry MV Ilala was conducted for a period of 1 yr in 2013. In the southern region where the MV Ilala does not
operate, the Fisheries Research Vessel, RV *Ndunduma*, and smaller boats were used. An onboard monitoring system was used to make continuous measurements of lake surface pCO$_2$, chlorophyll fluorescence, and temperature while the vessels were underway. On the MV Ilala and RV *Ndunduma*, valves were inserted into the sea-chest plumbing system, allowing lake surface water to be pumped into the onboard monitoring system. On the MV Ilala, the hull mounted intake was \( \sim 2 \text{ m} \) below the waterline and the time between intake and measurement was \( \sim 2 \text{ s} \). On the RV *Ndunduma*, the intake depth was \( \sim 2.4 \text{ m} \) and the time from intake to measurements was \( \sim 3 \text{ s} \). On smaller boats, intake tubing was submerged \( \sim 0.5 \text{ m} \) below the lake surface by attaching to a vertical pole mounted on the boat hull. The south–north round-trip cruise on the MV Ilala lasted on average about 6 d. For data analysis purposes, the lake was divided into five zones (Fig. 1) based on catchment characteristics (Kidd 1983), previous plankton and water quality observations (Bootsma 1993a; Patterson and Kachinjika 1995), and transect orientation, that is, whether the MV Ilala was traveling on a south–north or west–east direction. In each zone, surface-water samples (2 m) were collected from 2–5 stations, depending on the size of the zone, and filtered through GF/F glass fiber filters (nominal pore size = 0.7 \( \mu \text{m} \)). Filters were analyzed for Chl *a* following the method of Stainton et al. (1977). Filter samples for analysis of particulate C and N concentrations and carbon stable isotope ratios were analyzed on a Costech 4010 Elemental Analyzer System coupled by a Thermo Scientific CONFLO IV gas control module to a Thermo Scientific Delta-V Plus Isotope Ratio Mass Spectrometer. Each sample run was preceded by a tin foil blank and standards of acetaldehyde. During sample runs, an acetaldehyde control sample was run every 12th sample. \(^{13}\text{C} / ^{12}\text{C} \) ratios (expressed as \( \delta^{13}\text{C} \) values) were determined relative to the PDB carbonate standard and are expressed as \( \delta^{13}\text{C} \) (%o) values:

\[
\delta^{13}\text{C} = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000
\]

where \( R_{\text{sample}} / R_{\text{standard}} = \frac{^{13}\text{C}}{^{12}\text{C}} \)

Chl *a* measurements were made to determine the degree to which surface pCO$_2$ may be linked to phytoplankton biomass. Seston carbon stable isotope ratio may reflect variations in phytoplankton growth rate (Takahashi et al. 1991; Zohary et al. 1994; Gu and Schelske 1996; Ngochera and Bootsma 2011) and so these measurements were made along with Chl *a* to support the interpretation of pCO$_2$ temporal and spatial fluctuations.

Surface-water pCO$_2$ measurements were made using a real-time, in situ CO$_2$ measuring system. The CO$_2$ system consists of a “wet box” which includes a peristaltic pump (400–500 mL min$^{-1}$), temperature sensor, gas equilibrator (Membrana® minimodule membrane contactor, model G477), a flow-through fluorometer (WETLabs WETStar), and a “dry box” containing a Li-Cor LI-820 infrared gas analyzer (IRGA), an oxygen sensor, a Campbell Scientific CR-1000 controller/logger, and an air pump connected to tubing that circulates air between the equilibrator in the wet box and the gas sensors in the dry box. A length of Nafion® tubing, packed in silica gel, was placed in the air flow between the equilibrator and the IRGA to remove water vapor. Air–water 95% gas equilibration time is \(< 90 \text{ s} \) (Zagorski and Bootsma 2006). The dry box has a secondary air intake tube that allowed for measuring ambient air pCO$_2$, approximately 5 m above the lake surface. A solenoid valve was used to switch the air plumbing between the ambient air intake and water-equilibrated air on a 15 min cycle with 12 min of water sampling and 3 min of air sampling. A Garmin 16-HVS GPS receiver was attached to the logger, allowing all measurements to be georeferenced. Vessel speed reported by the GPS to the controller was used to switch the system on and off so that the system only operated while the vessel was underway.

