

Aquatic metabolism in the Everglades: Dominance of water column heterotrophy

Scot E. Hagerthey,^{a,*} Jonathan J. Cole,^b and Deborah Kilbane^{a,1}

^aEverglades Division, South Florida Water Management District, West Palm Beach, Florida

^bCary Institute of Ecosystem Studies, Millbrook, New York

Abstract

Using high-frequency measurements of free water dissolved oxygen (O_2), we assessed gross primary production (GPP), respiration (R), and net aquatic production (NAP) in the shallow-water Everglades peatland between 1996 and 2005. We distinguish NAP from net ecosystem production since the boundary for shallow aquatic ecosystems may include aboveground GPP of wetland biota. Metabolism was estimated for 68 sites distributed among nine habitats and yielded 1085 5-d deployments or 5425 site-days. Habitats differed in vegetation composition, trophic status, and hydrology. Systemwide O_2 averaged 3.8 ± 2.2 mg L^{-1} (mean \pm SD), or $49\% \pm 30\%$ of atmospheric saturation. GPP, R, and NAP averaged 103 ± 76 , 220 ± 79 , and -117 ± 65 mmol O_2 m^{-2} d^{-1} , respectively. Metabolism was greater during the summer-wet season when greater irradiance, temperature, and material flux stimulate primary production and decomposition. Paradoxically, GPP was inversely related to total phosphorus (TP), with oligotrophic (TP < 7 μ g L^{-1}) open-water habitats dominated by periphyton having the highest and eutrophic (TP > 35 μ g L^{-1}) habitats with dense emergent macrophytes the lowest rates. R was greatest for moderately enriched (TP = 15 μ g L^{-1}) open-water habitats with floating macrophytes. The prevalence of net heterotrophy, 96% of the 1085 NAP estimates, reveals the importance of aboveground biota in regulating aquatic metabolism and O_2 dynamics in shallow ecosystems. R is not only regulated by the influx of aboveground autochthonous carbon but also by aquatic GPP. Carbon turnover is greater in habitats where O_2 production by aquatic vegetation enables aerobic respiration. Conversely, water-column GPP is suppressed by dense emergent macrophytes, which limits O_2 availability, favors anaerobic respiration, and reduces carbon turnover.

The total metabolic balance of an ecosystem, termed net ecosystem production (NEP), is the difference between gross primary production (GPP) and ecosystem respiration (R) (Lovett et al. 2006). When NEP is positive (net autotrophic), fixation of inorganic carbon (C) through photosynthesis exceeds oxidation of organic C. Alternatively, when NEP is negative (net heterotrophic), the remineralization of organic C exceeds fixation of inorganic C. In aquatic ecosystems, the diurnal change in free water dissolved oxygen (O_2) can be used to estimate NEP (Odum 1956). With the use of instruments to obtain high-frequency measurements of O_2 and temperature (e.g., Hydrolab and YSI sondes), along with improvements in estimating atmospheric exchange (Cole and Caraco 1998; Cole et al. 2000), reliable estimates of whole-ecosystem metabolism can be made for aquatic systems with relatively simple and easily defined boundaries. This generally applies to systems with minimal wetland or littoral biota in which GPP is controlled by phytoplankton or periphyton and R may be strongly influenced by allochthonous organic matter. In contrast, the boundary for a shallow aquatic ecosystem is more likely to include wetland and littoral biota; thus, free water measurements of O_2 may not accurately reflect NEP because the autochthonous aboveground GPP of emergent, floating, woody, or herbaceous vegetation is not captured (Caraco and Cole 2002). We refer to the measurements of aquatic metabolism for shallow aquatic ecosystems as net aquatic production (NAP), thereby distinguishing it from estimates of NEP.

Wetlands, shallow ponds, and temporary ponds are examples of shallow aquatic ecosystems that are common, yet under-studied, landscape features (Wetzel 2001). A significant factor contributing to NAP and O_2 dynamics is the balance between the aquatic and terrestrial properties inherent to shallow aquatic ecosystems (McKenna 2003; Stanley et al. 2003; Cole et al. 2007). The vegetation structure of these systems may be dominated by phytoplankton, periphyton, submersed aquatic vegetation (SAV), floating leafed aquatic vegetation (FLAV), emergent macrophytes, herbaceous vegetation, or woody vegetation. Photosynthesis by phytoplankton, periphyton, and SAV contribute significantly to the oxygenation of the water column and aquatic GPP (Caraco and Cole 2002; Lauster et al. 2006; Goodwin et al. 2008), with periphyton and SAV production generally exceeding phytoplankton (Blindow et al. 2006). Aerial production by vascular plants can affect NAP by limiting light availability for in-water photosynthesis (Grimshaw et al. 1997; McCormick and Laing 2003) and increasing the supply of autochthonous organic matter (McKenna 2003; Stanley et al. 2003; Lauster et al. 2006). Reduced aquatic photosynthesis limits the production of free water O_2 , whereas increased organic matter loading stimulates bacterial production and increases aquatic R (Stanley et al. 2003). Further, R of the in-water parts of FLAV and emergent vegetation can contribute significantly to oxygen demand (Lovett et al. 2006). Another factor influencing shallow-system NAP and O_2 is the chemical oxygen demand created by the microbial processing of organic matter in sediments (Stanley et al. 2003; Torgersen and Branco 2007).

High-frequency measurements of free water O_2 provide valuable insight into ecosystem-level processes and habitat

* Corresponding author: shagerth@sfwmd.gov

¹ Present address: CSA International, Inc., Stuart, Florida

quality for shallow aquatic ecosystems. NAP estimates derived using this method have been used to examine the effects of eutrophication (McCormick et al. 1997), ecosystem restoration (Cronk and Mitsch 1994; McKenna 2003), variable hydrology (Tuttle et al. 2008), carbon cycling (Torgersen and Branco 2007), and pelagic–littoral differences (Lauster et al. 2006; Goodwin et al. 2008). O_2 measurements have been used to assess the habitat quality for fish and invertebrates (Caraco and Cole 2002; Goodwin et al. 2008). NAP studies in shallow aquatic ecosystems are limited in space and time, generally consisting of a few sites with measurements spanning 1 or 2 yr. Thus, there is considerable uncertainty regarding the variability and causal factors regulating NAP in shallow aquatic ecosystems.

In this study we utilized 10 yr of high-frequency O_2 measurements from 68 sites to examine the spatial and temporal dynamics of aquatic metabolism (GPP, R, and NAP) in a shallow aquatic ecosystem, the Everglades peatland. We compared aquatic metabolism among nine habitats common to the peatland. The habitats capture emergent and submersed vegetation structures that reflect important environmental drivers (e.g., water quality and hydrology). To identify factors that may regulate aquatic metabolism, we examined relationships between metabolism and several water-quality and environmental parameters. Finally, we examined temporal dynamics for seasonal patterns and long-term trends.

Study site—The Everglades was once a large subtropical, oligotrophic peatland that covered 1.1×10^4 km² of the southern portion of the Florida peninsula (Davis et al. 1994). A vast portion of the landscape consisted of a contiguous mosaic of sawgrass (*Cladium*) ridges, open-water sloughs, and tree islands, all oriented parallel with the unimpeded southward flow of water from Lake Okeechobee to Florida Bay (Sklar et al. 2005). With rainfall as the primary driver of both the predrainage (ca. 1850) hydrology and biogeochemistry, primary productivity was limited by the minimal supply of essential elements, especially P.

Agriculture and urban development over the past century, however, have reduced the areal extent to just 0.6×10^4 km² (Fig. 1) as the demand to control water resources for drainage, flood protection, and consumptive uses has increased. What presently exists is a series of large impoundments, called water conservation areas (WCA), and Everglades National Park (ENP) rather than one large contiguous peatland (see Web Appendix at http://www.aslo.org/lo/toc/vol_55/issue_2/0653a.pdf; Fig. A1). Development has also caused degradation in water quality that has negatively affected the ecosystem. Increased loading of P from agricultural and urban runoff has resulted in eutrophication, as evident by strong environmental gradients (P and dissolved ions) that emanate from water control structures (Sklar et al. 2005) leading to multiple ecosystem regime shifts (Hagerthey et al. 2008). Today the Everglades is characterized by a mosaic of habitats that differ in vegetation structure and reflect water quality and hydrologic conditions.



Fig. 1. Location of the Everglades peatland within the state of Florida. See the Web Appendix for a more detailed map that includes site locations.

Methods

Data sources—For this analysis we utilized data from 68 monitoring sites distributed throughout the Everglades that are part of a larger network designed to assess water quality and hydrologic effects on Everglades ecosystem structure and function (see Web Appendix). Since effects emanate from conveyance features (canals or structures), sites are distributed along transects that extend from existing or proposed conveyance features into the marsh interior (Table 1). Although the initiation, intensity, and frequency of sampling differed among transects located in WCA-1, WCA-2A, WCA-3A, WCA-3B, Shark River Slough (SRS), and Taylor Slough (TS), they shared a common suite of parameters consisting of dissolved oxygen (O_2), pH, specific conductivity (COND), temperature (TEMP), total phosphorus (TP), and total Kjeldahl nitrogen (TKN). The exception was dissolved organic carbon (DOC), which was routinely measured in WCA-1, WCA-2A, and WCA-3A but sporadically in WCA-3B, SRS, or TS. Additional DOC data for SRS and TS were obtained from the Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) program.

We used Hydrolab water-quality sondes (models Mini-sonde 4a and Minisonde MS5) fitted with a Clark Cell sensor to obtain high-frequency measures of free water O_2 . Before deployment, sondes were calibrated to atmospheric saturation and programmed to record at 30-min intervals. Since water depths in the Everglades are shallow (0.1 to 1 m), hydrolabs were suspended from polyvinyl chloride tripods such that the sonde bottom rested in the middle of the water column. Sondes were deployed in sets of 10 to 15 on a region-by-region basis (e.g., WCA-1). The frequency was typically quarterly but varied among regions depending on the study objective and environmental conditions

Table 1. Description of the monitoring transects in six regions of the Everglades, Florida. Conveyance feature describes the means by which water enters the marsh. Stressor describes the reason for establishing the monitoring transect (P, phosphorus; H, hydrology).

