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Hydrological Conditions Control P Loading and Aquatic Metabolism in an Oligotrophic, Subtropical Estuary

**Gregory R. Koch · Daniel L. Childers ·
Peter A. Staehr · René M. Price · Stephen E. Davis ·
Evelyn E. Gaiser**

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Abstract Using high-resolution measures of aquatic ecosystem metabolism and water quality, we investigated the importance of hydrological inputs of phosphorus (P) on ecosystem dynamics in the oligotrophic, P-limited coastal Everglades. Due to low nutrient status and relatively large inputs of terrestrial organic matter, we hypothesized that the ponds in this region would be strongly net heterotrophic and that pond gross primary production (GPP) and respiration (R) would be the greatest during the "dry," euhaline estuarine season that coincides with increased P availability. Results indicated that metabolism rates were consistently associated with elevated upstream total phosphorus and salinity concentrations. Pulses in aquatic metabolism rates were coupled to the timing of P supply from groundwater upwelling as well as a potential suite of hydrobiogeochemical interactions. We provide evidence that freshwater discharge has observable impacts on aquatic ecosystem function in the oligotrophic estuaries of the Florida Everglades by controlling the availability of P to the ecosystem. Future water management decisions in South Florida must include the impact of changes in water delivery on downstream estuaries.

Keywords Estuary · Everglades · Hydrology · Metabolism · Phosphorus

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G. R. Koch (✉) · E. E. Gaiser
Department of Biological Sciences and Southeast Environmental Research Center, Florida International University,
Miami, FL 33199, USA
e-mail: gkoch001@fiu.edu

D. L. Childers
School of Sustainability, Arizona State University,
Tempe, AZ 85287, USA

P. A. Staehr
Department of Marine Ecology, National Environmental Research Institute, Aarhus University,
Frederiksborgvej 399,
4000 Roskilde, Denmark

R. M. Price
Department of Earth and Environment and Southeast Environmental Research Center, Florida International University,
Miami, FL 33199, USA

S. E. Davis
Everglades Foundation,
18001 Old Cutler Rd,
Palmetto Bay, FL 33157, USA

Introduction

Estuaries and estuarine wetlands are ecologically and societally important systems, exhibiting high rates of primary production that fuel offshore secondary production (Odum 1968; Nixon 1980; Childers et al. 2000). Because they integrate entire upstream watersheds, estuarine ecosystems are recipients of nutrients and sediments from terrestrial sources (Milliman and Syvitski 1992; Smith and Hollibaugh 1993; Hobbie 2000; Howarth et al. 2002). Childers et al. (2006) suggested that, because of this loading, oligotrophic estuaries may be especially important as reference sites for investigating the effects of eutrophication in the coastal environment. Furthermore, hydrological processes play a central role in shaping estuarine ecosystem structure and function by controlling nutrient loading and the relative contributions of marine and terrestrial influences on the estuary. In this study, we used high-resolution measures of aquatic ecosystem metabolism from an oligotrophic estuary in the Florida Everglades to assess how hydrological conditions control water quality and aquatic ecosystem dynamics by regulating nutrient availability.

The Florida Coastal Everglades Long-Term Ecological Research Program (FCE LTER; http://fce.lternet.edu) has identified the estuarine ecotone of the southern Everglades as a focal point of research because this shallow, topographically flat freshwater–estuarine interface is strongly influenced by seasonal changes in water source and flow (Childers et al. 2006). In the southern Everglades, primary productivity is the greatest in the oligohaline ecotone (Ewe et al. 2006), a transition zone between freshwater sawgrass (*Cladium jamaicense*) marsh- and red mangrove (*Rhizophora mangle*)-dominated scrub forest. Childers (2006) proposed that these relatively higher rates of primary production in the ecotone are supported by dry season increases in the limiting nutrient—phosphorus (P)—that is regulated by the seasonal flushing of freshwater through the system (Childers et al. 2006; Fig. 1). High water column total phosphorus (TP) in the ecotone during the dry season may be derived from a number of sources. Price et al. (2006) show evidence for the discharge of high-P groundwater in the coastal Everglades, while Davis and Childers (2007) indicate internal recycling of P through biotic pathways. In addition, Caraco et al. (1989) demonstrate the potential for abiotic release of P from estuarine sediments. The focus of the FCE LTER program has largely been on wetland processes rather than on open water aquatic processes. Here, we examine the hypothesis of Childers (2006) from an aquatic perspective within the context of the ecotone ecosystem.

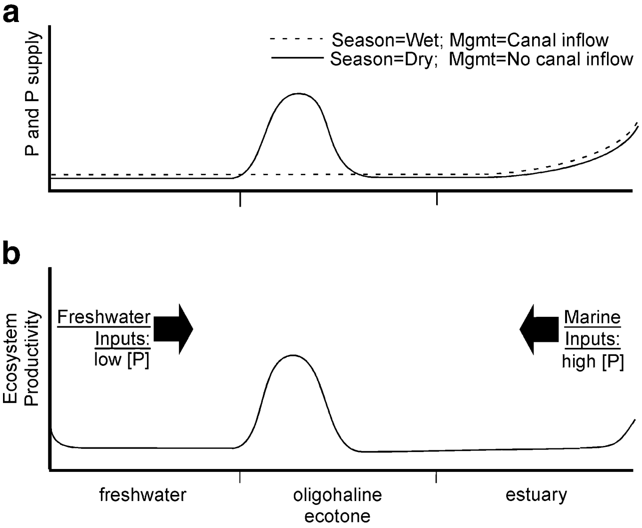

Fig. 1 Conceptual model illustrating the change in P supply and ecosystem productivity across the Southern Everglades landscape. Taylor River and the sites of this study are located within the oligohaline ecotone section of the figure. The freshwater section represents upstream freshwater marshes while the estuary section represents Florida Bay. Marine inputs refer to the Gulf of Mexico. Supply of freshwater to the watershed is controlled by seasonal rainfall and water management decision making. Modified from Childers (2006)