The temperature sensor in the wet box has an accuracy of \( \pm 0.1 \text{°C} \). Several times per day during cruises, a bucket was used to draw water directly from the lake and a hand-held thermometer used to record the lake’s surface temperature. These temperatures were compared with the pCO$_2$ system measurements to determine whether water temperature changed between the point of intake and the point of measurement, as this would affect pCO$_2$ measurements. These measurements indicated that the temperature in the gas equilibrator was slightly warmer than in situ temperature, and so measured temperatures were corrected using the relationship

\[
\text{LST} = 0.8289 \times L_T + 4.34 \quad (r^2 = 0.84, p < 0.0001), \quad \text{where LST is the corrected lake surface temperature and } L_T \text{ is the measured temperature.}
\]

Measured pCO$_2$ was then corrected for warming to determine in situ surface pCO$_2$. IRGA-reported pCO$_2$ values, which are normalized to a pressure of 1.0 atm, were corrected for local atmospheric pressure (recorded hourly at a lakeshore meteorological station at Senga Bay) to determine in situ pCO$_2$. The IRGA was regularly calibrated using 0 and 399 ppm (\( \pm 2\% \)) standard gases. Lake-atmospheric CO$_2$ flux was calculated as

\[
F = kK_H(p_{\text{CO}_2w} - p_{\text{CO}_2a})
\]

where pCO$_2w$ and pCO$_2a$ are the partial pressures (\( \mu \text{atm} \)) of CO$_2$ in surface water and air, respectively, \( K_H \text{ (mol m}^{-3} \text{ atm}^{-1}) \) is the aqueous phase solubility of CO$_2$ (Weiss 1974), and \( k \) is the vertical gas transfer coefficient (cm h$^{-1}$). Various empirical models have been applied to estimate the value of \( k \), with estimates varying by as much as fourfold. A commonly used model is that of Nightingale et al. (2000), but this model was parameterized for marine systems with windspeeds that are higher than those usually observed over Lake Malawi (winds speeds are predominately \(< 6 \text{ m s}^{-1} \)). Alternatively, Vachon and Prairie (2013) have proposed a model that accounts for both windspeed and lake surface area, but we found that this model results in extremely high \( k \) values when applied to a lake as large as Lake Malawi. Instead, we used an alternative model proposed by Vachon and
Prairie (2013) that was parameterized using a broad range of windspeeds and does not account for lake surface area:

\[ k_{600} = 2.58 \times \frac{U_{10}}{1.41} \quad (3) \]

where \( k_{600} \) is the transfer velocity at a temperature of 20°C (at which the Schmidt number for CO₂ is 600), and \( U_{10} \) is the wind speed (m s \(^{-1}\)) normalized to a height of 10 m above the water surface. This model results in \( k \) values that are intermediate between those derived using the two other models mentioned above. Wind speeds were adjusted to a height of 10 m using the power law relationship:

\[ U_{10} = U_t \times \left( \frac{z}{z_t} \right)^\alpha \quad (4) \]

where \( U_t \) is the wind speed at the reference height \( z_t \), \( U_{10} \) is the wind speed at 10 m, and \( \alpha \) is a parameter dependent on surface conditions and atmospheric stability, which was set to 0.14 (Peterson and Hennessey 1978). Wind speeds were measured hourly at Senga Bay, 10–20 m from the lakeshore. Based on analyses of long-term meteorological data sets for land-based stations around the lake, as well as over-lake measurements (Hamblin et al. 2003), we derived correction factors for each zone, season, and daily 6-hour quartile, which were used with the Senga Bay data to calculate daily windspeeds for each zone. \( k \) values were corrected for temperature following the method described by Jähne et al. (1987). Whole-lake monthly mean and standard deviations (SDs) of pCO₂ and CO₂ flux (\( F \)) for each month were determined by weighting the measurements for each zone according to the zone surface area.

On three dates in April, August, and October 2014 at a station near Nkhata Bay (11.5542°S, 34.3134°E; maximum depth = 400 m), deep profile samples were collected for measurements of SRP, along with CTD casts (Sea-Bird SBE 19 SEACAT profiler) to measure vertical profiles of temperature and pH. SRP concentrations were measured spectrophotometrically with the molybdate-ascorbic acid method (Stainton et al. 1977). Measurements we have made in a previous study (unpubl.) indicate that carbonate alkalinity in Lake Malawi is relatively constant, with values at depths < 200 m averaging 2175 μeq L \(^{-1}\) (SD = 36), and values in the anoxic hypolimnion averaging 2222 μeq L \(^{-1}\) (SD = 20). Therefore, we used pH measurements and alkalinity (Alk) to estimate total dissolved inorganic carbon (DIC) concentrations:

\[ \text{DIC} = \frac{\text{Alk} \left( [\text{H}^+]^2 + [\text{H}^+]K_1 + K_1K_2 \right)}{K_1 \left( [\text{H}^+] + 2K_2 \right)} \quad (5) \]

where \( K_1 \) and \( K_2 \) are the carbonic acid dissociation constants (Cai and Wang 1998). Equation 5 assumes that the contributions of H\(^+\) and OH\(^-\) to alkalinity are negligible, which is a valid assumption for the relatively high alkalinity of Lake Malawi.