Region	Sites	Conveyance feature	Stressor	Date initiated	Hydrolab deployments
WCA-1	9	L-7 canal	P	Jun 1997	245
WCA-2A	13	S10s culverts	P	Sep 1996	249
WCA-3A	12	L-28 canal	P	Mar 2000	154
WCA-3B	4	S345s (proposed)	H	Dec 1997	89
Shark River Slough	12	S12s and S355s	H	Dec 1997	169
Taylor Slough	17	S332 pump*	H	Aug 1997	245

* The S332 pump was decommissioned in 2000 and replaced with a degraded levee.

(e.g., sondes were not deployed during droughts). Deployments typically lasted for 5 d (Mon–Fri) but inclement weather could delay deployment or retrieval. Given the short deployment duration, biofouling of the sensors was generally not an issue. Sondes were postcalibrated immediately after retrieval. A total of 1085 sonde deployments was made between September 1996 and December 2005. This study makes use of 5425 site-days data.

To characterize the environmental conditions we paired O_2 data with concomitant measures of water quality (TP, TKN, DOC, COND, and pH) and environmental data (TEMP, depth, photosynthetically active radiation [PAR], the Palmer drought severity index [PDSI], and precipitation [PRECIP]). TP, TKN, and DOC were monitored monthly and analyzed using standard methods (McCormick et al. 1996). Hydrolabs were fitted with temperature, pH, and specific conductivity sensors and values obtained by averaging the multiday sonde deployments. Water depth was measured at the time of the deployment. PAR and air temperature data were obtained from meteorological stations positioned throughout the Everglades watershed (South Florida Water Management District's DBHYDRO database: www.sfwmd.gov) using the following region-specific station identifiers: LoxWS for WCA-1; S7WX for WCA-2A; S140W for WCA-3A; S331W for Shark River Slough and WCA-3B; and JBTS for Taylor Slough. Monthly PDSI and PRECIP values were obtained from the Drought Information Center, National Oceanographic and Atmospheric Administration (www.drought.noaa.gov). PDSI was added to the data set because it encompasses the temporal variability in the regional climate that drives hydrology systemwide (e.g., drought, normal, or wet year).

NEP, GPP, and R calculations—We used the method of Cole et al. (2000) to calculate daily NEP, GPP, and R for each deployment on the basis of the changes in water column O_2 (ΔO_2). Whereas NEP and R can be determined directly from the sonde data, GPP is estimated by difference. Within a 30-min interval it is assumed that

$$\Delta O_2 = \text{NEP} + D \quad (1)$$

where NEP captures the difference between GPP and R and D is the diffusive exchange of O_2 with the atmosphere. D is regulated by the difference in O_2 in the water column (O_2) from atmospheric equilibrium ($O_{2\text{sat}}$) and the temperature-dependent gas exchange coefficient for oxygen (k)

modeled as a function of wind speed (Cole and Caraco 1998):

$$D = k(O_{2\text{sat}} - O_2) \quad (2)$$

Positive and negative values of D reflect addition and removal of O_2 from the water column, respectively. Since wind speed estimates were not available for any of the 68 monitoring sites, we utilized wind speed measured at 10 m above ground surface from meteorological stations, listed above, located within each of the regions and as close to the monitoring transects as possible. We assumed that the mean daily wind speed measured at a nearby meteorological station would be a reasonable surrogate for the average daily wind conditions for sites located in open water but not for sites with dense emergent macrophytes. For these sites, we assumed that the emergent macrophytes would reduce wind speed at the air–water interface to effectively zero. Since the time-stamp for wind speed did not coincide with the sonde record, we applied a single k value to each 24-h period. Since GPP at night is zero (Cole et al. 2000), we assumed that the ΔO_2 within a 30-min interval during the night was attributed to R_{night} and D . Assuming that R at night equals R during the day (Cole et al. 2000; Lauster et al. 2006), GPP was estimated by adding daytime NEP and R. The 30-min estimates of NEP, R, and GPP were summed over each 24-h period. Daily values were then averaged for the deployment period, typically 4 d. The NEP we calculate is the oxygen balance solely for the water column. Because the emergent and floating leafed plants vent much of their photosynthetically produced O_2 to the atmosphere, but have root and biomass respiration in the water column, the NEP we measure here is not truly net “ecosystem” production but the aquatic moiety of it. Thus, we use NAP to express water-column NEP.

Data analyses—The long-term data set was analyzed several ways to identify spatial and temporal patterns and to identify ecological drivers. General spatial patterns were assessed by determining average values for individual sites and examining patterns within each region. To test the hypothesis that aquatic metabolism in shallow aquatic ecosystems is influenced by vegetation structure, we grouped the 68 sites into nine habitats on the basis of the dominant vegetation (Table 2). Six habitats were oligotrophic (low P), with the vegetation patterns distinguishing different geographic regions (northern and southern Everglades), hydrology (short hydroperiod, long hydro-

Table 2. Description of the nine Everglades peatland habitats and the associated stressor that the 68 sites were assigned.

Code	Habitat description	Stressor
SHMP	Short hydroperiod marl prairie dominated by calcareous periphyton mats. Little or no organic soils. Common to the margins of Shark River Slough and Taylor Slough.	None
OWEU	Open-water slough dominated by the emergent macrophyte <i>Eleocharis</i> and a submersed <i>Utricularia</i> -periphyton matrix. Soils are mostly organic. Common to WCA-3A, WCA-3B, Shark River Slough, and Taylor Slough.	None
OWNU	Open-water slough dominated by the emergent macrophyte <i>Nymphaea</i> and a submersed <i>Utricularia</i> -periphyton matrix. Soils are mostly organic. Common to WCA-1 and WCA-2A.	None
OWNC	Open-water slough dominated by the emergent macrophyte <i>Nymphaea</i> and a submersed calcareous <i>Utricularia</i> -periphyton matrix. <i>Chara</i> is also common. Soils are mostly calcitic. Common to WCA-2A.	Minerals
OWMF	Open-water sloughs located near the mangrove fringe and dominated by thick periphyton mats. Soils are a mixture of organic and calcitic muds. Restricted to southern Taylor Slough and Shark River Slough.	Salt water
OWCD	Open-water sloughs that have become degraded because of altered hydrology. While the submersed <i>Utricularia</i> -periphyton matrix is present, the emergent macrophyte sawgrass from the adjacent ridge is invading the slough. Soils are typically organic.	Hydrology
OWT	Open-water sloughs that are influenced by phosphorus. Characterized by high density of the floating macrophyte <i>Nymphaea</i> .	Phosphorus
TYPHA	Dense monoculture of the emergent macrophyte <i>Typha</i> (cattail). Soils are organic.	Phosphorus
SALIX	Dense mixture of <i>Salix</i> (willow) and <i>Typha</i> . Soils are organic.	Phosphorus

period, and altered hydrology), and dissolved ion content (hard water and soft water). The other three habitats were associated with varying degrees of eutrophication, from open-water sloughs with dense floating macrophytes to dense stands of emergent vegetation with little or no open water. Metabolism estimates among habitats were compared using analysis of covariance (ANCOVA) with temperature as the covariate since preliminary analysis indicated a strong seasonal pattern (Sokal and Rohlf 1981; Gotelli and Ellison 2004). Multiple comparisons were made using Tukey honestly significant difference (HSD) tests. The assumption of data independence was confirmed with spatial autocorrelation and semivariogram analysis for spatial independence and residual analysis for temporal independence. GPP and R were log-transformed to meet the assumptions of normality.

Temporal patterns were first investigated by comparing systemwide and habitat aquatic metabolism between the wet season (15 May–15 Nov) and dry season (16 Nov–14 May) using *t*-tests (Sokal and Rohlf 1981). Second, simple linear regression was used to examine the aquatic metabolism 10-yr trends for individual sites and each of the nine habitats; however, we only report results for the nine habitats since trends for individual sites were generally similar to the habitats.

Relationships of systemwide aquatic metabolism with water quality (log[TP], log[TKN], COND, pH) and environmental variables (depth, TEMP, PAR, PDSI, and PRECIP) were examined using Pearson product moment correlations. For each of the nine habitats, models were developed for log(GPP), log(R), and NAP using forward stepwise multiple regressions with water quality and environmental variables. To determine if the ecological drivers were similar among habitats, we compared the model variables among habitats types.

Results

For the 1085 sonde deployments made between September 1996 and December 2005, the systemwide aquatic GPP, R, and NAP averaged 103 ± 76 (mean \pm SD), 220 ± 79 , and -117 ± 65 mmol O₂ m⁻² d⁻¹, respectively (Fig. 2). O₂ averaged 3.8 ± 2.2 mg L⁻¹ (Fig. 2), or $49\% \pm 30\%$ of atmospheric saturation. R exceeded GPP by an average of 2.1-fold and positive values of NAP occurred for only 4% (38/1085) of the deployments. These results demonstrate that net heterotrophy is the norm for the Everglades water column. Among individual sites, mean GPP, R, and NAP varied 15-, 4-, and 29-fold, respectively (see Web Appendix, Table A1). Metabolism also differed among and within regions, with the greatest differences occurring in regions affected by P (see Web Appendix, Table A1). GPP increased with distance from water control structures in WCA-1, WCA-2A, and WCA-3A but no patterns were evident in the oligotrophic WCA-3B, SRS, or TS. For WCA-1, WCA-2A, and WCA-3A the greatest mean R and NAP values occurred between the enriched and oligotrophic sites (e.g., sites E4 and F4 in WCA-2A) but no trends were evident for WCA-3B, SRS, or TS.

