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Drivers of ecosystem metabolism in restored and natural prairie wetlands

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Abstract

Elucidating drivers of aquatic ecosystem metabolism is key to forecasting how inland waters will respond to anthropogenic changes. We quantified gross primary production (GPP), respiration (ER), and net ecosystem production (NEP) in a natural and two restored prairie wetlands (one “older” and one “recently” restored), and identified drivers of temporal variation. GPP and ER were highest in the older restored wetland, followed by the natural and recently restored sites. The natural wetland was the only net autotrophic site. Metabolic differences could not be definitively tied to restoration history, but were consistent with previous studies of restored wetlands. Wetlands showed similar metabolic responses to abiotic variables (photosynthetically active radiation, wind speed, temperature), but differed in the direct and interactive influences of biotic factors (submersed aquatic vegetation, phytoplankton). Drivers and patterns of metabolism suggested the importance of light over nutrient limitation and the dominance of autochthonous production. Such similarity in ecosystem metabolism between prairie wetlands and shallow lakes highlights the need for a unifying metabolic theory for small and productive aquatic ecosystems.

Key words: ecosystem restoration; gross primary production; net ecosystem production; prairie pothole wetlands; respiration; submersed aquatic vegetation.

30 **Introduction**

31 Accurate forecasting of the cumulative impacts of global change on aquatic ecosystems relies on
32 identification of key local and regional drivers of their metabolism (Staeher et al. 2012).
33 Ecosystem metabolism involves biologically mediated transformations of carbon and is defined
34 by three components: gross primary production (GPP), ecosystem respiration (ER), and net
35 ecosystem production (NEP), where $NEP = GPP - ER$ (Chapin et al. 2006). In lentic inland
36 waters, temperature, nutrients, and light availability have been identified as important abiotic
37 drivers of ecosystem metabolism (Hanson et al. 2003; Sand-Jensen and Staeher 2007; Staeher et al.
38 2010a; Hoellein et al. 2013; Klotz 2013; Solomon et al. 2013). However, drivers of metabolism
39 in freshwater systems vary over space and time (Smith and Hollibaugh 1997; Hanson et al. 2006;
40 Roberts et al. 2007), as well as between ecosystem types (Hoellein et al. 2013).

41 Our understanding of anthropogenic impacts on rates and drivers of metabolism of
42 aquatic ecosystems is in its infancy. As an integrative measure of the interactions among various
43 biological communities and their abiotic environment, ecosystem metabolism is a potentially
44 powerful tool for providing a holistic understanding of human effects on ecosystems. To date,
45 the effects of eutrophication on lake and stream ecosystem metabolism are perhaps the best
46 studied (e.g., Oviatt et al. 1986; D'Avanzo et al. 1996; Kemp et al. 2009; Davidson et al. 2015).
47 Insight into future consequences of climate change for freshwater metabolism comes from
48 observational (e.g., Roberts et al. 2007) and experimental (e.g., Moss 2010; Davidson et al. 2015;
49 Yvon-Durocher et al. 2017) studies. The impact of contaminants on aquatic metabolism has been
50 difficult to establish because of confounding effects of excess nutrient inputs (e.g., Aristi et al.
51 2015), and investigations in mesocosms (e.g., Wiegner et al. 2003; Brooks et al. 2004) may miss
52 key processes that operate at the whole-ecosystem scale. In the related field of ecosystem

restoration, i.e., facilitating the recovery of degraded ecosystems, ecosystem metabolism has been used to evaluate the recovery of restored streams (McTammany et al. 2007; Northington et al. 2011; Hoellein et al. 2012; Giling et al. 2013). Investigations of restored lakes (Dunalska et al. 2014) and wetlands (McKenna 2003) are less common and have generally been limited to short-term studies (14 or fewer days of metabolism data), but see Jeppesen et al. (2012).

We investigated drivers of GPP, ER, and NEP in three prairie wetlands at different stages of restoration. In North America, prairie wetlands, or “potholes”, have been frequently drained for agriculture, resulting in the loss of their many ecosystem functions and services. Restoration of drained wetlands seeks to reverse these losses. The studied wetlands included one site hydrologically restored in 2009 (hereafter “recently restored”), one restored in 1998 (“older restored”), and a wetland that had never been drained (“natural”). The study was based on a simple conceptual framework wherein drainage and subsequent restoration may affect the abiotic environment or biological communities in prairie wetlands (Fig. 1). In turn, ecosystem functions arise from complex interactions between the abiotic environment and wetland biota. Our goal was to identify variables that explain: 1) variation in daily metabolic rates within the wetlands; and 2) among-site differences in metabolic rates and their drivers (arrows 3a and 3b in Fig. 1). We previously documented that the recently restored wetland emitted more carbon dioxide and had lower NEP than the older restored and natural wetlands (box 2 in Fig. 1; Bortolotti et al. 2016a). We also showed that the abiotic environment and some biological communities (e.g., submersed aquatic vegetation [SAV]) are different in recently restored wetlands compared to more established wetlands (arrows 1a and 1b in Fig. 1; Bortolotti et al. 2016b). Given these previously described differences, we predicted that the recently restored wetland would be less

productive and have different metabolic drivers when compared to the older restored and natural wetlands.

Methods

Study area

We quantified ecosystem metabolism in the open-water zone of three wetlands during May-September 2013. This study followed a pilot investigation in 2012; those data are not analyzed here, but are published elsewhere (see Bortolotti et al. 2016a). The wetlands were chemically and biologically representative of three “restoration states” and were selected for in-depth study based on a survey of 24 sites in the central aspen parkland ecoregion of southeastern Saskatchewan, Canada (see Bortolotti et al. 2016b). Wetlands were hydrologically restored by Ducks Unlimited Canada by building earth berms across drainage ditches and allowing the basin to refill with precipitation and runoff. All three wetlands were naturally fishless and classified as semi-permanent (Class IV, characterized by hydroperiods lasting at least 5-6 months per year; Stewart and Kantrud 1971). All basins retained water during the entire course of this study and mean surface areas and depths were 0.41 ha and 0.77 m (natural wetland), 0.88 ha and 0.90 m (older restored wetland), and 0.27 ha 0.81 m (recently restored wetland). The two smaller sites experienced greater seasonal changes in area and volume than the older restored wetland. At each site, a ring of emergent vegetation dominated by cattails (*Typha*), bulrushes (*Scirpus* spp.), and/or sedges (*Carex* spp.) surrounded an open-water zone. SAV covered as much as 100 % of the wetland bottom, though in the deepest part of the wetland there was always open water above the vegetation from which to collect samples and measurements. The natural wetland was located on a 65 ha parcel of uncultivated and ungrazed land. In 2013, the older restored wetland

was also on land that was fallow, though it had been lightly grazed by cattle in some previous years. The recently restored wetland was situated on land cultivated with canola during the summer of 2013, but previously only lightly grazed by cattle.

