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Understanding drivers of aquatic ecosystem metabolism in freshwater subtropical ridge and slough wetlands

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Abstract. How climate and habitat drive variation in aquatic metabolism in wetlands remains uncertain. To quantify differences in seasonal aquatic metabolism among wetlands, we estimated aquatic ecosystem metabolism (gross primary productivity, GPP; ecosystem respiration, ER; net aquatic productivity, NAP) in subtropical ridge and slough wetlands of the Florida Everglades from more than 2 yr of continuously measured water column dissolved oxygen, photosynthetically active radiation (PAR), water temperature, and water depth. Gross primary productivity and ER were modeled from light, temperature, and water depth using non-linear minimization and maximum likelihood. Reaeration rates were estimated from wind speed. Dissolved oxygen was below saturation at all sites during both wet and dry seasons. Water depth interacted with vegetation to influence PAR, water temperature, and spatiotemporal patterns in aquatic metabolism. Gross primary productivity and ER were highest at the slough with lowest submerged aquatic vegetation (low-SAV slough), intermediate in the sawgrass (*Cladium jamaicense*) ridge site, and lowest at the slough with highest submerged aquatic vegetation (high-SAV slough). Ecosystem respiration was strongly positively correlated with GPP at the sawgrass ridge and low-SAV slough sites. Gross primary productivity increased with water temperature and PAR across all habitat types, whereas ER decreased (more respiration) with water temperature and PAR. Net aquatic productivity was negatively correlated with water temperature and positively correlated with PAR, suggesting that ER was more sensitive than GPP to water temperature. Aquatic metabolism was largely net heterotrophic in all wetlands, and high-SAV appeared to buffer seasonal variation in PAR and water temperatures that drive NAP in subtropical wetlands. Our results suggest that aquatic ecosystem metabolism in wetlands with seasonal hydrology is sensitive to changes in water depth and vegetation density that influence temperature and light. Expanding our understanding of how metabolic processes and carbon cycling in wetland ecosystems vary across gradients in hydrology, vegetation, and organic matter could enhance our understanding and protection of conditions that maximize carbon storage.

Key words: dissolved oxygen; floc; freshwater marsh; long-term ecological research; net aquatic ecosystem metabolism; subtropical.

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Introduction

Wetland ecosystems play a disproportionately large role in global carbon storage (Chmura et al. 2003, Mitsch et al. 2013). The ability to produce and store carbon varies across wetland types as a function of hydrogeomorphology and in response to shifts in the physiological activity of emergent vegetation with seasonal and changes in temperature and water level (Bernal and Mitsch 2012, Mitsch et al. 2013). A global meta-analysis of CO_2 fluxes among wetlands found that inland wetlands are small or neutral carbon storage sinks relative to coastal wetlands (Lu et al. 2017). Although primary productivity and ecosystem respiration in wetlands is largely driven by temperature and precipitation, as well as characteristics of emergent vegetation (Malone et al. 2014, Lu et al. 2017), understanding how hydrogeomorphology drives the balance between carbon gains and losses is needed to more accurately estimate the carbon sequestering capacity of wetlands ecosystems (Bernal and Mitsch 2012).

The Florida Everglades, the largest freshwater peatland in the United States, is a model ecosystem to study carbon storage dynamics of wetlands due to its seasonal hydrology and spatially heterogeneous habitat mosaics. The subtropical climate of South Florida has a distinct wet–dry seasonality in hydrology that interacts with higher elevation ridge and lower elevation slough vegetation to provide a range in wetland water depths from ~0 to 90 cm (McVoy et al. 2011). In the central Everglades, the ridge–slough habitat mosaic is an iconic feature that is thought to be maintained by seasonal hydrology and soil elevation feedbacks that promote bi-stable divergence and persistence in higher elevation (ridge) and lower elevation (slough) wetlands (Heffernan et al. 2013). Although carbon burial and accumulation derived from plant production in soils is the dominant biological pathway for storing carbon in ecosystems (Chapin et al. 2009), the relative contributions of water column processes and the influence of active forms of detrital organic matter on carbon storage vs. flux in wetlands remain uncertain.

In ridge and slough freshwater wetlands like the Everglades, flocculent organic matter (hereafter floc) is formed from submerged vegetation and periphyton, which can be entrained or transported downstream (Jaffé et al. 2001, Pisani et al. 2015). Characteristic of the Everglades, sawgrass (*Cladium jamaicense*) ridges form alongside sloughs dominated by submerged aquatic vegetation (SAV) that contribute to the formation of flocculent organic matter in long-hydroperiod freshwater marsh wetlands. Vertical fluxes of CO_2 suggest that Everglades freshwater wetlands are highly heterogeneous and can fluctuate from being a small source to a small sink of CO_2 annually depending on spatiotemporal changes in hydrology (Jimenez et al. 2012, Schedlbauer et al. 2012, Malone et al. 2014, Zhao et al. 2019). Emergent vegetation is believed to drive net aquatic productivity (NAP) in these wetlands (Ewe et al. 2006, Hagerthey et al. 2010). Water column metabolism is driven by photosynthesis and respiration from periphyton, submerged aquatic plants, algae, cyanobacteria, and emergent vegetation, and respiration from heterotrophic decomposition of organic matter (Davis and Ogden 1994, McCormick and Laing 2003, Hagerthey et al. 2010). Although NAP in the Everglades has been studied in response to variation in P concentrations (Davis and Ogden 1994, McCormick and Laing 2003, Iwaniec et al. 2006) and habitat type (Ewe et al. 2006, Hagerthey et al. 2010), we still do not fully understand the magnitude and the drivers of the temporal variation in aquatic carbon dynamics in freshwater subtropical ridge and slough wetlands, particularly related to water depth, vegetation density, and floc deposition.

We quantified the magnitude and variability in aquatic ecosystem metabolic rates in freshwater subtropical ridge and slough wetlands of the Florida Everglades. Specifically, we focused on differences between peat-dominated ridge wetlands that have shallower water depths than nearby peat-dominated slough wetlands that contain greater variation in vegetation density and higher floc deposition. We predicted that (1) NAP would become more heterotrophic (ecosystem respiration, ER > gross primary productivity, GPP) with lower water depths and higher floc deposition (during the dry season and in higher density vegetation) and (2) ER would be positively related to GPP during the dry season when lower water depths enable light to penetrate to the bottom of the wetland (Fig. 1) (Hagerthey et al. 2010). We expected the ridge (higher

