Science of the Total Environment 790 (2021) 147920

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Repeated large-scale mechanical treatment of invasive *Typha* under increasing water levels promotes floating mat formation and wetland methane emissions

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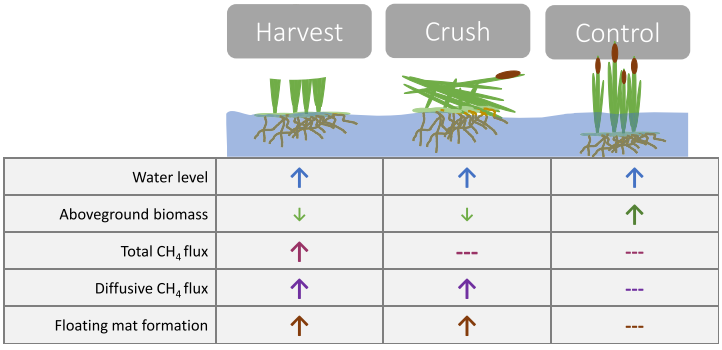
HIGHLIGHTS

- Five-year, large-scale study of biomass and carbon response to wetland management.
- We measured in-situ plant-mediated CH_4 flux and dissolved surface water CH_4.
- Crushing and harvesting *Typha* reduced biomass, even under high water levels.
- We found a positive correlation between floating mats and surface water CH_4.
- Harvested stands had total in-situ CH_4 flux rates twice as high as controls.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 5 February 2021
Received in revised form 12 May 2021
Accepted 15 May 2021
Available online 21 May 2021

Editor: Jan Vymazal

Keywords:
Carbon
Freshwater wetland
Management tradeoffs
Water level
Ecosystem services
Floating mats
Invasive *Typha*
Mechanical treatment

ABSTRACT

Invasive species management typically aims to promote diversity and wildlife habitat, but little is known about how management techniques affect wetland carbon (C) dynamics. Since wetland C uptake is largely influenced by water levels and highly productive plants, the interplay of hydrologic extremes and invasive species is fundamental to understanding and managing these ecosystems. During a period of rapid water level rise in the Laurentian Great Lakes, we tested how mechanical treatment of invasive plant *Typha* × *glauca* shifts plant-mediated wetland C metrics. From 2015 to 2017, we implemented large-scale treatment plots (0.36-ha) of harvest (i.e., cut above water surface, removed biomass twice a season), crush (i.e., ran over biomass once mid-season with a tracked vehicle), and *Typha*-dominated controls. Treated *Typha* regrew with approximately half as much biomass as unmanipulated controls each year, and *Typha* production in control stands increased from 500 to 1500 g-dry mass m^{-2} yr^{-1} with rising water levels (~10 to 75 cm) across five years. Harvested stands had total in-situ methane (CH_4) flux rates twice as high as in controls, and this increase was likely via transport through cut stems because crushing did not change total CH_4 flux. In 2018, one year after final treatment implementation, crushed stands had greater surface water diffusive CH_4 flux rates than controls (measured using dissolved gas in water), likely due to anaerobic decomposition of flattened biomass. Legacy effects of treatments were evident in 2019; floating *Typha* mats were present only in harvested and crushed stands, with higher frequency in deeper water and a positive correlation with surface water diffusive CH_4 flux. Our

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https://doi.org/10.1016/j.scitotenv.2021.147920
0048-9697/Published by Elsevier B.V.

Harvest
Methane

study demonstrates that two mechanical treatments have differential effects on *Typha* structure and consequent wetland CH_4 emissions, suggesting that C-based responses and multi-year monitoring in variable water conditions are necessary to accurately assess how management impacts ecological function.

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1. Introduction

Global change agents are fundamentally altering ecological processes that govern the carbon (C) balance of freshwater wetlands. In the Laurentian Great Lakes, the largest system of freshwater lakes on Earth, climate change is increasing the frequency and amplitude of extreme water level events, with higher highs, lower lows, and more rapid rates of water level change expected in the next century (Gronewold and Rood, 2019). Large-amplitude swings in water levels coupled with increased nutrient loading from agriculture and urban watersheds promotes invasion by dominant macrophytes (e.g., *Phragmites australis*, *Typha* × *glauca*) into freshwater coastal wetlands (Lishawa et al., 2010; Tulbure and Johnston, 2010; Woo and Zedler, 2002). Increased water level variability and invasive species dominance alter wetland vegetation structure, and in turn can dramatically affect wetland C dynamics (Duke et al., 2015; Liao et al., 2008).

In North America, it is estimated that freshwater wetlands are responsible for 45% of total wetland carbon dioxide (CO_2) uptake, but contribute 54% of the emissions of methane (CH_4; Bridgham et al., 2006), a potent greenhouse gas with 28 times the warming potential of CO_2 (Ciais et al., 2013). Wetland plants photosynthesize and assimilate CO_2 for biomass growth or storage in rhizomes as organic C (Ehrenfeld et al., 2005; Kayranli et al., 2010), and release C via internal gas transport through aerenchymatous tissue, transporting oxygen down to the rhizosphere and soil gases (i.e., CH_4) up to the atmosphere (Carmichael et al., 2014; Grosse et al., 1996; Laanbroek, 2010). Further, vegetation indirectly influences greenhouse gas flux by mediating the quantity and quality of C substrates for microbial activity (i.e., root exudates; Kayranli et al., 2010). Currently we lack a comprehensive understanding of how invasive plant management alters wetland C cycling, limiting our ability to consider trade-offs among C storage and other ecosystem services, such as biodiversity and water quality (Bennett et al., 2009; Peralta et al., 2017; Rodríguez et al., 2006).

Herbicide is the predominant control method for problematic wetland invasive plants in North America (Hazelton et al., 2014; Martin and Blossey, 2013), though increasing evidence suggests that chemical methods are neither viable long-term solutions nor desirable approaches in freshwater ecosystems (Lawrence et al., 2016; Judd and Francoeur, 2019; Quirion et al., 2018). Targeting feedbacks that sustain macrophyte dominance, such as internal nutrient cycling and biomass accumulation (Galatowitsch et al., 1999; Larkin et al., 2012; Suding et al., 2004), can improve wetland management outcomes. For example, cutting and removing (i.e., harvesting) invasive biomass disrupts litter accumulation (Keyport et al., 2019), a key mechanism that allows dominant macrophytes to maintain their dense monocultures (Farrer and Goldberg, 2009; Holdredge and Bertness, 2011; Vaccaro et al., 2009; Zedler, 2009). Mechanical techniques such as harvesting and crushing biomass can increase structural complexity, catalyze regrowth from the native seed bank, increase light penetration, and may ultimately sustain a less-invaded state (Lishawa et al., 2015; Osland et al., 2011; Zedler, 2009).