Quantification of ecosystem metabolism

We quantified ecosystem metabolism using the diel oxygen technique. Floating anchored rafts holding a sonde and small meteorological station were deployed over the deepest point of each wetland in the open-water zone. Sondes (one Hydrolab DS5 and two YSI EXO2) were deployed continuously from May-September apart from breaks for cleaning and calibration approximately every two weeks. Sondes were equipped with optical dissolved O₂, pH, temperature, and conductivity probes and logged every 20 minutes at a depth of 25 cm below the water surface. A single EXO total algae probe (excitation at 470 and 590 nm, emission at 685 nm) was rotated between the two YSI sondes. O₂ probes were calibrated in air-saturated water. The meteorological stations were equipped with a Met One 014A anemometer (at 1 m height), a Young 61302V barometer, a Kipp & Zonen PQS1 photosynthetically active radiation (PAR) sensor, and a Campbell Scientific CR800 or CR10X datalogger programmed to log readings every 20 minutes.

The diel O₂ method for calculating ecosystem metabolism is based on the premise that, during the day, observed changes in O₂ concentrations are the result of two metabolic processes (production of O₂ by autotrophs and consumption of O₂ through respiration by all organisms) and exchange of O₂ with the atmosphere (Odum 1956). Photochemical changes in O₂ are not modeled (Cole et al. 2000). At night, GPP = 0 so that respiration and atmospheric exchange are the only processes affecting O₂ concentrations. By assuming that daytime and nighttime

respiration rates (R_{day} and R_{night}) are equal, it is then possible, after accounting for atmospheric exchange, to compute daily: a) ER as the hourly R_{night} rate multiplied by 24 hours; b) GPP from the sum of changes in O_2 concentration for each time step ($\Delta O_2/\Delta t$) during the day plus daytime respiration (the sum of R_{day}); and c) NEP rate as $GPP - ER$ (Cole et al. 2000; Staehr et al. 2010b). Thus, positive NEP denotes net autotrophy and negative NEP equates to net heterotrophy. It is likely that $R_{\text{day}} > R_{\text{night}}$ (Pace and Prairie 2005; Tobias et al. 2007; Hotchkiss and Hall 2014; though see Bachmann et al. 2000), which causes an underestimation of GPP and ER, but does not affect estimates of NEP.

Calculation of metabolic rates followed Cole et al. (2000). Briefly, the change in O_2 concentration over time was considered a product of the balance of O_2 production by photosynthesis and O_2 consumption by respiration, and the diffusive exchange of O_2 with the atmosphere (F) in the mixed layer (Z_{mix} = mixed layer depth). Due to the shallow depth of the wetlands, we assumed that $Z_{\text{mix}} = Z_{\text{max}}$, although this might not have always been the case. F can be calculated as follows:

$$F = k_{O_2}(O_{2\text{sat}} - O_{2\text{meas}})$$

where k_{O_2} is the piston velocity (m/s) calculated from k_{600} (Cole and Caraco 1998) and Schmidt coefficient (Jähne et al. 1987), and $(O_{2\text{sat}} - O_{2\text{meas}})$ is the difference between the concentration of O_2 in equilibrium with the atmosphere ($O_{2\text{sat}}$) and the measured O_2 concentration in water ($O_{2\text{meas}}$). All calculations were made in the R programming environment (R Development Core Team 2012).

Measurements of drivers of metabolism

We quantified several environmental variables that might explain variation in ecosystem metabolism, including climatic variables (PAR, wind speed), nutrient concentrations (inorganic nitrogen, phosphorus), and water column properties (water temperature at both the surface and bottom of the water column, light attenuation). We also measured possible biological drivers of metabolism, like substrates for microbial respiration (dissolved organic carbon [DOC], sediment OC) and proxies of primary producer abundance (chlorophyll *a* [chl *a*], SAV cover, dissolved organic nitrogen [DON]).

Daily average PAR and wind speed were calculated from meteorological station readings. Daily average surface water temperature was calculated from sonde readings. Water samples were collected weekly into HDPE bottles to quantify water chemistry, including total phosphorus (TP), ammonium (NH_4^+), nitrite + nitrate ($\text{NO}_2 + \text{NO}_3^-$), total dissolved nitrogen (TDN), DOC, and chl *a*. Samples were processed and preserved the same day, then stored in the dark at 5°C or frozen until being analyzed at the CALA- (Canadian Association for Laboratory Accreditation) accredited University of Alberta Biogeochemical Analytical Service Laboratory (see supplementary information for details of the analytical methods used). On > 60 % of days, $\text{NO}_2 + \text{NO}_3^-$ concentrations were below detection limit ($2 \mu\text{g L}^{-1}$), and concentrations were always small relative to NH_4^+ . Given that NH_4^+ is the form of inorganic nitrogen most often preferred by primary producers (Graham and Wilcox 2000), we did not include $\text{NO}_2 + \text{NO}_3^-$ in subsequent statistical analyses. We used linear interpolation between sampling days to obtain daily estimates of these water chemistry variables so that they could be included in models of metabolism.

HOBO pendant temperature data loggers recorded temperatures at both the surface and bottom of the water column. We calculated the temperature difference between the surface and

bottom water (hereafter, ΔT) as a proxy of thermal stratification and, inversely, the potential for mixing events. ΔT ranged from -0.02 to 7.33, with only one instance of $\Delta T < 0$. Approximately every 2 weeks, we measured a vertical profile of PAR in the water column of the wetlands using a LI-COR 192SA underwater quantum radiation sensor. From these readings, we calculated the vertical light extinction coefficient (k_d) as:

$$k_d = \frac{\ln I_0 - \ln I_z}{z}$$

where I_0 is the photon flux density a few cm below the water surface, and I_z is the photon flux density at depth z (in this case, the bottom of the wetland).