The hydrologic conditions of the Everglades have undergone extensive compartmentalization over the last 100 years that has reduced freshwater flows to the estuaries (Light and Dineen 1994; Sklar et al. 2005). This diminished freshwater delivery to downstream estuaries has resulted in increased salinities in the coastal zone and landward transgression of salt-tolerant vegetation communities (Ross et al. 2000; Gaiser et al. 2006). The Comprehensive Everglades Restoration Plan (www.evergladesplan.org) aims to restore freshwater delivery to Everglades wetlands, ultimately resulting in increased freshwater flow to Everglades estuaries. With successful restoration, the southern Everglades mangrove ecotone should ultimately experience increased flow of freshwater that more closely approximates historical levels. Thus, it is important to understand how Everglades estuaries interact with freshwater inputs in order to guide restoration efforts.

The extreme seasonal and interannual variability in water flow and source in our system affords the opportunity to examine the sensitivity of ecosystem metabolic processes to hydrologic forcing and variable supplies of the limiting nutrient, P. Ecosystem metabolism includes whole system photosynthesis and respiration. Ecosystems with positive net ecosystem production (NEP; or gross primary production (GPP)>ecosystem respiration (R)) are net autotrophic and produce excess organic matter, whereas those exhibiting negative NEP (GPP<R) are net heterotrophic and ultimately depend on allochthonous sources of organic carbon (Odum 1956; Dollar et al. 1991; Smith et al. 1991; Duarte and Prairie 2005). In this study, we investigated the FCE LTER hypotheses regarding P supply and ecosystem productivity as presented in Childers (2006). Specifically, we characterized long-term variation in southern Everglades estuarine water quality as well as spatiotemporal variation of aquatic, whole-ecosystem metabolism. We then evaluated the contribution of seasonally changing water quality drivers to variation in aquatic ecosystem metabolism rates. We hypothesized that ecosystem GPP and R would be the greatest during the dry, euhaline estuarine season coinciding with increased availability of water column P. We further expected to find net heterotrophy (NEP>0) throughout the year, sustained by low productivity and high inputs of allochthonous carbon.

Methods

Site Description

Taylor Slough is one of two major drainage basins within Everglades National Park, Florida, USA (Fig. 2). Histori-

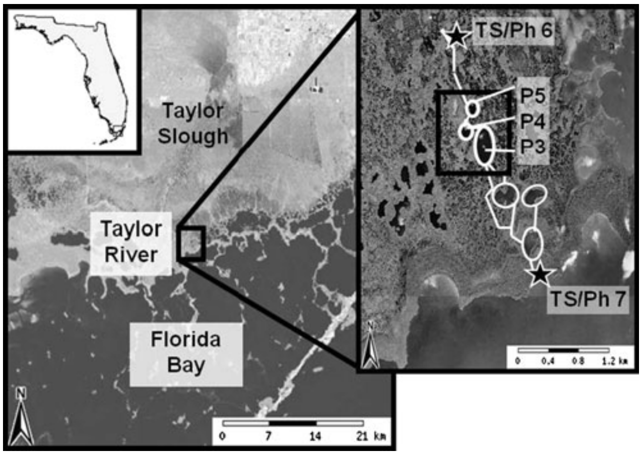

Fig. 2 Satellite imagery showing the location of Taylor River (outlined in *white*) within the Taylor Slough watershed of Everglades National Park. This study was conducted in three ponds (from south to north: pond 3, pond 4, and pond 5) midway between FCE LTER sites TS/Ph-6 (upstream) and TS/Ph-7 (downstream). Note the abundance of small ponds in the southern Everglades landscape

cally, water entered this watershed largely via local precipitation, but the water budget now includes managed canal inputs (Light and Dineen 1994; Childers et al. 2006). Taylor River (the estuarine portion of Taylor Slough) is one of the most important hydrologic connections between Taylor Slough freshwater marshes and northeastern Florida Bay (Davis et al. 2001; Sutula et al. 2003) and is characterized by a series of connected ponds and creeks meandering through extensive scrub mangrove wetlands. We estimated ecosystem metabolism in three centrally located Taylor River ponds: pond 3 (4.69 ha, 25.2035° N, 80.6437° W), pond 4 (0.66 ha, 25.2057° N, 80.6464° W), and pond 5 (0.60 ha, 25.2075° N, 80.6453° W; Fig. 2). These ecosystems, as with the Greater Everglades landscape in general, are P-limited, oligotrophic and very sensitive to changes in P availability (Boyer et al. 1999; Noe et al. 2001; Gaiser et al. 2004). In addition, South Florida's climate is subtropical and marked by a wet season from June through November and a dry season from December through May (Duever et al. 1994). This estuarine system experiences minimal astronomical tide and has minimal topographic relief. The ecotone is a mangrove-dominated basin separated from Florida Bay by the Buttonwood Ridge, a higher elevation coastal berm. Surface water exchange between Taylor River and Florida Bay occurs where the river incises the ridge. Freshwater flows down Taylor River and into Florida Bay during the wet season, while wind-forced excursions of high-salinity Florida Bay water move upriver during the dry season. Surface water in Taylor River is in direct hydraulic connection with groundwater in the underlying Biscayne Aquifer. The Biscayne Aquifer is a karstic, carbonate aquifer, and one of the most permeable aquifers in the world (Fish and Stewart 1991). In the mangrove ecotone region of Taylor River, up to 2 m of peat deposits overly this carbonate aquifer.

