1
2 **Main Manuscript for**
3 Coupled CH_4 production and oxidation support CO_2 supersaturation in a
4 tropical flood-pulse lake (Tonle Sap Lake, Cambodia)
5

6 Benjamin Lloyd Miller[1,2†], Gordon William Holtgrieve[1], Mauricio Eduardo Arias[3],
7 Sophorn Uy[4,5], and Phen Chheng[6]
8   1. University of Washington, School of Aquatic and Fishery Sciences
9   2. University of Washington, School of Environmental and Forest Sciences
10   3. University of South Florida, Department of Civil and Environmental Engineering
11   4. Cambodian Inland Fisheries Research and Development Institute
12   5. Royal University of Agriculture, Faculty of Fisheries
13   6. Cambodian Fisheries Administration
14

15 [†]Corresponding author
16

17 **Email:** blm8@uw.edu
18

19 **Author Contributions:** BLM, GWH, and MEA initiated the research and designed the
20 study approach. BLM, GWH, MEA, SU, and PC designed the field sampling effort, and
21 BLM, SU, and PC carried out field sampling. BLM conducted lab and data analyses.
22 BLM and GWH wrote the manuscript.
23

24 **Competing Interest Statement:** There are no competing interests.
25

26 **Classification:** Biological Sciences—Ecology, Physical Sciences—Environmental
27 Sciences
28

29 **Keywords:** Carbon dioxide supersaturation, methane oxidation, flood-pulse, lake
30

31 **This PDF File Includes:**
32   Main Text
33   Figures 1 to 3
34   Table 1
35   References
36

Abstract

Carbon dioxide (CO_2) supersaturation in lakes and rivers worldwide is commonly attributed to terrestrial-aquatic transfers of organic and inorganic carbon (C) and subsequent, *in-situ* aerobic respiration. Methane (CH_4) production and oxidation also contribute CO_2 to freshwaters, yet this remains largely unquantified. Flood-pulse lakes and rivers in the tropics are hypothesized to receive large inputs of dissolved CO_2 and CH_4 from floodplains characterized by hypoxia and reducing conditions. We measured stable C isotopes of CO_2 and CH_4, aerobic respiration, and CH_4 production and oxidation during two flood stages in Tonle Sap Lake (Cambodia) to determine whether dissolved CO_2 in this tropical flood-pulse ecosystem has a methanogenic origin. Mean CO_2 supersaturation of $11,000 \pm 9,000$ µatm could not be explained by aerobic respiration alone. ^{13}C depletion of dissolved CO_2 relative to other sources of organic and inorganic C, together with corresponding ^{13}C enrichment of CH_4, suggested extensive CH_4 oxidation. A stable isotope mixing model shows that the oxidation of ^{13}C depleted CH_4 to CO_2 contributes between 47% and 67% of dissolved CO_2 in Tonle Sap Lake. ^{13}C depletion of dissolved CO_2 was correlated to independently measured rates of CH_4 production and oxidation within the water column and underlying lake sediments. However, mass balance indicates that most of this CH_4 production and oxidation occurs elsewhere, within inundated soils and other floodplain habitats. Seasonal inundation of floodplains is a common feature of tropical freshwaters, where high reported CO_2 supersaturation and atmospheric emissions may be explained in part by coupled CH_4 production and oxidation.

Significance Statement

Freshwaters inextricably link flows of carbon between the land, oceans, and atmosphere. Resulting carbon dioxide supersaturation relative to the atmosphere in most of the world's lakes and rivers has long been assumed to come from aerobic respiration. Although carbon dioxide also comes from the oxidation of anaerobically produced methane, this has been largely ignored within freshwaters. Here, we use stable isotopes of carbon dioxide and methane to show that a nontrivial proportion of the total dissolved carbon dioxide in a tropical flood-pulse lake comes from methane oxidation. Seasonal pulses of flooding are common in the tropics, suggesting that coupled methane production and oxidation likely contribute more broadly to flows of carbon between the land, understudied tropical freshwaters, and atmosphere.

Main Text

Introduction

Globally, most lakes and rivers are supersaturated with dissolved carbon dioxide (CO_2) relative to the atmosphere, highlighting their outsized role in transferring and transforming terrestrial carbon (C) (1,2,3). Terrestrial-aquatic transfers of C can include CO_2 dissolved in terrestrial ground- and surface waters (3,4,5,6), dissolved inorganic carbon (DIC) from carbonate weathering (7,8), or organic C from various sources that is subsequently respired in lakes and rivers (9,10). Initially, oceanic export was thought to be the only fate for terrestrial-aquatic transfers of C, but a growing body of research on sediment burial of organic C and CO_2 emissions from freshwaters prompted the "active pipe" revision to this initial set of assumptions (11). Although freshwaters are now recognized as focal points for transferring and transforming C on the landscape, most of this research has been conducted within temperate freshwaters (2,11,12). Few studies focus on the mechanisms of CO_2 supersaturation in tropical lakes and rivers, with most conducted in just one watershed, the Amazon (4,13,14,15).

CO_2 supersaturation within tropical freshwaters is likely influenced by their unique flood-pulse hydrology. The canonical Flood-pulse Concept (FPC) hypothesizes that annual flooding of riparian land will lead to organic C mobilization and respiration (16). Partial pressures of CO_2 (pCO_2) have been measured in excess of 44,000 μatm in the Amazon River (13), 16,000 μatm in the Congo River (18), and 12,000 μatm in the Lukulu River (18). Richey et al. (13), Borges et al. (17), and Zuidgeest et al. (18) have each shown that that riverine pCO_2 scales with the amount of land flooded in these watersheds. Yet, it was only recently that Abril and Borges (19) proposed the importance of flooded land to the "active pipe." These authors differentiate uplands that unidirectionally drain water downhill (via ground- and surface water) from floodplains that bidirectionally exchange water with lakes and rivers (19). They conceptualize how floodplains combine high hydrologic connectivity, high rates of primary production, and high rates of respiration to transfer relatively large amounts of C to tropical freshwaters (19).