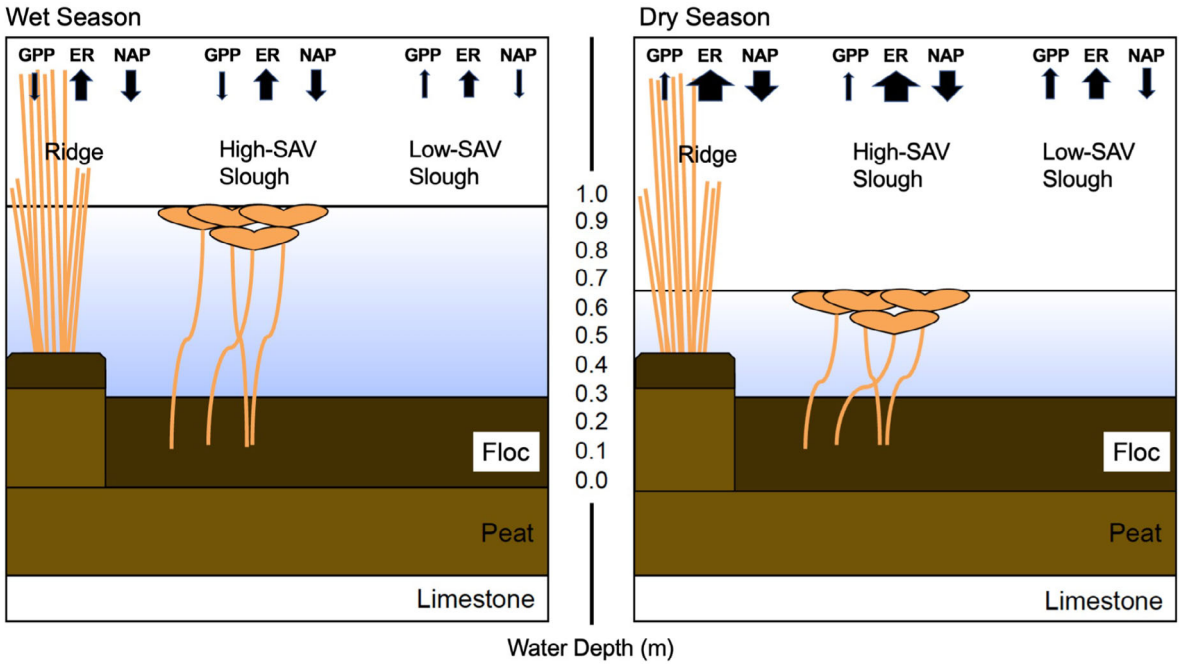


Fig. 1. A conceptual model of aquatic ecosystem metabolism (gross primary productivity, GPP; ecosystem respiration, ER; net aquatic productivity, NAP) during wet and dry season differences in water depth. Freshwater marsh wetlands include sawgrass (*Cladium jamaicense*) ridge and sloughs with high- and low-density submerged aquatic vegetation (SAV) habitats of the Florida Everglades (South Florida, USA). Photo credit: John Kominoski.

vegetation density, lower water depth) to be more heterotrophic than sloughs due to light attenuation from emergent vegetation (Fig. 1) (Hagerthey et al. 2010). We also hypothesized that the slough habitat with higher density SAV (high-SAV slough) would have higher ER and lower NAP (more heterotrophic) than the slough habitat with lower density SAV (low-SAV slough), as greater light attenuation was expected at higher SAV density as well as higher microbial oxygen demand from higher floc deposition (Fig. 1).

Materials and Methods

Site description

Our study site (25.780859°, −80.726742) was located in ridge and slough wetlands of the southern Water Conservation Area 3A (WCA-3A) about 1.6 km North of Tamiami Trail with Everglades National Park to the South (Fig. 2). We selected three sampling locations, all within 20 m of each other, two within a single slough and one in the adjacent sawgrass (*C. jamaicense*) ridge (Fig. 2). The slough was ~50 m wide; the ridge ~30 m wide; and the ridge sampling point was located ~3 m into the ridge. The high-SAV slough site contained water lily (*Nymphaea odorata*), spikerush (*Eleocharis cellulosa*), and bladderwort (*Utricularia foliosa* and *U. purpurea*), and the low-SAV slough site was dominated by few water lily (*N. odorata*) (Fig. 2). A benthic layer of unconsolidated floc—a heterogeneous mixture of algal and detrital organic matter—generally is found covering the peat of the sloughs and the ridges to a thickness that varies from 0 to 25 cm thick (McVoy et al. 2011, Pisani et al. 2015). The thickness of the layer may be thinner on the sawgrass ridges than in the sloughs, but on ridges, the thickness can be obscured by visible fragments of dead sawgrass leaves (C. McVoy, *personal observation*).

Dissolved oxygen and temperature

We deployed dissolved oxygen (DO) loggers (D-Opto SDI-12 Optical DO Sensor; ENVCO Global, Auckland, New Zealand) by attaching them to vertical tripods adjusted every 60 d to

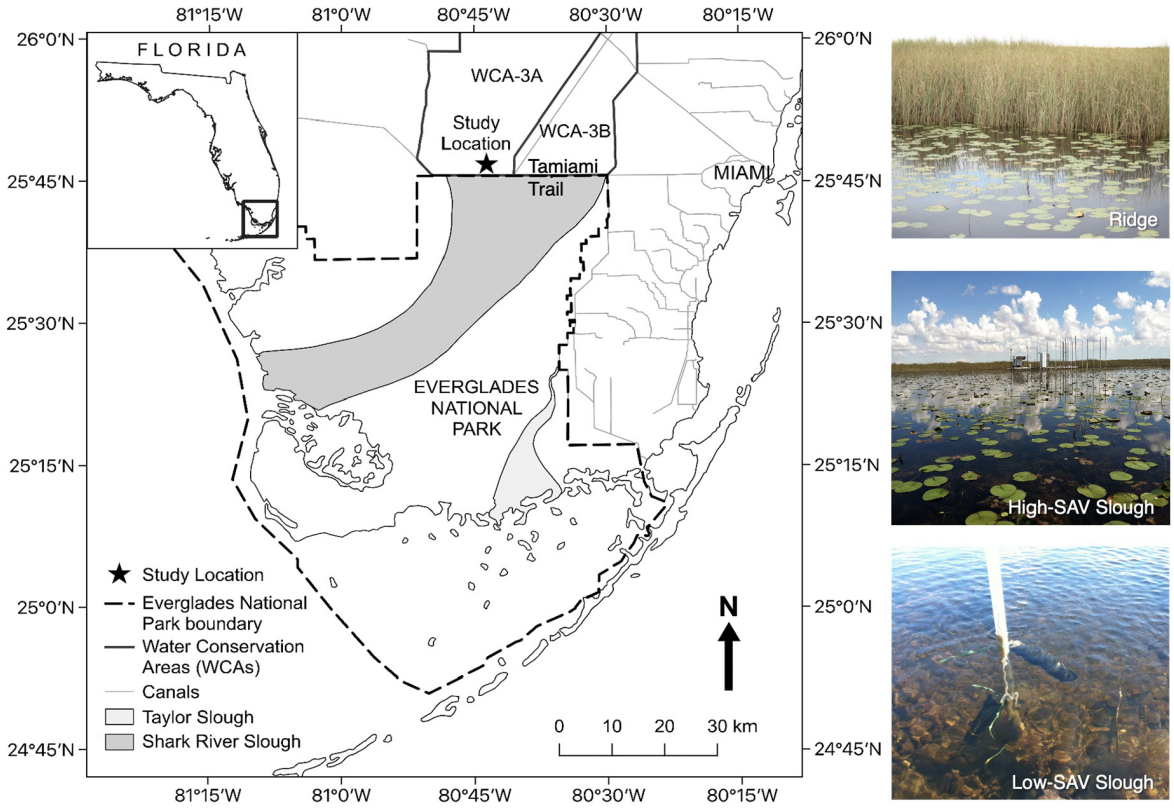


Fig. 2. Location of the study sites within freshwater marsh wetlands with ridge and slough habitats of the Florida Everglades, North of Everglades National Park (South Florida, USA). Map produced by Mike Rugge.