In addition to using surface pCO₂ measurements to determine lake-atmosphere CO₂ exchange, we estimated internal fluxes of DIC and SRP between the hypolimnion, metalimnion, and epilimnion to determine whether these fluxes promote net CO₂ uptake or outgassing. Accepting that phosphorus is the nutrient limiting phytoplankton production (Hecky et al. 1996; Ngochera and Bootsma 2018) and that the annual supply of P to the epilimnion is dominated by internal loading (Bootsma and Hecky 2019), the net uptake of inorganic carbon in the epilimnion (\( U_{\text{DIC}} \)) can be expressed as a product of the net flux of SRP into the epilimnion (\( F_{\text{SRP}} \)) and the C : P ratio of phytoplankton (C : Pphyto):

\[ U_{\text{DIC}} = F_{\text{SRP}} \times C : P_{\text{phyto}} \quad (6) \]

Under steady-state conditions, \( U_{\text{DIC}} \) must be balanced by the sum of DIC flux from the metalimnion (\( F_{\text{DIC}} \)) and the lake-atmosphere CO₂ flux (\( F_{\text{atm}} \)):

\[ U_{\text{DIC}} = F_{\text{DIC}} + F_{\text{atm}} \quad (7) \]

If net annual \( U_{\text{DIC}} \) is greater than \( F_{\text{DIC}} \), the lake is expected to be a net sink for atmospheric CO₂ (\( F_{\text{atm}} \) is positive), and vice versa. Estimates of DIC and SRP vertical fluxes were made using vertical profile measurements of DIC and SRP, combined with estimates of vertical mixing rates (\( k \)) between lake strata as revealed by chlorofluorocarbon-12 (CFC-12) profiles (Vollmer et al. 2002), following the method described by Bootsma et al. (2003):

\[ F = k \frac{V_2}{V_1} (C_2 - C_1) \frac{V_1}{A} \quad (8) \]

where \( F = \) flux rate (mg m \(^{-2}\) yr \(^{-1}\)), \( k = \) vertical exchange coefficient, \( V_1 \) and \( V_2 \) are volumes of adjacent strata (upper and lower, respectively), \( A \) is lake surface area (to which all fluxes were normalized; 29,500 km \(^2\)), and \( C_1 \) and \( C_2 \) are the volume-weighted average concentrations of DIC or SRP in the adjacent strata:

\[ C = \frac{\sum (\Delta Z_i A_i C_i)}{\sum (\Delta Z_i A_i)} \quad (9) \]

where \( \Delta Z_i \) is the thickness of a depth layer within a stratum (set at 1 m intervals), \( A_i \) is the horizontal area of a layer, and \( C_i \) is the dissolved SRP or DIC concentration within the layer. While the CFC-12 measurements are not contemporaneous with our CO₂ and SRP measurements, CFC-12 profiles reflect mixing rates integrated over multiyear time scales, and a comparison of thermal structure during this study with that measured in previous studies (Li et al. 2018; Bootsma and Hecky 2019) reveals no major differences. To account for any long-term change in the concentration and distribution of SRP and DIC and the potential error in our DIC estimates based on pH measurements, we supplemented the data collected in this
study with that collected in two other studies, one in 1997 (Bootsma and Hecky 2019) and one in 2014 (Li et al. 2018).

An approach similar to that described above is to compare the ratio of excess DIC (EDIC) to SRP in the metalimnion and hypolimnion with epilimnetic seston C : P ratios. EDIC represents the difference between the volume-weighted mean annual DIC concentration in the metalimnion or hypolimnion and the DIC concentration in the epilimnion. If the EDIC : SRP ratio in the deeper layers is greater than the phytoplankton C : P ratio, the lake can be expected to lose a portion of the phytoplankton, which appears to be valid for the pelagic zone of large lakes (Hecky et al. 1993; Sterner and Elser 2002).

Data analyses (descriptive statistics, two-way ANOVA and post hoc tests) were performed using SigmaPlot12.5 and OriginPro8 software to test for significant spatial and temporal variability in the measured parameters. Differences between means were considered significant at $p < 0.05$.

**Results**

Meteorological conditions display a clear seasonality, with temperatures coolest between June and August, coinciding with high wind speeds (Fig. 2). During this period, persistent southeasterly winds blow across the lake. Temperature profiles for the three seasons indicate that in the cool, windy period, mean water column temperatures at the southern end of the lake are similar to those recorded in the metalimnion and hypolimnion further to the north, likely due to upwelling of deep, cold water at the southern end of the lake at this time of year. The wet season (December–April) is characterized by relatively higher air temperatures (mean of 29°C) and low wind speeds (mean of less than 2 m s$^{-1}$).

To determine if there were significant differences in surface pCO$_2$ over time and among zones, the data set from each zone was partitioned into three periods that coincide with meteorological and hydrological conditions, that is, the hot, wet season (October–April), the cool, windy mixing season (May–September), and the hot, stratified season (October–November). The partitioned data were then subjected to a two-way ANOVA with location and season as the two factors. Significant differences were observed among seasons ($p < 0.001$). A pairwise multiple comparison (Tukey test) showed that pCO$_2$ in the hot, stratified season was significantly greater than in other seasons (Fig. 3a). The cool, windy season was not significantly different from the hot, wet season. However, within the cool, windy season, there was a whole-lake transition from relatively CO$_2$ supersaturation early in the season to undersaturation later in the season (Fig. 3a). A similar trend was observed in the hot, wet season when whole-lake pCO$_2$ transitioned from supersaturation to as low as 350 μatm in late February (Fig. 3b). Spatially, the annual mean pCO$_2$ in the southernmost region (zone 5) was above saturation and significantly greater than the individual annual means for zones 1–4 (Fig. 3c and Table 1). However, there is high pCO$_2$ variability in zone 5 than the rest of the zones with lowest and highest values recorded in February and June, respectively. No significant difference was observed among zones 1–4 ($p > 0.05$). While there was some spatial variation in surface pCO$_2$, the seasonal pattern was similar for most zones. As a result, there was no statistically significant interaction between zone and season ($p = 0.973$).