Methanogenesis inevitably results on floodplains after dissolved oxygen (O_2) and other electron acceptors for anaerobic respiration such as iron and sulfate are consumed (16,19). Horizontal gradients in dissolved O_2 and reducing conditions have been observed extending from the center of lakes and rivers through their floodplains in the Mekong (20,21), Congo (22), Pantanal (23), and Amazon watersheds (4). CH_4 production and oxidation occur along such redox gradients (4,16,19,23). CH_4 is produced by acetate fermentation (eq. 1) and carbonate reduction (eq. 2) within freshwaters (24,25). CH_4 production coupled with aerobic oxidation results in CO_2 (eq. 3; 25), yet no studies have quantified the relative contribution of coupled CH_4 production and oxidation to CO_2 supersaturation within tropical freshwaters.

$$CH_3COOH \rightarrow CO_2 + CH_4 \tag{1}$$

$$CO_2 + 8H^+ + 8e^- \rightarrow CH_4 + 2H_2O \tag{2}$$

122
123    $CH_4 + 2O_2 \rightarrow CO_2 + 2H_2O$ (3)
124
125   The relative contribution of coupled CH_4 production and oxidation to CO_2
126   supersaturation within tropical freshwaters can be traced with stable C isotopes of CO_2
127   and CH_4. Methanogenesis results in CH_4 that is depleted in ^{13}C ($\delta^{13}C$=-65 to -50‰ from
128   acetate fermentation, -110‰ to -60‰ from carbonate reduction) compared to other
129   potential sources of organic and inorganic C ($\delta^{13}C$=-37 to -7.7‰; see Methods)
130   (24,25,26). The oxidation of this ^{13}C depleted CH_4 results in ^{13}C depleted CO_2
131   (24,25,26). At the same time, CH_4 oxidation enriches the $^{13}C/^{12}C$ of residual CH_4 as
132   bacteria and archaea preferentially oxidize ^{12}C-CH_4 (25). This means that the $^{13}C/^{12}C$ of
133   CO_2 and CH_4 can serve as powerful tools to determine the source of CO_2 supersaturation
134   within freshwaters.
135
136   Tonle Sap Lake (TSL) is Southeast Asia's largest lake and an understudied flood-pulse
137   ecosystem that supports a regionally important fishery (21,22,27). Each May through
138   October, monsoonal rains and Himalayan snowmelt increase discharge in the Lower
139   Mekong and cause one of its tributaries, the Tonle Sap River, to reverse course from
140   southeast to northwest (21). During this course reversal, the Tonle Sap River floods TSL.
141   The TSL flood-pulse increases lake volume from 1.6 km^3 to 60 km^3 and inundates 12,000
142   km^2 of floodplain for 3-6 months per year (21,27). Holtgrieve et al. (22) have shown that
143   aerobic respiration is consistently greater than primary production in TSL (i.e., net
144   heterotrophy), with the expectation of consistent CO_2 supersaturation. But, the partial
145   pressures, C isotopic compositions, and ultimately the source of dissolved CO_2 in TSL
146   remain unquantified.
147
148   To quantify CO_2 supersaturation and its origins in TSL, we measured the partial pressures
149   of CO_2 and CH_4 and compared their C isotopic composition to other potential sources of
150   organic and inorganic C. We carried out these measurements in distinct lake
151   environments during the high-water and falling-water stages of the flood-pulse,
152   hypothesizing that CH_4 production and oxidation on the TSL floodplain would support
153   CO_2 supersaturation during the high-water stage. We found that coupled CH_4 production
154   and oxidation account for a nontrivial proportion of the total dissolved CO_2 in all TSL
155   environments and during both flood stages, showing that anaerobic degradation of
156   organic C at aquatic-terrestrial transitions can support CO_2 supersaturation within tropical
157   freshwaters.
158
159   **Results**
160
161   pCO_2 and pCH_4 in TSL were consistently supersaturated relative to atmospheric
162   equilibrium. pCO_2 averaged 13,000 ± 6,000 µatm (mean ± 1 SD) across sites during the
163   high-water stage and 13,000 ± 12,000 µatm during the falling-water stage (Table 1).
164   pCH_4 was significantly greater during the high-water stage (11,000 ± 2,000 µatm) than
165   during the falling-water stage (600 ± 300 µatm) (p<0.001, d=1.8). By contrast, pCO_2 and
166   pCH_4 at sea level are approximately 400 µatm and 1.8 µatm, respectively.
167

168   CO_2 supersaturation exceeded dissolved O_2 deficits, indicating sources of dissolved CO_2

169   other than aerobic respiration (Figures 1a and 1b). CO_2 supersaturation is expected to

170   vary with dissolved O_2 deficits in a -1/1 O_2:CO_2 ratio as one µmol of dissolved O_2 is

171   consumed for each µmol of dissolved CO_2 produced. Instead, ratios of -0.1/1 were

172   observed during both the high-water and falling-water stages. During the high-water

173   stage, the greatest CO_2 supersaturation occurred under the most hypoxic conditions

174   (Figure 1a).

175

176   The intercept of the relationship between 1/CO_2 and $\delta^{13}C$-CO_2 can be used to determine

177   the source of dissolved CO_2 (Keeling Intercepts, Table S1) (28,29). In TSL, the inverse

178   of $p$$CO_2$ was strongly correlated with ^{13}C depletion of CO_2. The intercept of $\delta^{13}C$-CO_2

179   was as low as -51‰ during the high-water stage and -43‰ during the falling-water stage.

180   This indicates a ^{13}C depleted source of dissolved CO_2 relative to the other sources of

181   organic and inorganic C measured, which ranged from -37‰ to -7.7‰ (Figure 2a).

182   Observed ^{13}C depletion of dissolved CO_2 coincided with ^{13}C enrichment of dissolved

183   CH_4 (Table 1, Figures 3a and 3b). Acetate fermentation produces $\delta^{13}C$-CH_4 ranging

184   from -65‰ to -50‰ and carbonate reduction produces $\delta^{13}C$-CH_4 ranging from -110‰ to

185   -60‰ (24,25,26). By contrast, $\delta^{13}C$-CH_4 averaged -36 ± 2‰ during the high-water

186   stage. During this flood stage, dissolved CO_2 became more ^{13}C depleted and dissolved

187   CH_4 became more ^{13}C enriched from open-water environments ($\delta^{13}C$-CO_2=-37 ± 4‰,

188    $\delta^{13}C$-CH_4=-45 ± 9‰) to edge environments ($\delta^{13}C$-CO_2=-39 ± 6‰, $\delta^{13}C$-CH_4=-38 ± 6‰)

189   to floodplain environments ($\delta^{13}C$-CO_2=-41 ± 7‰, $\delta^{13}C$-CH_4=-34 ±2‰). Net

190   fractionation between $\delta^{13}C$-CO_2 and $\delta^{13}C$-CH_4 (simply, $\delta^{13}C$-CO_2 – $\delta^{13}C$-CH_4) of

191   typically <10‰ in TSL indicates substantial CH_4 oxidation (25) (Figures 3a, 3b).

192

193   A two-source isotope mixing model for $\delta^{13}C$-CO_2 was used to estimate fractional

194   contributions to dissolved CO_2 by CH_4 oxidation compared with other potential sources

195   of organic and inorganic C (Figure 2a). Assuming oxidation of CH_4 produced by acetate

196   fermentation only, the fractional contributions by CH_4 oxidation to dissolved CO_2 range

197   from 63% to 85% across the distinct lake environments and flood stages of TSL (Table

198   S3). Assuming oxidation of CH_4 produced by both acetate fermentation and carbonate

199   reduction, these contributions by CH_4 oxidation fall to a more conservative 47% to 67%.

200   Apparent fractionation between $\delta^{13}C$-CO_2 and $\delta^{13}C$-CH_4 (simply, $\delta^{13}C$-CO_2/$\delta^{13}C$-CH_4)

201   of typically <1.055 in TSL indicate substantial CH_4 production by acetate fermentation

202   with some carbonate reduction (24,25) (Figure 2b).