mid-depth of the water column level at the two slough locations (~15 to 45-cm depth) and one ridge location (~5 to 30-cm depth). We positioned DO sensors facing upward and above benthic substrates to ensure that measurements were made in the water. When the DO sensor in the ridge site was above the water during peak dry periods, we were able to detect and exclude these data recorded as supersaturated %DO. The ENVCO Global loggers recorded DO concentrations and temperature at 15-min intervals at each location from 14 February 2014 to 23 March 2016. Sites were visited every 60 d to download data, remove any fouling of the sensors, check calibration, and vertically reposition the DO loggers at mid-depth in the water column, if necessary. Prior to deploying DO loggers, each logger was calibrated in air-saturated water (water that had been aerated with an airstone for 20 min). Upon retrieval from the field, DO loggers were tested for potential drift assessed by recording DO and temperature in air-saturated water and adjusted as necessary.

Meteorological and stage measurements

At the research platform, photosynthetically active radiation (PAR) ($\mu mol \cdot s^{-1} \cdot m^{-2}$) was measured continuously at approximately 3 m above the water surface and averaged every 15 min (Apogee Model SQ-100, Logan, Utah, USA). Barometric pressure was recorded every 15 min (WXT-520; Vaisala, Helsinki, Finland). Stage in the slough was recorded at 15-min intervals using a level transducer installed in a PVC tube at a set depth (KPSI Model 500 SDI-12, 0-4 PSI range, 0.05% accuracy, TE Connectivity, Schaffhausen, Switzerland) and converted to water depths (cm) using the peat elevations of the bottom of the slough and surface of the ridge. Due to proximity (<20 m) and the absence of any hydrological barriers, it was assumed that stages at both slough locations and at the ridge location

were identical. Wind speed (m/s) at approximately 3 m above water surface was measured using a sonic anemometer (Vaisala WXT-520).

Surface water physicochemistry

In October 2014, during the peak of the wet season when water depths were highest, we recorded depth-specific PAR using triplicate measures at 15–20 cm depth intervals from the surface of the water to the surface of the soil in each habitat. We generated PAR attenuation curves for each site to quantify the change in light from the surface with increasing water depth. We used these discrete depth-specific PAR attenuation measurements to help interpret modeled estimates of metabolism from continuous water depth and surface PAR measurements. In 2014 and 2015, we collected triplicate grab water samples from mid-depth of the water column at each site during dry and wet seasons, placed on ice in the field, and returned them to the laboratory for dissolved organic carbon (DOC), total nitrogen (TN), and total phosphorus (TP). A total of $N = 36$ water samples were analyzed for water chemistry. Total P was analyzed following Solórzano and Sharp (1980), and TN was measured with an Antek TN analyzer (Antek Instruments, Houston, Texas, USA). Dissolved organic carbon was analyzed on filtered (0.7-mm GF/F filters; Whatman, Maidstone, UK) samples using a Shimadzu TOC Analyzer (Shimadzu, Columbia, Maryland, USA). Water chemistry analyses were conducted at the Southeast Environmental Research Center Nutrient Analysis Laboratory (SERC-NAL). SERC-NAL followed strict internal and external QA assurance practices and is NELAC Certified for non-potable water-General Chemistry under State Lab ID E76930.

Diel dissolved oxygen and aquatic ecosystem metabolism

Oxygen flux was estimated by fitting the following model to the oxygen data (Van de Bogert et al. 2007, Hall et al. 2015)

$$O_i = O_{i-t} + \frac{\text{GPP} \times \text{PPFD}_t}{z \times \sum \text{PPFD}} + \frac{\text{ER} \times \Delta t}{z} + K(O_s - O) \times \Delta t \quad (1)$$

where O_2 at time i is equal to O_2 at the previous time $(i-1)$ plus time step-specific rates of GPP and ER, z is water depth, and K is air–water gas exchange coefficient per unit time (based on the reaeration flux $K(O_s - O)$, and the difference between dissolved O_2 and O_2 at saturation for a given temperature and barometric pressure). O_s is saturated oxygen concentration, estimated as a function of barometric pressure and water temperature (Garcia and Gordon 1992), and $O_s - O$ is the saturation deficit. PPFD_t is photon flux density during the time interval t (μmol photons·m^{-2}·s^{-1}). In this model, ER is a negative O_2 flux because O_2 is being consumed. The time step (Δt) is the measurement interval of logged O_2 data for each DO sonde. We assumed that GPP was a linear function of light (Van de Bogert et al. 2007) and that ER was constant throughout the day. During our measurements, we rarely observed DO saturation (see below *Results*). Net aquatic productivity (NAP) was measured as the change in DO after accounting for diffusive exchange with the atmosphere or reaeration (K) (Hagerthey et al. 2010).

$$\text{NAP}_t = \text{GPP}_t - \text{ER}_t \quad (2)$$

$$K_t = 0.5 \times 10^{0.15} \times w_t \quad (3)$$

In aquatic ecosystems, K_t is generally modeled as a function of wind speed (w_t) (Cole and Caraco 1998, Caffrey 2004, Hagerthey et al. 2010, Solomon et al. 2013), although studies have shown that commonly used wind speed/gas exchange relationships may overestimate the gas transfer velocity in wetland ecosystems (Ho et al. 2018).

To estimate GPP and ER, we fit the model of diel whole-stream metabolism to the measured oxygen data by finding estimates of GPP and ER that minimized the negative log-likelihood of the model to the data using function *nlm*() in R (Hall et al. 2015). We compared modeled estimates and fits based on the minimized log-likelihood estimate (LLE). We used the following exclusion criteria for modeled GPP and ER: We eliminated positive estimates of ER, repeated values for subsequent dates, and used LLE (values > 600) combined with the determination of realistic estimates of GPP and ER based on the distribution of all modeled values. Exclusion of data based on these criteria accounted for 3–20% of daily

estimates of GPP and ER (ridge: $n = 97$ of 525; high-SAV slough: 122 of 597; low-SAV slough: 18 of 611), leaving $n = 428$ (ridge), $n = 475$ (high-SAV slough), and $n = 593$ (low-SAV slough) diel estimates (total $N = 1496$). See Kominoski (2021) for the full dataset from this study.

Data analyses

We used ordinary non-parametric bootstrapping to estimate uncertainty in modeled estimates of GPP and ER with 10,000 repeated samples. We detected low uncertainty and strong positive correlation (0.86) between GPP and ER with a standard error of 0.009 and 95% confidence interval range of −0.878 to −0.843. Therefore, we used all estimates of GPP and ER that had minimized LLE and realistic estimates (see Diel dissolved oxygen and aquatic ecosystem metabolism).