To quantify sediment OC content we collected triplicate sediment cores on five occasions between May and mid-July 2013 from each of the three wetlands using a 7.6 cm diameter polycarbonate tube. We sectioned off and froze the top two cm of each core. These sections were subsequently freeze-dried, homogenized, and analyzed for OC content by loss on ignition for 4 hours at 550 °C (Heiri et al. 2001).

We determined three proxies for SAV biomass to avoid excessive disturbance of the wetlands from SAV harvest. The first proxy was % SAV cover within the wetland, linearly interpolated to get a daily estimate of SAV cover. The second biomass proxy was a categorical measure (SAV_{cat}) with levels of “low”, “medium”, and “high” cover. These categories corresponded to 0-25 %, 26-50 %, and 51-100 % cover, respectively. Although there is generally a positive relationship between SAV area and biomass, this relationship varies with species (Armstrong et al. 2003) and cover estimates cannot capture all changes in SAV biomass (e.g., when SAV stands become denser). Therefore, the third proxy for SAV biomass, dissolved organic nitrogen (DON), was not based on SAV cover. We calculated DON by subtracting the

concentration of inorganic species (NH_4^+ and $\text{NO}_2 + \text{NO}_3^-$) from TDN. DON, along with DOC, increased seasonally in these wetlands, a pattern typical of prairie wetlands attributable to release of exudates by submersed macrophytes and algae (Berman and Bronk 2003; Waiser 2006). Exudates and their organically bound nutrients are linked to photosynthesis by, not degradation of, submersed macrophytes (Demarty and Prairie 2009). Supporting our interpretation of autochthonous generation of DON and DOC, C:N molar ratios declined seasonally (Fig. S1). Because DON concentrations are also influenced by evapoconcentration and algal biomass (including epiphytes associated with the SAV), they are an imperfect proxy for SAV alone. However, DON was unrelated to chl *a* concentrations (Fig. S2) and the relationship between DON and SAV cover (Fig. S3) suggests that, despite these previously mentioned limitations, DON captured changes in SAV biomass that % SAV cover did not.

Statistical analyses

We used generalized least squares regression (gls in the nlme package in R; Pinheiro et al. 2014) to identify predictors of metabolic rates as gls regression allows model errors to be both correlated and have unequal variance (Zuur et al. 2009). As for most time series data, metabolic rates were autocorrelated through time (evaluated using the Durban-Watson statistic; Scheiner and Gurevitch 2001). There was also evidence of heteroskedasticity in GPP and ER model residuals. We used an exponential variance function structure and a first-order autoregressive structure as required to account for the heteroskedasticity and autocorrelation, respectively.

Drivers of metabolic rates were initially modeled with all sites together, including site and site by predictor variable interactions (e.g., site x temperature) because of possible site-specific responses to metabolic drivers. However, given that the best models for GPP, ER, and

NEP each included 3 or 4 site-predictor interactions, we ultimately decided to model each site separately. There were $n = 128$ observations for the older restored site and $n = 130$ for the recently restored site. Although we had 138 daily metabolism measurements for the natural site, malfunction of the HOBO dataloggers in mid-August limited metabolism models to a total of 98 observations.

We considered 10 potential predictors in GPP models including temperature, PAR, wind speed, ΔT , NH_4^+ , TP, chl a , and one of DON, SAV, or SAV_{cat} . DON, SAV, and SAV_{cat} represent alternative proxies for the same variable (SAV biomass) and thus only one measure was used per model. Five covariates were considered in ER models: wind speed, ΔT , DOC, and one of surface or bottom temperature. In NEP models, we considered eight variables: temperature, PAR, wind speed, ΔT , chl a and one of DON, SAV, or SAV_{cat} . Temperature was eventually dropped from models of NEP due to problems of collinearity, and no substantive relationship with NEP. We considered quadratic effects of variables only when indicated by initial data exploration and visualization. Predictor variables were standardized before modelling. Two variables, k_d and sediment OC, were not measured with sufficient frequency to include in the regressions.

To select the most parsimonious model of metabolism, and to examine the relative support for models including different proxies for SAV biomass, we used an information-theoretic approach (Akaike's Information Criterion corrected for small sample size; AIC_c). We followed criteria outlined in Burnham and Anderson (2002), wherein the model with the lowest AIC_c is deemed best, and models with ΔAIC_c values ≤ 2 and < 4 (ΔAIC_c being the difference between the best-approximating and lower ranked models) are considered well-supported and plausible, respectively. We report models within $4 \Delta \text{AIC}_c$, though not those containing

uninformative parameters (Arnold et al. 2010). Akaike weights (ω_i) were also used to make inferences about relative support for competing models (Burnham and Anderson 2002). AIC_c were calculated with the `AICcmodavg` package in R (Mazerolle 2015). Predictor variables in the final models were tested for collinearity by ensuring that all variance inflation factors were less than ~ 5 (Zuur et al. 2009). Model selection was done using maximum likelihood estimation, but parameters were calculated using restricted maximum likelihood estimation. We report $\beta \pm SE$ of the best models unless otherwise stated. Following convention, we calculated ER rates as negative numbers (and are presented that way in Fig. 2), but β were calculated from models where ER rates were positive to make the direction of the relationship between ER and its drivers more intuitive.

We characterized differences among sites with respect to the possible drivers of metabolism in two ways. First, we used principal components analysis (PCA) of square root-transformed data, including only measured (i.e., not interpolated) values to characterize the three sites with respect to their water chemistry and thermal environment (i.e., water temperature, ΔT). Second, we used Analysis of Covariance (ANCOVA) to evaluate whether the variables used in the metabolism models varied by site, changed with date, and whether there was a site by date interaction. Randomization tests (Manly 1997) were used to assess the significance of the ANCOVAs because these data violated the statistical assumption of independent observations. We used `lmp` in the `lmPerm` package in R (Wheeler and Torchiano 2016). Observations were randomly assigned (999 permutations) to a site, and the P -value was calculated based on the number of times the randomly generated test statistics exceeded the test statistic derived from the original data. We described the relationship between GPP and ER using standardised major axis (SMA) estimation, calculated in the `smatr` package in R (Warton et al. 2012).