A similar two-way ANOVA was conducted for CO$_2$ flux, which revealed significant differences of lake-atmosphere CO$_2$ flux among both seasons and locations ($p < 0.001$), with no significant interaction of season and location ($p = 0.816$). Net CO$_2$ uptake by the lake was observed during the rainy season and the latter half of the cool, windy season in all zones, while net CO$_2$ efflux was observed at the onset of the cool, windy season and during the hot, stratified season. The largest CO$_2$ flux into the lake was observed in September at the end of the windy season, while

**Fig. 2.** Variation of (a) daily mean air temperature (solid line) and whole-lake mean monthly water temperature (symbol and dashed line), (b) daily mean wind speed, and (c) daily total rainfall recorded at Senga Bay Research Station.
The highest evasion to the atmosphere was in May (Fig. 4, entire lake). For most of the year, zones 1–4 were either net sinks of CO2 or close to equilibrium with the atmosphere. By contrast, while zone 5 was a net CO2 sink in some months, over the entire year it was a net CO2 source. The highest pCO2 was recorded during the cool, windy season while the lowest were observed in the hot, wet season (Figs. 3, 4). Post hoc analysis indicates that there was no significant difference in CO2 flux between the rainy and windy seasons ($p > 0.05$), and no significant difference was observed among zones 1–4 ($p > 0.05$). The area-weighted mean annual CO2 flux was estimated as $-748 \pm 89$ (95% confidence interval [CI]) mmol C m$^{-2}$ yr$^{-1}$, for the lake indicating that the lake is a net sink of CO2 from the atmosphere (Table 1). Overall, Lake Malawi assimilates a total of $2.17 \pm 0.25$ (95% CI) $\times 10^{10}$ mol C yr$^{-1}$ from the atmosphere.

**Table 1.** Zone surface area, annual mean wind speed, mean surface pCO2, and associated CO2 flux calculated using flux equation of Vachon and Prairie (2013). CO2 fluxes include 95% CI for each zone.

| Location | Surface area (km$^2$) | Mean wind speed (m s$^{-1}$) | Mean surface pCO2 (μatm) | CO2 flux (mmol C m$^{-2}$ d$^{-1}$) |
|----------|-----------------------|------------------------------|--------------------------|-----------------------------------|
| Zone 1   | 14,194                | 2.49                         | 380.42                   | $-2.21 \pm 0.15$                  |
| Zone 2   | 5683                  | 1.67                         | 369.42                   | $-2.07 \pm 0.26$                  |
| Zone 3   | 1282                  | 2.86                         | 376.37                   | $-2.69 \pm 0.27$                  |
| Zone 4   | 7541                  | 2.98                         | 392.25                   | $-1.79 \pm 0.18$                  |
| Zone 5   | 300                   | 3.45                         | 429.79                   | $+2.25 \pm 1.31$                  |

Daily weighted mean CO2 flux (mmol C m$^{-2}$ d$^{-1}$) $-2.05 \pm 0.27$

Annual mean CO2 flux (mmol C m$^{-2}$ yr$^{-1}$) $-748 \pm 89$

Annual whole-lake CO2 flux (mol C yr$^{-1}$) $-2.17 \pm 0.25 \times 10^{10}$
Fig. 4. Mean monthly CO₂ fluxes and associated standard error (SE) bars for the five lake zones. The lower right figure displays monthly mean area-weighted CO₂ fluxes for the entire lake. Text at the upper right of each plot is the mean annual CO₂ flux. Positive fluxes indicate net evasion from the lake to the atmosphere while negative values are invasion into the lake. Note the different CO₂ flux scale for zone 5.