Habitat patterns—Measures of O₂ and ecosystem metabolism differed significantly among the nine habitats (Fig. 3; Table 3). Mean O₂ ranged from 0.5 to 7.6 mg L⁻¹ (Fig. 3A) and percentage saturation from 5% to 92% (Fig. 3B). Lower values were associated with eutrophic habitats. Mean GPP varied sixfold across habitats and differed significantly (Fig. 3C; Table 3). The highest values were associated with oligotrophic (TP < 7 μg L⁻¹) open-water sloughs, especially those characterized by the emergent macrophyte *Eleocharis* and the SAV *Utricularia*-periphyton matrix (OWEU) or by the cohesive

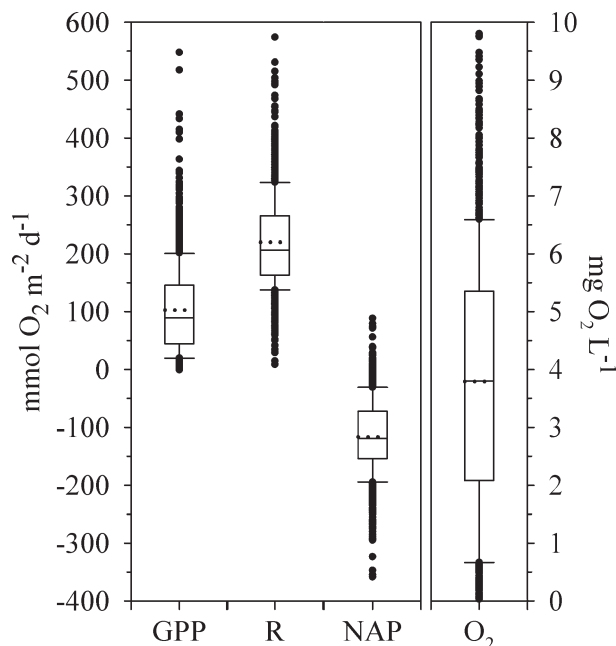


Fig. 2. Box-plot summary statistics of aquatic metabolism estimates (GPP, R, and NAP $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and dissolved oxygen ($\text{mg O}_2 \text{ L}^{-1}$) for all shallow aquatic habitats in the Everglades made between 1996 and 2005. $n = 1085$. Box represents the 75th and 25th percentiles, the solid line the median, and the dashed line the mean.

periphyton mats common to short-hydroperiod marl prairies (SHMP). Both of these habitats tend to occur in the southern Everglades (WCA-3A and ENP) and had GPP values greater than the oligotrophic *Nymphaea*-dominated habitats (OWNU and OWNC) typical of the northern Everglades (WCA-1 and WCA-2A). Although the mean GPP for open-water habitats influenced by P (OWT) was lower than similarly vegetated oligotrophic habitats (OWNU), the difference was not significant. Similarly, GPP did not differ between oligotrophic habitats with different ionic strengths (OWNC = OWNNU). In contrast, GPP for habitats degraded by poor hydrologic conditions (OWCD) were significantly lower than comparable undegraded habitats (OWEU). The lowest GPP values were associated with P-enriched habitats ($\text{TP} > 30 \mu\text{g L}^{-1}$) and dominated by either dense stands of the emergent macrophyte *Typha* (TYPHA) or a mixture of the herbaceous tree *Salix* and *Typha* (SALIX).

Aquatic R varied twofold among habitats (Fig. 3D; Table 3). Open-water sloughs with elevated P concentrations (OWT) had the highest mean R and differed significantly from adjacent oligotrophic open-water habitats within the same region (OWNU and OWNC). The lowest mean R was associated with the open-water habitat located at the mangrove fringe (OWMF). R did not differ significantly between the southern and northern Everglades oligotrophic open-water habitats (OWEU and OWNNU). The oligotrophic habitat type with greater ionic strength (OWNC) had R values 17% lower than the habitat with lower ionic strength (OWNNU). For the hydrologically affected habitat (OWCD), R was 20% lower than the long-

hydroperiod habitat (OWEU) but similar to the short-hydroperiod habitat (SHMP). R for the P-enriched habitats TYPHA and SALIX were significantly lower than the oligotrophic reference habitats OWEU and OWNNU.

None of the habitats had a mean positive NAP and values differed significantly among habitats (Fig. 3E; Table 3). The least negative mean, $-20 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, was associated with the open-water mangrove fringe (OWMF). This habitat, like the SHMP (NAP = $-61 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), has dense cohesive periphyton mats and little emergent vegetation. The oligotrophic habitats in the southern Everglades (OWEU) were significantly less net heterotrophic than the northern Everglades (OWNNU). Hydrologic differences did not affect NAP (OWEU = OWCD). Habitats with greater ionic content had less negative NAP (OWNC < OWNNU). The open-water, P-enriched habitat (OWT) had the most negative value, $-191 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$, followed by the TYPHA and SALIX habitats.

Temporal trends—GPP, R, and NAP differed between the wet (15 May–15 November) and dry (16 November–14 May) seasons. Mean GPP was significantly greater in the wet season ($115 \pm 85 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) than dry season ($88 \pm 89 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) (t -test ratio = 5.9; $\text{df} = 1083$, $p < 0.0001$). R was similarly different (wet = 238 ± 84 ; dry = $198 \pm 66 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$; t -test ratio = 8.6; $\text{df} = 1083$, $p < 0.0001$). NAP was significantly more heterotrophic in the wet season ($-123 \pm 66 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) than dry season ($-110 \pm 62 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) (t -test ratio = -3.3 ; $\text{df} = 1083$, $p = 0.0009$). However, seasonal patterns differed among habitats (Fig. 4). For each of the nine habitats, R was significantly greater in the wet season than dry season. GPP was significantly greater in the wet season for the oligotrophic open-water habitats OWEU, OWMF, OWNNU, and SHMP. NAP values for OWEU, OWMF, and OWT did not differ between seasons (t -test; $p > 0.05$).

The trend over time for our period of measurements for NAP indicated that net heterotrophy increased for the majority of habitats (Fig. 5). The only habitats where no change in NAP was observed were open-water *Nymphaea-Utricularia* sloughs (OWNNU; $p = 0.7221$) and cattail stands (TYPHA; $p = 0.4318$). NAP declined (i.e., net heterotrophy increased) significantly for the oligotrophic habitats open-water *Eleocharis-Utricularia* sloughs (OWEU; $p < 0.0001$), open-water *Nymphaea* calcareous periphyton sloughs (OWNC; $p < 0.0376$), open-water mangrove fringe (OWMF; $p = 0.0271$), short-hydroperiod marl prairies (SHMP; $p = 0.0257$), and the P-enriched willow habitat (SALIX; $p = 0.0049$). Marginally significant declines were observed for open-water transitional sloughs (OWT; $p = 0.0696$). The annual rate of decline among these habitats ranged between -3.9 and $-9.7 \text{ mmol O}_2 \text{ m}^{-2} \text{ yr}^{-1}$.

Temporal patterns of GPP over the last decade differed among the habitat classifications. Significant declines in GPP with time were observed for OWMF ($p = 0.0013$), open-water *Cladium* degraded sloughs (OWCD; $p = 0.0048$), and willow thickets (SALIX; $p < 0.0001$). The annual decline in GPP for these habitats ranged between -7.0 and $-11.6 \text{ mmol O}_2 \text{ m}^{-2} \text{ yr}^{-1}$. GPP increased with