Mechanical disturbance to invasive plant biomass could shift vegetation structure in ways that directly increase wetland CH_4 emissions, as repeated cutting or bending of aboveground biomass damages belowground rhizome networks and reduces oxidation of the rhizosphere (Sale and Wetzel, 1983; Jordan and Whigham, 1988), and may amplify methanogenesis or decrease CH_4 oxidation. Further, cut macrophyte stems can act as a conduit for CH_4 transport from the soil to the atmosphere, as both waterfowl-grazed (Dingemans et al., 2011; Winton and Richardson, 2017) and mechanically cut stems (Kasak et al., 2020; Zhu et al., 2007) have been found to increase wetland CH_4 emissions. In contrast, Rietl et al. (2017) found aboveground clipping of multiple plant species had no immediate effect on CH_4 emissions from wetland mesocosms, and Kandel et al. (2013) found that harvest of reed canary grass led to decreased soil CH_4 emissions within 3 months of treatment, but did not affect aboveground biomass or CO_2 uptake. These divergent responses to mechanical disturbance may be due to differences in C pools or limited post-treatment monitoring periods, and necessitate that plant biomass metrics, aqueous C, and C gas flux be monitored during invasive plant management studies.

Repeated mechanical treatment of flooded wetlands may also promote the formation of floating mats. Floating mats consist of live belowground biomass of common emergent plants (e.g., *Carex*, *Cladium*, *Cyperus*, *Phragmites*, *Typha*), dead organic matter, and mineral sediments that are held together by a network of low density roots and rhizomes, all floating above wetland sediments (Azza et al., 2006; Farrell et al., 2010; Lieffers, 1983). CH_4 bubbles trapped under floating mats further promote buoyancy to overcome the downward force from biomass (Hogg and Wein, 1988a). Floating mat formation has been associated with increased anaerobic decomposition (Hogg and Wein, 1988a), eutrophication (Sarneel et al., 2010), and flooding (Azza et al., 2006), which are processes linked to varying degrees of wetland C uptake and release. Overall, it is still unclear how a vegetation structural shift such as floating mat formation in response to invasive plant management and water level change will affect wetland C services.

The limited spatial and temporal scopes of wetland invasive plant control and restoration research have hindered restoration (Kettenring and Adams, 2011; Wagner et al., 2008), and have motivated large scale, multi-year investigations to address how environmental variabilities (e.g., water level fluctuation) affect management outcomes. We leveraged a 25-ha, five-year field experiment to examine how repeated mechanical treatment (harvesting, crushing) of a wetland invasive macrophyte (*Typha* × *glauca*, hereafter *Typha*) affects biomass production, floating mat formation, and plant-mediated C metrics. Invasive *Typha* is a common wetland management target throughout eastern North America because it creates dense, tall stands that outcompete native species (Bansal et al., 2019; Carson et al., 2018; Zedler and Kercher, 2005) and alters biogeochemical processes (Tuchman et al., 2009). We predicted that repeated mechanical treatment of *Typha* would decrease aboveground biomass production and net ecosystem production (NEP) yet increase the frequency of floating mats and CH_4 emissions relative to unmanipulated, *Typha*-dominated controls.

2. Materials and methods

2.1. Study site

Typha has been a management concern in the northern Great Lakes region for >20 years. Our study site at Cheboygan Marsh (Michigan, USA) has been a focal point of research investigating the impacts of *Typha* invasion, as *Typha* dominates (>99%) aboveground biomass production (Larkin et al., 2012; Tuchman et al., 2009). Cheboygan Marsh is a lacustrine open-embayment wetland (palustrine emergent marsh) on northern Lake Huron (lat 45°39′N, long 84°28′W) that is a benchmark site in the Great Lakes Coastal Wetland Monitoring Project (Uzarski et al., 2017), and is a model freshwater coastal system used to

investigate restoration strategies (Berke, 2017; Keyport et al., 2019; Lishawa et al., 2015).

2.2. Experimental design

Experimental treatments were implemented in 60 m × 60 m plots for three continuous years (2015–2017). We established 15 plots throughout a 25-ha *Typha*-dominated (>75% total plant cover) area in 2015 and randomly assigned three management treatments ($n = 5$): harvest, crush, and control (Fig. 1). Harvest treatments were implemented with a low ground pressure amphibious harvester (Loglogic Softrak, Devon, UK) that cut biomass ~20 cm above the water surface, shredded, and collected it into a tippable hopper; harvests occurred in mid-July and early September each year. Harvested biomass was removed from the wetland complex and used to test viability as a bioenergy or compost feedstock (Carson et al., 2018). Crush treatments were implemented in mid-July each year; biomass was crushed by driving over plots with a low ground pressure amphibious vehicle (Ontario Drive & Gear Limited Argo, Ontario, CA), but biomass and litter were not removed. Control treatments were unmanipulated *Typha*-dominated reference plots. To quantify treatment responses over time, we established five subplots within each 60 m × 60 m plot; one placed in the center and four equidistant between center and corners, to minimize edge effects. We estimated *Typha* biomass in years 2015–2019 and quantified a range of C responses during the 2016–2019 growing seasons.

2.3. Biomass & floating mats

We estimated *Typha* aboveground biomass during the peak of the growing season (July) in years 2015–2019. Within 1 m × 1 m quadrats, we quantified *Typha* stem height and water depth at all five subplots in each plot. We utilized a site-specific allometric equation by regressing stem height and dry biomass to estimate *Typha* aboveground biomass (g dry biomass/m^2; Lishawa et al., 2015). In 2019, we noted the presence or absence of floating mats at each subplot. We estimated floating mat frequency by calculating the proportion of subplots with floating mats for each plot.