Fig. 5. Seasonal and spatial variation of Chl a (a, b) and carbon stable isotope ratios (c, d) in surface waters. SE bars are included in (a, c). Interpretation of (b, d) is as for Fig. 3.
Table 2. Calculated volumes for each depth strata; vertical exchange coefficients (k); volume-weighted annual mean DIC, EDIC, and SRP concentrations; EDIC : SRP ratios; and vertical DIC and SRP flux rates. k values are from Vollmer et al. (2002). DIC and SRP fluxes values represent annual flux to a stratum from that underlying it. SD values (±) represent variability among measurements made in three separate studies: 1997 (Bootsma and Hecky 2019), 2014 (Li et al. 2018), and the present study.

| Stratum        | Volume (km³) | k (yr⁻¹) | DOC (µmol L⁻¹) | DIC (µmol L⁻¹) | SRP (µmol L⁻¹) | EDIC (µmol L⁻¹) | EDIC:SRP | DIC flux (mmol C m² yr⁻¹) | SRP flux (mmol P m² yr⁻¹) |
|---------------|--------------|----------|----------------|----------------|---------------|----------------|-----------|---------------------------|---------------------------|
| Epilimnion    | 2754         | 0.27     | 55–150         | 2153 ± 30      | 0.49 ± 0.09   | 0              | —         | 1797 ± 72                  | 19.05 ± 0.25              |
| (0–105 m)     |              |          |                |                |               |                |           |                           |                           |
| Metalimnion   | 2310         | 0.056    | 45–150         | 2237 ± 65      | 1.37 ± 0.23   | 108 ± 32       | 182 ± 30  | 873 ± 94                  | 11.61 ± 0.88              |
| (105–220 m)   |              |          |                |                |               |                |           |                           |                           |
| Hypolimnion   | 2711         | —        | 40–160         | 2404 ± 68      | 3.59 ± 0.85   | 160 ± 34       | 91 ± 23   | —                         | —                         |
| (> 220 m)     |              |          |                |                |               |                |           |                           |                           |

Seston δ¹³C and Chl a concentrations followed similar seasonal patterns of variation (Fig. 5a,c). Spatially, the southernmost zone 5, which is considered the most productive area in the lake, showed higher Chl a concentrations and more ¹³C-enriched seston than the rest of the lake (Fig. 5b,d). A two-way ANOVA indicated that both seston δ¹³C and Chl a concentration varied significantly among seasons (p < 0.02) and zones (p < 0.02), with no significant interaction of season and zone (p > 0.75). A negative correlation is observed between pCO₂ and Chl a (−0.063, p = 0.847) and seston δ¹³C (−0.026, p = 0.521) although the relationship is not significant. In contrast, a positive correlation and significant relationship exists between Chl a and δ¹³C (0.655, p = 0.021).

Concentrations of DIC, EDIC, and SRP increased with depth (Table 2). The EDIC : SRP ratio in the metalimnion (182 ± 30) is greater than the Redfield ratio, but slightly lower than the mean epilimnetic seston C : P ratio of ~ 200:1 (Ngochera and Bootsma 2018). The hypolimnetic EDIC : SRP ratio of 91 ± 23 is less than half the epilimnetic seston C : P ratio. DIC and SRP fluxes from the metalimnion to the epilimnion represent the sum of material recycled within the metalimnion plus material loaded to the hypolimnion from the metalimnion. The fluxes presented in Table 2 indicate that hypolimnetic recycling contributes ~ 49% of the DIC vertical flux to the epilimnion while it contributes ~ 61% of the P flux.

Discussion

The results presented here show distinct differences in pCO₂ and CO₂ fluxes over time and location that appear to be linked to hydrological and hydrodynamic conditions. With some exceptions, the seasonal pattern of surface CO₂ conforms to what might be expected based on previously observed patterns of phytoplankton productivity (Bootsma 1993b; Patterson and Kachinjika 1995; Patterson et al. 2000). In a whole-lake study of phytoplankton photosynthesis, Bootsma (1993b) measured the highest photosynthetic rates during the mixing (June–September) and rainy (December–January) seasons, the same periods when surface pCO₂ was below saturation in the present study. Although phosphorus supply to the epilimnion is dominated by internal loading (Bootsma and Hecky 2019), the CO₂ undersaturation observed in the rainy season in Lake Malawi suggests that the lake also responds rapidly to external nutrient loading. This is perhaps because a significant portion of the river nutrient load is confined to the epilimnion and upper metalimnion rather than being diluted over the entire water column (Patterson and Kachinjika 1995; Kingdon et al. 1999). Other studies have also shown that rainfall can affect the seasonal dynamics of CO₂ in aquatic systems, but many of these studies are in smaller lakes where inputs of CO₂-rich groundwater result in higher lake surface pCO₂ during the rainy season (Marotta et al. 2010; Rasilo et al. 2012; Macklin et al. 2018). Rainfall can also result in increased loading of organic carbon, which might be expected to promote heterotrophy (Cole et al. 1994; Hanson et al. 2003). There is evidence that organic carbon input to the surface waters of Lake Malawi increases during the rainy season, but concentrations of organic C in the lake and its tributaries are low compared to many lakes (Ramlal et al. 2003), and our results suggest that the effects of rainy season nutrient loading on lake-atmosphere CO₂ exchange outweigh those of organic carbon loading.