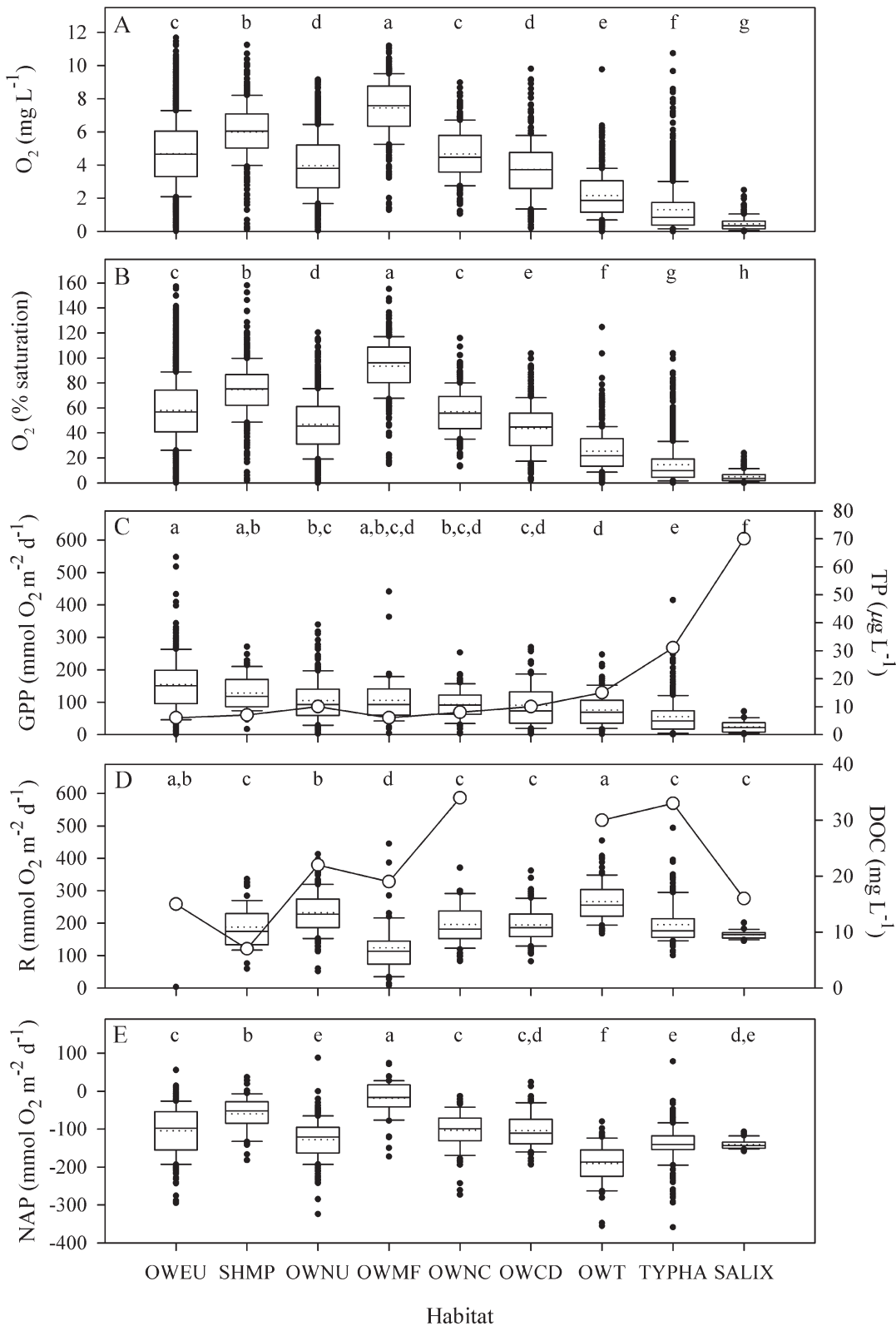


Fig. 3. Box-plot summary statistics of (A) O₂ concentrations, (B) % saturation, and (C–E) aquatic metabolism estimates (GPP, R, and NAP mmol O₂ m⁻² d⁻¹) for the nine different habitats common to the Everglades, Florida peatland. Habitats are described in Table 2. Average TP (μg L⁻¹) and DOC (mg L⁻¹) for each habitat are presented on the second y-axis. Habitats with the same letter are not significantly different (ANCOVA results Table 4; Tukey HSD, $p > 0.05$). Box represents the 75th and 25th percentiles, the solid line the median, and the dashed line the mean.

Table 3. Analysis of covariance (ANCOVA) results comparing aquatic dissolved oxygen (O_2 and % saturation) and metabolism (GPP, R, and NAP) among the nine different habitats common to the Everglades peatland with water temperature as the covariate. Habitats are described in Table 2. $n_{O_2} = 6690$; $n_{\%O_2} = 6404$; $n_{\text{metabolism}} = 1138$.

	Source			
	Model	Habitat	Temperature	Interaction
O_2 concentration				
df	17,6672	8,17	1,17	8,17
F	390	784	134	8.8
p	<0.0001	<0.0001	<0.0001	<0.0001
O_2 % saturation				
df	17,6386	8,17	1,17	8,17
F	402	750	0.3	17.5
p	<0.0001	<0.0001	0.5811	<0.0001
GPP				
df	17,1063	8,17	1,17	8,17
F	28.0	43.2	23.6	2.3
p	<0.0001	<0.0001	<0.0001	0.0168
R				
df	17,1063	8,17	1,17	8,17
F	35.3	55.6	67.5	1.6
p	<0.0001	<0.0001	<0.0001	0.1105
NAP				
df	17,1063	8,17	1,17	8,17
F	29.8	57.1	2.8	2.1
p	<0.0001	<0.0001	0.0961	0.0335

time for OWNC ($p = 0.0002$) and OWT ($p = 0.0491$). The rates of increase for these two habitats were 6.9 and 4.1 $\text{mmol } O_2 \text{ m}^{-2} \text{ yr}^{-1}$, respectively. Trends with time were not evident for OWEU ($p = 0.6767$), OWNU ($p = 0.6987$), SHMP ($p = 0.9237$), or TYPHA ($p = 0.5009$). Residuals for individual habitats tended to be positively correlated with environmental variables, especially TEMP, but were not related to TP or TKN.

Trends of aquatic R also differed among the habitats. R increased with time in the oligotrophic habitats OWEU ($p < 0.0001$), OWNC ($p < 0.0001$), OWT ($p = 0.0010$), and perhaps SHMP ($p = 0.0879$). The annual rate of increase ranged between 4.1 and 11.2 $\text{mmol } O_2 \text{ m}^{-2} \text{ yr}^{-1}$. R decreased for the SALIX ($p = 0.0159$) at a rate of 3.4 $\text{mmol } O_2 \text{ m}^{-2} \text{ yr}^{-1}$. R did not change with time for OWNU ($p = 0.6027$), OWCD ($p = 0.2099$), OWMF ($p = 0.1099$), or TYPHA ($p = 0.9766$). As with GPP, residuals for individual habitats were positively correlated with environmental variables but not with TP or TKN.

Patterns with water quality and environmental variables—Systemwide aquatic GPP, R, and NAP were poorly correlated with water quality and environmental variables (Table 4); however, the slopes for many of the variables differed significantly from zero. Water-quality variables (DOC, TKN, TP, COND) were negatively related to GPP, R, and NAP, whereas environmental variables (TEMP, PAR, PRECIP) were positively related. The poor relation-

ship resulted from the high variability in metabolism that occurred in oligotrophic habitats. For example, 57% of the GPP estimates had corresponding TP values $< 10 \mu\text{g L}^{-1}$, yet GPP ranged from 0.14 to 547 $\text{mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$ (Fig. 6). Positive relationships with TEMP, PAR, and PRECIP captured seasonal dynamics; mainly metabolism tended to be greater during the wet season than the dry season (Table 4). Water depth was positively related to R and negatively related to NAP. No relationship was found between water depth and GPP. Aquatic metabolism was not related to the PDSI, a measure of the overall climate of south Florida.

Water quality and environmental variables were poor predictors of systemwide GPP, R, and NAP. The coefficient of determinations (r^2) estimated using forward multiple stepwise linear regressions for GPP, R, and NAP were 0.28, 0.18, and 0.19, respectively.

For multiple regression models for individual habitats, r^2 values ranged between 0.07 and 0.70 for GPP, 0.16 and 0.67 for R, and 0.14 and 0.63 for NAP. The principal elements of the GPP and R models for the open-water oligotrophic habitats OWEU, SHMP, OWNU, OWMF, OWNC, and OWCD were the environmental variables TEMP and PDSI, whereas the water-quality variables DOC and TP were the primary elements for the vegetated eutrophic SALIX and TYPHA habitats. In contrast, for the eutrophic open-water habitat OWT, the environmental variables TEMP and PDSI were associated with GPP and the water-quality variable DOC was associated with R.

Discussion

Our long-term study revealed that dissolved oxygen is persistently low and undersaturated in the shallow surface waters of the Everglades. The low O_2 is caused by the metabolic imbalance of the water column where net heterotrophy is far more prevalent than net autotrophy. For the decade of 1996–2005, R exceeded GPP for 96% of the 1085 estimates of aquatic metabolism. Heterotrophy persisted even though GPP, R, and NAP differed significantly among habitats reflective of different environmental conditions (e.g., oligotrophic–eutrophic, short–long hydroperiod) (Fig. 3). The spatial patterns in NAP suggest that water column heterotrophy is driven by the large standing crop (Turner et al. 1999) and high primary productivity (Ewe et al. 2006) of emergent and floating leafed macrophytes (i.e., aboveground autochthonous C). Differences among habitats reflect variability in the amount and type of aboveground autochthonous organic matter, SAV–periphyton production, and environmental conditions. Further, emergent and floating leafed macrophytes vent most of their photosynthetically produced oxygen into the atmosphere, but the respiration of their underwater parts consume significant amounts of water-column oxygen (Caraco and Cole 2002; Caraco et al. 2006).

Gross primary production—Aquatic GPP in shallow aquatic ecosystems is regulated more by SAV and periphyton production than phytoplankton (Belanger et al. 1989; Stanley et al. 2003; Lauster et al. 2006). Unlike