2.4. Carbon fluxes

In July and August 2017, we measured continuous CO_2 and CH_4 concentrations using a PVC-framed chamber (0.25 m × 0.25 m × 2-m tall) wrapped with transparent UV-resistant PVC film, with two internal

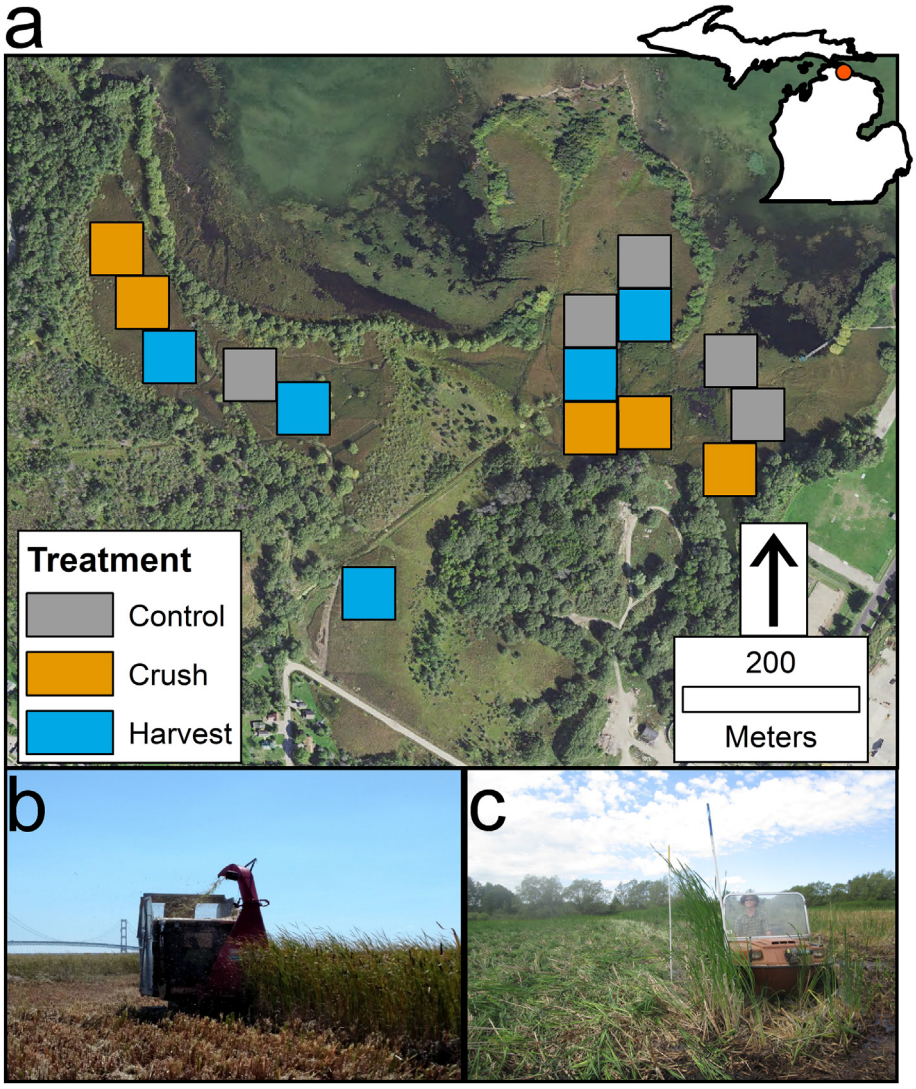

Fig. 1. (a) Map of invasive *Typha* management treatment plots (60 × 60 m) at Cheboygan Marsh (Cheboygan, Michigan, USA) implemented during 2015–2017 growing seasons. Control: unmanipulated *Typha*-dominated references. Base map imagery from 2018 NAIP: USDA Farm Service Agency, 2018. National Agriculture Imagery Program (NAIP). (b) Harvest: *Typha* biomass was cut and removed with an amphibious tractor twice per growing season. (c) Crush: *Typha* biomass was crushed with amphibious vehicle once per growing season.

fans to circulate air, a vent tube, sampling port, and temperature sensor (Holland et al., 1999). Because clear chambers were placed over *Typha* stems, measurements represent net fluxes; CO_2 fluxes approximate net ecosystem exchange (NEE), as they integrate photosynthetic uptake and autotrophic and heterotrophic respiration; a negative NEE value indicates net uptake, and a positive NEE value indicates net release. The inverse of NEE is Net Ecosystem Production (NEP), and from hereafter we refer to our CO_2 fluxes in terms of NEP; a positive NEP value indicates net uptake, and a negative NEP value indicates net release. CH_4 fluxes encompass the net effect of plant transport and water-atmosphere diffusive flux ("total CH_4 flux" hereafter). Because we transported our gas analyzer on a large-tracked amphibious vehicle that would disturb our long-term subplots, we sampled near three of the four corners associated with the 60 m × 60 m plots, instead of closer to the middle; we drove the vehicle ~5 m into the interior of each plot and walked on a 2-m long aluminum plank with step stools attached on either end (to minimize soil disturbance) to place chambers ~7 m from plot edges. We sampled between 10 am and 3 pm and set the chamber in a floating foam base that was placed over plants and connected to a Picarro g2201-*i* cavity ring-down spectrometer (Picarro, California, USA) via Teflon tubing from the sampling port. A vacuum pump drew chamber air into the instrument (~30 mL/min) during a 10-minute deployment. During gas sampling, we measured photosynthetically active radiation (PAR) 2.35 m above the soil surface and at the water surface with a Li-Cor LI-189 quantum sensor (Li-Cor Biosciences, Nebraska, USA), and we recorded air and water temperatures adjacent to the chamber.

For in-situ gas flux calculations, measurements that indicated chamber error, such as chamber tipping during incubation or elevated initial concentrations due to ebullition, were excluded from analysis; 3% of CO_2 rates and 20% of CH_4 rates were excluded due to chamber error. We calculated flux rate as the linear change in concentration over time, corrected for chamber temperature, atmospheric pressure, and chamber volume, based on the ideal gas law using original R script (Martin and Moseman-Valtierra, 2015). Correlation tests were used to test whether the slope of gas concentration over time differed from zero; *p*-values >0.05 were concluded to have zero flux rates. Any non-linear change ($R^2 < 0.8$) was re-calculated using only the half of the incubation (linear change over first 5 min), and subsequently excluded from analysis if re-calculation did not improve fit; 2% of CO_2 flux rates and 22% of CH_4 flux rates were excluded due to non-linearity. We calculated percent light penetration by dividing PAR at the water surface by PAR 2.35 m above the substrate (soil) surface and multiplying by 100.