Long-Term Hydrologic and Water Quality Variables

Two water quality monitoring stations are located along the reach of Taylor River as part of the FCE LTER Program (TS/Ph 6 and TS/Ph 7) where water quality has been continuously monitored since 1996 (Fig. 2). Here we investigate intra-annual variability in salinity and TP concentrations collected from 1996 to 2010 in Taylor River in order to relate these abiotic drivers to aquatic ecosystem metabolism estimates. Each FCE LTER station has an automated ISCO water sampler to collect samples from the middle of the water column. The data presented here are 1 L water samples integrated either daily (four subsamples collected every 6 h) or tri-daily (four subsamples collected every 18 h; see Childers et al. 2006 for details). Autosamplers were serviced monthly by FCE LTER staff, and unfiltered water samples were returned to the lab for TP and salinity analysis. TP concentrations were determined using the dry ashing/acid hydrolysis technique (Solorzano and Sharp 1980). Salinity was measured using either a refractometer or YSI salinometer (Childers et al. 2006). We also obtained Taylor River discharge data from US Geologic Survey (USGS) gauging stations located near FCE LTER sites. These data are publically available through the USGS South Florida Information Access website (http://sofia.usgs.gov). Lastly, we obtained regional rainfall data from the Royal Palm Ranger Station located in northern Taylor Slough, Everglades National Park. These data are made available through the LTER Network and US Forest Service Climate and Hydrology Database Projects (CLIMDB/HYDRODB; http://www.fsl.orst.edu/climhy). To approximate salinity concentrations at our study sites, which were located in the middle reach of Taylor River between FCE LTER and USGS monitoring stations (Fig. 2), we used the arithmetic mean between upstream and downstream salinity measurements.

Ecosystem Metabolism from Buoy Measurements

We estimated daily GPP, R, and net ecosystem production (NEP=GPP−R) of three ponds in the Taylor River system (Fig. 2) from November 2008 through May 2010. GPP, R, and NEP were determined from free-water, diel changes in dissolved oxygen (Odum 1956; Staehr et al. 2010a). At the center of each pond, we deployed a buoy with sensors measuring dissolved oxygen, water temperature, wind speed, surface irradiance, and underwater PAR. Data were collected continuously at 10-min intervals. Each buoy contained one OxyGuard® 525 membrane dissolved oxygen sensor (OxyGuard International A/S, Denmark), three HOBO® #UA-002-64 underwater temperature and PAR sensors, one HOBO® #S-LIA-M003 surface PAR sensor, and one HOBO® #S-WSA-M003 anemometer attached to a HOBO® #H21-002 micro-station datalogger (Onset Computer Corp., USA) housed within a waterproof case. The dissolved oxygen sensor was powered by a 12-V battery recharged by a solar panel. Buoys were visited monthly to perform sensor cleaning, maintenance, calibration, and data retrieval.

Oxygen concentrations were used to calculate daily volumetric rates (millimoles O_2 per cubic meter per day) of GPP, R, and NEP according to governing equation:

$$\Delta O_2/\Delta t = \mathrm{GPP} - \mathrm{R} - F$$

where $\Delta O_2/\Delta t$ is the change in dissolved oxygen over a known period of time, GPP is gross primary production, R is respiration, and F is diffusive exchange of oxygen between the water column and the atmosphere (Odum 1956). We assumed that no GPP occurs during night and that nighttime R is equal to daytime R. For ease of comparison, we present GPP values as positive and R values as negative. Atmospheric diffusion (F) was modeled as:

$$F = k(O_{2\mathrm{meas}} - O_{2\mathrm{sat}})$$

where k is piston velocity, $O_{2\mathrm{meas}}$ is the measured dissolved oxygen concentration, and $O_{2\mathrm{sat}}$ is the oxygen saturation of the water corrected for both temperature and salinity (Staehr et al. 2010a). Piston velocity is defined as:

$$k = k_{600} \times (Sc/600)^{-0.5}$$

where k_{600} is k for a Schmidt number of 600 and Sc is the Schmidt number for the time step (Jähne et al. 1987). k_{600} was determined from wind speed at 10 m height above the water surface (Cole and Caraco 1998):

$$k_{600} = 2.07 + 0.215(\mathrm{wind}_{10\mathrm{m}})^{1.7}$$

However, since wind measurements are not typically taken at 10 m height, we modeled wind speed at 10 m from wind speed at a known height according to Smith (1985):

$$\mathrm{wind}_{10\mathrm{m}} = \mathrm{wind}_z\left(1.4125\left(z^{-0.15}\right)\right)$$

where wind_z is the wind speed measured at height z. Finally, we derived the Schmidt number (Sc), an indicator of gaseous molecular movement, for each time step from water temperature (Wanninkhof 1992):

$$Sc = 0.0476(T)^3 + 3.7818(T)^2 - 120.1(T) + 1,800.6$$

where T is water temperature (degree Celsius). For a detailed discussion of the calculations and assumptions used to estimate ecosystem metabolism via this method, please refer to Staehr et al. (2010a).