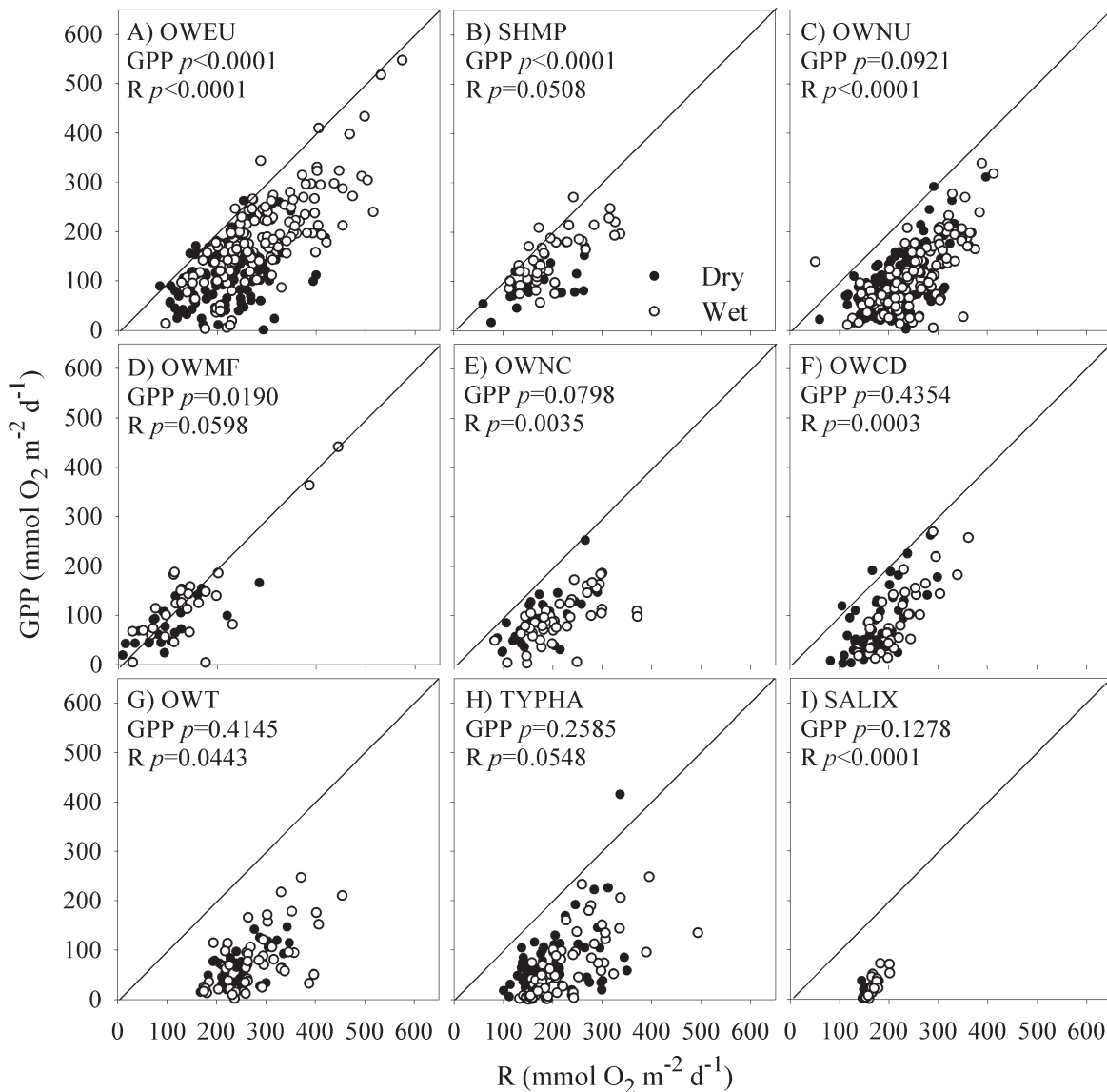


Fig. 4. (A–I) Relationships between wet- (15 May–15 Nov) and dry- (16 Nov–14 May) season GPP and R for each habitat. The line represents the 1:1 ratio where GPP and R are in balance. Above and below the line represent net autotrophy and net heterotrophy, respectively. The p -values represent the significance of a t -test comparing the mean seasonal values for GPP and R.

other aquatic ecosystems (Hanson et al. 2003), aquatic GPP in these systems is negatively related to eutrophication (Fig. 6). Whereas turbidity is the causal mechanism for many shallow systems (Wetzel 2001; Blindow et al. 2006), the paradox for shallow clear water systems arises because of eutrophication increasing the standing stock of emergent vegetation, which results in light limitation of SAV and periphyton production (Blindow et al. 2006). This is evident in the Everglades by the expected positive relationship between P and periphyton biomass-specific productivity ($\text{mmol O}_2 \text{ g}^{-1} \text{ ash-free dry mass } \mu\text{mol photons m}^{-2}$); however, when adjusted to biomass per unit area ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), a negative relationship with P emerges (McCormick et al. 1998). In *Typha* stands, where the canopy can reduce PAR by 85% (Grimshaw et al. 1997), periphyton biomass is nearly absent (McCormick et al. 1998), whereas in open-water habitats periphyton biomass can be substan-

tial, ranging from 2 to 6262 g m^{-2} (Turner et al. 1999; Gaiser et al. 2006; Iwaniec et al. 2006), and GPP 10- to 218-fold greater than in *Typha* (McCormick et al. 1998). Thus, the lower aquatic GPP for TYPHA, SALIX, and OWT habitats relative to oligotrophic open-water habitats can be attributed to a lower SAV–periphyton standing stock.

Aquatic GPP differences among and within open-water habitats were also likely due to variability in SAV and periphyton. In open-water habitats (OWEU, OWNU, OWNC, and OWCD), the aquatic community is generally comprised of metaphytic, epiphytic, or epipellic periphyton, several species of *Utricularia* (*Utricularia purpurea* and *Utricularia foliosa*), or the macroalga *Chara* sp. In contrast, the SHMP and OWMF habitats are comprised mostly of cohesive epibenthic and epiphytic periphyton mats. Differences in primary production have been recorded among the vegetation that comprises the SAV–periphyton complex.

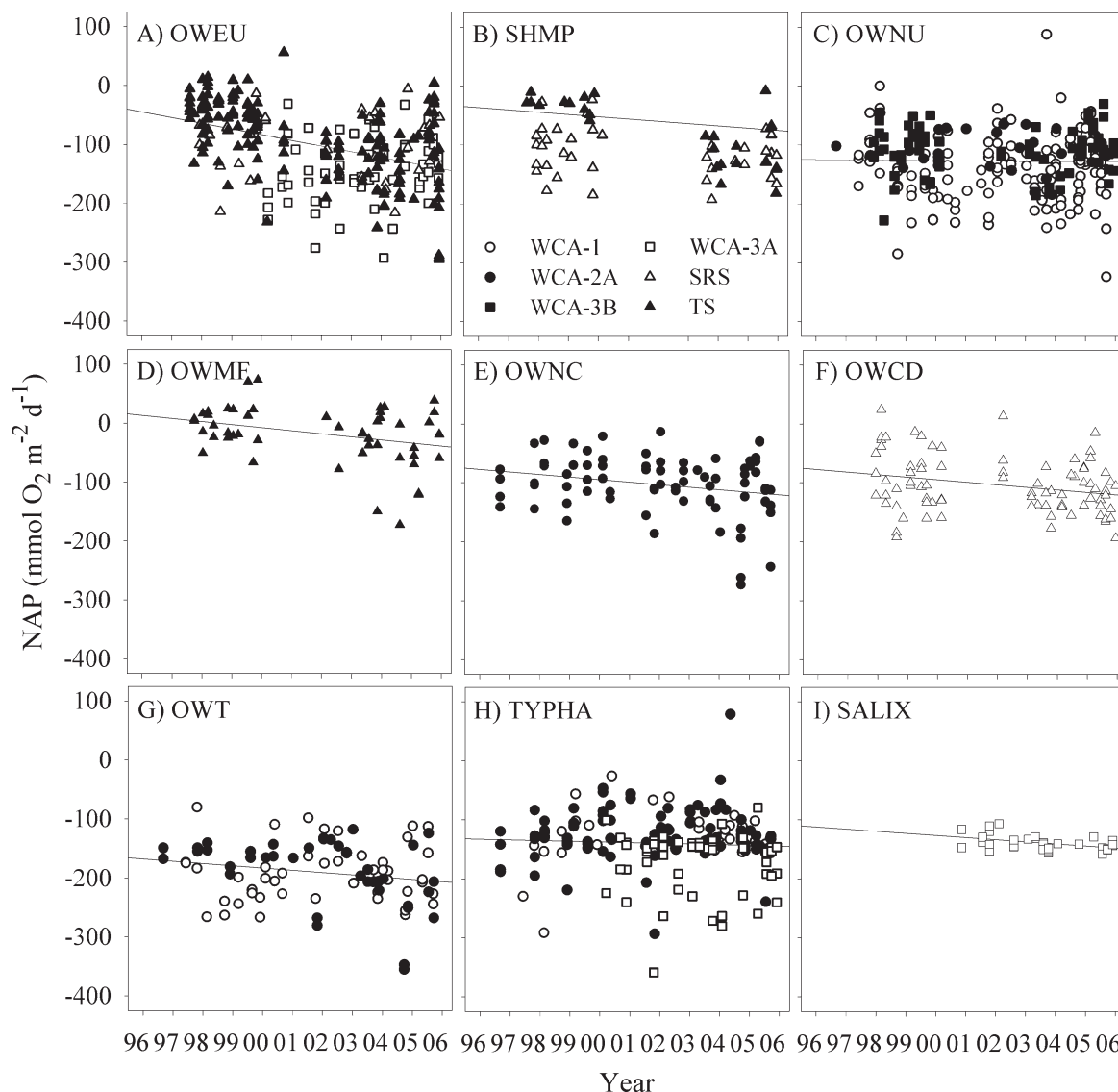


Fig. 5. (A–I) Trends of NAP ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) between 1996 and 2005 for each habitat. Habitats are described in Table 2. Symbols indicate the region, Water Conservation Area or Everglades National Park, where the estimate of NAP was obtained.

For example, reported GPP ranges for periphyton are 4–31,000 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (McCormick et al. 1998; Iwaniec et al. 2006; S. E. Hagerthey unpubl.), 29–1469 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for *Chara* (S. E. Hagerthey unpubl.), and 101–228 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for *Utricularia* (S. E. Hagerthey unpubl.). Phytoplankton production, in contrast, is typically less than 2 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Belanger et al. 1989). The high GPP estimates associated with the mangrove fringe sites in TS and the SHMP are consistent with high periphyton biomass (Gaiser et al. 2006; Iwaniec et al. 2006).

Respiration—The aquatic R in shallow water systems reflects the contribution of heterotrophic metabolism from different biotic components. In our study, where R was determined using ΔO_2 , these components consisted of SAV and periphyton, the underwater parts of emergent and floating plants, mineralization of DOC, and sediment metabolism. If, however, we had used CO_2 to assess R,

then remineralization chemical reactions that do not require oxygen (e.g., photo-oxidation of DOC and redox reactions) would also have contributed (Torgersen and Branco 2007). For example, inorganic C dynamics in regions with short hydroperiods (SHMP), along the freshwater–estuarine ecotone (OWMF), and in the interior of WCA-2A (OWNC) are influenced by CaCO_3 precipitation by cyanobacteria (Browder et al. 1994). Differences among habitats (Fig. 4) may not only result from dissimilarity in the contributions of each biotic component but also from the quality and quantity of organic C substrates available for heterotrophic metabolism.