High concentrations of Chl a and enriched δ¹³C values were observed in the wet (December–March) and mixing periods (May–August) when nutrient inputs to the surface mixed layer are highest. In contrast, low Chl a concentrations and depleted δ¹³C values were observed during the period of strongest stratification (October and November), when epilimnetic nutrient inputs and photosynthetic rates are low (Bootsma 1993b; Guildford et al. 2007). Similar results were observed by Ngochera and Bootsma (2011) who attributed the enriched seston δ¹³C during the rainy and mixing seasons to enhanced phytoplankton growth rates during those periods. The
similarities between seasonal patterns of surface pCO₂, Chl a, and seston δ¹³C in this study and phytoplankton/nutrient dynamics observed in previous studies suggest that lake-atmosphere CO₂ exchange over much of the lake is regulated by phytoplankton productivity, which in turn is regulated by SRP supply (Guildford et al. 2007). An exception to this relationship was observed at the southernmost part of the lake (zone 5), where pCO₂ was high at the same time that phytoplankton biomass and photosynthesis are usually high (Bootsma 1993b). This is the opposite of what we expected. The low surface temperatures during the cool, windy season in zone 5 suggest that there was upwelling at that time, which was accompanied by elevated Chl a concentrations (mean = 1.8 μg L⁻¹). While this upwelling water is a major source of nutrients to the epilimnion (Hamblin et al. 2003), it appears that there is a lag in community metabolism response to these nutrients. In the initial stage of upwelling, the supply of EDIC exceeds the assimilative capacity of the phytoplankton. This is highlighted by a comparison of lake-atmosphere CO₂ flux rates during the May–July period with potential CO₂ input to zone 5 due to upwelling. The loss of DIC in zone 5 due to degassing to the atmosphere during this period, expressed as volumetric concentration (ΔDICₐ), is determined as:

\[
\Delta \text{DIC}_a = \frac{F_{\text{atm}} \cdot d}{Z}
\]  

(10)

where \(F_{\text{atm}}\) = mean lake-atmosphere CO₂ flux (14.5 ± 1.7 mmol m⁻² d⁻¹), \(d\) = number of days (92), and \(Z\) = mean depth of zone 5 (30 m). The resultant ΔDICₐ is 44 ± 5.2 μmol L⁻¹. The cool surface temperatures observed in zone 5 during this period (23.2°C) are comparable to those in the hypolimnion (23°C), suggesting that much of the water in this zone is replaced by upwelling hypolimnetic water during the mixing season, a conclusion supported by model simulations of Hamblin et al. (2003). If it is assumed that all of this water is from the hypolimnion, where the DIC concentration is approximately 251 ± 74 μmol L⁻¹ greater than in the epilimnion (Table 2), then the net accumulation of DIC in the epilimnion during this period, after lake-atmosphere flux is accounted for, is ~ 207 ± 74 μmol L⁻¹. In order to assimilate this EDIC and return zone 5 to a state of atmospheric CO₂ equilibrium at the end of this period (Fig. 4), phytoplankton photosynthesis would need to account for a net uptake of ~ 68 ± 24 mmol C m⁻² d⁻¹. Photosynthesis rates measured in this part of the lake using the ¹⁴C tracer method can exceed 80 mmol C m⁻² d⁻¹ at this time of year (Bootsma 1993b). Hence, it appears that phytoplankton are capable of assimilating much of the EDIC that is introduced by upwelling on a time scale of months, but rapid upwelling at the beginning of the windy/mixing season results in a DIC influx that temporarily exceeds photosynthetic C assimilation, resulting in a loss of some CO₂ to the atmosphere. Similar observations have been made for some marine systems, such as the Oregon coast, where nearshore-offshore gradients of surface pCO₂ during upwelling events are similar to the south–north gradient observed in Lake Malawi during the windy season (Hales et al. 2005).

Our observations for Lake Malawi do not conform to the common tenet that oligotrophic lacustrine and marine systems tend to be net heterotrophic (del Giorgio et al. 1997; Duarte and Agusti 1998; Cole 1999; Duarte and Prairie 2005). The prevalence of net heterotrophic aquatic ecosystems is attributed to inputs of allochthonous organic carbon (Prairie et al. 2002; Hanson et al. 2003; Duarte and Prairie 2005), which would seem to be supported by a positive correlation between pCO₂ and DOC concentration (Jonsson et al. 2003, 2008; Sobek et al. 2005; Lapierre and del Giorgio 2012). However, the generalization of net heterotrophy in oligotrophic systems has been viewed with some skepticism from both the freshwater (Carignan et al. 2000) and marine perspective (Karl et al. 2003). In Lake Malawi, DOC concentrations are low, usually well below 100 μmol L⁻¹ (Ramal et al. 2003). This may be due in part to the low watershed: lake area ratio (3.4), a mechanism also invoked by Borges et al. (2014) to explain apparent autotrophy in Lake Kivu, another meromictic African lake. Climate and land use may also influence DOC loading to Lake Malawi. Unlike in many temperate rivers, DOC concentrations in Lake Malawi tributaries are low (Hecky et al. 2003; Ramal et al. 2003).