Results

Metabolic rates varied both temporally and spatially among the three wetlands (Fig. 2). GPP and ER were highest in the older restored wetland, followed by the natural and recently restored wetlands, with each site displaying unique seasonal patterns of these rates (Fig. 2a-c, Table 1). ER was strongly coupled to GPP in all wetlands (Fig. 3). However, SMA estimation showed that GPP and ER were more closely coupled in the natural ($\beta = 1.19 \pm 0.05$, $P < 0.001$, $R^2 = 0.78$) and recently restored ($\beta = 0.99 \pm 0.04$, $P < 0.001$, $R^2 = 0.80$) wetlands than in the older restored wetland ($\beta = 0.97 \pm 0.06$, $P < 0.001$, $R^2 = 0.57$). With all sites combined, $\beta = 1.03 \pm 0.03$, $P < 0.001$, and $R^2 = 0.74$.

NEP was highest in the natural wetland, the only site to have a net autotrophic signal over the course of the open-water season (Fig. 2d-f, Table 1). In contrast, both restored wetlands were net heterotrophic overall, with the recently restored wetland more strongly so (Fig. 2d-f, Table 1). The natural and older restored wetlands showed similar seasonal changes in NEP, with numerous autotrophic days in mid-summer.

Drivers of ecosystem metabolism

Tables 2-4 show the top models of GPP, ER, and NEP and Table 5 contains the parameter estimates for variables in the best-approximating model for each site and metabolic rate. Drivers of GPP differed among the three sites, with some measure of SAV being the only variable appearing in the best-approximating models of all three sites. The best-approximating model of GPP in the natural wetland included PAR, wind speed, ΔT , and DON ($\omega_i = 1.000$; Table 2). In contrast, the best-approximating model for the older restored wetland ($\omega_i = 0.684$) included

PAR, chl *a*, and an orthogonal second-order polynomial of DON. In the recently restored wetland, the best-approximating model ($\omega_i = 0.461$) included temperature, ΔT , TP, chl *a*, and SAV_{cat}. Other measures of SAV abundance (SAV, DON) appeared in plausible models. GPP increased with PAR and temperature, but decreased with greater ΔT (Table 5). Although GPP decreased with increasing wind speeds in the natural wetland (i.e., lower GPP when the water column is presumably better mixed), contrary to the relationship with ΔT (i.e., higher GPP when the water column is better mixed), the effect of ΔT on GPP was both greater and better estimated than that of wind speed (Table 5). In both the natural and recently restored wetlands, GPP was positively related to SAV. In contrast, GPP in the older restored wetland showed a unimodal relationship to DON, with maximum GPP at intermediate DON concentrations. The GPP-chl *a* relationship was positive in the recently restored wetland, but negative and poorly estimated in the older restored wetland.

Drivers of ER rates generally included some measure of water temperature and water column mixing (Table 3). Only in the recently restored wetland was there an ER-DOC relationship (Table 5). At all sites, greater ER was associated with higher water temperatures and lower ΔT . ER was also positively related to wind speed.

PAR and wind speed were in the best-approximating model of NEP for all sites (Table 4), but the wetlands differed with respect to NEP-producer relationships — SAV influenced the natural wetland whereas chl *a* affected the recently restored wetland (Table 5). At all sites, higher NEP was associated with greater PAR and lower wind speeds (Table 5). The best NEP models for the natural ($\omega_i = 1.000$) and older restored ($\omega_i = 0.291$) sites each included some proxy for SAV biomass (Table 4). The best models of NEP in the older restored and recently restored sites also included chl *a*. NEP and SAV cover were positively related in the natural

wetland (Table 5) whereas the NEP-SAV relationship was slightly negative in the older restored site, though other measures of SAV and a well-supported model including the second-order polynomial of DON suggested this relationship was non-linear (Table 4). The NEP-chl *a* relationship was positive in the recently restored wetland, but negative in the older restored wetland (Table 5).

Differences in environmental variables among wetlands

In the spring, there was little difference among the sites with respect to their water chemistry and thermal environment (Fig. 4). However, as the season progressed, the recently restored site was differentiated based on its greater TP and chl *a*, whereas temporal changes in the older restored and natural wetlands were more strongly related to NH_4^+ and DON (Figs. 4, 5, Table 6). Results from the ANCOVAs support this interpretation, with a significant site or site x date interaction for NH_4^+ , TP, and chl *a* (Fig. 5). The site effect for DOC and DON was not statistically significant, but the recently restored wetland differed from the other sites (i.e., had non-overlapping confidence intervals; Table 6). The variables measured too infrequently to be included in models of metabolism, k_d and sediment OC, also varied by site. Until late June, k_d was similar among wetlands and it did not change seasonally in the natural wetland (Fig. 6). In contrast, from late June onwards, k_d was elevated in the recently restored wetland and, to a lesser extent, the older restored wetland. Mean ($\pm$ standard deviation) surface sediment OC content was highest in the older restored wetland (60.0 ± 11.0 %), followed by the natural (39.1 ± 13.8 %) and recently restored (26.7 ± 14.5 %) wetlands.

Discussion

Metabolic rates in the three wetlands were high relative to other lentic ecosystems (Laas et al. 2012; Solomon et al. 2013), each showing distinct magnitudes and drivers of GPP, ER, and NEP. Although the wetlands showed, as expected, similar metabolic responses to abiotic variables such as PAR and temperature, they differed in terms of the direct and interactive influences of biotic factors, such as SAV and phytoplankton abundance. In particular, SAV better explained variation in NEP in the older restored and natural wetlands while phytoplankton appeared to be stronger drivers of NEP in the recently restored wetland. Below, we offer potential explanations for our key findings.

Drivers of daily variation in ecosystem metabolism

The abiotic drivers that most influenced GPP and NEP were PAR and proxies of water column stratification. Only in the recently restored wetland was there evidence that nutrients (i.e., TP) might influence GPP. Greater GPP and NEP were associated with greater PAR, but stratification proxies had opposite effects; GPP was lower when the water column was less well mixed (i.e., high ΔT) whereas NEP was elevated (i.e., higher NEP with lower wind speeds). The relationship between stratification proxies and metabolism likely reflects variable incorporation of benthic production and respiration to observed rates. That GPP increased with decreased ΔT could be the result of various processes; for example, that benthic processes contributed to production, consistent with a shallow system with light transmission to the benthos. Alternatively, greater GPP when the water column is well mixed could reflect nutrient resuspension or effects of water circulation on the light climate. However, the negative NEP-wind speed relationship indicated

that the wetland benthos may have contributed more to respiration than production. Investigations of drivers of metabolic rates in wetlands have been few to date, making it difficult to compare our findings to any general understanding of factors affecting metabolism in freshwater wetlands (Hoellein et al. 2013). However, the drivers identified here are common to lakes, especially small and shallow lakes and ponds (e.g., Sand-Jensen and Staehr 2007; Coloso et al. 2008; Staehr et al. 2010a; Hoellein et al. 2013; Klotz 2013).