We used simple linear regressions to compare goodness of fits between water depth and submerged PAR levels for each habitat type. Linear regressions were also used to compare the relationships between GPP and ER at each habitat type. We also created a matrix of all pairwise Pearson's correlation coefficients and examined univariate density plots and loess curves using the ggpairs function in the GGally package in R (Schloerke et al. 2018) for the daily variables: NAP, GPP, ER, water temperature, PAR, and water depth (Appendix S1: Figs. S1–S4).

To understand differences in aquatic metabolism among ridge and low- and high-SAV slough habitats, we evaluated the effect of water depth (cm), PAR, and water temperature (°C) on daily NAP, GPP, and ER using generalized additive models (GAM) with the *gam* function in the "mgcv" package (Wood 2012) in R. We built separate GAMs for each habitat type. Generalized additive models use smooth functions to model non-linear functional relationships between predictors and the response. This approach separates linear trends from any general non-linear trends and determines whether the significance of a smoothed variable is associated with a simple linear trend or a more complicated pattern. We used Quantile-Quantile (Q-Q) plots of the residuals to evaluate whether the appropriate distribution, identity, and log-link were used. The Durbin-Watson statistic, with the *durbinWatsonTest* function in the "car" package (Fox and Weisberg 2011), was used to determine the AR(1) correlation coefficient. We then specified the AR(1) correlation coefficient and used the *gam.check* function to evaluate the convergence of the smoothness selection optimization and run diagnostic tests to evaluate whether the dimension choices were adequate. We then proceeded by updating the original GAM model. A P value of ~0.05 was used to determine the inclusion of independent variables (water temperature, PAR, and water depth), and the explanatory powers of the final models were compared using the R^2 statistic and the percent deviance explained. We recognize that P-values are not straightforward, as is the case with mixed models and machine learning approaches. With GAM models, P-values should not be used for harsh cutoffs and low P values are sufficient for statistical significance. For the standard Gaussian setting in mgcv, we can use R^2 as a measure of the variance explained. This approach also provides a "deviance explained" (DEV), which is nearly identical to the unadjusted R^2 for our model settings, but for non-Gaussian models, the deviance explained is preferred. All statistical analyses were performed in R v.3.6.1 and RStudio v. 1.2.1335 (R Development Core Team 2020).

Results

Surface water physicochemistry

Median water depth was consistently 30 cm greater in slough sites than the ridge site due to higher elevation in the ridge (Fig. 3A–C). Median (range: minimum–maximum) water depth was 38 cm (20–101 cm) in the ridge, 91 cm (53–108 cm) in the high-SAV slough, and 99 cm (50–135 cm) in the low-SAV slough (Fig. 3A–C). Light (PAR) exponentially decreased with water depth at each site but varied among sites as a function of depth (Fig. 4A–C). Water chemistry was similar among the sites, so the values reported here are the composite mean. Mean (±SE) concentrations (mg/L) of DOC (13.0 ± 0.55), TN (0.45 ± 0.02), and TP (0.01 ± 0.00) were measured.

Diel dissolved oxygen and aquatic ecosystem metabolism

All habitats had evident diel changes in DO during both dry and wet seasons, but there were habitat-specific differences in DO saturation

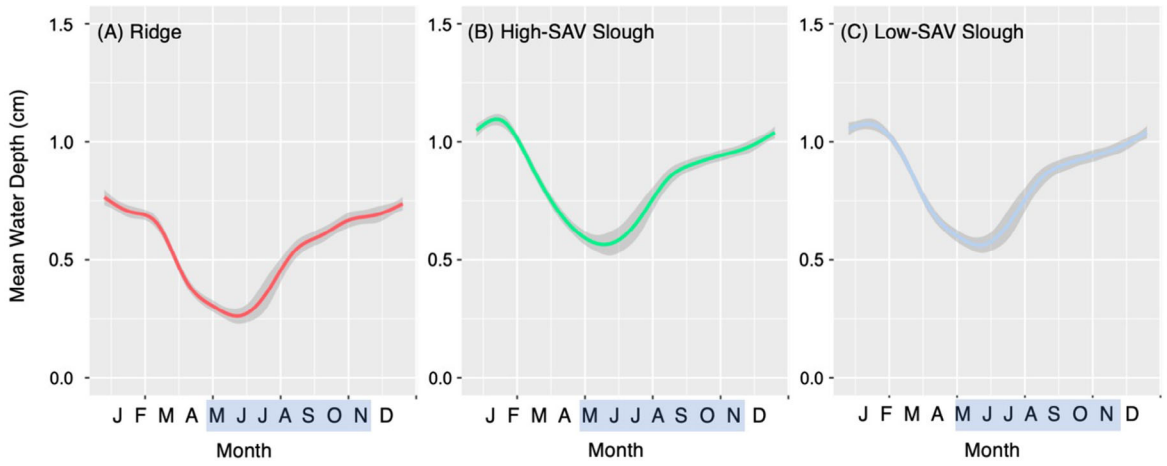


Fig. 3. Water depths in ridge and slough habitats of freshwater marsh wetlands of the Florida Everglades (South Florida, USA). Data trends were estimated from mean daily water depth and smoothed with generalized additive models. Blue shaded months on the *x*-axis label (letters denote abbreviated months) indicate the wet season (May–November).

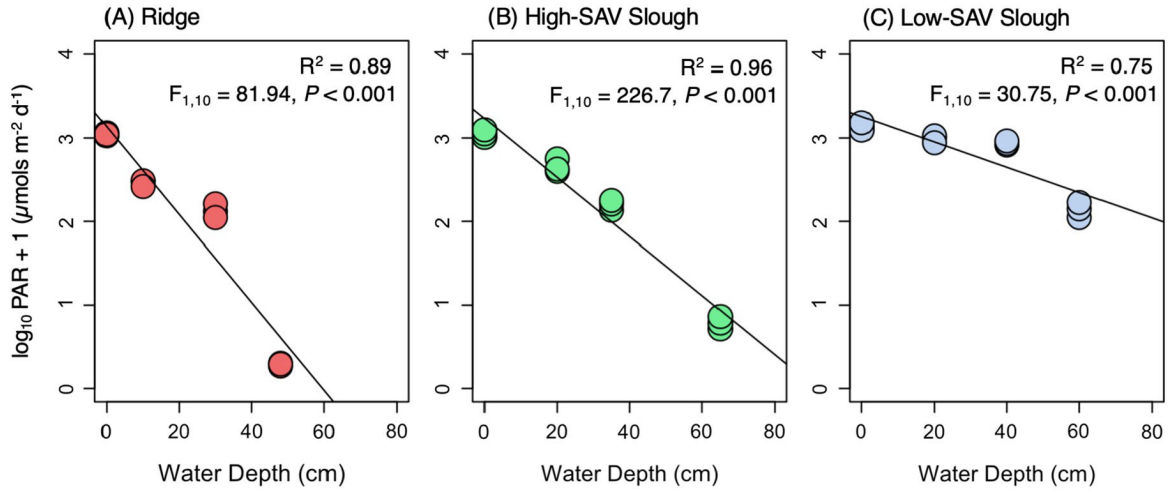


Fig. 4. Attenuation of photosynthetically active radiation (PAR) with water depth in ridge and slough habitats of freshwater marsh wetlands of the Florida Everglades (South Florida, USA). Triplicate measurements were made at 15–20 cm depth intervals from the surface of the water to the surface of the soil in each habitat.