Water Residence Time Estimation

We estimated water residence time (WRT) in estuarine ponds from 1999 to 2009 following the equation:

$$\mathrm{WRT} = A_\mathrm{p} \times Z/(Q + \mathrm{ET} \times A_\mathrm{p})$$

where A_p is the surface area of the pond, Z is water depth, Q is surface water discharge, and ET is evapotranspiration. Pond area was estimated from aerial photography via Google Earth. Pond depth was determined from USGS stage data from site TS/Ph-6; however, USGS stage data are reported as relative to the North American Vertical Datum of 1988 (NAVD88). Since we did not know the elevation of the pond bed relative to NAVD88, we approximated water depth by assuming that the 10-year mean stage was equal to a 1-m water depth. Thus, deviations from the overall stage mean corresponded to equal deviations from 1 m pond depth. We assumed that surface water discharge from the ponds was equal to discharge measured at TS/Ph-6. Finally, we used ET data at nearby Joe Bay obtained from the South Florida Water Management District DBHydro database (http://my.sfwmd.gov/dbhydroplsql/show_dbkey_info.main_menu). Although water loss to groundwater recharge likely occurred at certain times, Taylor River received water input from groundwater over the long term, and this input is captured in TS/Ph-6 discharge rates (Zapata-Rios 2009). Lastly, we also obtained discharge data measured in freshwater Taylor Slough, made available by Everglades National Park, in order to compare managed inputs of freshwater to estimates of estuarine WRT.

Groundwater Sampling

Groundwater samples were collected monthly from June 2008 to June 2009 from four wells at TS/Ph-7 and three wells at TS/Ph-6. The wells were located along transects oriented perpendicular to the main river channel. The wells were constructed from 2.5 or 5 cm diameter PVC pipe and placed to depths of about 0.75 m at TS/Ph-6 and 1.5 m at TS/Ph-7, corresponding with the depth of the peat/limestone interface. A complete description of well construction and locations can be found in Zapata-Rios (2009). Prior to sample collection, each well was purged of at least three-well volumes of water using a peristaltic pump. During that time, specific conductance, salinity, temperature, pH, and dissolved oxygen were monitored in the discharge water until stable readings were obtained using a YSI-85 meter. Samples were then collected into helium-purged and vacuum-sealed collection bags to preserve the anoxic state of the groundwater. We stored samples on ice for immediate transport to the Southeast Environmental Research Center nutrient laboratory at Florida International University for TP analysis according to Solorzano and Sharp (1980).

Statistical Analyses

We summarized Taylor River surface water hydrologic and nutrient variables by calculating arithmetic means for each month in the 1996–2010 FCE LTER dataset. In addition, we calculated an overall monthly mean across all sampled years (e.g., one mean for all January data, etc.). In order to reduce short-term noise and because the data used this study were collected at differing frequencies, all data were also summarized into weekly arithmetic means for statistical comparison. We tested all data for normality using Shapiro–Wilk tests. Differences between upstream vs. downstream stations and wet vs. dry seasons were then tested using either Student's *t* tests on normally distributed data or Mann–Whitney rank sum tests on non-normal data. In order to test for significant seasonal differences in measured variables, we defined "wet" season as occurring when surface water salinities were at or near zero (September–February) and "dry" season as all other times (March–August). This is in contrast to the conventional wet/dry distinctions based on rainfall in South Florida (May–November=wet season and December–April=dry season; Duever et al. 1994). Our adjusted seasonal demarcation is more closely linked to the timing of seasonal freshwater pulses through the estuary.

Relationships between metabolic, physical, and chemical variables were examined using Pearson's correlation analysis. We explored controls on the variation in estuarine metabolism rates using multiple regression analysis; however, time series data commonly violate regression assumptions about the independence of data points. After testing for the presence of autocorrelation within the time series using Durbin–Watson tests, we used an autoregressive model that accounts for autocorrelation (Proc Autoreg using SAS 9.2, SAS Institute Inc., USA). The autoregressive model is nearly identical to ordinary multiple regression models except that significant relationships between previous data points within the time series may be included as parameters in the model. Thus, variation is explained that would otherwise be attributed to model error and the model gains predictive power. Correcting for autocorrelation in regression models has been used in the statistics and economics fields for decades (e.g., Durbin 1960; Beach and MacKinnon 1978) but has gained increasing use in ecological studies in recent years (e.g., Carpenter et al. 1998; Lichstein et al. 2002; Staehr et al. 2010b). We used a backward stepwise autoregressive model to identify and include only significant orders of autocorrelation. It should be noted that in this procedure "stepwise" refers to the elimination of insignificant orders of autocorrelation in the model and not to the elimination of insignificant model predictors. We initially included a suite of independent predictor variables in the regression model based on the results of the correlation analysis. We then iteratively removed insignificant predictors one at a time and the model with the lowest corrected Akaike's Information Criterion (AICc; Burnham and Anderson 2002) was selected. Occasionally, removal of an insignificant predictor variable caused deterioration in model AICc. In these cases, we chose to include the insignificant predictor if it did not show antagonistic effects with the other predictors in the model. Model parameters were determined using maximum likelihood estimation. Both correlation and regression analyses were performed on weekly means of variables for each pond as well as for a combined mean across all ponds. We used α=0.05 to determine significance for all statistical tests in this study.

Results

Long-Term Water Quality Patterns

Taylor River discharge rates exhibited temporal variability closely matching variation in rainfall with exceptionally wet years having elevated rates of discharge and exceptionally dry years have depressed rates of discharge (e.g., 1999 vs. 2004, Fig. 3a). Discharge at the upstream TS/Ph 6 site ranged from −0.3 to 0.8 m^3/s, with a 14-year mean of 0.3 m^3/s. At the downstream TS/Ph 7 site, discharge ranged from −0.7 to 5.5 m^3/s and averaged 1.1 m^3/s. Discharge was significantly higher at the river mouth (TS/Ph-7) than at the upstream gauge (TS/Ph-6; p<0.0001) as downstream TS/Ph-7 integrated more of the mangrove wetland ecotone and was the only local cut through the Buttonwood Ridge. In addition, estuarine discharge rates showed a repeating, seasonal pattern with the highest discharge rates occurring 1–2 months after peak regional rainfall (Fig. 3a). Examining intra-annual patterns in discharge using polar plots showed that the highest discharge rates at both sites consistently occurred during September–February while the lowest discharge rates at both monitoring sites occurred during May (Fig. 4a, b).