In 2018 and 2019, increased water levels and floating mats precluded us from collecting in-situ gas fluxes, as navigating to plots with the gas sampling equipment was not feasible. Therefore, we collected surface water samples to quantify dissolved CH_4 concentrations using the headspace equilibration method (Jahangir et al., 2012). In July 2018, we collected triplicate samples of surface water from three of five subplots per plot, and in July 2019, we collected surface water samples from all five subplots per plot. We used a YSI multimeter probe (YSI Inc., Ohio, USA) to quantify dissolved oxygen (mg/L), pH, temperature (°C), and electrical conductivity (μS/cm). We collected 2 mL of surface water with a nylon syringe and injected samples into evacuated 10-mL Exetainers with double-wadded septa (Labco, England). Vials were stored in the dark until they were filled with 8 mL of helium and then agitated for 5 min at 1500 RPM in the laboratory to strip all CH_4 from the water into the headspace. Headspace CH_4 was analyzed using a Thermo Scientific Delta V Advantage magnetic sector gas isotope mass spectrometer interfaced to a Thermo Scientific Gasbench II. CH_4 flux from surface water to atmosphere was then estimated from the dissolved CH_4 concentration (ppm) by correcting for the ideal gas law, conductivity, solubility of CH_4, and the estimated amount of water per day equilibrating with atmospheric air, based on values from lakes with similar area to our study site (k_{600} = 0.44 m/d; Cole et al., 2010; Jähne et al., 1987).

2.5. Aqueous carbon

Dissolved organic carbon (DOC) was measured in 2016 (3/5 subplots per plot) and 2019 (5/5 subplots per plot) to quantify potential C substrates available for methanogenesis. To quantify DOC, a 45 mL surface water sample was collected using a nylon syringe and filtered in the field through a 0.45-μm filter into an amber vial. Vials were stored at 4 °C until DOC was quantified on a Shimadzu Total Organic Carbon Analyzer (2016) or an OI Total Organic Carbon Analyzer (2019) using EPA Method 415.1. Acetate was also estimated from 0.45-μm filtered surface and pore water samples collected from all 5 subplots in each plot during 2016 and 2019 using a Dionex high-performance ion chromatograph.

2.6. Statistical analyses

Within each growing season, data were analyzed using linear mixed effects models (lmer; *lmer* package in R version 3.4.1), with plot as a random factor to account for repeated measures and spatial variation. Linear models (lm; *lm* package in R version 3.4.1) were used when there was only one data point per plot. We interpreted significant effects via ANOVA Type III on model coefficients at an alpha value of 0.05 with Satterthwaite approximation for degrees of freedom. When categorical coefficients (i.e., treatment, date) were significant, we performed *post-hoc* pairwise comparisons on model coefficients using difference of least squares means (*emmeans* package in R version 3.4.1). When continuous numeric coefficients (e.g., water depth) were significant, we plotted the parameter to observe the trend. All means are presented as un-transformed means ±1 SE.

Aboveground biomass data were analyzed at the subplot level to maintain the highest spatial resolution possible, and were tested for the effect of treatment, surface water depth (measured at same subplot of biomass sampling) and their interaction. We analyzed floating mat data at the plot level in order to test for the effect of treatment and water depth on floating mat frequency (which was calculated as number of subplots with floating mat present/total subplots × 100).

Gas flux data were also left at higher resolution (subplot level) because we collected all parameters of interest simultaneously at the subplot level; 2017 total plant-mediated flux data were initially analyzed by gas species (CO_2, CH_4) to test for effects of treatment, date, surface water depth, above-canopy PAR (ambient variation in light availability that may affect photosynthesis and stomatal conductance), and the interaction of treatment with the three other terms. There were no significant effects of surface water depth or light availability on our response variables, so these fixed effects were removed for final analysis. 2018 and 2019 surface diffusive flux data were tested for treatment effects. Finally, to assess the relationship between floating mats and CH_4 at the subplot level, we used *lm* to test for the effect of floating mat presence and frequency on CH_4 flux, and the effect of floating mat frequency on CH_4 flux.

Aqueous carbon (DOC and acetate) data were aggregated to the plot level in order to include plot-level water depth (average of subplot data taken at biomass subplots) as a covariate in tests for treatment effects, because dissolved compounds may be diluted by deeper water. For 2016 data, *lmer* was used with plot as factor to account for repeated measurements (July, August). In 2019 data, *lm* was used because there was only one sampling campaign.

3. Results

3.1. Biomass & floating mats

Typha biomass varied among treatments ($F_{2,14} = 28.78$, $p \le 0.0001$), year ($F_{4,14} = 51.89$, $p \le 0.0001$), and their interaction ($F_{8,14} = 17.38$, $p \le 0.0001$). Within-year analyses revealed that experimental mechanical treatment (crush, harvest) reduced *Typha* aboveground biomass

relative to unmanipulated *Typha*-dominated controls in all years following initial treatments (Fig. 2). Prior to treatment implementation in 2015, we observed differential biomass production (crush > control), but aboveground biomass was more than twice as abundant in controls relative to treatment plots after treatment initiation. Within control plots and across all years and subplots, *Typha* biomass was positively correlated with water level ($R^2 = 0.39$, $p < 0.0001$). Treatment differences persisted with increasing water levels in the marsh, where we observed a greater than six-fold increase in mean water levels between 2015 (12.6 ± 1.6 cm) and 2019 (76.7 ± 2.7 cm).

Prior to treatment initiation in 2015, no floating mats were observed at Cheboygan Marsh. In 2019, two years after last treatment implementation, we found an interactive effect of treatment and water depth on floating mat frequency ($F_{2,9} = 7.47$, $p = 0.012$), with the greatest abundance of floating mats in harvested areas with deep water (Fig. 3).

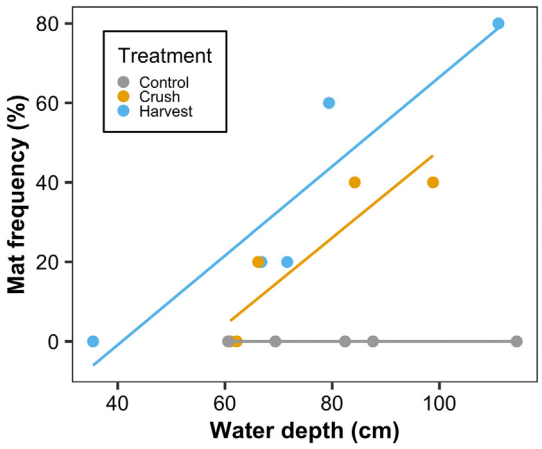

Fig. 3. Regression lines of floating mat frequency (%) and water depth (cm) for invasive *Typha* treatments in July 2019. Floating mats were most frequent in harvested, deep-water plots. Each point represents the percentage of subplots within a 60 × 60-m plot with floating mats (subplots with floating mats/total subplots × 100). For crush treatment, the regression equation is $y = 0.0110x - 0.62$, $R^2 = 0.76$, and for harvest: $y = 0.012x - 0.46$, $R^2 = 0.81$. There was no significant effect of water depth on mat frequency in the control plots.