203

204    $\delta^{13}C$-CO_2 was strongly correlated to independent measurements of net CH_4 oxidation in

205   the water column during the high-water stage (Figures 3c and 3d). The same significant

206   relationship was observed between $\delta^{13}C$-CO_2 and gross CH_4 production within the

207   sediments (Figures 3e and 3f). Despite these relationships, CO_2 mass balance indicates

208   that CH_4 production and oxidation within the water column and underlying sediments

209   contribute at most 9% to dissolved CO_2 in TSL (Table S4).   Of these two processes, CH_4

210   production contributes 1-2 orders of magnitude more CO_2 than CH_4 oxidation. Other

211   processing of C within the water column and underlying sediments, such as aerobic

212   respiration, also contribute a relatively small share of total dissolved CO_2 (13 ± 8%).

213

Discussion

Contributions of CH_4 production and oxidation to CO_2 supersaturation are understudied within tropical freshwaters, where extensive flooding, dissolved O_2 deficits, and reducing conditions at aquatic-terrestrial transitions make such contributions likely. The subtropics and tropics are home to many high order flood-pulse rivers, such as the Amazon, Orinoco, Congo, Zambezi, and Mekong, which are collectively responsible for over 30% of global mean annual discharge [30]. Along this tropical "active pipe" lays 52% of the world's floodplains, transferring and transforming C at relatively high rates [20,31]. Using a combination of isotopic tracers and mass balance, we show that a substantial fraction this transfer and transformation of C occurs through coupled CH_4 production and oxidation in TSL.

A majority of our measured $\delta^{13}C$-CO_2 fell between the ^{13}C depleted CO_2 known to result from CH_4 oxidation, and the relatively more ^{13}C enriched phytoplankton, periphyton, macrophytes, and terrestrial C3 vegetation measured in TSL (Figure 2a). Because there is little fractionation during aerobic respiration of organic C, measured $\delta^{13}C$-CO_2 in lakes can be expected to fall inside the range of $\delta^{13}C$ observed for commonly considered sources of organic and inorganic C [31,32]. Instead, our observed $\delta^{13}C$-CO_2 fell outside of this range. Potential sources of organic and inorganic C in TSL ranged from $\delta^{13}C$=-37‰ for macrophytes to $\delta^{13}C$=-7.7‰ for atmospheric CO_2 in equilibrium with water. De Kluiver and others [33,34] have reported relatively ^{13}C depleted phytoplankton ($\delta^{13}C$=-41‰, Table S2). However, the net heterotrophy and CO_2 supersaturation consistently observed in TSL and other lakes [34] makes substantial contributions to dissolved CO_2 from aquatic primary producers such as phytoplankton unlikely, because these ecosystems are inferred to receive greater inputs of terrestrial organic C than aquatic organic C. Accordingly, the $\delta^{13}C$ of dissolved CO_2 measured by De Kluiver et al. [34] ranges from -21‰ to -9‰, suggesting that the aerobic respiration of relatively ^{13}C depleted phytoplankton in net heterotrophic lakes does not substantially impact $\delta^{13}C$-CO_2. Furthermore, our most ^{13}C depleted dissolved CO_2 was sampled on the TSL floodplain, where the water column and underlying sediments are largely shaded by macrophytes and other emergent vegetation, limiting phytoplankton production [20]. Ultimately, methanogenesis is the only possible source of the ^{13}C depleted dissolved CO_2 observed in TSL. We can therefore use a two-source stable isotope mixing model to estimate relative contributions to dissolved CO_2 by 1) potential sources of organic and inorganic C and 2) CH_4 oxidation. This mixing model shows that CH_4 oxidation contribute between 47% and 67% of dissolved C-CO_2 across the distinct lake environments and flood stages of TSL, which is unprecedented in the aquatic C cycling literature.

High CO_2 supersaturation and an imbalance with dissolved O_2 such as we observed in TSL (Figures 1a and 1b) have previously been attributed to autotrophic and heterotrophic respiration of macrophytes and other, emergent aquatic vegetation on flooded land [15,16,18,35]. Macrophytes and other emergent aquatic vegetation fix primarily atmospheric CO_2, acting more as terrestrial primary producers than aquatic primary producers. Melack and Engle [35] have shown that floating macrophytes dominate

6

260 primary production and provide the bulk of organic C to an Amazon floodplain lake.
261 Abril et al. (15) have further suggested that floodplain and riparian wetland vegetation in
262 the Amazon could export fully half of its primary production on an annual basis. Data
263 from TSL supports a more nuanced interpretation. The most ^{13}C depleted source of
264 organic C in TSL was an individual macrophyte (δ^{13}C=-37‰, mean δ^{13}C=-33 ± 4‰).
265 Even so, 70% of our dissolved CO_2 measurements were depleted in ^{13}C below -37‰. As
266 confirmed by our stable isotope mixing model, this means that aerobic respiration of
267 macrophytes can contribute to but not explain the C isotopic depletion of dissolved CO_2
268 observed in TSL.
269
270 Corresponding ^{13}C enrichment of dissolved CH_4 indicated a fractionating loss process,
271 further supporting the interpretation that CH_4 oxidation supports CO_2 supersaturation in
272 TSL. Acetate fermentation within tropical lake sediments from the Amazon and Pantanal
273 has been shown to produce δ^{13}C-CH_4 values ranging from -86‰ to -61‰ (36,37). The
274 same studies showed concurrent carbonate reduction producing CH_4 even more depleted
275 in ^{13}C (36,37). By contrast, we measured an overall mean δ^{13}C-CH_4 of -43 ± 9‰ in TSL,
276 with some values as high as -11‰ (Table 1, Figures 3a, 3b). Similar values were
277 measured by Barbosa et al. (38) on Amazon River floodplains (δ^{13}C-CH_4=-70.1‰ to -
278 14.8‰). Independently measured rates of CH_4 production and oxidation in TSL support
279 this conclusion. Both net CH_4 oxidation in the water column of TSL (Figures 3b, 3c) and
280 gross CH_4 production within the sediments (Figures 3d and 3e) were strongly correlated
281 to δ^{13}C-CO_2.
282
283 Despite these relationships, CH_4 production and oxidation and aerobic respiration within
284 the water column and underlying sediments typically contribute less than 15% of
285 dissolved CO_2 in TSL (Table S4). In our mass balance, we solve for CO_2 advected from
286 elsewhere, within inundated soils and other floodplain habitats, and infer that this is a far
287 greater contributor to CO_2 supersaturation. This was initially hypothesized by Junk et al.
288 (17) and later combined with the "active pipe" by Abril and Borges (20). Yet, it has been
289 empirically tested using dissolved CO_2 and CH_4 in only two other locations (15,18), and
290 never with the C isotopic composition of these dissolved gases.
291
292 The ^{13}C depletion of CO_2, ^{13}C enrichment of CH_4, and their correlations to independently
293 measured rates of CH_4 production and oxidation suggest that these coupled processes
294 support CO_2 supersaturation in TSL. By extension, coupled CH_4 production and
295 oxidation are disproportionately responsible for CO_2 emissions from TSL. Lauerwald et
296 al. (13) estimate that >50% of global riverine CO_2 emissions occur in the tropics,
297 emphasizing the importance of tropical "active pipes." Data on the stable C isotopes of
298 both CO_2 and CH_4 are rarely reported for freshwaters, though ^{13}C enriched dissolved CH_4
299 (>-50‰) reported in tropical and temperate lakes, wetlands, peatlands, and the Amazon
300 River implies widespread oxidation of CH_4 to CO_2 (Table S5). Coupled CH_4 production
301 and oxidation have thus been understudied, but may support CO_2 supersaturation and
302 CO_2 emissions from other tropical freshwaters with large amounts of seasonally or
303 perennially flooded land. The extent of this flooding will most likely change under the
304 twin stressors of hydropower development and climate change in the tropics (21),