Interannual variability in salinity was similar to patterns in precipitation and discharge (Fig. 3b). Unlike discharge rates, however, both TS/Ph 6 and TS/Ph 7 exhibited similar magnitudes of change in salinity each year: salinity at TS/Ph 6 ranged from 0.0 to 46.6 psu with a mean of 8.7 psu, while salinity at TS/Ph 7 ranged from 0.0 to 46.5 psu with a mean of 14.2 psu. Polar plot analysis revealed that the highest salinity concentrations in Taylor River surface water

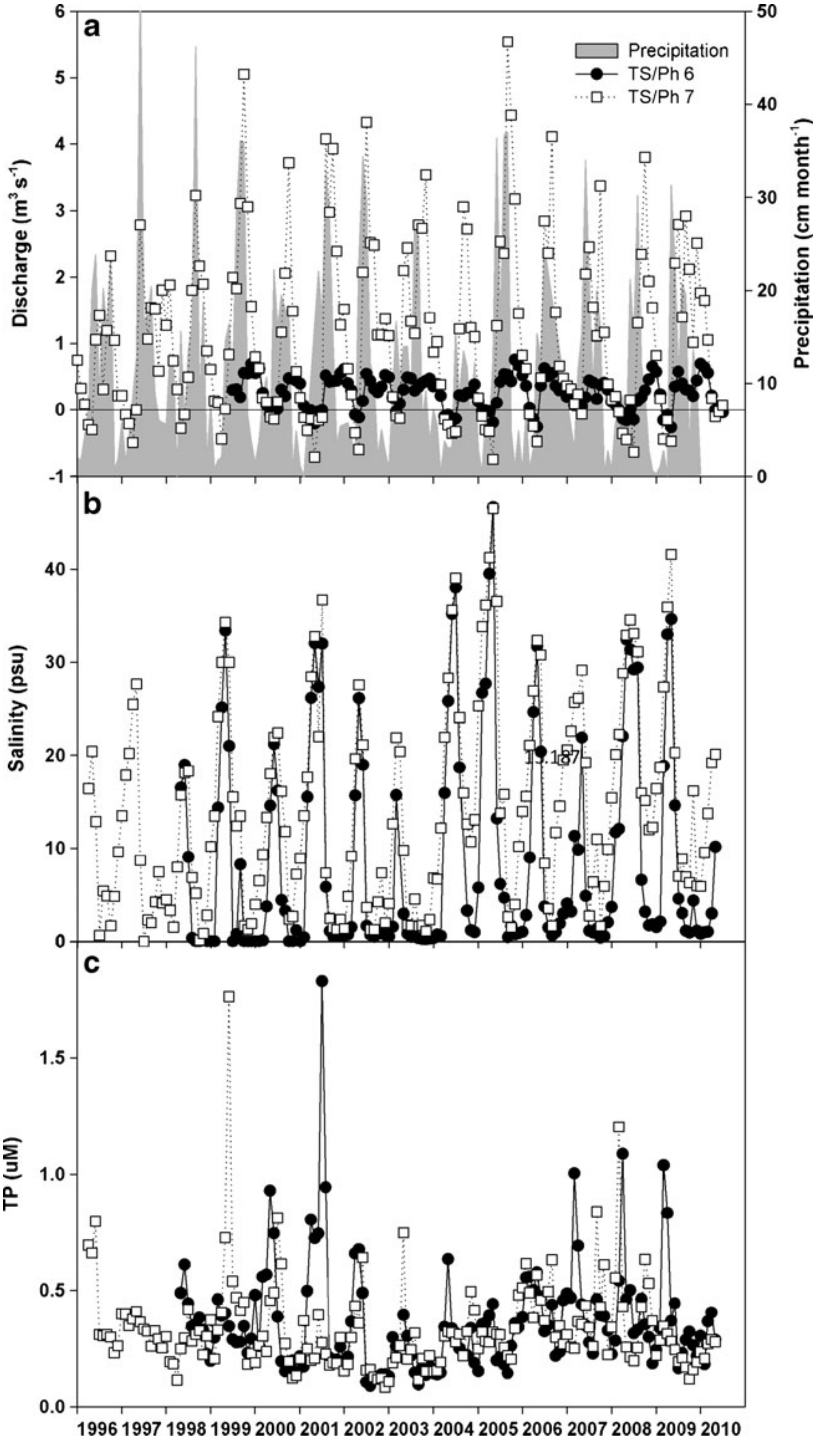

Fig. 3 Monthly mean discharge (cubic meters per second, **a**), salinity (practical salinity units, **b**), and TP (micromolars, **c**) data from sites TS/Ph-6 (*filled circles*) and TS/Ph-7 (*open squares*). Monthly total precipitation data (centimeters per month, **a**) were measured at the Royal Palm station in Taylor Slough, north of Taylor River

occurred from March through August when discharge rates were the lowest (Fig. 4c, d).