3.2. Carbon fluxes

Total plant-mediated CH_4 fluxes differed among treatments ($F_{2,27} = 8.84$, $p = 0.001$), as we observed higher flux rates with *Typha* harvest (Fig. 4a). However, we did not detect differences between July and August 2017 sampling campaigns ($F_{1,27} = 2.06$, $p = 0.16$), nor a treatment by sampling campaign interaction ($F_{2,27} = 0.24$, $p = 0.79$; Fig. 4a). For NEP, we observed an interaction between treatment and sampling campaign ($F_{2,35} = 10.72$, $p = 0.002$; Fig. 4b). Crushing and harvesting *Typha* biomass in late July reduced net CO_2 uptake during our August campaign (Fig. 4b).

Surface CH_4 diffusive flux estimates in 2018 and 2019 were an order of magnitude lower than total CH_4 flux measurements in 2017 (Figs. 4, 5). We observed treatment differences in CH_4 diffusive fluxes in 2018 ($F_{2,14} = 4.8$, $p = 0.025$), but not in 2019 ($F_{2,15} = 1.49$, $p = 0.26$), and surface water characteristics were similar across treatments (Table 1). In July 2018, one year after final treatment, crushed plots

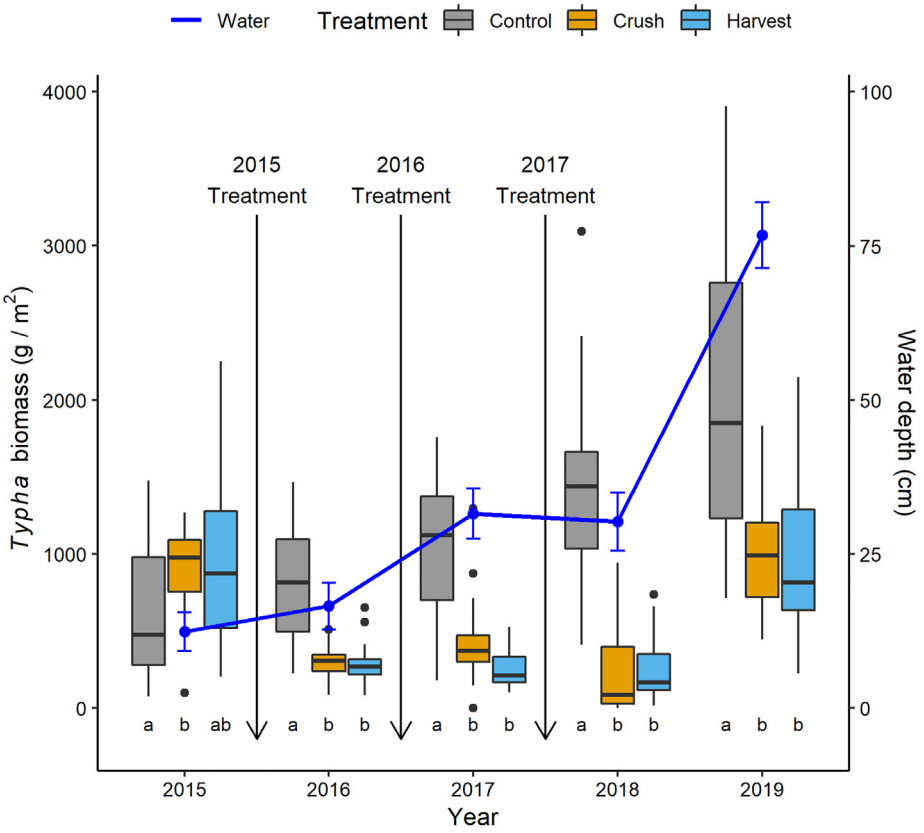

Fig. 2. Boxplots (boxes indicate interquartile range, whiskers encompass values 1.5 times the interquartile range, single points indicate outliers) of aboveground *Typha* biomass (2015–2019) varied across management treatment plots ($n = 5$). Treatments were implemented annually 2015–2017; pre-treatment biomass estimates occurred prior to treatment implementation in 2015. Biomass measurements from 2016 to 2018 estimate *Typha* biomass one-year post-treatment after each annual treatment, and 2019 measurements estimate biomass two years post- final treatment. Non-overlap of letters indicates within year treatment differences, based on least squares means *post-hoc* comparisons. Mean (± SE) water level averaged across plots are overlaid to highlight increasing water levels over time and relationship with biomass.

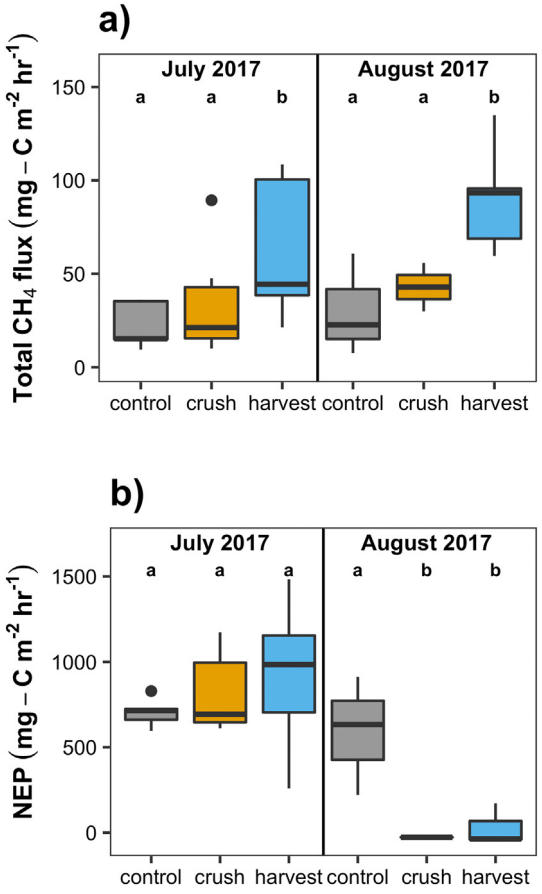

Fig. 4. Boxplots (boxes indicate interquartile range, whiskers encompass values 1.5 times the interquartile range, single points indicate outliers) of in-situ (a) total plant-mediated methane (CH_4) flux and (b) net ecosystem production (NEP; net CO_2 uptake) among experimental treatments of invasive *Typha* in July 2017 (one year after 2016 management) and in August 2017 (<one month after 2017 management). Non-overlap of letters indicates differences in flux rates based on least-square means *post-hoc* comparisons. Note total CH_4 flux was log-transformed prior to statistical analysis, but untransformed data are presented here.