(Fig. 5A–F). All sites were under-saturated; there were distinct differences in patterns among habitats and seasons. During the dry season, DO in ridge and low-SAV slough sites were both approximately 2 mg/L below saturation (Fig. 5A, E) compared to the high-SAV slough being up to 8 mg/L below saturation (Fig. 5C). In contrast, during the wet season, DO concentrations at all sites were approximately 6 mg/L below saturation (Fig. 5B, D, F). Dissolved oxygen concentrations in the high-SAV slough were nearly the same during both dry and wet seasons (Fig. 5C, D). Correcting DO for reaeration resulted in minimal changes to diel DO patterns in all habitats and seasons (see red lines, Fig. 5A–F).

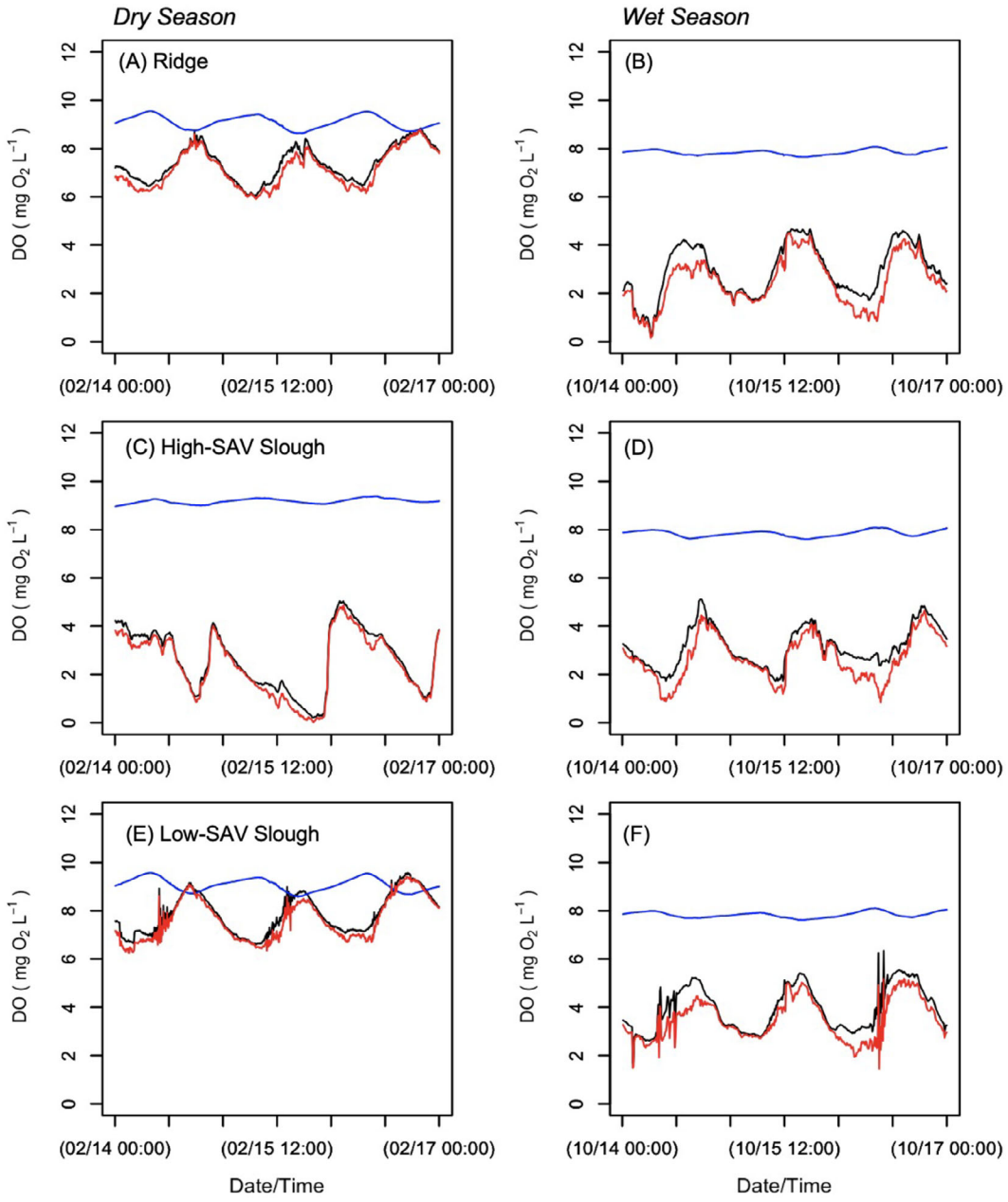


Fig. 5. Examples of typical dissolved oxygen (DO) measurement (black lines) and DO saturation (blue lines) in freshwater subtropical ridge and slough wetlands of the Florida Everglades (South Florida, USA). Measurements were made during dry and wet seasons in a sawgrass (*Cladium jamaicense*) ridge (A, B) and sloughs with high- (C, D) and low-density (E, F) submerged aquatic vegetation (SAV). Diel dissolved oxygen was corrected (red lines) for estimated reaeration modeled from wind speed.

Modeled rates of aquatic GPP (Fig. 6A–C) and ER (Fig. 6D–F) in ridge and slough wetlands were highest during periods of the dry season when water levels decreased and during periods of the wet season water levels increased. The lowest GPP and ER levels in ridge and slough wetlands generally occurred during times of the year when water depths are typically lowest