Periphyton and DOC are unlikely to contribute significantly to Everglades aquatic R. Although R varies considerably for Everglades periphyton (range 4 to 9115 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), GPP:R for periphyton is consistently greater than 1 (range 1.8 to 7.8; Belanger et al. 1989; Iwaniec et al. 2006). Thus, although some of the

Table 4. Pearson product moment correlations (r) for Everglades aquatic GPP, R, and NAP with water quality and environmental variables. n for DOC = 580, TKN = 984, TP = 1024, pH = 1078, COND = 1073, Depth = 1076, Temperature = 1081, PAR = 1085, PDSI = 1085, and PRECIP = 1085.

	GPP		R		NAP	
	r	p	r	p	r	p
Water quality						
DOC (log)	-0.25	<0.0001	-0.25	<0.0001	-0.02	0.5840
TKN (log)	-0.32	<0.0001	-0.21	<0.0001	-0.12	<0.0001
TP (log)	-0.38	<0.0001	-0.17	<0.0001	-0.23	<0.0001
pH	0.16	<0.0001	-0.17	<0.0001	0.40	<0.0001
COND	-0.30	<0.0001	-0.14	<0.0001	-0.17	<0.0001
Environmental variables						
Depth	0.03	0.3602	0.12	<0.0001	-0.12	<0.0001
Temperature	0.34	<0.0001	0.29	<0.0001	0.04	0.2315
PAR	0.12	<0.0001	0.13	<0.0001	-0.01	0.6502
PDSI	0.03	0.2675	-0.01	0.8589	0.05	0.1292
PRECIP	0.16	<0.0001	0.16	<0.0001	-0.01	0.7210

O₂ within the periphyton complex diffuses into the water column, O₂ concentrations within the periphyton complex remain high and likely maintain internal R (Hagerthey et al. in press). DOC quantity and quality are key drivers regulating R in most aquatic ecosystems (del Giorgio and Peters 1994; Cole et al. 2000; Hanson et al. 2003). In the Everglades, the quantity of DOC declines from north to south (see Web Appendix; Qualls and Richardson 2003; Stern et al. 2007) and quality varies as a function of vegetation type (Maie et al. 2006; Osborne et al. 2007), production, decomposition, and sorption equilibrium with peat (Qualls and Richardson 2003). However, R for the water column is small (< 2 mmol O₂ m⁻² d⁻¹) (Belanger et al. 1989; S. E. Hagerthey unpubl.) relative to aquatic R (mean 220 mmol O₂ m⁻² d⁻¹), the inference being that most R is associated with the sediments.

Sediment biological oxygen demand can have a strong influence on R in shallow aquatic ecosystems (Gutknecht et al. 2006; Torgersen and Branco 2007). In our study,

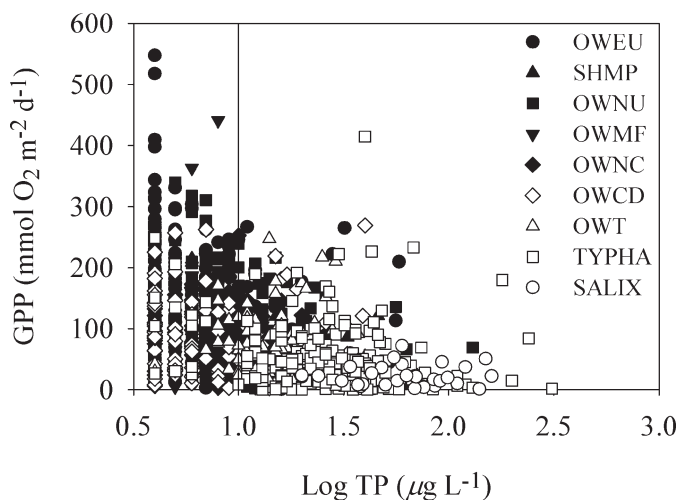


Fig. 6. Scatter plot of total phosphorus ($\mu\text{g L}^{-1}$) and GPP ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) by habitat. Habitats are described in Table 2. $n = 1080$. $\text{GPP} = -57.68 - 78.8 \log(\text{TP})$; $r^2 = 0.135$.

differences within and among habitats can almost certainly be accounted for by variability in bacterial remineralization of epipellic periphyton, detrital-flocculent organic matter (floc), and peat. Comprised mostly of photoautotrophs, epipellic periphyton is unlikely to significantly contribute to aquatic R. Floc is an integral component of the Everglades landscape, varying in quantity and quality (Bruland et al. 2006; Corstanje et al. 2006; Hagerthey et al. 2008). Defined as the unconsolidated pourable fraction of organic material overlying soil, it is comprised of plant and periphyton matter in various states of decomposition. C mineralization of the floc and peat soil is affected by substrate quality (nutrient content and susceptibility of organic C microbial breakdown), water depth, and O₂ availability. In general, O₂ availability and P loading accelerates C turnover (DeBusk and Reddy 1998, 2003; Corstanje et al. 2007), decreasing water levels increase C flux (DeBusk and Reddy 2003), decomposition is greater in the floc than in underlying peat (DeBusk and Reddy 1998, 2005), and C turnover is on the order of days for floc but years for peat soils (DeBusk and Reddy 1998; Stern et al. 2007). O₂ metabolism for floc ranges between 20 and 900 mmol m⁻² d⁻¹ (Belanger et al. 1989; S. E. Hagerthey unpubl.).

The high aquatic R measured in oligotrophic open-water habitats (OWEU, OWNU, OWCD, and OWNC) and in the moderately enriched open-water habitat (OWT) likely resulted from the rapid decomposition of floc stimulated by the availability of O₂ produced by SAV-periphyton photosynthesis. The average O₂ and GPP for the oligotrophic habitats exceeded 3.5 mg L⁻¹ and 88 mmol O₂ m⁻² d⁻¹, respectively. The subtle differences among these habitats may be due to heterogeneity in vegetation composition regulating the amount and type of C substrates available for mineralization (Osborne et al. 2007). In contrast, the relatively lower aquatic R for the oligotrophic SHMP and OWMF habitats were likely due to a lack of floc and greater epipellic periphyton abundance. Core incubation studies of Everglades floc and soil indicate that the anaerobic C mineralization rates are roughly one-third of aerobic rates (DeBusk and Reddy 1998); thus, we

likely underestimated aquatic R for eutrophic habitats with low O_2 (TYPHA and SALIX) because anaerobic processes that generate CO_2 were not accounted for (Torgersen and Branco 2007).

Net aquatic production—We found that the aquatic ecosystem of the Everglades was consistently net heterotrophic. The magnitude and range of heterotrophy ($NAP = -117 \pm 6 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$; range -359 to $88 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$) is similar to NAP values reported for temperate wetlands (McKenna 2003) and temperate bogs (Lauster et al. 2006) and NEP values for estuaries (Caffrey 2004) and rivers (Colangelo 2007). Compared with NEP for oligotrophic and mesotrophic temperate lakes (Cole et al. 2000; Lauster et al. 2006), the degree of heterotrophy in the Everglades is an order of magnitude greater. However, our NAP estimates capture only aquatic processes and therefore do not represent NEP. Shallow aquatic ecosystem NEP requires the inclusion of aboveground autochthonous production, which when accounted for generally reveals that shallow aquatic ecosystems are net autotrophic (McKenna 2003). This is likely the case for the Everglades peatland, as it is for macrophyte beds in some rivers (Goodwin et al. 2008).

Differences in NAP among the nine habitats (Fig. 3) reflect differences in habitat structure and function that influence the balance between GPP and R. The contribution of GPP to NAP was greatest for oligotrophic open-water habitats where photosynthesis was not light-limited by aboveground vegetation. Heterotrophy was greatest for open-water habitats with floating and emergent macrophytes due to greater loading of organic C increasing sediment R. The lowest heterotrophy values were for SHMP and OWMF, habitats dominated by periphyton (high GPP) with little vascular plant production (low R). Interestingly, the GPP and R estimates for these oligotrophic habitats are equivalent to values for eutrophic estuaries (Caffrey 2004) and lakes (Lauster et al. 2006). The OWT habitat was the most heterotrophic because of high R values associated with P enrichment increasing floating macrophyte growth rates and organic C loading (Hagerthey et al. 2008). NAP for the vegetative dense eutrophic habitats (TYPHA and SALIX) were intermediate among all the habitats and regulated by R. The lower R values and low O_2 concentrations associated with these habitats indicate that organic C remineralization is controlled by slower anaerobic processes (DeBusk and Reddy 1998).

Our results contradict previous measures of Everglades aquatic metabolism that suggested balanced autotrophy and heterotrophy ($GPP:R \sim 1$) for oligotrophic open-water habitats (Belanger and Platko 1986; McCormick et al. 1997; McCormick and Laing 2003). This difference may simply reflect temporal patterns since the earlier study covered 1979–1985, whereas ours spanned 1996–2005. However, another possible factor may be the diffusive-exchange parameter (D ; Eq. 2) used in the O_2 models to estimate metabolism (Eq. 1), McCormick et al. (1997) applied a diffusion rate on the basis of water depth and a fixed diffusion coefficient of $1.68 \text{ g } O_2 \text{ m}^{-2} \text{ d}^{-1}$ to the entire

1979–1985 data set. Our metabolism estimates assumed a more dynamic diffusion coefficient that varied as a function of the difference between the water-column O_2 concentration and the atmospheric equilibrium concentration and modeled gas exchange as a function of wind speed (Cole et al. 2000).