Total P concentrations were generally below 0.5 μM although we did observe higher TP values at both sites during exceptionally dry years (Fig. 3c). Total P at the upstream TS/Ph 6 site ranged from 0.1 to 1.8 μM with a mean of 0.4 μM while TP at TS/Ph 7 ranged from 0.1 to 1.8 μM with a mean of 0.3 μM. Median TP concentrations at the two sites were not significantly different; however, from the polar plots it is clear that TP at upstream TS/Ph 6 exhibited a larger seasonal range and variability than TP at downstream TS/Ph 7 (Fig. 4e, f). While mean water column TP was relatively

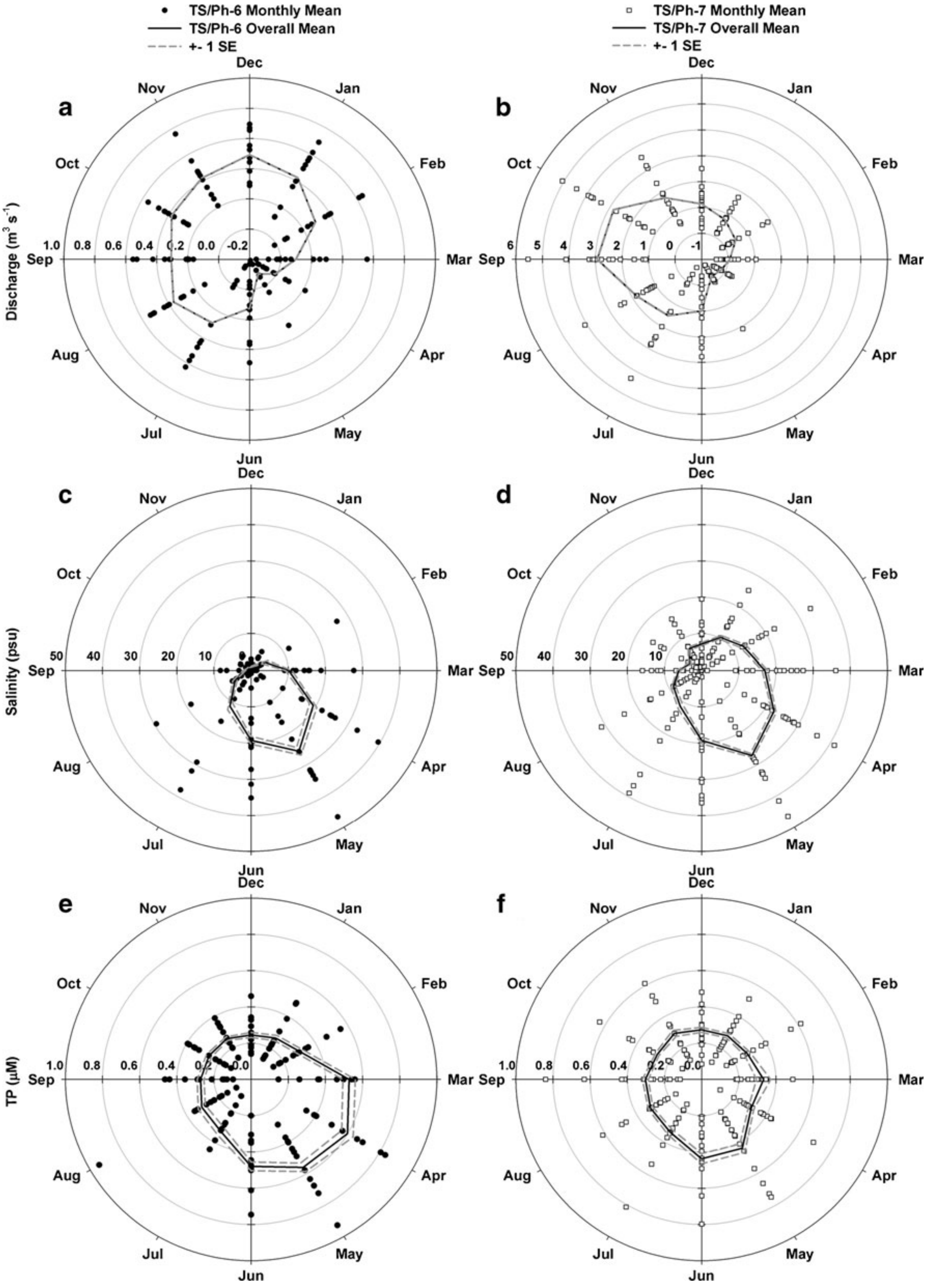

Fig. 4 Polar plots of monthly mean discharge (cubic meters per second; **a**, **b**), salinity (practical salinity units; **c**, **d**), and TP (micromoles per liter; **e**, **f**) data from sites TS/Ph-6 (*filled circles*, *left column*) and TS/Ph-7 (*open squares*, *right column*) for the years 1996–2010. The *solid black line* in all plots indicates an overall monthly mean for the data record with *gray dashed lines* indicating ±1 SE of the overall mean. Months progress clockwise around the plot. Magnitude of data points is represented by radial distance from the center of the plot

consistent throughout the year at TS/Ph 7, TP was the highest during the dry season at the TS/Ph 6 site.

Ecosystem Metabolism Dynamics

Aquatic ecosystem GPP in Taylor River showed a clear seasonal pattern during 2008–2010 (Fig. 5a). Gross primary production was the highest during the nutrient rich 2009 dry season while the 2010 dry season showed a similar but smaller peak in ecosystem GPP. Furthermore, GPP was the lowest during the 2009 wet season. Ecosystem R followed a temporal pattern similar to that of GPP (Fig. 5b), with a baseline rate of roughly 100–200 mmol $O_2 m^{-3}$ day^{-1}. Respiration was much more variable during the 2010 dry season than during preceding periods of the study. We found sustained net heterotrophy (GPP<R; NEP<0) in all three Taylor River ponds throughout the study period (Fig. 5c). There was a brief period of net autotrophy (GPP>R; NEP>0) during January 2010 that coincided with the passage of a cold front across South Florida that reduced water temperature below 10°C, with a minimum of 7.9°C. The switch from heterotrophic to autotrophic conditions was related to a reduction in pond respiration (from ~200 to 100 mmol $O_2 m^{-3}$ day^{-1}) during a simultaneous period of enhanced GPP (from >100 to 200 mmol $O_2 m^{-3}$ day^{-1}).