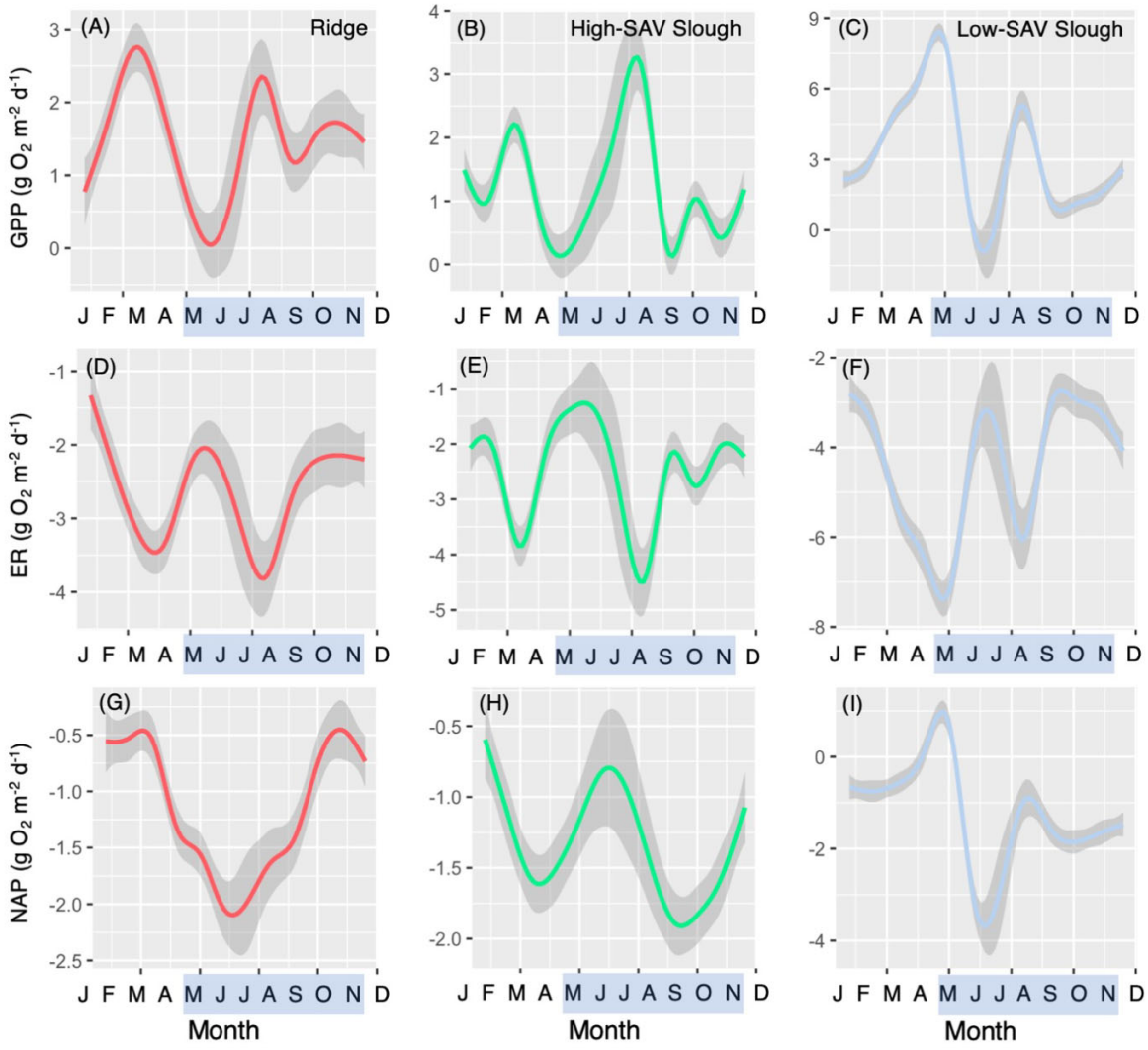


Fig. 6. Generalized additive model predictions and the effect of smoothed date on (A–C) gross primary productivity (GPP), (D–F) ecosystem respiration (ER), and (G–I) net aquatic productivity (NAP) in ridge and slough habitats. Blue shaded months on the *x*-axis label (letters denote abbreviated months) indicate the wet season (May–November).

(Fig. 6A–F). The lowest GPP and ER rates were at the high-SAV slough site (Fig. 6B, E). Ridge and slough aquatic metabolism was largely net heterotrophic (negative NAP; Fig. 6G–I), except for the low-SAV slough during the peak dry season (April; Fig. 6I). Ecosystem heterotrophic state was highest during the lowest water depths in ridge and low-SAV slough wetlands, whereas the strongest negative NAP values were measured during periods of intermediate depth in the high-SAV slough (Fig. 6G–I). Rates of ER were strongly positively related to GPP at the ridge and low-SAV slough sites and less correlated at the high-SAV slough site (Fig. 7A–C).

Drivers of aquatic metabolism by habitat

In ridge and slough habitats, smoothed water temperature ($P < 0.001$; Fig. 8A), PAR ($P < 0.001$; Fig. 8B), and water depth ($P < 0.001$; Fig. 8C) explained patterns in GPP (DEV = 60%). In

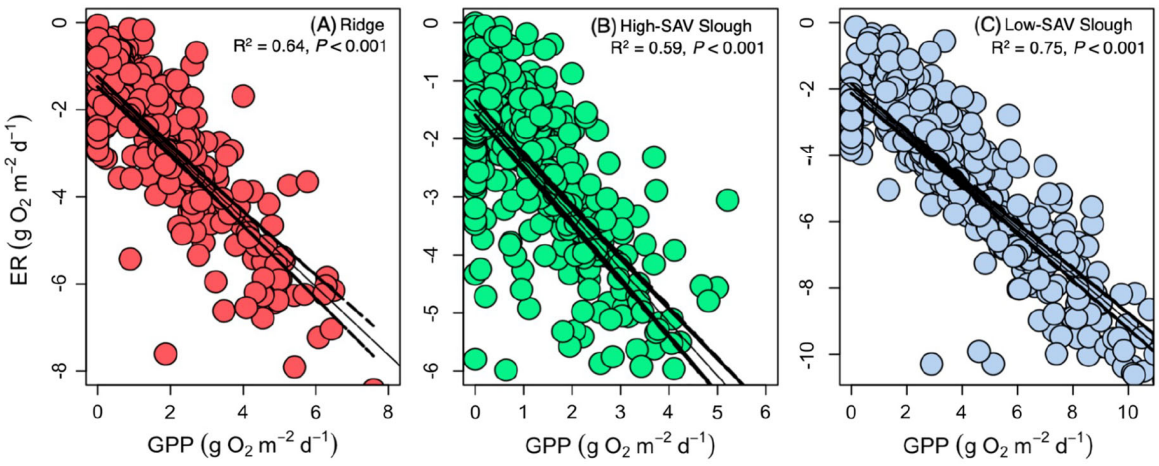


Fig. 7. Relationships between aquatic ecosystem respiration (ER) and gross primary productivity (GPP) (A–C) and between net aquatic productivity in freshwater marsh wetlands from sawgrass (*Cladium jamaicense*) ridge and sloughs with high- and low-density submerged aquatic vegetation (SAV) habitats of the Florida Everglades (South Florida, USA).

general, GPP increased with water temperature up to ~26°C (Fig. 8A) and with PAR across all habitat types (Fig. 8B). Gross primary productivity had a variable relationship with water level (Fig. 8C) and differences between habitats were greatest for the response to smoothed water depth.

In Everglades freshwater ridge and slough wetlands, smoothed water temperature ($P < 0.001$), PAR ($P < 0.001$), and water depth ($P < 0.001$) explained patterns in ER (DEV = 50%), which mirrored the relationships observed for GPP (Fig. 8D–F). In general, ER decreased (higher respiration) with water temperature up to ~26°C ($P < 0.001$; Fig. 8D), and with PAR ($P < 0.001$; Fig. 8B) across all habitat types. Similar to patterns observed in GPP, differences in ER between habitats were greatest for the response to smoothed water depth.

Patterns in NAP resulted from shifts in GPP and ER, which were differentially influenced by non-linear relationships with water temperature ($P < 0.001$; Fig. 8G), PAR ($P < 0.001$; Fig. 8H), and water depth ($P < 0.001$; Fig. 8I; DEV = 28%). Across habitat types, NAP was negatively correlated with water temperature and positively correlated with PAR, suggesting that ER was more sensitive than GPP to water temperature, and GPP drove patterns with PAR. The ridge had the highest NAP at greater water depths, while at lower water depths, the high-SAV slough had higher NAP (Fig. 8I). The low-SAV slough site had the highest NAP at a water depth ranging from 50 to 75 cm (Fig. 8I).