SAV was the most consistently important biological driver of GPP and NEP, but its effect on metabolism was complex and sometimes site-specific. In the natural wetland, GPP and NEP were positively related to SAV. In contrast, in the older restored wetland, peak GPP and NEP were observed at intermediate SAV abundance. The GPP-SAV relationship was positive and linear in the recently restored wetland, but SAV was unrelated to NEP at this site and it was the only site where chl *a* concentrations were positively related to GPP and NEP. Without having measured benthic metabolism or epipellic abundance, it is difficult to identify the exact contributions of benthic producers versus SAV to wetland metabolism. However, we generally emphasize the importance of SAV over epipelon, while acknowledging that the relative contribution of these communities to GPP likely changed seasonally. The depth of the photic zone ranged from 0.65 m (in the recently restored wetland) to 3.4 m (in the natural wetland). Most of the time, the depth of the photic zone was greater than wetland depth. However, light attenuation measurements were always made in unvegetated areas and thus overestimate illumination of the benthos. For ~ two thirds of the study period, most of the wetland bottom was covered in SAV (Fig. 5h), undoubtedly shading the sediments. Thus, we expect that the contribution of the phytobenthos to GPP is likely greatest in the spring. Prairie wetlands also support significant emergent vegetation communities (Stewart and Kantrud 1971). Emergent

374 macrophyte leaves exchange gases directly with the atmosphere, so their immediate production
375 and respiration are not captured in estimates of metabolism in the open-water zone. Only the
376 decomposition of these plants, usually those from the previous growing season, may be captured
377 in open-water O_2 measurements. Overall, the consistent inclusion of SAV abundance (or some
378 proxy for it) in GPP models underscores the importance of this community to prairie wetland
379 production.

380 Drivers of ER were consistent across the three wetlands, with greater ER observed at
381 warmer temperatures, when the water column was likely to be well mixed (i.e., small ΔT and/or
382 high wind speeds), and when GPP was high. There was not strong support for an ER-DOC
383 relationship, though Solomon et al. (2013) also did not detect a significant relationship in a
384 synthesis of respiration in lakes. The coupling of ER and GPP (Fig. 3) suggested that
385 autochthonous material supported much of the respiration in these wetlands. The strength of
386 coupling between GPP and ER in this system (slopes > 0.9 , R^2 values of 0.57-0.80) was close to
387 predictions and measurements for oligotrophic lakes (Solomon et al. 2013), which was surprising
388 for a productive wetland ecosystem. Background respiration (i.e., the intercept of the regression
389 line; Solomon et al. 2013) varied among sites, with levels in the two restored wetlands (~ 75
390 $\text{mmol } O_2 \text{ m}^{-3} \text{ day}^{-1}$) exceeding the natural wetland ($-103.1 \text{ mmol } O_2 \text{ m}^{-3} \text{ day}^{-1}$). However, in an
391 analysis of the three sites together, the intercept was not significantly different from zero,
392 suggesting very low background respiration in these wetlands. Low background respiration is
393 indicative of low rates of respiration of allochthonous and recalcitrant autochthonous organic
394 carbon (Solomon et al. 2013). Our findings are similar (with respect to regression slope and
395 intercept) to a study of small lakes that, although oligotrophic, were SAV-dominated (Martinsen

et al. 2017), again suggesting a major role for SAV in shaping the metabolism of shallow lentic ecosystems.

Insights into wetland function and resemblance to shallow lakes

The general absence of nutrients in models of GPP was consistent with evidence from shallow lakes wherein nutrient limitation is less common than light limitation in nutrient-rich systems or when producers can access nutrients from the sediments (e.g., Sand-Jensen and Staehr 2007; Kragh et al. 2017). Although DOC is an important regulator of light attenuation in many aquatic ecosystems, in prairie wetlands, phytoplankton generally determine turbidity (Zimmer et al. 2016) as we found with the k_d -chl a relationship being stronger than the k_d -DOC relationship (Fig. S4). Similarly, the greatest light attenuation was measured in the recently restored site, which had the highest chl a but lowest DOC concentrations of the three wetlands. Thus, although the same amount of PAR reached the water surface at the three sites (Fig. 5a, Table 6), phytoplankton likely limited light availability to other primary producers (SAV, epiphytes, and epipelon). In the recently restored wetland, periods of elevated light attenuation and chl a coincided with high TP concentrations (Fig. 7). Despite little support for nutrient limitation of primary production, phosphorus may have played a role in stimulating phytoplankton blooms and thus contributing to turbid conditions. Also, even though nutrients did not explain much variation in daily metabolic rates, it does not discount the potential for nutrients to drive variation in metabolism at other scales.

SAV had an important role in shaping light conditions and, thus, the metabolism of prairie wetlands. There was always some measure of SAV in the top models of GPP (Table 2), consistent with studies of shallow lakes that emphasized the role of SAV in driving production

(e.g., Brothers et al. 2013; Kragh et al. 2017). In contrast, SAV or a SAV proxy only appeared in top models of NEP for the natural and older restored sites; DON concentrations were significantly lower in the recently restored wetland (Table 6). The natural wetland had low k_d throughout the open-water season (Fig. 6), associated with high SAV abundance and low chl a concentrations, despite sometimes high nutrient concentrations. Given that macrophyte community composition affects the stability of the clear-water conditions (Hilt 2015) and some species of SAV can impede the development of phytoplankton (Mjelde and Faafeng 1997), SAV taxonomic identity may be more important than SAV biomass to preserving clear-water conditions. We suggest that by maintaining clear-water conditions and associated minimal light attenuation, the SAV may have created conditions that maximized not only SAV photosynthetic rates, but also epiphytic and benthic production, resulting in conditions of net autotrophy. Vesterinen et al. (2016) documented that production by periphyton can be significant and contributes to the net autotrophic status of small boreal lakes. In contrast, the recently restored wetland, the most net heterotrophic of the three sites, supported both abundant SAV and phytoplankton and showed seasonally increasing light attenuation (Fig. 6). Phytoplankton may have suppressed production by other primary producers by modifying light availability. Some studies of shallow lakes are consistent with our findings and describe phytoplankton-dominated systems as less productive and more heterotrophic than macrophyte-dominated ones, often due to shading by phytoplankton (e.g., Blindow et al. 2006; Brothers et al. 2013). However, manipulations of lakes between clear and turbid states (e.g., Jeppesen et al. 2012; Zimmer et al. 2016) have noted no changes in GPP and NEP between states.