Like Lake Malawi, Lake Superior has a small watershed: surface area ratio (1.6) and low water column DOC concentrations (67–267 μmol L⁻¹; Urban et al. 2005). However, Lake Superior appears to be net heterotrophic (Urban et al. 2005; Atilla et al. 2011; Lin and Guo 2016). An obvious difference between these two systems is thermal structure (meromictic vs. dimictic), which has consequences for redox conditions. Lake Superior is well oxygenated throughout the water column while Lake Malawi is permanently anoxic below ~ 200 m. Anoxic conditions may slow the decomposition of organic carbon while promoting the recycling of P (Nürnberg 1984; Benitez-Nelson et al. 2007; Sobek et al. 2009). That this may be occurring in Lake Malawi is evidenced by the EDIC: SRP ratios in the hypolimnion and metalimnion (Table 2), which are low relative to the mean epilimnetic seston C: P ratio (~ 200:1, Ngochera and Bootsma 2018). The difference between seston C: P ratios and deep-water EDIC: SRP ratios suggests that sinking particulate P is recycled more efficiently than particulate C. Therefore, recycled P that is returned to the epilimnion is more than sufficient to support photosynthetic assimilation of recycled CO₂. Unlike large temperate lakes, this assimilation occurs at relatively high rates throughout the year, due to consistently high temperatures and irradiance. As a result, phytoplankton CO₂ uptake over the lake as a whole exceeds the flux of CO₂ from the hypolimnion to the surface layer, creating a demand for atmospheric CO₂. If Eqs. 9, 10 are solved using the fluxes in Table 2 and a phytoplankton C: P ratio of 200:1, the photosynthetic assimilation of CO₂ (UDIC) is determined as 3.8 ± 0.1 mol C m⁻² yr⁻¹ while the flux of DIC from the metalimnion to the epilimnion (FDIC) is 1.8 ± 0.1 mol C m⁻² yr⁻¹.
The difference between the two, 2 mol C m⁻² yr⁻¹, must be made up by the flux of atmospheric CO₂ into the lake (F). By comparison, the CO₂ flux from the atmosphere into the lake, based on lake and atmosphere pCO₂ measurements, is 0.75 ± 0.09 mol C m⁻² yr⁻¹ (Table 1). Hence, both approaches indicate that the lake is a net CO₂ sink. The difference between the two estimates of lake-atmosphere CO₂ flux may be due in part to the time scales over which these approaches are relevant. We measured lake-atmosphere CO₂ flux over one annual cycle, whereas the vertical mixing rates used to derive vertical fluxes are appropriate for multiyear time scales (Vollmer et al. 2002). We have also not accounted for external C and P loads which, as suggested by the seasonal patterns of pCO₂, Chl a, and seston δ¹³C, may be significant. River chemistry measurements reported by Kingdon et al. (1999) indicate a mean total organic C : P ratio of 179, which is slightly below the mean epilimnetic seston C : P of 200. The influence of river loading on lake-atmosphere CO₂ flux will depend on a number of factors, including the bioavailability of the various C and P forms and the depths to which they sink immediately after entering the lake. If all of the riverine P and organic C are made available to the epilimnion, the difference between the riverine and epilimnetic C : P ratios suggests that river loading would slightly reinforce the autotrophic conditions that appear to be promoted by differential internal recycling of C and P.

Our measured mean lake surface pCO₂ of 385 μatm and CO₂ flux of ~0.75 mol C m⁻² yr⁻¹ differ from earlier estimates for Lake Malawi (pCO₂ = 844 μatm; C flux = 5.3 mol C m⁻² yr⁻¹) made by Alin and Johnson (2007), who concluded that Lake Malawi is a net CO₂ source to the atmosphere. They did not measure pCO₂ directly but calculated it using published pH, alkalinity, and DIC concentrations. Their ability to accurately determine whole-lake mean pCO₂ was likely limited due to limited spatial and temporal coverage of data, and errors that can result from calculating CO₂ based on other variables of the inorganic carbon system (Abril et al. 2015). While we did not observe epilimnetic pCO₂ values as high as those reported by Alin and Johnson (2007) (the maximum we observed was 758 μatm), it is possible that their measurements may have been influenced by episodic, localized mixing events that resulted in high surface pCO₂. Because the data available to Alin and Johnson (2007) did not afford them a temporal analysis like that presented here, their ability to explore mechanisms regulating lake-air CO₂ exchange was also limited.