305   impacting the future role of floodplains in the transfer and transformation of C from
306   terrestrial to aquatic ecosystems.
307
308   **Materials and Methods**
309
310   *Field Sampling*
311
312   Field sampling was conducted during the high-water and falling-water stages of the
313   annual flood-pulse in October 2015 and March 2016, respectively, representing the
314   typical hydrological range in TSL. Flood stages were assessed using historical data from
315   a gauging station at Kampong Luong (See SI, Figure S1) (21). Sampling focused on
316   three locations in the southwest (Kampong Preah), central (Anlang Reang), and
317   northwest (Prek Konteil) basins of TSL. Transects designed to capture horizontal
318   gradients in dissolved O_2 and reducing conditions were established at each location.
319   These transects consisted of six points extending through the distinct open-water
320   (Transect Point 1), edge (Transect Point 2) and floodplain environments of TSL (Transect
321   Points 4-6).   The edge environments were characterized by a transition from open-water
322   environments to emergent, permanently rooted floodplain vegetation.
323
324   *Partial Pressures of CO_2 and CH_4*
325
326   Partial pressures of CO_2 and CH_4 at each transect point and flood stage in TSL were
327   quantified as the average of three duplicates collected at 0.1 m below the water surface
328   and at 0.5 m above the lake bottom where water depth exceeded 0.5 m (n=143 duplicates,
329   n=47 replicates). Water was collected into 74 mL gas-tight serum bottles using a van
330   Dorn sampler, preserved in the field with 74 μL of 50% mass/volume zinc chloride
331   solution, and placed on ice for transport to the Royal University of Phnom Penh, where
332   they were stored at 4 °C until analysis. For analysis, samples were displaced with helium
333   to roughly equal parts headspace and water, left to equilibrate for 12 h, and analyzed for
334   headspace pCO_2 and pCH_4 using gas chromatography (SRI 8610*c* GC) by referencing to
335   certified standards of known concentrations.
336
337   *Stable C Isotopes of CO_2 and CH_4*
338
339   Following analysis for partial pressures, samples were re-sealed with Apiezon grease,
340   inverted, placed on ice, and transported to the University of Washington for C isotopic
341   analysis (n=47). A 20 mL headspace sample was analyzed for the $^{13}C/^{12}C$ of CO_2 and
342   CH_4 simultaneously using a cavity ring-down spectrometer (Picarro G2201*i*) with a small
343   sample introduction module (Picarro A0314 SSIM). Following Malowany et al. (39), a
344   column of reduced copper shavings was installed on the small sample introduction
345   module to eliminate interference by hydrogen sulfide with isotopic measurements.
346   Samples exceeding 300 μatm CH_4 were diluted with ultra-high purity nitrogen to further
347   eliminate interference by high concentrations of this gas with isotopic measurements.
348   Stable C isotopes of CO_2 and CH_4 are each expressed in delta (δ) notation relative to
349   Vienna Pee Dee Belemnite by referencing to certified CO_2 and CH_4 standards of known
350   concentrations and $^{13}C/^{12}C$.

Stable C Isotopes of Organic and Inorganic C

Grab samples of floating macrophytes (*Eichhornia sp.*), terrestrial C3 vegetation, periphyton, and phytoplankton were collected across the distinct lake environments and flood stages of TSL, combined, and considered a single, lake-wide sample with a minimum of four replicates. Phytoplankton were collected using a Wisconsin net sampler (Wildco 40-A50), and periphyton was scraped from the benthos and the surfaces of floating macrophytes and emergent aquatic vegetation. Macrophytes ($\delta^{13}C$=-33 ± 4‰, n=4), terrestrial C3 vegetation ($\delta^{13}C$ =-29 ± 2‰, n=7), periphyton ($\delta^{13}C$=-28 ± 4‰, n=18), and phytoplankton ($\delta^{13}C$=-24 ± 4‰, n=6) in TSL were freeze dried, ground, and analyzed for bulk $^{13}C/^{12}C$ using an elemental analyzer (CE Instruments 2500 NA) interfaced with an Isotope Ratio Mass Spectrometer (DeltaV IRMS). Laboratory working standards were glutamic acid 1 ($\delta^{13}C$=-28.3‰ vs. VPDB), glutamic acid 2 ($\delta^{13}C$=-13.7‰), and sockeye salmon ($\delta^{13}C$=-21.3‰). DIC ($\delta^{13}C$=-13.8 ± 0.4‰, n=98) samples from another sampling effort across the same lake environments and flood stages were acidified, displaced with a helium headspace, analyzed on a DeltaV IRMS, and considered a lake-wide sample as described previously.

Depth-integrated Gross Primary Production & Aerobic Respiration

Gross primary production (GPP) and aerobic respiration were modeled across the distinct lake environments and flood stages of TSL using diel dissolved O_2 data in the "LakeMetabolizer" R package (n=16) (40,41). Model inputs include hourly dissolved oxygen (mmol L^{-1}), hourly water temperature (°C), and hourly photon flux for photosynthetically active radiation (PAR; $\mu E\ s^{-1}\ m^{-2}$). Continuously logging dissolved O_2 and water temperature sensors were deployed for a minimum of 20 h (Precision Measurement Engineering miniDO$_2$T Logger, accuracy + / - 0.16 mg $O_2\ L^{-1}$ and + / - 0.1 °C). Accuracy of dissolved O_2 sensors was verified prior to field deployment using the Winkler titration method. PAR was not measured directly, but calculated from full-spectrum irradiance based on latitude, longitude, aspect, slope, and transmissivity data and the "astrocalc4r" function in the "fishmethods" R package (42). GPP and aerobic respiration were converted to mmol $CO_2\ m^{-3}\ d^{-1}$ using an assimilation efficiency of 1.2 for photosynthesis (43,44) and a conversion efficiency of 1.0 for respiration.