As in other shallow lake systems (e.g., Attermeyer et al. 2017; Martinsen et al. 2017), autochthonous production was important in shaping ER. Although there was little evidence that

DOC drove day-to-day variation in ER, the highest ER rates were observed in the site with the greatest DOC and sediment OC pools (i.e., the older restored wetland), suggesting that among-wetland differences in ER could have been driven by the availability of substrates for microbial respiration. Although DOC concentrations are influenced by evapoconcentration, the patterns observed cannot be accounted for by estimated volumetric changes (L.E. Bortolotti, unpublished data). Given the relatively close coupling of ER and GPP in this system (i.e., GPP is an important source of OC for respiration), GPP may also have explained differences in ER rates among sites. Given that autochthonous and allochthonous DOC often differ with respect to characteristics such as colour and incorporation into food webs (Karlsson et al. 2012), systems with predominantly autochthonous DOC may not fit neatly into limnological paradigms about DOC (e.g., Bogard et al. 2019). Furthermore, sediment OC may be especially important to ER in shallow ecosystems. In the older restored wetland, we measured higher sediment OC content and less coupled GPP and ER ($R^2 = 0.57$) compared to the other sites ($R^2 > 0.77$), though background respiration was just as high in the recently restored wetland. ER fueled by sediment OC, which is derived from emergent macrophytes grown during previous open-water seasons, would contribute to the decoupling of GPP and ER by releasing heterotrophic organisms from dependence on (recent) production-generated carbon. Although we did not attempt to elucidate why the older restored wetland has greater sediment OC content, anecdotally, that site has a greater area of emergent vegetation in and around the basin than the other wetlands. Given that the older restored wetland had abundant SAV and relatively low chl *a* and k_d , which support high rates of GPP, it is possible that the net heterotrophy observed in this site could be attributable to higher benthic respiration rates fueled by sediment OC.

Influence of restoration history

In addition to having unique drivers of metabolism, the three sites showed different rates of metabolism and site characteristics, with the recently restored site standing out from the other two most often, especially with respect to TP, chl *a*, and k_d (Figs. 4, 5, 6) and its lower GPP, ER, and NEP (Table 1). Previous research showed that recently restored wetlands have less sediment OC, higher carbon dioxide concentrations, lower pH, more TP, and different SAV community composition than natural and older restored wetlands (i.e., there is an effect of restoration on both the abiotic environment and biological communities — arrows 1a and 1b, Fig. 1; Bortolotti et al. 2016b). These factors are all plausibly related to metabolic rates (arrows 3a and 3b in Fig. 1) and align with the finding that the recently restored wetland was less productive, had lower ER rates, and was the most net heterotrophic of the three wetlands. Previous work has shown that older restored and natural wetlands are similar with respect to water chemistry and the taxonomic composition of SAV, benthic producer communities (Bortolotti et al. 2016b) and emergent vegetation (Puchniak 2002). Thus, differing metabolic rates between the older restored and natural wetlands in this study (Table 1) may instead reflect wetland variation that is unrelated to the restoration history of the sites. Ultimately, it is impossible, due to the constraints imposed by our study design and resources available for this study, to conclusively relate site characteristics or restoration history to the observed differences in ecosystem metabolism — to comment more definitively we would need to measure ecosystem metabolism in a greater number of sites.

Conclusions

Our study adds to the evidence that small, shallow, non-forested aquatic systems are neither consistently net autotrophic nor net heterotrophic — rather, they oscillate between these two

488 states (e.g., Sand-Jensen and Staehr 2007; Laas et al. 2012; Klotz 2013; Martinsen et al. 2017).
489 Prairie wetlands displayed coupling of GPP and ER on par with lakes, and showed great
490 similarity to shallow lakes with respect to ecosystem metabolism. In particular, the importance of
491 SAV and the benthos, light limitation, and strong autochthonous production set prairie wetlands
492 (which could also be described as ponds) and shallow lakes apart from larger lakes where
493 production is most strongly correlated with levels of TP and allochthonous inputs and colored
494 DOC shape metabolic rates (e.g., Hanson et al. 2003). Given the abundance of small aquatic
495 ecosystems and their importance in global biogeochemical cycles (Downing 2010; Holgerson
496 and Raymond 2016), there would be great merit in developing a more unifying theory of the
497 functioning of these systems in a rapidly changing world. Further research is clearly needed to
498 better characterize and understand the impacts of anthropogenic perturbations and subsequent
499 restoration efforts on the ecosystem metabolism of not only lakes, but also ponds and wetlands.

500

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Table 1. Mean $\pm$ standard deviation of gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) in $\text{mmol O}_2 \text{ m}^{-3} \text{ day}^{-1}$ in three prairie wetlands in May-September 2013. The three sites included a natural wetland (i.e., has never been drained), an older restored wetland (restored in 1998), and a recently restored wetland (restored in 2009).