We tested the influence of a static vs. a dynamic diffusive-exchange parameter on metabolism estimates utilizing a subset of our data. We compared metabolism estimates made using the model of Stephens and Jennings (1976; referred to as the S&J model) following the method of McCormick et al. (1997) with those made using the model of Cole et al. (2000; the Cole model). The subset included 42 sonde deployments for sites and dates that overlapped our study and that of McCormick and Laing (2003) (WCA-2A Sep 1996, Oct 1997, Feb 1998; WCA-1 Jun 1997, Oct 1997, and Feb 1998). There was a moderately good relationship for GPP, with the major differences occurring when GPP was $> 100 \text{ mmol } O_2 \text{ m}^{-2} \text{ d}^{-1}$ (Fig. 7A). The magnitude of GPP difference varied from 0.3 to 3.3. There was a poor relationship for R (Fig. 7B), with the Cole model being twofold greater than the S&J model. Although there was a moderately strong relationship for NAP (Fig. 7C), the Cole model predicted much higher rates of heterotrophic metabolism. $GPP:R$ was likewise strongly related (Fig. 7D), with estimates obtained using the Cole model approximately half those obtained using the S&J model. Since it is unlikely that diffusion would remain constant over time, we believe that the metabolism estimates obtained using a dynamic diffusion coefficient are more accurate and reflective of the environment. Therefore, we believe that aquatic GPP and R in the Everglades are generally not in balance ($GPP:R = 1$), as has been reported (McCormick et al. 1997; McCormick and Laing 2003). Confirmation of the low $GPP:R$ values comes from the actual O_2 concentrations. If $GPP:R$ were consistently ≥ 1 , water-column O_2 would be close to or above the atmospheric saturation concentration. Our data show that daily mean O_2 was below 100% saturation 94% of the time, averaging $49\% \pm 31\%$ saturation (Fig. 3B). The low dissolved oxygen concentration is a direct consequence of the R in excess of GPP.

Drivers—Patterns of O_2 vary across spatial and temporal scales (diel to decades) because of differential effects of drivers (irradiance, temperature, and material flux) on aquatic biological, physical, and chemical processes (Hanson et al. 2006). The spatial patterns along transects (see Web Appendix; McCormick et al. 1997) and among habitats (Fig. 4) reflect the long-term effects of P enrichment (material flux). The seasonal pattern of higher GPP, R, and NAP in the summer-wet season coincides, as expected, with maximal irradiance, temperature, and material flux. However, systemwide and habitat aquatic metabolism estimates varied considerably within and among years and were not well correlated to water quality or environmental variables. It is likely that combinations of these variables interact in complex fashions to directly regulate habitat vegetation biomass, which ultimately regulates GPP and R. We did not measure biomass but

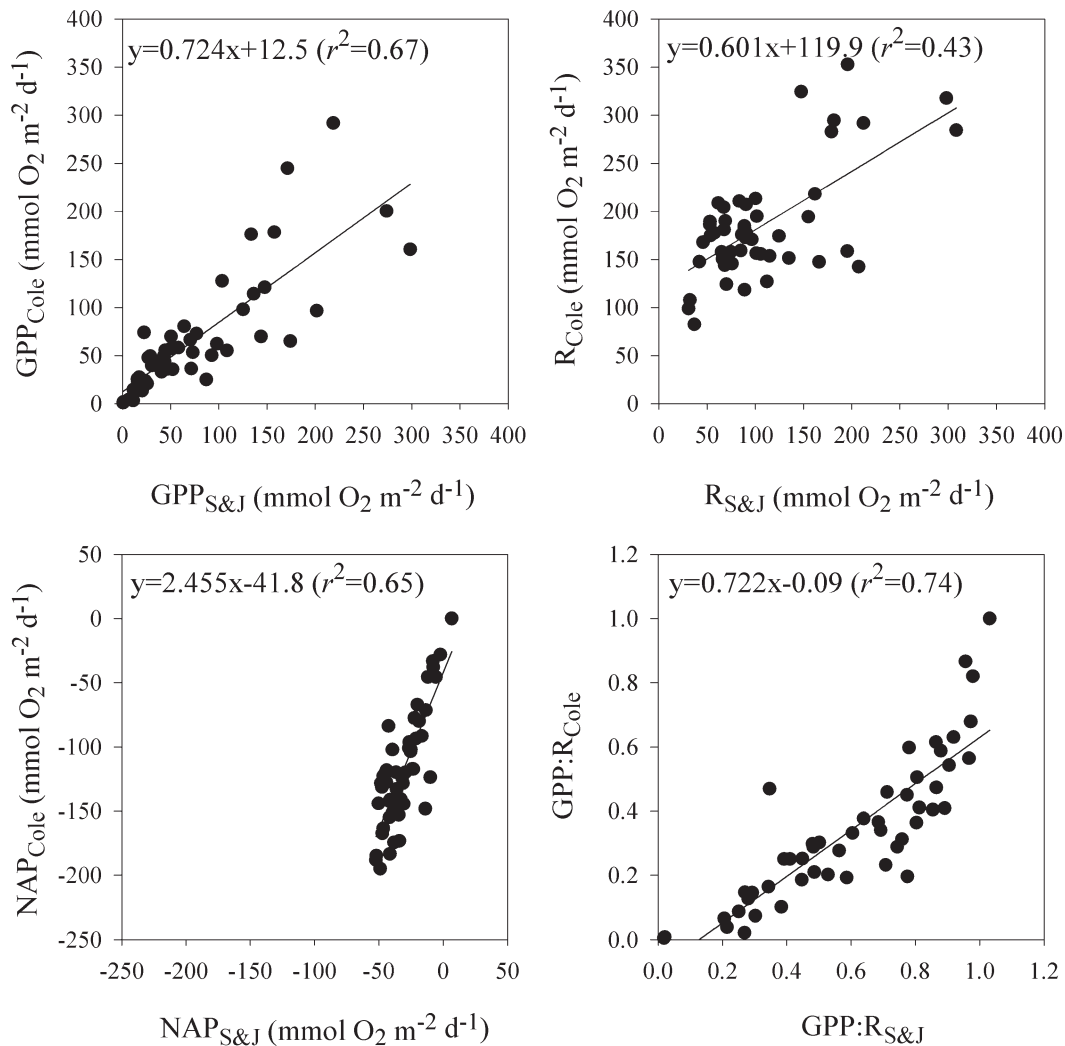


Fig. 7. Comparison of (A) GPP, (B) R, (C) NAP, and (D) production:respiration (GPP:R) obtained using the diel-oxygen models of Stephens and Jennings (1976) and Cole et al. (2000). Models differed only in the assumptions of diffusion.

spatial and short-term (3 yr) surveys of SAV, periphyton, and aboveground vegetation indicated a high degree of variability (Turner et al. 1999; Ewe et al. 2006; Iwaniec et al. 2006). Identifying the ecological drivers operating at intra- and interannual temporal scales for shallow aquatic ecosystems like the Everglades is a difficult task because of a lack of long-term records of biomass and the unresolved complex interactions between the primary drivers (water quality and hydrology). In addition, shallow aquatic ecosystems are more susceptible to extreme climatic events (drought and hurricanes) and time-lag effects between vegetation production and decomposition (i.e., last year's production is this year's decomposition).

Aquatic metabolism is the balance of GPP and R. In most aquatic ecosystems, R is subsidized by allochthonous external sources of C, primarily hydrologic transport of DOC, or from direct input of terrestrial plant material (e.g., leaves and coarse woody debris). In many oligotrophic lakes, heterotrophy persists because the input of allochthonous DOC from the watershed is greater than plankton production. Wetlands, however, are fundamentally differ-

ent in that a significant source C to aquatic metabolism comes from emergent macrophytes or herbaceous vegetation located directly within, or in proximity to (meters), the surface water. Our results indicate that the broad-scale spatial patterns (among habitats) and seasonal temporal patterns in aquatic metabolism can be attributed to differences in the drivers (irradiance, temperature, and material flux). Yet, these same drivers cannot directly account for variability across temporal scales of years, indicating that the complex interactions or extreme events that regulate local ecosystem structure in the Everglades are not well understood. The tendency for R to exceed GPP results in the Everglades having low water-column O_2 concentrations relative to other aquatic ecosystems. The lower O_2 concentrations have a profound effect on the ecosystem by directly affecting biogeochemical processes and restricting faunal diversity. Our results strongly suggest that *Typha* expansion and the loss of slough habitat (Sklar et al. 2005; Hagerthey et al. 2008) have significantly altered the aquatic metabolism of the Everglades by increasing the influx of aboveground autochthonous carbon, reducing

aquatic GPP, and resulting in very low oxygen concentrations. If we are correct, a large-scale *Typha* removal project (underway) will result in dramatically higher oxygen concentrations and higher GPP in the water column.

Acknowledgments

As this study encompassed a decade of environmental monitoring, many individuals contributed to the collection of the data presented here. We single out Paul McCormick, Susan Newman, and David Rudnick, for they conceived the monitoring network. Special thanks go to the numerous field assistants, pilots, and laboratory technicians that labored over the years. Brent Bellinger, Greg Koch, and two anonymous reviewers provided insightful comments that greatly improved the manuscript. We thank Sue Hohner for making the map. Dissolved organic carbon data for Shark River Slough and Taylor Slough were provided by the Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) program.

This material is based upon work supported by the National Science Foundation through the FCE LTER program under grant 9910514.