Global analyses indicate that most small, tropical lakes are CO₂-supersaturated (Marotta et al. 2009; Aufdenkampe et al. 2011), which has been attributed to higher frequency of flooding (Raymond et al. 2013) and high temperature-dependent mineralization rates (Kosten et al. 2010). Warm temperatures may also promote carbon fixation, so there is no obvious reason why temperature alone should promote low photosynthesis : respiration ratios in the euphotic zone. However, in tropical lakes where much of the water column is deeper than the euphotic zone, the warm temperatures can be expected to promote high respiration rates in the aphotic zone, leading to net heterotrophy at the whole ecosystem scale. As Lewis (2010) points out, this trend will be offset to some degree by the depletion of electron acceptors in the deep waters of tropical lakes if they are anoxic. We suggest that, by inhibiting respiration and accelerating P recycling, low redox conditions in the hypolimnion of Lake Malawi more than offset the effects of warm temperature on the photosynthesis : respiration ratio, making the lake a CO₂ sink, unlike temperate lakes of similar size and smaller tropical lakes. This mechanism may also be important in other tropical, meromictic lakes. Like Lake Malawi, Lake Tanganyika is meromictic and has a deep, anoxic hypolimnion. Alin and Johnson (2007) calculated pCO₂ for Lake Tanganyika ranging from 403 to 504 μatm. These values suggest slight supersaturation, but they are lower than the mean pCO₂ that Alin and Johnson (2007) calculated for Lake Malawi (620 μatm), and Alin and Johnson (2007) point out that the small number of measurements used in their calculations likely resulted in a bias toward CO₂ supersaturation. Lake Kivu, another African meromictic lake, appears to be a net source of CO₂, but this is due to large inputs of inorganic C at depth from geothermal springs. Based on a carbon mass balance for the lake, Borges et al. (2014) have determined that the lake would be a net CO₂ sink if not for these deep inputs. They attribute this autotrophy to low river input of organic carbon. However, as in Lake Malawi, deep-water dissolved P concentrations are high (Bootsma and Hecky 1999), and decomposition of organic carbon in the anoxic hypolimnion is slow (Pasche et al. 2012), so internal carbon and nutrient dynamics may also promote autotrophy in this system. Lake Victoria is not meromictic, but its hypolimnion does become anoxic for several months of the year. To our knowledge, no direct measurements of CO₂ concentrations have been published for the lake, but Alin and Johnson (2007) report an estimated pCO₂ of 93 μatm based on measurements of pH and total alkalinity. Likewise, Lake Batur (Indonesia), which has an anoxic hypolimnion (Fukushima et al. 2017), is a net CO₂ sink (Macklin et al. 2018). Hence, there is some evidence that hypolimnetic redox conditions may regulate CO₂ dynamics in tropical lakes. However, the potential for differential C and P recycling to promote autotrophy will depend on a number of factors in addition to an anoxic hypolimnion. In particular, the concentration of iron and sulfide in the hypolimnion will determine whether recycled P is made available to the euphotic zone, or trapped in the hypolimnion due to coprecipitation with iron oxyhydroxides at the oxic-anoxic interface (e.g., McParland et al. 2015).

Measured organic carbon burial rates in Lake Malawi range from 800 to 1000 mmol C m⁻² yr⁻¹ (Otu et al. 2011). These rates are comparable to the whole-lake annual net CO₂ influx measured in our study, suggesting that allochthonous inputs make a relatively small contribution to carbon burial. This is in agreement with the findings of Piksalkn (2004), who observed sedimentation rates in the cool, windy season, when phytoplankton production is greatest, that were several orders of magnitude lower than those in the temperate summer months.
magnitude greater than those in the rainy season. Our results suggest that sedimentary carbon burial would be significantly less if carbon and phosphorus were recycled with similar efficiencies in the water column. At steady state, the rate of P burial in sediments must equal the rate of P loading to the lake, but the rate of C burial will depend on how efficiently P is recycled within the lake. This relationship needs to be considered when using the lake's long sedimentary record to reconstruct paleolimnological and paleoclimatological conditions.

**Conclusion**

The data presented here reveal distinct seasonal changes in pCO2 related to hydrodynamic and meteorological conditions. At a whole-lake scale, the observed temporal patterns of both pCO2 and lake-atmosphere CO2 fluxes are generally in agreement with trends of phytoplankton biomass and photosynthesis, which appear to be regulated by in-lake mixing and river inflow. On an annual basis, Lake Malawi appears to be a net CO2 sink. The CO2 drawdown in tropical Lake Malawi is driven by phytoplankton production during the wet and mixing season, while evasion to the atmosphere is driven by the physical resupply of DIC from deep waters to the epilimnion at the onset of the mixing season and the high respiration to photosynthesis ratios in the hot, stratified season. The observed spatial trends indicate that although the southern region of the lake is the most nutrient-rich and most productive, CO2 emission from this region is high at the beginning of the cool, mixing season, suggesting that the capacity of phytoplankton to assimilate upwelled CO2 may depend in part on the rate at which CO2 and SRP are advected into the euphotic zone. Other regions of the lake, where delivery of DIC- and SRP-enriched water to the epilimnion is more gradual, either by local mixing or horizontal transport from the southern end, are CO2 sinks throughout the year.

Although there is a tendency for oligotrophic lakes to be net heterotrophic, this does not appear to be the case for Lake Malawi. We suggest that net autotrophy in Lake Malawi is due to a higher efficiency of P recycling vs. C recycling in the anoxic hypolimnion, which results in a low DIC : SRP supply ratio to the epilimnion.

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Conflict of Interest

None declared.

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