Patterns in whole system metabolism were surprisingly pond-specific (Table 1). Pond 3 and pond 4 GPP was negatively correlated with surface irradiance (I_0) while pond 5 GPP was positively correlated with I_0. Salinity and TP concentration were positively correlated with GPP in pond 4 and pond 5 but not with GPP in pond 3. Phosphorus flux estimates were negatively correlated with GPP in pond 4 and pond 5. Furthermore, watershed P retention was positively correlated to GPP in pond 5 but not correlated to GPP in pond 3 or pond 4. Combined average pond GPP was positively correlated with I_0, salinity, upstream [TP], and *P* retention, while negatively correlated to both upstream and downstream P fluxes. Ecosystem R was positively correlated with GPP in pond 4 and pond 5 but not correlated with GPP in pond 3. Respiration was also positively correlated with salinity and upstream [TP] across all ponds as well as with temperature and downstream [TP] in pond 3 and pond 5. Respiration was negatively correlated with both upstream and downstream P fluxes in pond 4 and pond 5 but positively correlated with P retention in pond 5. When the ponds were combined, R was positively correlated with GPP, I_0, temperature, salinity, upstream [TP], and P retention while negatively correlated with P fluxes from both upstream and downstream. Net ecosystem production was positively correlated with GPP in ponds 3 and 5 and negatively correlated with R in all ponds. Net ecosystem production was negatively correlated with salinity in ponds 3 and 4. In addition, NEP was negatively correlated with both I_0 and temperature in pond 3 and pond 5. In addition, NEP was negatively correlated with upstream [TP] only in pond 3. Combined NEP was negatively correlated to R, I_0, salinity, and temperature.

The ability of environmental driver variables to predict variation in metabolism rates was also pond-specific (Table 2). In pond 3, GPP was best predicted using both I_0 and salinity; however, I_0 was the only significant contributor to GPP variation. In contrast, pond 4 GPP was best predicted from upstream (TS/Ph-6) TP concentration, with salinity and upstream TP flux included as insignificant predictors. Salinity and water temperature were significant predictors of pond 5 GPP although upstream [TP] was also included. Salinity and temperature best explained variation in GPP combined across all ponds. Models of ecosystem R always included GPP as a significant predictor at all ponds. In pond 3, R was best explained by temperature, GPP, upstream [TP], salinity, and downstream [TP]. The best pond 4 R model included GPP, salinity, and upstream [TP]. In pond 5, R was best modeled as a function of salinity, GPP, temperature, upstream P flux, and upstream [TP]. Regression analysis on combined R data revealed that GPP, temperature, salinity, upstream P flux, and upstream [TP] were the best predictors of R across all ponds. NEP was best predicted by temperature and upstream [TP] in pond 3, while the best model of pond 4 NEP included salinity, upstream [TP], and I_0. Pond 5 NEP was best predicted by temperature, upstream P flux, salinity, and upstream [TP]. Finally, NEP combined across all ponds was best predicted by temperature, salinity, upstream P flux, and upstream [TP].

Water Residence Time

Estimates of WRT in estuarine Taylor River ponds were consistently between 1 and 5 days (Fig. 6). Pond size was directly related to WRT, with the largest pond (pond 3) exhibiting the longest residence times. Furthermore, WRT increased in all ponds during dry season months. This seasonal effect was most pronounced in larger ponds as well as during years with very low freshwater flow within the Taylor Slough watershed (e.g., 2001, 2004, and 2007).

Groundwater Dynamics

Groundwater salinity values were 20–30 psu at both TS/Ph-6 and TS/Ph-7 from June 2008 through June 2009 (Fig. 7a, b), and annual groundwater and surface water salinity medians were not significantly different from each other at either site. Similarly, groundwater salinity did not