had higher diffusive CH_4 flux rates than controls (Fig. 5a). While we did not see direct effects of mechanical treatment on diffusive CH_4 flux in July 2019, plots with floating mats had higher diffusive flux rates than those without ($F_{1,13} = 9.37$, $p = 0.01$; Fig. 6a), and floating mat abundance was positively linearly related with diffusive CH_4 flux ($R^2 = 0.49$, $p = 0.002$; Fig. 6b).

3.3. Aqueous carbon

In 2016, a year after initial treatment, water depth and treatment had an interactive effect on surface water DOC ($F_{2,23} = 9.17$, $p = 0.001$; Table 2). At water depths less than 25 cm, crushing resulted in less DOC than in harvest and control plots, and when water depth was greater than 25 cm, crushing led to higher DOC than harvest and control plots (Fig. A1). In 2019, two years after the last treatment, we did not detect an effect of treatment, water depth, or their interaction on surface water DOC (Table 2). There was an interactive effect of treatment and sampling campaign on 2016 pore water acetate ($F_{2,25} = 4.59$, $p = 0.02$; .1). In July 2016, a year after initial management, neither crush nor harvest differed from control, while crushed plots had twice as much acetate as harvested plots. In August, <one month after 2016 management, pore water acetate did not differ among treatments, and in 2019, two years after the last treatment, we did not detect an effect of treatment, water depth, or their interaction on surface water acetate (Table A1).

4. Discussion

Repeated mechanical treatment (twice a season for three consecutive seasons) of invasive *Typha* via harvesting or crushing reduced aboveground biomass and increased the frequency of floating mats, indirectly causing greater surface water diffusive flux of CH_4. When we accounted for plant transport of CH_4, total flux rates were an order of magnitude higher than diffusive-only flux estimates, and harvesting was the only treatment that resulted in elevated CH_4 flux rates at multiple time scales (two weeks, one year after treatment implementation). While the increase in diffusive flux is largely explained by floating mat frequency in harvested and crushed stands, total CH_4 flux is likely further increased by the presence of standing dead litter and freshly

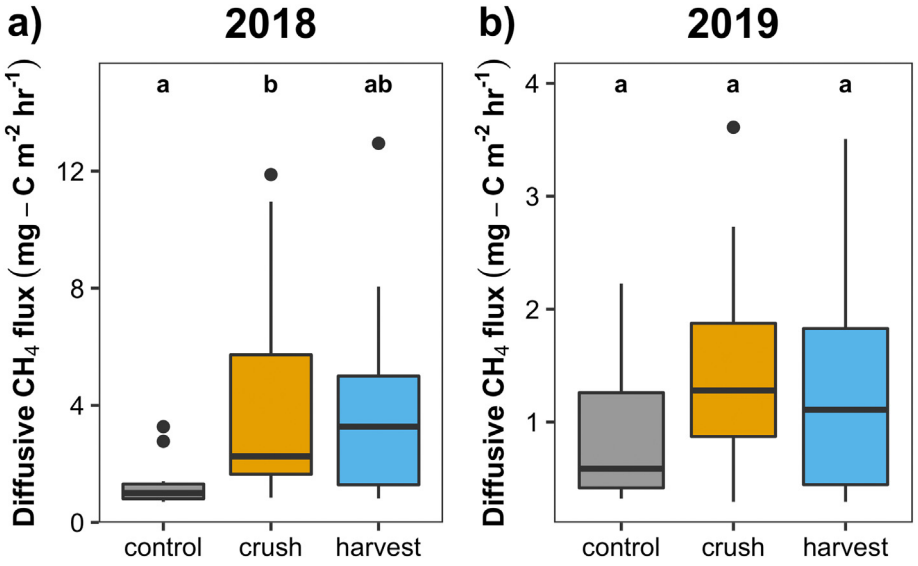

Fig. 5. Boxplots (boxes indicate interquartile range, whiskers encompass values 1.5 times the interquartile range, single points indicate outliers) of surface water diffusive methane (CH_4) flux calculated from surface water samples collected in (a) July 2018 and (b) July 2019 (one and two years after final management, respectively, of invasive *Typha*). Note y-axis scales differ between Figs a and b. Non-overlap of letters indicates differences in flux rates within year based on least-square means *post-hoc* comparisons.

Table 1
Environmental variables (mean ± SE) associated with surface water dissolved methane (CH_4) sampling in July 2018 and 2019 for experimental treatments (control, crush, harvest) of invasive *Typha*.

	Temperature (°C)		pH		Electrical conductivity (μS/cm)	
	2018	2019	2018	2019	2018	2019
Control	22.6 ± 0.22	21.7 ± 0.32	7.2 ± 0.05	6.8 ± 0.07	418.6 ± 42.6	297.8 ± 29.5
Crush	23.9 ± 0.58	21.3 ± 0.58	7.2 ± 0.33	6.8 ± 0.07	447.0 ± 52.6	345.2 ± 37.9
Harvest	24.1 ± 0.21	20.9 ± 0.58	7.4 ± 0.14	6.8 ± 0.09	492.5 ± 62.0	502.0 ± 159.9

Subplot measurements were averaged to estimate plot means for each treatment (±SE; n = 5). Environmental variables did not differ among treatments during 2018 or 2019 sampling events.