Discussion

We quantified the magnitude and variability in aquatic metabolic rates in freshwater subtropical ridge and slough wetlands of the Florida Everglades. We found that seasonal variation in water depths interacted with habitat type and density to drive patterns of net heterotrophy in wetlands. Rates of NAP were strongly explained by light attenuation and temperature, which varied seasonally with water depths but also interacted with slough SAV density. Contrary to our predictions, rates of NAP during the dry season were less heterotrophic—despite more negative ER—where rates of GPP increased to more than half the rate of ER. The high-SAV slough site had higher net heterotrophic conditions during interseasonal periods of intermediate water depth compared to the ridge and low-SAV slough sites that were most net heterotrophic when water levels were lowest. In support of our predictions, ER was positively related to GPP (but less so for the high-SAV slough site), as was observed in other studies of aquatic metabolism in the Everglades (Hagerthey et al. 2010, Schedlbauer et al.

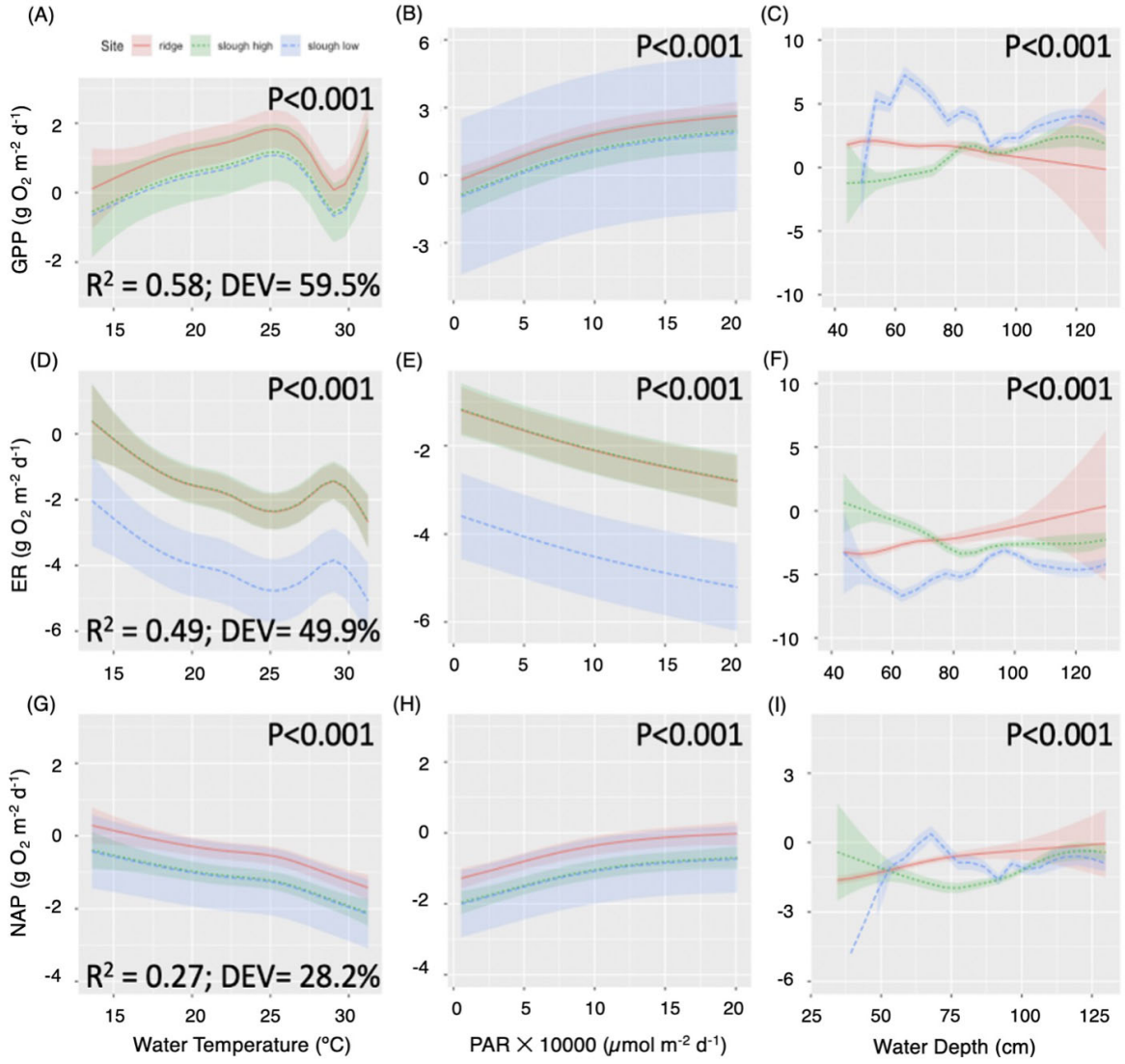


Fig. 8. Generalized additive model predictions, and the effect of smoothed (A, D, G) water temperature (Twater), (B, E, H) of photosynthetically active radiation, and (C, F, I) water depth on (A–C) gross primary productivity (GPP), (D–F) ecosystem respiration (ER), and (G–I) net aquatic productivity (NAP) in ridge and slough habitats.

2012). We expected aquatic metabolism in the ridge to be more heterotrophic than in both low- and high-SAV sloughs due to light attenuation from emergent vegetation (Hagerthey et al. 2010), and we measured negative rates of NAP consistent with seasonal declines in water depth at the ridge site. However, variation in NAP in both slough sites interacted with SAV density and water depths, causing more spatiotemporal variability in NAP as well as the most negative overall rates of NAP detected (in the low-SAV slough).

Light and temperature associated with changes in water depth and interactions with vegetation strongly drove seasonal trends of aquatic metabolism in ridge and slough wetlands. Aquatic metabolism was more heterotrophic with increasing temperature and decreasing water

depth, despite higher PAR levels during that period of the wet season (May through August) (Fig. 8G–I). The high-SAV slough site had lower magnitude but more temporally variable heterotrophic NAP than the low-SAV slough throughout both wet and dry seasons (Fig. 6G, H). Our results suggest that although dense SAV blocks light consistently throughout the year and at different water levels, higher SAV density at the high-SAV slough site buffered rates of ER that increased DO consumption in ridge and low-SAV sites with increased temperature and PAR (Fig. 8D–F). Aquatic metabolism in the ridge and low-SAV slough sites had similar patterns during both wet and dry seasons compared to the high-SAV slough site (Fig. 6). Collectively, our findings suggest that ridges and low-SAV sloughs attenuate PAR similarly when water levels are low, whereas high-SAV sloughs are more buffered from seasonal variation in PAR as well as water temperatures that drive NAP. In addition, strong relationships between ER and GPP in ridge and low-SAV slough wetlands are evidence that autotrophic respiration influences NAP. Therefore, although emergent vegetation does attenuate light and affect NAP in Everglades wetlands (Hagerthey et al. 2010), we found that water levels and density of SAV were important factors explaining year-round patterns of metabolism among freshwater ridge and slough wetlands.