Volumetric rates were multiplied by mixing depths to obtain areal rates in terms of mmol $CO_2\ m^{-2}\ d^{-1}$. Mixing depths were evaluated with dissolved O_2 profiles at each site using a multi-parameter sonde calibrated just prior to deployment with water-saturated air (YSI 6920). Dissolved O_2 data were plotted over depth (m), smoothed using a loess spanning function of 0.2, and interrogated for inflection points in R (41). The depth of these inflection points at each transect was considered the mixing depth.

Depth-integrated CH$_4$ Production & Oxidation

Gross CH$_4$ production within lake sediments was quantified as the average of three, duplicate sediment incubations. At each transect point and flood stage in TSL, sediment

397   cores were taken with a stainless-steel corer. The upper 1 cm^3 of each core was sealed
398   inside a 74 mL gas-tight serum bottle (*n*=72 duplicates, *n*=24 replicates). The remaining
399   volume of the bottle was filled with bottom water collected 0.5 m above the sediments.
400   Three additional bottles were filled with bottom water, only, and three with water
401   collected 0.1 m below the water surface. All bottles were incubated at ambient air
402   temperatures (25-33 4 °C), which were typically <4 °C different from water temperatures
403   in TSL, and sampled daily from a helium headspace for seven days. pCH_4 was analyzed
404   as described previously and corrected for progressively decreasing headspace:water
405   ratios. Net CH_4 oxidation in surface waters was multiplied by mixing depths to obtain
406   areal rates as above. Net oxidation in bottom waters was added to net CH_4 production
407   measured in the bottles containing a combination of sediment cores and bottom water and
408   considered gross CH_4 production. Following incubation, each sediment core was dried at
409   100 °C for three hours and weighed. Gross CH_4 production rates were then corrected for
410   sediment core weight and scaled to nmol CH_4 m^{-3} d^{-1}. Previously published studies of
411   CH_4 production in lake sediment cores show that rates measured at the sediment-water
412   interface are consistent to a sediment depth of 0.1 m (25,45). Volumetric rates of CH_4
413   production were thus multiplied by 0.1 m to obtain areal rates in terms of nmol CH_4 m^{-2}
414   d^{-1}. Because one mol of CO_2 is produced for each mol of CH_4 produced during acetate
415   fermentation, presumed to be dominant in TSL (Figure 2b) and within freshwaters more
416   broadly (24,25), rates were also considered in terms of nmol CO_2 m^{-2} d^{-1}. Each transect
417   sampled included negative control incubations amended with a 74 µL of 50%
418   mass/volume zinc chloride solution.
419
420   *Mass Balance*
421
422   A mass balance for dissolved CO_2 in TSL was created from processes resulting in a gain
423   or loss of CO_2:
424
425    $$CO_{2,Measured} = CO_{2,Advected} + CO_{2,Respiration} - CO_{2,GPP} + CO_{2,MProd} + CO_{2,MOx}$$
426
427   where $CO_{2,Respiration}$ is the CO_2 gained from modeled aerobic respiration (mmol m^{-2} d^{-1}),
428    $CO_{2,GPP}$ is the CO_2 lost from modeled GPP (mmol m^{-2} d^{-1}), $CO_{2,MProd}$ is the CO_2 gained
429   from measured gross CH_4 production within sediments (mmol m^{-2} d^{-1}), and $CO_{2,MOx}$ is
430   the CO_2 gained from measured net CH_4 oxidation in the water column (mmol m^{-2} d^{-1}).
431    $CO_{2,Measured}$ is the pCO_2 measured within the water column of TSL and multiplied by a
432   temperature dependent Henry's constant and mixing depth to yield dissolved CO_2 in
433   mmol m^{-2} on the day of sampling. Diffusion of CO_2 from TSL to the atmosphere was
434   modeled using $CO_{2,Measured}$ following Cole and Caraco (46). CO_2 diffusion reflects an
435   atmospheric loss subsequent to $CO_{2,Measured}$ and was ultimately excluded from the mass
436   balance. $CO_{2,Advected}$ is the remaining CO_2 in the mass balance assumed to result from
437   aerobic respiration and anaerobic degradation of organic C elsewhere, within inundated
438   soils and other floodplain habitats under steady state conditions (mmol m^{-3} d^{-1}). Mean
439   daily $CO_{2,Advected}$ ± 1 SE was quantified using normal distributions—based on sample
440   size, mean, and standard deviation—of other terms in the mass balance over 10,000
441   Monte Carlo simulations in R (41).
442

443 *Stable Isotope Mixing Model*
444
445 The C isotopic composition of CO_2 measured in TSL fell between the $^{13}C/^{12}C$ produced
446 by 1) the oxidation of ^{13}C depleted CH_4 to CO_2 (-110‰ to -50‰) and 2) that of other
447 potential organic and inorganic sources of CO_2 (-37‰ to -7.7‰). Here, the sole concern
448 is the fraction of CO_2 derived from CH_4 oxidation. Thus, a two-source ("Methane"
449 versus "Other") stable isotope mixing model was deemed appropriate. The model also
450 accounted for CO_2 losses from primary production and atmospheric diffusion, and took
451 the form:
452
453 $\delta^{13}CO_2 = \left(\delta^{13}C_{Methane} \cdot f_{Methane}\right) + \left(\delta^{13}C_{Other} \cdot f_{Other}\right)$
454 $\qquad - \left(\left(\delta^{13}CO_{2,Measured} + \varepsilon_{GPP}\right) \cdot f_{GPP}\right)$
455 $\qquad - \left(\left(\delta^{13}CO_{2,Measured} + \varepsilon_{Diffusion}\right) \cdot f_{Diffusion}\right)$
456
457 where $\Sigma f_i = 1.00$. $\delta^{13}C_{Methane}$ was modeled as a continuous uniform distribution of $\delta^{13}C$-
458 CH_4 values produced by methanogenesis, ranging from -110‰ to -50‰ (Figure 2a)
459 (24,25,26). $f_{Methane}$ is the fraction of CO_2 resulting from CH_4 oxidation. Because
460 $\delta^{13}C_{Methane}$ encompasses the range of $\delta^{13}C$ values produced by both acetate
461 fermentation (-65‰ to -50‰)—presumed to be dominant in TSL and within freshwaters
462 more broadly (24,25)—and carbonate reduction (-110‰ to -60‰), the model results in a
463 conservative estimate of $f_{Methane}$ for this freshwater lake (Figure 2b).
464
465 $\delta^{13}C_{Other}$ was also modeled as a continuous uniform distribution of $\delta^{13}C$ values
466 encompassing other potential sources of organic and inorganic C (See SI, Figure S2).
467 This distribution ranges from the most ^{13}C depleted source of organic C measured in
468 TSL, macrophytes ($\delta^{13}C$=-37‰), to the most ^{13}C enriched source of inorganic C,
469 atmospheric CO_2 in equilibrium with water ($\delta^{13}C$ =-7.7‰) (47). $\delta^{13}C_{Other}$ therefore
470 encompasses the $\delta^{13}C$ of terrestrial C3 vegetation, periphyton, phytoplankton, and DIC
471 measured in TSL and the $\delta^{13}C$ of emergent aquatic C4 grasses ($\delta^{13}C$=-12.2 ± 0.3‰)
472 measured by Hedges et al. (48) in the Amazon. With multiple sources of organic and
473 inorganic C that overlap in $\delta^{13}C$ and no prior information on the relative importance of
474 each, the most parsimonious option was to treat them as a group with equal probability
475 across the full range of $\delta^{13}C$ values. However, multiple alternative models were also
476 tested (See SI, Table S3).
477
478 $\delta^{13}C_{CO_{2,Measured}}$ and mass-dependent fractionations for photosynthesis (f_{GPP}) and
479 diffusion to the atmosphere ($f_{Diffusion}$) in the model were quantified by this study and its
480 mass balance (See SI, Table S4). The kinetic fractionation factors for photosynthesis and
481 diffusion, ε_{GPP} and $\varepsilon_{Diffusion}$, are -19‰ and -1.1‰, respectively (47). Following the
482 IsoSource mixing model by Phillips et al. (49), $f_{Methane}$ and f_{Other} were assigned possible
483 values between 0.00 and 1.00 by 0.05 and $\delta^{13}CO_2$ was solved for iteratively in R (41). If
484 the resulting $\delta^{13}CO_2 = \delta^{13}CO_{2,Measured} \pm 1‰$ and $f_{Other} > 0.15$ (allowing a minimum
485 f_{Other} of 20%), then $f_{Methane}$ was saved. Sensitivities of the continuous uniform
486 distributions generated by the model were quantified over 10,000 Monte Carlo