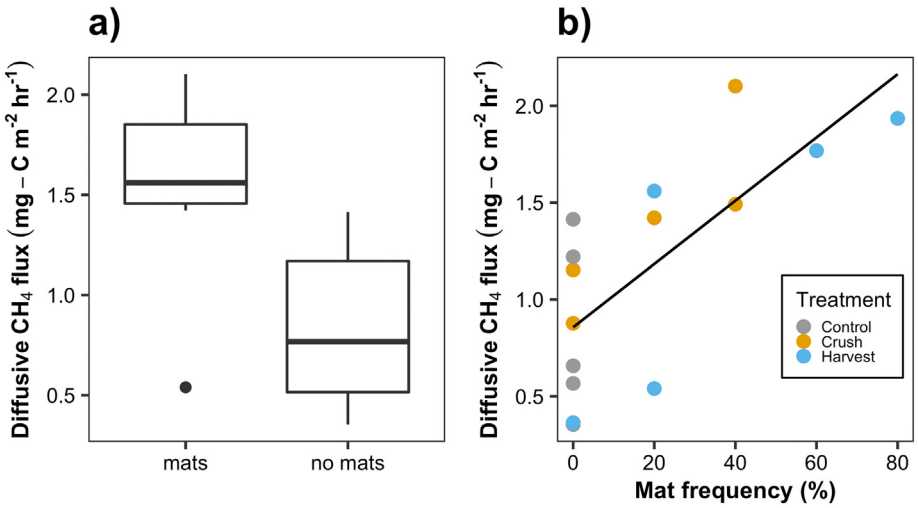

Fig. 6. July 2019 (two years after final management of invasive *Typha*) (a) boxplot (boxes indicate interquartile range, whiskers encompass values 1.5 times the interquartile range, single points indicate outliers) of diffusive methane (CH_4) flux was greater in treatment plots where floating mats were present than treatment plots where no floating mats were present, and (b) mat frequency was positively related to diffusive CH_4 flux, $y = 1.63x + 0.86$, $R^2 = 0.49$.

cut stems in harvested stands. Thus, the two mechanical management treatments, when implemented under flooded conditions, appear to have differential effects on *Typha* structure and consequently on wetland CH_4 emissions.

Water levels in the Lakes Michigan-Huron reached near historic levels in summer 2019, within 15 cm of the record high water level reached in October 1963 (Gronewold et al., 2018). Once established, invasive macrophytes often increase in dominance and stem density with rising water levels (Farrell et al., 2010; Gathman et al., 2005). Over the course of our five-year study (2015–2019) we observed a more than six-fold increase in water levels across Cheboygan Marsh, and we found increased aboveground biomass production in our unmanipulated *Typha*-dominated control plots as water levels rose (Fig. 2). In contrast, both crushing and harvesting treatments reduced invasive *Typha* aboveground biomass relative to controls under high water conditions, consistent with other mechanical management studies (Lishawa et al., 2015; Osland et al., 2011; Wilcox et al., 2018), and reductions in biomass persisted through the duration of the study, at least two years after our mechanical treatments ceased (Fig. 2). Evidence suggests that repeated cutting may be more effective at reducing biomass than a one-time harvest (Jinadasa et al., 2008; Lishawa et al., 2020; Wilcox et al., 2018). While our study documents a common case of an established invasive macrophyte increasing dominance and stem density with rising water levels, it also demonstrates how wetland mechanical disruption followed by increased deep water can sustain reductions in invasive *Typha* biomass. Our results support the growing consensus that effective invasive plant control requires a combination of management approaches (Bansal et al., 2019), especially given the projected increased variability of water level changes in the Laurentian Great Lakes (Gronewold and Rood, 2019).

Table 2
Dissolved organic carbon (DOC) treatment means (± SE) of surface water from three sampling campaigns conducted during 2016 and 2019. In 2016, there was an interactive effect of treatment for invasive *Typha* (control, crush, harvest) and water depth; crush had less DOC than control and harvest at water depths <25 cm, and greater DOC at water depths >25 cm.

	DOC (mg/L)		
	July 2016	Aug 2016	July 2019
Control	17.0 ± 9.4	20.3 ± 12.4	8.4 ± 2.2
Crush	17.1 ± 2.6	24.5 ± 5.5	11.3 ± 1.4

Subplot measurements were averaged to estimate plot means. In 2016, experimental treatments were implemented between the July and August sampling campaign.

While management-induced reductions in invasive *Typha* biomass tend to promote native plant richness and waterbird food resources (Lishawa et al., 2015; Lishawa et al., 2019; Lishawa et al., 2020), our present study found that mechanical treatment combined with flooding also promoted floating mat formation. In 2019, two years after final treatment implementation, floating mats were present in more than a third of harvested subplots (36% ± 14) and had moderate frequency in crushed subplots (20% ± 8%), while there were no floating mats in controls. To our knowledge, this is the first documentation of how repeated mechanical treatment of an invasive macrophyte under high water levels can promote the formation of floating mats. We observed a treatment by water level interaction, with floating mat frequency increasing at deeper water in harvest and crush plots, but not in control plots (Fig. 3). Floating mats of macrophyte vegetation have important consequences for present and future ecosystem services provided by wetlands. In constructed and nutrient-rich wetlands, floating mats of *Typha* can improve water quality via removal of algal bloom-causing nutrients (i.e., phosphorous, nitrogen) as roots draw water directly from

the water instead of through the soil (Chua et al., 2012; Hubbard, 2010; Ijaz et al., 2016; Keizer-Vlek et al., 2014). The high water levels we observed may limit traditional revegetation efforts (Brown and Bedford, 1997; van der Valk and Baalman, 2018), but native plants can germinate from the seed bank and survive on the floating mats, which sit above the water column (Cherry and Gough, 2006; Farrell et al., 2010). Regarding plant- and wildlife-based services, floating *Typha* mats in our treatment plots appeared to serve as a seedbed of a rich assemblage of native sedges and forbs, creating habitat heterogeneity in an otherwise monotypic stand of invasive *Typha*. While *Typha* mats can reduce habitat for waterfowl who cannot navigate through the mats (Krusi and Wein, 1988), they can create habitat for other species who prefer mat surfaces such as aerial insects, rodents, reptiles (Hill et al., 1987), and wading birds. Regarding C-based services, our study provides new evidence that floating mat formation increases surface water CH_4 emissions (Fig. 6), which could counter-balance C storage provided by wetlands. Thus, while temperature often has a greater direct impact than water level on freshwater wetland CH_4 emissions (Pugh et al., 2018; Strachan et al., 2015; Turetsky et al., 2014), increased water levels can indirectly impact CH_4 emissions via increased floating mat formation.