The role of organic matter in driving aquatic biogeochemical cycling and ecosystem metabolism is least understood in wetlands compared to other aquatic ecosystems (Hagerthey et al. 2010, Bernhardt et al. 2018). Peatlands store carbon primarily as partially decomposed plant matter ("peat"). In the Everglades, peat soils form within the ridge and slough habitats, often building deep layers of stored carbon. In contrast, floc that is composed of decaying periphyton and detritus, and carbonates (Noe et al. 2003) can be more accessible and labile than detritus and is an important base of the food web for freshwater marshes of the Everglades (Belicka et al. 2012). Periphyton can be an important seasonal contributor to floc (Neto et al. 2006, Pisani et al. 2013), as well as filamentous green algae (Gao et al. 2007) and SAV (Troxler and Richards 2009). Although wetland organic matter has low mobility, both floc and periphyton are mobilized from upstream to downstream in freshwater marshes of the ridge and slough Everglades (Jaffé et al. 2001, Pisani et al. 2013), providing an essential and active resource for metabolic demand in these ecosystems (Belicka et al. 2012, Trexler et al. 2014) and a possible mechanism for retaining ridge and slough geomorphology (Heffernan et al. 2013). In addition, the contribution of periphyton and SAV to floc can vary seasonally (although unlikely at our sites), as periphyton increases in biomass during the wet season (McCormick et al. 1997). Our continuous measurements of DO at all sites from just above the soil surface—where floc deposition is the highest—resulted in immediate depletion of DO to zero (data not included in this study, J. Kominoski, *personal observation*). The high deposition detritus-based floc with low rates of bioreactivity in these peat-dominated ridge and slough wetlands likely explains a year-round stratification of under-saturated but higher concentrations of DO water situated directly above an anoxic floc layer. The relative contribution of floc to NAP in subtropical ridge and slough wetlands that vary in algal and detrital contributions to floc (Pisani et al. 2013) is an area in need of further study.

Although results from our study focused on peat-dominated ridge and slough wetlands where organic carbon predominates, studies that quantify carbonate formation–dissolution processes are needed to capture inorganic carbon fluxes that can offset primary productivity (organic carbon) gains with net ecosystem total carbon (inorganic and organic) losses (Malone et al. 2021). Values of NAP measured in a long-hydroperiod peat-dominated freshwater marsh and a short-hydroperiod marl-dominated freshwater marsh (Malone et al. 2021; mean: ~−0.5 g $O_2 \cdot m^{-2} \cdot d^{-1}$) were less heterotrophic (higher NAP) compared to more heterotrophic (lower NAP) from our current study (range: ~−4.0 to −0.50 g $O_2 \cdot m^{-2} \cdot d^{-1}$), which is likely explained by the general lack of periphyton presence at our study sites (see photographs in Fig. 2). The role of inorganic carbon (i.e., carbonates) in driving net ecosystem carbon flux is complex but beginning to emerge more clearly. A recent study that compared nested aquatic and land surface CO_2 fluxes at eddy covariance towers in short- and long-hydroperiod freshwater marshes in the Everglades revealed that NAP explained very little variation in ecosystem CO_2 fluxes (Malone

et al. 2021). Another recent study in a nearby seagrass meadow in Florida Bay detected higher CO_2 emissions during the day than at night, resulting in a net source of CO_2 to the atmosphere (Van Dam et al. 2021). Collectively, these findings suggest that carbonate ecosystems can be sources of atmospheric CO_2 and that the source of CO_2 for GPP may be from the production of calcium carbonate ($CaCO_3$). This result may explain why Everglades short-hydroperiod marl prairies become a more substantial source for CO_2 under inundated conditions even when ER is expected to decline (Zhao et al. 2019, Malone et al. 2021). As many carbonate wetlands exist worldwide, our ability to understand the net carbon storage capacity of all wetlands requires a strong understanding of the relative controls on organic and inorganic carbon fluxes.

Understanding carbon storage in ecosystems requires balancing carbon production, transformation, and export of organic and inorganic carbon (Chapin et al. 2006). Wetlands have traditionally been understood to be highly productive ecosystems with low organic matter decomposition rates due to anaerobic conditions (Odum et al. 1995, Chmura et al. 2003, Mitsch et al. 2013). Their high productivity compared to other inland aquatic ecosystems is believed to result from emergent vegetation, which creates a vertical separation of the net autotrophic and net heterotrophic components of these ecosystems (Chmura et al. 2003, Mitsch et al. 2013). Shallow regions of aquatic ecosystems tend to be net autotrophic at the ecosystem scale, often exporting particulate and dissolved organic matter to support respiration in adjacent regions of a water body (Kemp et al. 1997; Caffrey et al. 1998; Van de Bogert et al. 2007). Our findings challenge previously held assumptions that net ecosystem metabolism in wetlands is driven by emergent vegetation (Hagerthey et al. 2010). We found that net aquatic metabolism was similarly driven by seasonal changes in water depth (and subsequent changes in temperature and light) in emergent wetlands and wetlands with less dense submerged vegetation, whereas wetlands with dense SAV are more metabolically buffered from seasonal temperature and light regimes. Despite relatively consistent net heterotrophic aquatic conditions within wetlands, the carbon balance of wetland ecosystems can vary among substantially when integrating across emergent, submergent, and open-water components (Zhao et al. 2019, Morant et al. 2020*a*, *b*, Malone et al. 2021). In addition, the global contribution of wetlands to methane production is substantial, and the production of methane from wetlands rising water temperatures increases faster than GPP (Camacho et al. 2017). Collectively, the capacity of wetlands—as all ecosystems—to store carbon is a function of the relative organic and inorganic production vs. losses of multiple forms and ages of carbon (Chapin et al. 2006).

Inland aquatic ecosystems are largely net heterotrophic (Solomon et al. 2013, Bernhardt et al. 2018), and changes in hydrology that affect ecosystem metabolism can be critical control points driving net carbon storage or loss (Bernhardt et al. 2017). The hydrogeomorphology of inland waters, including wetlands, explains variation in the relative carbon storage capacity among aquatic ecosystems (Heffernan et al. 2013, Mitsch et al. 2013, Lu et al. 2017, Zhao et al. 2019). In wetland ecosystems that store massive amounts of carbon as well as carbonates, changes in hydrology, such as seasonal rainfall, drought, and water management, can shift ecosystems trophic state from net autotrophic to net heterotrophic (Schedlbauer et al. 2012, Malone et al. 2013, Zhao et al. 2019). Although wetlands store more carbon per unit area than rivers and streams, wetlands release nearly twice as much carbon compared to other inland aquatic ecosystems (Aufdenkampe et al. 2011). An important, yet understudied component of net carbon fluxes in wetlands is lateral transport; a predominant component of coastal and tidal wetlands (Aufdenkampe et al. 2011, Lu et al. 2017). Expanding our understanding of how metabolic processes and carbon cycling in wetland ecosystems vary across gradients in hydrology, vegetation, and organic matter (Hagerthey et al. 2010, Zhao et al. 2019, Morant et al. 2020*b*, Malone et al. 2021) will enhance our understanding and protection of wetlands that maximize the persistence of structural and functional features that store carbon (Heffernan et al. 2013).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3849/full