487 simulations in R (41). The mean of all saved $f_{Methane}$ values was then reported as the
488 fraction of CO_2 resulting from CH_4 production and oxidation. Variance around these
489 saved $f_{Methane}$ values is based on different continuous uniform distributions generated at
490 random by the mixing model and was ultimately not reported.
491
492 *Statistical Analyses*
493
494 Normality in the data was assessed using quantile-quantile plots and Shapiro-Wilk tests.
495 Homogeneity of variance in the data was assessed using Levene's tests. pCH$_4$ and δ^{13}C-
496 CO_2 followed non-normal distributions and were log-transformed for parametric
497 comparisons along with pCO$_2$ and δ^{13}C-CH$_4$ across the distinct lake environments and
498 flood stages of TSL using ANOVA. Multiple pairwise-comparisons between means in
499 the open-water, edge, and floodplain environments during the high-water and falling-
500 water stages were carried out subsequently using Tukey Honest Significant Differences.
501 Our Bonferroni-corrected critical alpha-value for multiple pairwise comparisons was
502 0.025 (for linear regression, our critical alpha-value remained 0.050). To assess whether
503 differences between means were independent of sample size, we also calculated effect
504 sizes using Cohen's d, where d=0.2-0.4 corresponds to a small effect and low support for
505 differences between means, d=0.5-0.7 corresponds to a medium effect, and d>0.9
506 corresponds to a large effect and high support for differences (50). All statistical
507 analyses were conducted using R (41).
508
509 **Acknowledgements**
510

522
523 **References**
524

525 1. J.J. Cole, N.F. Caraco, G.W. Kling, T.K. Kratz, Carbon dioxide supersaturation in
526   the surface waters of lakes. Science, 265(5178), 1568-1570 (1994).
527   doi:10.1126/science.265.5178.1568
528 2. P.A. Raymond, J. Hartmann, R. Lauerwald, S. Sobek, C. McDonald, M. Hoover,
529   D. Butman, R. Striegl, E. Mayorga, C. Humborg, P. Kortelainen, H. Duerr, M.
530   Meybeck, P. Ciais, P. Guth, Global carbon dioxide emissions from inland waters.
531   Nature, 503, 355-359 (2013). doi:10.1038/nature12760
532 3. G.W. Kling, G.W. Kipphut, M.C. Miller, Arctic lakes and rivers as gas conduits

533   to the atmosphere—Implications for tundra carbon budgets. Science, 251, 298-
534   301 (1991). doi:10.1126/science.251.4991.298

535   4. J.E. Richey, A.H. Devol, S.C. Wofsy, R. Victoria, M.N.G. Riverio, Biogenic
536   gases and the oxidation and reduction of carbon in Amazon River and floodplain
537   waters. Limnol. Oceanogr., 33(4), 551-561 (1988). doi:10.4319/lo.1988.33.4.0551

538   5. J.B. Jones, P.J. Mulholland, Carbon dioxide variation in a hardwood forest
539   stream—An integrative measure of whole catchment soil respiration. Ecosystems,
540   1, 183-196 (1998). doi:10.1007/s100219900014

541   6. P.A. Raymond, J.E. Saiers, W.V. Sobczak, Hydrological and biogeochemical
542   controls on watershed dissolved organic matter transport—Pulse-shunt concept.
543   Ecology, 97(1), 5-16 (2016). doi:10.1890/14-1684.1

544   7. P. Lopez, R. Marce, J. Armengol, Net heterotrophy and CO_2 evasion from a
545   productive calcareous reservoir—Adding complexity to the metabolism-CO_2
546   evasion issue. J. Geophys. Res., 116, G02021 (2011). doi:10.1029/2010JG001614

547   8. R. Marce, B. Obrador, J.A. Morgui, J.L. Riera, P. Lopez, J. Armengol, Carbonate
548   weathering as a driver of CO_2 supersaturation in lakes. Nat. Geosci., 8, 107-111
549   (2015). doi:10.1038/NGEO2341

550   9. P.A. Del Giorgio, J.J. Cole, N.F. Caraco, R.H. Peters, Linking planktonic biomass
551   and metbolism to net gas fluxes in northern temperate lakes. Ecology, 80(4),
552   1422-1431 (1999). doi:10.1890/0012-9658(1999)080[1422:LPBAMT]2.0.CO;2

553   10. J.J. Cole, N.F. Caracao, Carbon in catchments—Connecting terrestrial carbon
554   losses with aquatic metabolism. Mar. Freshwater Res., 52, 101-110 (2001).
555   doi:10.1071/MF00084

556   11. J.J. Cole, Y.T. Prairie, N.F. Caraco, W.H. McDowell, L.V. Tranvik, R.G. Streigl,
557   C.M. Duarte, P. Kortelainen, J.A. Downing, J.J. Middleburg, J. Melack, Plumbing
558   the global carbon cycle—Integrating inland waters into the terrestrial carbon
559   budget. Ecosystems, 10, 171-184 (2007). doi:10.1007/s10021-006-9013-8

560   12. R. Lauerwald, G.G Laruelle, J. Hartmann, P. Ciais, P.A.G. Regnier, Spatial
561   patterns in CO2 evasion from the global river network. Global Biogeochem. Cy.,
562   29, 534-554 (2015). doi:10.1002/2014GB004941.