There is still scientific debate over the relative radiative forcing sink versus source potential of freshwater wetlands (Bridgham et al., 2006; Mitsch et al., 2013; Neubauer, 2014; Petrescu et al., 2015), and C dynamics may continue to shift as wetlands are invaded by dominant macrophytes or managed to promote native species. To clarify the driving factors responsible for variability in wetland CH_4 emissions, our study included plant biomass metrics, aqueous C, and C gas flux responses to repeated mechanical treatment. Our in-situ chamber-based measurements indicated that harvesting (cutting and removing) invasive *Typha* stems directly increased total CH_4 flux rates (Fig. 4a). Previous studies investigating the effects of single aboveground *Typha* harvests did not find differences in daytime CH_4 flux between controls and harvested areas (Günther et al., 2015; Keyport et al., 2019), though it should be noted these previous studies measured soil-only flux, not total (soil + plant) flux, and were observed under lower surface water levels. We found that elevated total CH_4 flux rates persisted at least a year after harvesting, which may be a function of scale and treatment frequency, as at our large scale, repeated harvests more likely reduced the vigor of a rhizomatous macrophyte than a one-time clipping of small areas (Zhu et al., 2007). Reduced *Typha* biomass with repeated mechanical treatment likely reduced rhizospheric oxidation, which coupled with increased availability of organic substrates from decomposing roots and organic matter and prolonged flooded conditions, generates ideal conditions for methanogenesis (Inglett et al., 2012; Morrissey et al., 2014).

Despite similar reductions in aboveground biomass as harvesting, crushing did not directly increase total CH_4 flux rates relative to controls, suggesting the importance of cut stems in moderating total CH_4 emissions, especially when cut stems are not flooded, as was the case with our harvesting equipment. Residual cut stems that remain emerged above the water surface can continue to function as conduits well past treatment implementation, venting subsurface CH_4 as well as CH_4 translocated from other *Typha* ramets connected via rhizome networks (Brix et al., 1992). Surface water diffusive flux rates (which do not account for stem transport) from harvested treatments were similar to controls (Fig. 5), and magnitudes lower than total flux, further suggesting transport through cut stems is the primary means by which harvest increases CH_4 emissions. Elevated surface water DOC concentrations in deep water crush treatment plots (Table 2, Fig. A1) suggests an ample supply of organic substrate for CH_4 production (Morrissey et al., 2014; Inglett et al., 2012; Zak et al., 2015), and crushing biomass led to greater diffusive CH_4 flux than in control treatments in 2018 (Fig. 5a). Additionally, nutrients leaching from freshly crushed *Typha* may have stimulated microbial processes to increase diffusive CH_4 flux rates (Rietl et al., 2017; Grasset et al., 2017). Thus, the two treatments likely had different mechanisms of increasing CH_4 emissions; greenhouse gas diffusing through cut stems in harvested stands (Laanbroek, 2010; Dingemans et al., 2011) and water column anaerobic decomposition releasing CH_4 from surface water in crushed stands (Megonigal et al., 2004). It is important to note the single season of total flux measurements (2017, after *Typha* had been harvested and crushed the previous two years) is a limited time scale. Extended temporal replication of total flux measurements could help clarify mechanistic distinctions that are important for regional or global models in order to include management scenarios and specific CH_4 transport pathways in wetland C budget projections (Xu et al., 2016).

Increased CH_4 emissions via cut stems and surface water may be outweighed by the benefits of increased plant diversity and nutrient uptake by newly-formed floating mats. While our study investigated the effects of mechanical treatment on aboveground biomass and C fluxes, further research on how repeated, long-term harvests impact belowground biomass could elucidate other tradeoffs in treatment effects. Accumulation of dead roots and rhizomes plays a key role in floating mat formation (Hogg and Wein, 1988b), so analyzing changes in belowground biomass would improve understanding of how repeatedly harvesting *Typha* creates floating mats. Future efforts could explore if cut stem CH_4 emissions are mitigated by mowing plant biomass below the water, a method that has the additional benefit of more effectively reducing invasive *Typha* dominance than above-water harvesting (Lishawa et al., 2020). Ultimately, our understanding of the role that managed and restored wetlands play in present and future landscapes would benefit from further research on the interaction of water level, vegetation and greenhouse gas flux (i.e., McNicol et al., 2017).

As stressors from climate change (i.e., water level shifts, atmospheric greenhouse gas concentrations) and human land-use (i.e., nutrient runoff from agriculture) continue to grow, it is increasingly important to understand ecosystem services provided by freshwater wetlands, and to accurately assess the effectiveness of wetland management efforts (Moreno-Mateos et al., 2012). The balance of radiative forcing, nutrient uptake, and plant diversity responses to management will depend on the timing and frequency of implementation. Since our study implemented two harvests per season, we observed cumulative effects of a mid-season and late-season harvest. Evidence from Kasak et al. (2020) suggests harvesting in autumn when CH_4 emissions are lower than mid-summer, and before leaf nutrients are translocated belowground would reduce CH_4 flux. Management later in the growing season may also be ideal for CO_2 uptake and C sequestration, in effect delaying the reduction in NEP we observed with mechanical treatment during peak of growing season (Fig. 4b). In terms of longer-term timing, crushing *Typha* increased surface water CH_4 flux through the following year post-treatment, but this surface water flux increase did not persist two years after treatment. Ultimately, C-based responses and multi-year monitoring in variable water conditions are necessary to accurately assess how invasive plant management impacts wetland ecological function.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.147920.

CRediT authorship contribution statement

Olivia F. Johnson: Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Abha Panda:** Investigation, Writing – original draft, Writing – review & editing. **Shane C. Lishawa:** Conceptualization, Formal analysis, Writing – review & editing, Visualization, Funding acquisition. **Beth A. Lawrence:** Conceptualization, Investigation, Resources, Writing – original draft, Writing - review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We appreciate financial support from the U.S. Environmental Protection Agency's Great Lakes Restoration Initiative (Project #'s GL-00E01925 and GL-00E1293), National Science Foundation and Department of Defense (AGS-1659338: REU Program "Climate Change in the Great Lakes Region"), and the University of Michigan's Biological Station summer research and housing grant. Rose Martin and Serena Moseman-Valtierra provided R-script to calculate gas flux from in-situ chamber measurements. Field and laboratory assistance were provided by Brendan Carson, Andrew Monks, Brian Ohsowski, Timothy Veverica, and other valiant members of "Team Typha." The manuscript was improved by feedback from Ashley Helton, Jack Clausen, Richard Grosshans, and two anonymous reviewers. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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