	Natural ($n = 138$)	Older restored ($n = 128$)	Recently restored ($n = 130$)
GPP	461 ± 178	545 ± 181	296 ± 172
ER	-444 ± 211	-605 ± 190	-375 ± 169
NEP	17 ± 99	-60 ± 118	-80 ± 76

Table 2. Ranking of models explaining variation in gross primary production in three prairie wetlands in May-September 2013. Only those models within 4 ΔAIC_c and the statistical null model are presented. Variables included in the models were photosynthetically active radiation (PAR), wind speed (Wind), water temperature (Temp), the temperature difference between surface and bottom waters as a proxy for stratification (ΔT), ammonium concentrations (NH_4^+), total phosphorus concentrations (TP), chlorophyll *a* concentrations (Chl), and one of three measures of submersed aquatic vegetation abundance (SAV, % cover of submersed vegetation; SAV.cat, submersed vegetation cover as a categorical variable with levels “low”, “medium”, and “high”; DON, dissolved organic nitrogen concentrations). Akaike’s information criterion corrected for small-sample bias (AIC_c) is an estimator of the expected Kullback-Leibler information (i.e., the discrepancy between the candidate model and the true model generating the data). ΔAIC_c is the difference between the AIC_c of the candidate model and the minimum AIC_c (1053.84). Akaike weight (ω_i) is the likelihood that the candidate model is the best model in the set, given the data and the other models in the set. *K* is the number of estimable parameters.

Site	Model structure	AIC_c	ΔAIC_c	ω_i	<i>K</i>
Natural	PAR, Wind, ΔT , DON	1208.85	0	1.000	8
	Intercept and model structure only (statistical null)	1239.69	30.84	< 0.001	4
Older restored	PAR, Chl, DON^2	1529.33	0	0.684	8
	PAR, DON^2	1531.91	2.57	0.189	7
	PAR, Temp, TP, Chl	1532.7	3.36	0.127	8
	Intercept and model structure only (statistical null)	1583.42	54.09	< 0.001	4
Recently restored	Temp, ΔT , TP, Chl, SAV.cat	1523.52	0	0.461	10
	Temp, ΔT , TP, Chl, SAV	1523.95	0.43	0.372	9
	Temp, ΔT , Chl, DON	1525.54	2.02	0.168	8
	Intercept and model structure only (statistical null)	1572.21	48.69	< 0.001	4

Table 3. Ranking of models explaining variation in ecosystem respiration in three prairie wetlands in May-September 2013. Only those models within 4 ΔAIC_c and the statistical null model are presented. Variables included in the models were wind speed (Wind), surface or bottom water temperatures (Temp, BTemp), the temperature difference between surface and bottom waters as a proxy for stratification (ΔT), and dissolved organic carbon (DOC).

Site	Model structure	AIC_c	ΔAIC_c	ω_i	K
Natural	BTemp, ΔT	1241.92	0	0.641	6
	Temp, ΔT	1243.08	1.16	0.359	6
	Intercept and model structure only (statistical null)	1265.57	23.65	< 0.001	4
Older restored	Wind, BTemp, ΔT	1566.67	0	0.437	7
	Wind, Temp, ΔT	1567.07	0.40	0.358	8
	Wind, BTemp	1568.18	1.51	0.205	7
	Intercept and model structure only (statistical null)	1589.14	22.47	< 0.001	4
Recently restored	Global (Wind, Temp, ΔT , DOC)	1553.86	0	0.444	8
	Wind, DOC	1554.40	0.54	0.339	6
	Global (Wind, BTemp, ΔT , DOC)	1555.30	1.44	0.216	8
	Intercept and model structure only (statistical null)	1614.43	60.57	< 0.001	4

Table 4. Ranking of models explaining variation in net ecosystem production in three prairie wetlands in May-September 2013. Only those models within 4 ΔAIC_c and the statistical null model are presented. Variables included in the models were photosynthetically active radiation (PAR), wind speed (Wind), the temperature difference between surface and bottom waters as a proxy for stratification (ΔT), chlorophyll *a* concentrations (Chl), and one of three measures of submersed aquatic vegetation abundance (SAV, % cover of submersed vegetation; SAV.cat, submersed vegetation cover as a categorical variable with levels “low”, “medium”, and “high”; DON, dissolved organic nitrogen concentrations).

Site	Model structure	AIC _c	ΔAIC_c	ω_i	K
Natural	PAR, Wind, SAV.cat	1077.68	0	1.000	7
	Intercept and model structure only (statistical null)	1172.18	94.50	< 0.001	3
Older restored	PAR, Wind, Chl, DON	1454.83	0	0.291	7
	PAR, Wind, SAV.cat	1455.23	0.40	0.238	7
	PAR, Wind, Chl, SAV	1455.71	0.88	0.188	7
	PAR, Wind, SAV	1456.70	1.87	0.114	6
	PAR, Wind, Chl, DON ²	1456.85	2.02	0.106	8
	PAR, Wind, DON	1457.91	3.08	0.062	6
	Intercept and model structure only (statistical null)	1507.83	53.00	< 0.001	3
Recently restored	PAR, Wind, Chl	1354.45	0	1.000	6
	Intercept and model structure only (statistical null)	1442.03	87.58	< 0.001	3

Table 5. Parameter estimates from the best-approximating models of gross primary production (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) in three prairie wetlands in May-September 2013. Variable abbreviations include: photosynthetically active radiation (PAR), wind speed (Wind), surface water temperature (Temp), bottom water temperature (BTemp), the temperature difference between surface and bottom waters as a proxy for stratification (ΔT), total phosphorus concentrations (TP), chlorophyll *a* concentrations (Chl), dissolved organic carbon (DOC), and one of three measures of submersed aquatic vegetation abundance (SAV.cat, submersed vegetation cover as a categorical variable with levels “low”, “medium”, and “high”; DON, dissolved organic nitrogen concentrations).

Rate	Natural		Older restored		Recently restored	
	Variable	β (SE)	Variable	β (SE)	Variable	β (SE)
GPP	PAR	87.65 (13.15)	PAR	86.97 (12.25)	Temp	66.55 (21.61)
	Wind	-38.28 (13.01)	Chl	-34.44 (16.01)	ΔT	-35.89 (10.37)
	ΔT	-116.98 (22.96)	DON ²	-596.05 (168.20)	TP	-69.50 (28.56)
	DON	70.16 (18.18)			Chl	104.87 (21.00)
					SAV.cat	116.00 (30.63)
ER	BTemp	55.45 (15.73)	Wind	32.87 (14.25)	Wind	35.51 (10.61)
	ΔT	-103.05 (18.20)	BTemp	85.81 (14.81)	Temp	29.35 (18.09)
			ΔT	-31.51 (15.86)	ΔT	-29.39 (13.32)
					DOC	81.33 (14.81)
NEP	PAR	77.79 (6.15)	PAR	60.90 (8.30)	PAR	32.06 (4.87)
	Wind	-26.10 (6.79)	Wind	-33.25 (9.89)	Wind	-38.35 (5.43)
	SAV.cat	32.54 (16.92)	Chl	-25.12 (9.58)	Chl	16.33 (5.61)
			DON	-17.92 (7.90)		