563   13. J.E. Richey, J.M. Melack, A.K. Aufdenkampe, V.M. Ballester, L.L. Hess,
564   Outgassing from Amazonian rivers and wetlands as a large tropical source of
565   atmospheric CO2. Nature, 416, 617-620 (2002). doi:10.1038/416617a

566   14. G. Abril, J. Martinez, L.F. Artigas, P. Moreira-Turcq, M.F. Benedetti, L. Vidal, T.
567   Meziane, J. Kim, M.C. Bernardes, N. Savoye, J. Deborder, E.L. Souza, P.
568   Alberic, M.F. Landem de Souza, F. Roland, Amazon River carbon dioxide
569   outgassing fuelled by wetlands. Nature, 505, 395-398 (2014).
570   doi:10.1038/nature12797

571   15. J.H.F. Amaral, V.F. Farjalla, J.M. Melack, D. Kasper, V. Scofield, P.M. Barbosa,
572   B.R. Forsberg, Seasonal and spatial variability of CO_2 in aquatic environments of
573   the central lowland Amazon basin. Biogeochemistry, 143, 133-149 (2019).
574   doi:10.1007/s10533-019-00554-9

575   16. W.J. Junk, P.B. Bayley, R.E. Sparks, "The flood pulse concept in river-floodplain
576   systems" in Proceedings of the International Large River Symposium, D.P.
577   Dodge, Ed. (Canadian Special Publication of Fisheries and Aquatic Sciences,
578   1989), pp. 110-127.

579   17. A.V. Borges, G. Abril, F. Darchambeau, C.R. Teodoru, J. Deborde, L.O. Vidal, T.
580   Lamber, S. Bouillion, Divergent biophysical controls of aquatic CO_2 and CH_4 in
581   the world's two largest rivers. Sci. Rep., 5, 15614 (2015). doi:10.1038/srep15614
582   18. A. Zuijdgeest, S. Baumgartner, B. Wehrli, Hysteresis effects in organic matter
583   turnover in a tropical floodplain during a flood cycle. Biogeochemistry, 131, 49-
584   63 (2016). doi:10.1007/s10533-016-0263-z

585 19. G. Abril, A.V. Borges, Ideas and perspectives—Carbon leaks from flooded land—Do we
586   need to replumb the inland water active pipe? Biogeosciences, 16, 769-784 (2019).
587   doi:10.5194/bg-16-769-2019
588 20. M.E. Arias, T.A. Cochrane, T. Piman, M. Kummu, B.S. Caruso, T.J. Killeen, Quantifying
589   changes in flooding and habitats in the Tonle Sap Lake (Cambodia) caused by water
590   infrastructure development and climate change in the Mekong Basin. J. Environm
591   Manage., 112, 53-66 (2012). doi:10.1016/j.envman.2012.07.003
592 21. G.W. Holtgrieve, M.E. Arias, K.N. Irvine, D. Lamberts, E.J. Ward, M. Kummu, J.
593   Koponen, J. Sarkkula, J.E. Richey, Patterns of ecosystem metabolism in the Tonle Sap
594   Lake, Cambodia with links to capture fisheries. PLoS One, 8(8), e71395 (2013).
595   doi:10.1371/journal.pone.0071395
596 22. Borges, S.V., F. Darchambeau, T. Lambert, C. Morana, G.H. Allen, E. Tambwe, A.T.
597   Sembaito, T. Mambo, J.N. Wabakhangazi, J.P. Descy, C.R. Teodoru, and S. Bouillon,
598   Variations in dissolved greenhouse gases (CO_2, CH_4, N_2O) in the Congo River
599   overwhelmingly driven by fluvial wetland connectivity. Biogeosciences, 16, 3801-3834
600   (2019). doi:10.5194/bg-16-3801-2019
601 23. S. K. Hamilton, S.J. Sippel, D.F. Calheiros, J.M. Melack, An anoxic event and other
602   biogeochemical effects of the Pantanal wetland on the Paraguay River. Limnol.
603   Oceanogr., 42(2), 257–272 (1997). doi:10.4319/lo.1997.42.2.0257
604 24. M.J. Whiticar, E. Faber, Methane oxidation in sediment and water column
605   environments—Isotopic evidence. Org. Geochem, 10(4-6), 759-768 (1986).
606   doi:10.1016/S0146-6380(86)80013-4
607 25. M.J. Whiticar, Carbon and hydrogen isotope systematics of bacterial formation and
608   oxidation of methane. Chem. Geol., 161, 291-314 (1999). doi:10.1016/S0009-
609   2541(99)00092-3
610 26. E.R. Hornibrook, F.J. Longstaffe, and W.S. Fyfe, Evolution of stable C isotope
611   compositions for methane and carbon dioxidein freshwater wetlands and other anaerobic
612   environments. Geochim. Cosmochim. Acta, 64(6), 1013-1027 (2000).
613 27. W. Burnett, G. Wattayakorn, R. Supcharoen, K. Sioudom, V. Kum, S. Chanyotha, R.
614   Kritsananuwat, Groundwater discharge and phosphorus dynamics in a flood-pulse
615   system—Tonle Sap Lake, Cambodia. J. Hydrol., 549, 79-91 (2017).
616   doi:10.1016/j.jhydrol.2017.03.049
617 28. C.D. Keeling, The concentration and isotopic abundance of carbon dioxide in rural areas.
618   Geochim. Cosmochim. Acta, 13, 322-334 (1958). doi:10.1016/0016-7037(58)90033-4
619 29. C.D. Keeling, The concentration and isotopic abundance of carbon dioxide in rural and
620   marine air. Geochim. Cosmochim. Acta, 24, 277-298 (1961). doi:10.1016/0016-
621   7037(61)90023-0
622 30. A. Dai, K.E. Trenberth, Estimates of freshwater discharge from continents—Latitudinal
623   and seasonal variations. J. Hydrometeorol., 3(6), 660-687 (2002). doi:10.1175/1525-
624   7541(2002)003<0660:EOFDFC>2.0.CO;2
625 31. J.F. Pekel, A. Cottam, N. Gorelick, A.S. Belward, High-resolution mapping of global
626   surface water and its long-term changes. Nature, 540, 418-422 (2016).
627 32. B.J. Peterson, B. Fry, Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst., 18,
628   293-320 (1987). doi:10.1146/annurev.es.18.110187.001453
629 33. A. De Kluijver, P.L. Schoon, J.A. Downing, S. Schouten, J.J. Middleburg, Stable carbon
630   isotope biogeochemistry of lakes along a trophic gradient. Biogeosciences, 11, 6615-

6646 (2014). doi:10.5194/bgd-11-6615-2014

34. S.L. McCallister, P.A. Del Giorgio, Direct measurement of the d13C signature of carbon respirared by bacteria in lakes—Linkages to potential carbon sources, ecosystem baseline metabolism, and CO2 fluxes. Limnol. Oceanogr., 53(4), 1204-1216 (2008). doi:10.4319/lo.2008.53.4.1204

35. J.M. Melack, D.L. Engle, An organic carbon budget for an Amazon floodplain lake. Verh. Internat. Verein. Theor. Angew. Limnol., 30(8), 1179-1182 (2009). doi:10.1080/03680770.2009.11923906