References

- BELANGER, T. V., AND J. R. PLATKO, II. 1986. Dissolved oxygen budgets in the Everglades WCA-2A. South Florida Water Management District.
- , D. J. SCHEIDT, AND J. R. PLATKO, II. 1989. Effects of nutrient enrichment on the Florida Everglades. *Lake Reserv. Manage.* **5**: 101–111.
- BLINDOW, I., A. HARGEBY, J. MEYERCORDT, AND H. SCHUBERT. 2006. Primary production in two shallow lakes with contrasting plant form dominance: A paradox of enrichment? *Limnol. Oceanogr.* **51**: 2711–2721.
- BROWDER, J. A., P. J. GLEASON, AND D. R. SWIFT. 1994. Periphyton in the Everglades: Spatial variation, environmental correlates, and ecological implications, p. 379–418. *In* S. M. Davis and J. C. Ogden [eds.], *Everglades: The ecosystem and its restoration*. St. Lucie Press.
- BRULAND, G. L., S. GRUNWALD, T. Z. OZBOURNE, K. R. REDDY, AND S. NEWMAN. 2006. Spatial distribution of soil properties in Water Conservation Area 3 of the Everglades. *Soil Sci. Soc. Am. J.* **70**: 1662–1676.
- CAFFREY, J. M. 2004. Factors controlling net ecosystem metabolism in U.S. Estuaries. *Estuaries* **27**: 90–101.
- CARACO, N. F., AND J. J. COLE. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecol. Appl.* **12**: 1496–1509.
- , S. FINDLAY, AND C. WIGAND. 2006. Vascular plants as engineers of oxygen in aquatic systems. *Bioscience* **56**: 219–225.
- COLANGELO, D. J. 2007. Response of river metabolism to restoration of flow in the Kissimmee River, Florida, U.S.A. *Freshwat. Biol.* **52**: 459–470.
- COLE, J. J., AND N. F. CARACO. 1998. Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF₆. *Limnol. Oceanogr.* **43**: 647–656.
- , M. L. PACE, S. R. CARPENTER, AND J. F. KITCHELL. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. *Limnol. Oceanogr.* **45**: 1718–1730.
- , AND OTHERS. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems* **10**: 171–184.
- CORSTANJE, R., S. GRUNWALD, K. R. REDDY, T. Z. OSBOURNE, AND S. NEWMAN. 2006. Assessment of the spatial distribution of soil properties in a northern Everglades marsh. *J. Env. Qual.* **35**: 938–949.
- , K. R. REDDY, J. P. PRENGER, S. NEWMAN, AND A. V. OGRAM. 2007. Soil microbial eco-physiological response to nutrient enrichment in a sub-tropical wetland. *Ecol. Indic.* **7**: 277–289.
- CRONK, J. K., AND W. J. MITSCH. 1994. Aquatic metabolism in four newly constructed freshwater wetlands with different hydrologic inputs. *Ecol. Eng.* **3**: 449–468.
- DAVIS, S. M., L. H. GUNDERSON, W. A. PARK, J. R. RICHARDSON, AND J. E. MATTSO. 1994. Landscape dimension, composition, and function in a changing Everglades ecosystem, p. 419–444. *In* S. M. Davis and J. C. Ogden [eds.], *Everglades: The ecosystem and its restoration*. St. Lucie Press.
- DEBUSK, W. F., AND K. R. REDDY. 1998. Turnover of detrital carbon in a nutrient-impacted Everglades marsh. *Soil Sci. Soc. Am. J.* **62**: 1460–1468.
- , AND ———. 2003. Nutrient and hydrology effects on soil respiration in a Northern Everglades marsh. *J. Env. Qual.* **32**: 702–710.
- , AND ———. 2005. Litter decomposition and nutrient dynamics in a phosphorus enriched Everglades marsh. *Biogeochemistry* **75**: 217–240.
- DEL GIORGIO, P. A., AND R. H. PETERS. 1994. Patterns in planktonic P:R ratios in lakes: Influence of lake trophicity and dissolved organic carbon. *Limnol. Oceanogr.* **39**: 772–787.
- EWE, S., E. GAISER, D. CHILDERS, D. IWANIEC, V. RIVERA-MONROY, AND R. TWILLEY. 2006. Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater–estuarine transects in the Florida Coastal Everglades. *Hydrobiologia* **569**: 459–474.
- GAISER, E. E., D. L. CHILDERS, R. D. JONES, J. RICHARDS, L. J. SCINTO, AND J. C. TREXLER. 2006. Periphyton responses to eutrophication in the Florida Everglades: Cross-system patterns of structural and compositional change. *Limnol. Oceanogr.* **51**: 617–630.
- GOODWIN, K., N. CARACO, AND J. COLE. 2008. Temporal dynamics of dissolved oxygen in a floating leaved macrophyte bed. *Freshw. Biol.* **53**: 1632–1641.
- GOTELLI, N. J., AND A. M. ELLISON. 2004. *A primer of ecological statistics*. Sinauer.
- GRIMSHAW, H. J., AND OTHERS. 1997. Shading of periphyton communities by wetland emergent macrophytes: Decoupling of algal photosynthesis from microbial nutrient retention. *Arch. Hydrobiol.* **139**: 17–27.
- GUTKNECHT, J. L. M., R. M. GOODMAN, AND T. C. BALSER. 2006. Linking soil process and microbial ecology in freshwater wetland ecosystems. *Plant Soil* **289**: 17–34.
- HAGERTHEY, S. E., B. BELLINGER, K. WHEELER, M. GANTAR, AND E. GAISER. *In press*. Everglades periphyton: A biogeochemical perspective. *Crit. Rev. Environ. Sci. Technol.*
- , S. NEWMAN, K. RUTCHY, E. P. SMITH, AND J. GODIN. 2008. Multiple regime shifts in a subtropical peatland: Community-specific thresholds to eutrophication. *Ecol. Monogr.* **78**: 547–565.
- HANSON, P. C., D. BADE, S. R. CARPENTER, AND T. K. KRATZ. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. *Limnol. Oceanogr.* **48**: 1112–1119.
- , S. R. CARPENTER, D. E. ARMSTRONG, E. H. STANLEY, AND T. K. KRATZ. 2006. Lake dissolved inorganic carbon and dissolved oxygen: Changing drivers from days to decades. *Ecol. Monogr.* **76**: 343–363.
- IWANIEC, D. M., D. L. CHILDERS, D. RONDEAU, C. J. MADDEN, AND C. SAUNDERS. 2006. Effects of hydrologic and water quality drivers on periphyton dynamics in the southern Everglades. *Hydrobiologia* **569**: 223–235.

- LAUSTER, G. H., P. C. HANSON, AND T. K. KRATZ. 2006. Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. *Can. J. Fish. Aquat. Sci.* **63**: 1130–1141.
- LOVETT, G. M., J. J. COLE, AND M. L. PACE. 2006. Is net ecosystem production equal to ecosystem carbon accumulation? *Ecosystems* **9**: 152–155.
- MAIE, N., R. JAFFÉ, T. MIYOSHI, AND D. L. CHILDERS. 2006. Quantitative and qualitative aspects of dissolved organic carbon leached from senescent plants in an oligotrophic wetland. *Biogeochemistry* **78**: 285–314.
- MCCORMICK, P. V., M. J. CHIMNEY, AND D. R. SWIFT. 1997. Diel oxygen profiles and water column community metabolism in the Florida Everglades, U.S.A. *Arch. Hydrobiol.* **140**: 117–129.
- , AND J. A. LAING. 2003. Effects of increased phosphorus loading on dissolved oxygen in a subtropical wetland, the Florida Everglades. *Wetlands Ecol. Manage.* **11**: 199–216.
- , P. S. RAWLIK, K. LURDING, E. P. SMITH, AND F. H. SKLAR. 1996. Periphyton–water quality relationships along a nutrient gradient in the northern Florida Everglades. *J. N. Am. Benthol. Soc.* **15**: 433–449.
- , R. B. E. SHUFORD, III, J. B. BACKUS, AND W. C. KENNEDY. 1998. Spatial and seasonal patterns of periphyton biomass and productivity in the northern Everglades, Florida, USA. *Hydrobiologia* **362**: 185–208.
- MCKENNA, J. E., JR. 2003. Community metabolism during early development of a restored wetland. *Wetlands* **23**: 35–50.
- ODUM, H. T. 1956. Primary production in flowing water. *Limnol. Oceanogr.* **1**: 102–117.
- OSBORNE, T. Z., P. W. INGLET, AND K. R. REDDY. 2007. The use of senescent plant biomass to investigate relationships between potential particulate and dissolved organic matter in a wetland ecosystem. *Aquat. Bot.* **86**: 53–61.
- QUALLS, R. G., AND C. J. RICHARDSON. 2003. Factors controlling concentration, export, and decomposition of dissolved organic nutrients in the Everglades of Florida. *Biogeochemistry* **62**: 197–229.
- SKLAR, F. H., AND OTHERS. 2005. The ecological–societal underpinnings of Everglades restoration. *Front. Ecol. Environ.* **3**: 161–169.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry. The principles and practice of statistics in biological research*, 2nd ed. W. H. Freeman.
- STANLEY, E. H., M. D. JOHNSON, AND A. K. WARD. 2003. Evaluating the influence of macrophytes on algal and bacterial production in multiple habitats of a freshwater wetland. *Limnol. Oceanogr.* **48**: 1101–1111.
- STEPHENS, D. W., AND M. E. JENNINGS. 1976. Determination of primary productivity and community metabolism in streams and lakes using diel oxygen measurements. U.S. Geological Survey.
- STERN, J., Y. WANG, B. GU, AND J. NEWMAN. 2007. Distribution and turnover of carbon in natural and constructed wetlands in the Florida Everglades. *Appl. Geochem.* **22**: 1936–1948.
- TORGENSEN, T., AND B. BRANCO. 2007. Carbon and oxygen dynamics of shallow aquatic systems: Process vectors and bacterial productivity. *J. Geophys. Res.* **112**: G03016, doi:10.1029/2007JG000401.
- TURNER, A. M., J. C. TREXLER, F. JORDAN, S. J. SLACK, P. GEDDES, J. H. CHICK, AND W. F. LOFTUS. 1999. Targeting ecosystem features for conservation: Standing crops in the Florida Everglades. *Conserv. Biol.* **13**: 898–911.
- TUTTLE, C. L., L. ZHANG, AND W. J. MITSCH. 2008. Aquatic metabolism as an indicator of the ecological effects of hydrologic pulsing in flow-through wetlands. *Ecol. Indic.* **8**: 795–806.
- WEBSTER, J. R., AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. *Ann. Rev. Ecol. Syst.* **17**: 567–594.
- WETZEL, R. G. 2001. *Limnology: Lake and river ecosystems*. Academic Press.

Associate editor: Luc De Meester

*Received: 14 May 2009
Accepted: 19 October 2009
Amended: 25 November 2009*