Table 6. Least squares means, 95 % confidence intervals, and sample sizes from linear models examining the effect of site, date, and their interaction on: photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{sec}^{-1}$), wind speed (m sec^{-1}), water temperature ($^{\circ}\text{C}$), difference in water temperature between surface and bottom waters (ΔT , $^{\circ}\text{C}$), ammonium concentration (NH_4^+ , $\mu\text{g L}^{-1}$), total phosphorus concentration (TP, $\mu\text{g L}^{-1}$), chlorophyll *a* concentration (Chl *a*, $\mu\text{g L}^{-1}$), submersed aquatic vegetation % cover (SAV), dissolved organic carbon (DOC, mg L^{-1}), dissolved organic nitrogen (DON, $\mu\text{g L}^{-1}$) in three prairie wetlands. Only measured values (i.e., non-interpolated values) were included in these calculations and all measurements were made between May and September 2013.

	Natural	Older restored	Recently restored
PAR	700.8 (663.0, 738.7) <i>n</i> = 138	756.3 (716.8, 795.7) <i>n</i> = 128	747.4 (708.5, 786.4) <i>n</i> = 130
Wind speed	1.9 (1.8, 2.0) <i>n</i> = 138	2.2 (2.0, 2.3) <i>n</i> = 128	2.4 (2.3, 2.6) <i>n</i> = 130
Temperature	19.4 (18.8, 20.0) <i>n</i> = 138	19.4 (18.8, 20.0) <i>n</i> = 128	17.6 (17.0, 18.2) <i>n</i> = 130
ΔT	2.6 (2.3, 3.0) <i>n</i> = 98	1.9 (1.7, 2.2) <i>n</i> = 128	3.0 (2.8, 3.3) <i>n</i> = 130
NH_4^+	23 (2, 44) <i>n</i> = 19	94 (71, 116) <i>n</i> = 17	23 (1, 45) <i>n</i> = 17
TP	134 (100, 169) <i>n</i> = 19	84 (47, 120) <i>n</i> = 17	277 (240, 313) <i>n</i> = 17
Chl <i>a</i>	8.6 (-2.5, 19.6) <i>n</i> = 19	9.4 (-1.9, 20.7) <i>n</i> = 18	49.1 (38.1, 60.1) <i>n</i> = 19
SAV	67 (57, 77) <i>n</i> = 18	49 (38, 60) <i>n</i> = 14	67 (57, 78) <i>n</i> = 16
DOC	30.2 (29.0, 31.4) <i>n</i> = 19	31.1 (29.8, 32.3) <i>n</i> = 17	25.9 (24.7, 27.2) <i>n</i> = 17
DON	2395 (2313, 2477) <i>n</i> = 19	2562 (2476, 2649) <i>n</i> = 17	2106 (2019, 2193) <i>n</i> = 17

FIGURE CAPTIONS

Figure 1. A framework for the effects of drainage and hydrological restoration on ecosystem attributes including the abiotic environment, biological communities, and ecosystem function. Arrow and box labels are explained in the text.

Figure 2. Daily estimates of ecosystem metabolism ($\text{mmol O}_2 \text{ m}^{-3} \text{ day}^{-1}$) in three prairie wetlands in May-September 2013. The left column of panels corresponds to the natural wetland (i.e., has never been drained), the center column to the wetland hydrologically restored in 1998 (older restored), and the right column to the wetland hydrologically restored in 2009 (recently restored). (a-c) Gross primary production (GPP; black circles) and ecosystem respiration (ER; open circles). (d-f) Net ecosystem production (NEP; grey circles). Positive NEP values indicate net autotrophy and negative values net heterotrophy.

Figure 3. Relationship between ecosystem respiration (ER) and gross primary production (GPP) in three prairie wetlands in May-September 2013. The dotted line represents the 1:1 line and the solid line the standardised major axis estimation for the site. The R^2 and P -values are the statistics associated with that estimation.

Figure 4. Association of sites and environmental variables in a recently restored (black), older restored (grey), and natural (white) prairie wetland based on principal components analysis of water chemistry (ammonium $[\text{NH}_4^+]$, dissolved organic carbon [DOC], dissolved organic nitrogen [DON], chlorophyll a [Chl a], and total phosphorus [TP]) and thermal environment

(difference in water temperature between surface and bottom waters [ΔT], water temperature [Temp]) data. Point size is proportional to sampling date.

Figure 5. Predicted drivers of ecosystem metabolism in three prairie wetlands in May-September 2013. Restoration state is indicated by symbol colour: open/white = natural, grey = older restored, and black = recently restored. Only measured (i.e., non-interpolated values) are shown here. Metabolic drivers include a) photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{sec}^{-1}$); b) wind speed (m sec^{-1}); c) water temperature ($^{\circ}\text{C}$); d) difference in water temperature between surface and bottom waters as a proxy for stratification (ΔT , $^{\circ}\text{C}$); e) ammonium concentration ($\mu\text{g L}^{-1}$); f) total phosphorus concentration ($\mu\text{g L}^{-1}$); g) chlorophyll *a* concentration ($\mu\text{g L}^{-1}$); h) % submersed aquatic vegetation cover; and i) dissolved organic carbon (DOC, mg L^{-1} ; circles) and dissolved organic nitrogen (DON, mg L^{-1} ; triangles). Above each panel is the significance of the effects of site, date, and a site x date interaction on the associated variable in an ANCOVA (significance determined by permutation testing). Significance levels are denoted as: *** at $P = 0.001$, ** at $P = 0.01$, * at $P = 0.05$, and n.s. (not significant).

Figure 6. Vertical light extinction coefficients (k_d ; m^{-1}) in three prairie wetlands in May-September 2013.

Figure 7. Total phosphorus (TP) and chlorophyll *a* (chl *a*) concentrations in the recently restored prairie wetland in May-September 2013. TP concentrations are depicted as triangles, and chl *a* as circles. Black circles are values determined by fluorometric methods from water collected ~

824 every two weeks. Grey circles are non-quantitative, high-frequency chl *a* readings from a total
825 algae probe on a multiparameter sonde.

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