36. R. Conrad, M. Klose, P. Claus, A. Enrich-Prast, Methanogenic pathway, 13C isotope fractionation, and archaeal community composition in the sediment of two clear-water lakes of Amazonia. Limnol. Oceanogr., 55(2), 689-702 (2010). doi:10.4319/lo.2010.55.2.0689

37. R. Conrad, M. Noll, P. Clause, M. Klose, W.R. Bastos, A. Enrich-Prast, Stable carbon isotope discrimination and microbiology of methane formation in tropical anoxic lake sediments. Biogeosciences, 8, 795-814 (2011). doi:10.5194/bg-8-795-2011/

38. P.M. Barbosa, V.F. Farjalla, J.M. Melack, J.H.F. Amaral, J.S. da Silva, B.R. Forsberg, High rates of methane oxidation in an Amazon floodplain lake. Biogeochemistry, 137, 351-365 (2018). doi:10.1007/s10533-018-0425-2

39. K. Malowany, J. Stix, A. Ven Pelt, G. Luic, H2S interference on CO_2 isotopic measurements using a Picarro G1101-i cavity ring-down spectrometer. Atmos. Meas. Tech., 8, 4075-4082 (2015). doi:10.5194/amt-8-4075-2015

40. L.A. Winslow, J.A. Zwart, R.D. Batt, H.A. Dugan, R.I. Woolway, J.R. Corman, J.S. Read, LakeMetabolizer—An R package for estimating lake metabolism from free-water oxygen using diverse statistical models. Inland Waters, 6(4), 622-636 (2016). doi:10.1080/IW-6.4.883

41. R Core Team, R—A language and environment for statistical computing, version 4.1.0 (R Foundation for Statistical Computing, 2019).

42. G.A. Nelson, fishmethods—Fishery Science Methods and Models (R package version 1.11-1, 2019). http://CRAN.R-project.org/package=fishmethods

43. G.E. Likens, "Primary production of inland aquatic ecosystems" Primary Productivity of the Biosphere, H. Leith, R.H. Whittaker, Eds. (Springer, 1975), pp. 185-202.

44. J.M. Melack, Primary productivity and fish yields in tropical lakes. Trans. Am. Fish. Soc., 105(5), 575-580 (1976). doi:10.1577/1548-8659(1976)105<575:PPAFYI>2.0.CO;2

45. B. Thebrath, F. Rothfuss, M.J. Whiticar, R. Conrad, Methane production in littoral sediment of Lake Constance. FEMS Microbiol. Lett., 102(3-4), 279-289 (1993). doi:10.1016/0378-1097(93)90210-S

46. J.J. Cole, N.F. Caraco, Atmospheric exchange of carbon dioxide in a low wind oligotrophic lake measured by the addition of SF6. Limnol. Oceanogr., 43(4), 647-656 (1998). doi:10.4319/lo.1998.43.4.0647

47. M.H. O'Leary, Carbon isotope fractionation in plants. Phytochemistry, 20, 553-567 (1981). doi:10.1016/0031-9422(81)85134-5

48. J.I. Hedges, W.A. Clark, P.D. Quay, J.E. Richey, A.H. Devol, M. Santos, Compositions and fluxes of particulate organic material in the Amazon River. Limnol. Oceanogr., 31(4), 717-738 (1986). doi:10.4319/lo.1986.31.4.0717

675 49. D.L. Phillips, S.D. Newsome, J.W. Gregg, Combining sources in stable isotope mixing
676   models—Alternative methods. Oecologia, 144, 520-527 (2005). doi:10.1007/s00442-
677   004-1816-8
678 50. J. Cohen, Statistical Power Analysis for the Behavioral Sciences, (Lawrence Earlbaum
679   Associates, 1988), pp. 1-567.
680

Figure 1. **a)** Dissolved O_2 deficit and CO_2 supersaturation relative to atmospheric equilibrium in open-water, edge, and floodplain environments of TSL during the high-water and **b)** falling-water stages of the flood-pulse. Dissolved O_2 deficit and CO_2 supersaturation are calculated as the difference between atmospheric equilibrium according to Henry's Law. Orange lines show atmospheric equilibrium at 0 μmol L^{-1} dissolved O_2 or CO_2. A slope (*m*) of -1.0 for represents the equimolar consumption of dissolved O_2 and production of dissolved CO_2 expected during aerobic respiration (black dashed line). Instead, a slope of -0.1 was observed during both the high-water and falling-water stages. O_2 deficits were strongly correlated to CO_2 supersaturation during the high-water stage, but there was no such correlation during the falling-water stage.

Figure 2. **a)** Measured $\delta^{13}C$-CO_2 (blue) relative to other potential sources of organic and inorganic C during the high-water and falling-water stages of the flood-pulse. "Other" potential sources of organic and inorganic C measured by this study in TSL include macrophytes, terrestrial C3 vegetation, periphyton, phytoplankton, and DIC. Emergent aquatic C4 grasses, measured by Hedges et al. (48) in the Amazon, and atmospheric CO_2 in equilibrium with water (47) are also included. Isotopic values quantified by this study are in blue and white, and those quantified by other studies (24,25,26,47,48) are in gray. **b)** Apparent fractionation between $\delta^{13}C$-CO_2 and $\delta^{13}C$-CH_4 (α_{app}) indicated substantial CH_4 production through acetate fermentation with some carbonate reduction in TSL (24,25). Therefore, a two-source isotope mixing model was created using 1) a continuous uniform distribution of $\delta^{13}C$-CO_2 known to result from the oxidation of CH_4 produced by both pathways (gray boxes) and 2) a continuous uniform distribution of $\delta^{13}C$-CO_2 from DIC and the aerobic respiration of potential organic C sources (white box).

Figure 3. **a)** $\delta^{13}C$-CO_2, $\delta^{13}C$-CH_4, in open-water, edge, and floodplain environments of TSL during the high-water and **b)** falling-water stages of the flood-pulse, modified from Whiticar (25). Zones of CH_4 production by acetate fermentation, CH_4 production by carbonate reduction, and CH_4 oxidation based on apparent fractionation between $\delta^{13}C$-CO_2 and $\delta^{13}C$-CH_4 (ε_C) are shaded in grey. **c)** ^{13}C depletion of CO_2 was strongly correlated to independent measurements of net CH_4 oxidation in the water column during the high-water stage, **d)** though not during the falling-water stage. **e)** ^{13}C depletion of CO_2 was also strongly correlated to gross CH_4 production within sediments during the high-water stage, **f)** though not during the falling-water stage.

Table 1. Mean partial pressures (μatm) $\pm$ 1 SD and $\delta^{13}C$ (‰) $\pm$ 1 SD for CO_2 and CH_4 in open-water, edge, and floodplain environments of TSL during the high-water and falling-water stages of the flood-pulse. Mean partial pressures (μatm) and $\delta^{13}C$ (‰) across all lake environments for the high-water and falling-water stages are also shown.