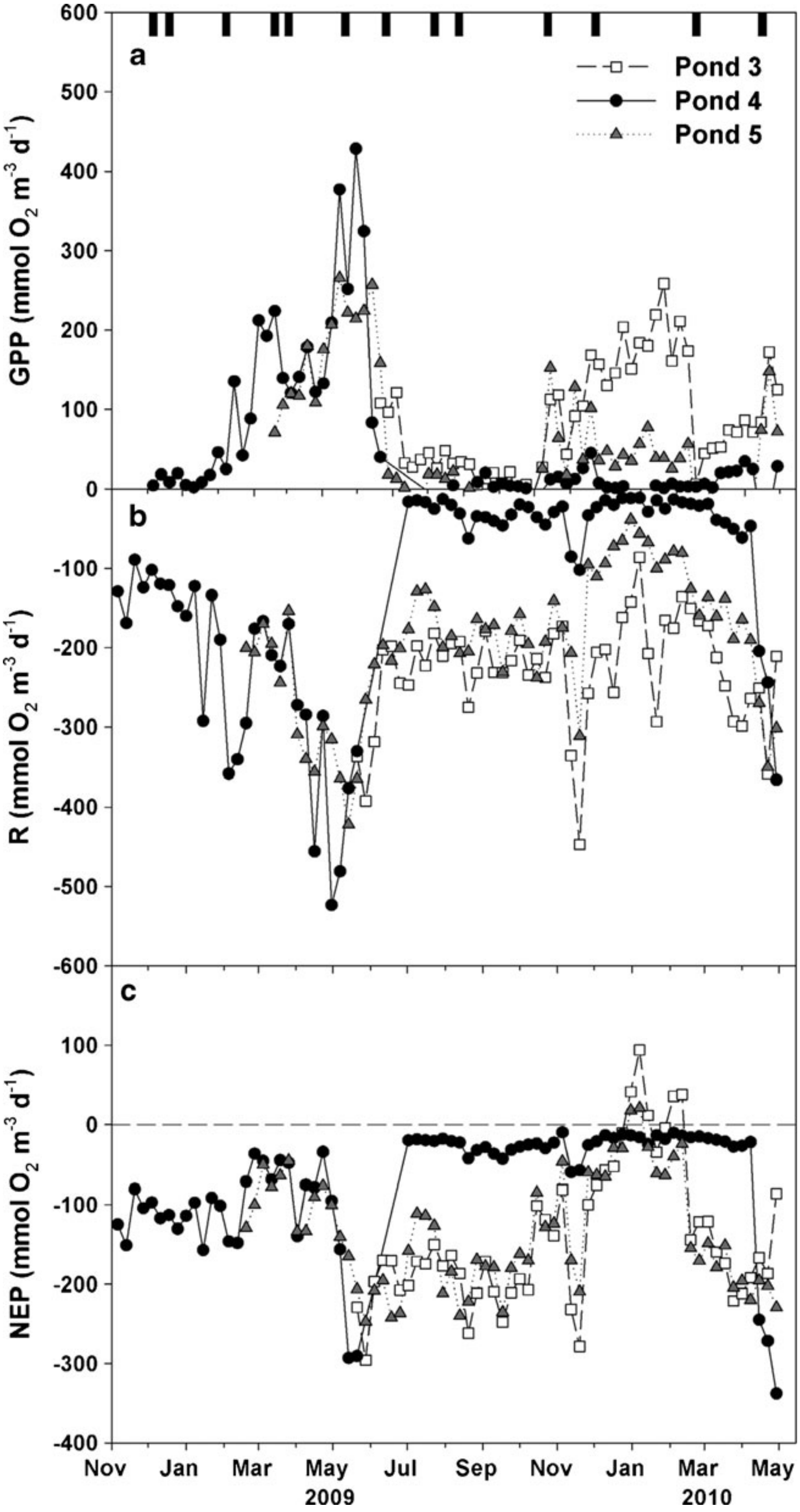

Fig. 5 GPP (**a**), *R* (**b**), and NEP (**c**) from Taylor River ponds 3 (*open squares*), 4 (*black circles*), and 5 (*gray triangles*). Metabolism components are reported as weekly means of daily, volumetric rates (millimoles O_2 per cubic meter per day). *Black bars at the top of the figure* indicate calibration dates

exhibit significant seasonal differences at either site, but we found significant seasonal shifts in surface water from hypersaline to oligohaline conditions both upstream (p= 0.008, n=5) and downstream (p<0.001, n=5).

Groundwater TP concentrations at TS/Ph-6 were significantly higher compared with surface water TP (p=0.011, n= 10; Fig. 7c, d), but this pattern was not found at TS/Ph-7. No significant seasonal difference in TP concentrations were

Table 1 Pairwise Pearson correlation coefficients between metabolism rates (GPP, R, NEP) and environmental driving variables: I_0 = surface irradiance, Temp = water temperature at 50cm depth, $\mathrm{Wind}_{10\mathrm{m}}$ = wind speed at 10m above the water surface, salinity, TP concentration measured at upstream TS/Ph-6 and downstream TS/Ph-7, upstream and downstream flux of P, and P retention (upstream flux−downstream flux). Correlation analyses were performed using weekly means of variables

		I_0	Temp	$\mathrm{Wind}_{10\mathrm{m}}$	Salinity	TS/Ph-6 [TP]	TS/Ph-7 [TP]	TS/Ph-6 P flux	TS/Ph-7 P flux	P retention	*R*	NEP
Pond 3 (*n*=51)	GPP	−0.60***	−0.60***	0.27	0.04	0.09	0.07	0.14	−0.10	0.16	0.11	0.68***
	R	0.17	0.40**	−0.07	0.57***	0.51***	0.17	−0.06	−0.25	0.26	–	−0.66***
	NEP	−0.58***	−0.75***	0.31*	−0.40**	−0.32*	−0.08	0.16	0.11	−0.07		–
Pond 4 (*n*=75)	GPP	−0.44***	0.05	0.38***	0.75***	0.65***	0.21	−0.45***	−0.34*	0.20	0.82***	−0.19
	R	0.42***	0.10	0.43***	0.82***	0.44***	0.27*	−0.42**	−0.36*	0.19	–	−0.72***
	NEP	0.18	−0.11	−0.18	−0.50***	−0.00	−0.20	0.18	0.19	0.53		–
Pond 5 (*n*=65)	GPP	0.31*	−0.03	0.42***	0.78***	0.57***	0.28*	−0.57***	−0.59***	0.30*	0.63***	0.32*
	R	0.64***	0.51***	0.27*	0.78***	0.38*	0.28*	−0.33**	−0.48***	0.27*	–	−0.53***
	NEP	−0.47***	−0.66***	0.13	−0.08	0.14	−0.03	−0.19	−0.07	0.00		–
Combined (*n*=75)	GPP	0.32**	−0.08	0.45***	0.74***	0.57***	0.11	−0.43***	−0.41***	0.27*	0.71***	0.16
	R	0.55***	0.37***	0.32**	0.83***	0.44***	0.12	−0.30**	−0.38***	0.25*	–	−0.58***
	NEP	−0.41***	−0.62***	0.08	−0.30**	0.05	−0.04	−0.08	0.05	−0.02		–

$^*p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$

detected in groundwater at either site, and surface water TP concentration only differed between seasons at TS/Ph-7 (p= 0.043, n=5).

Discussion

We combined high-resolution measures of aquatic ecosystem metabolism with water quality data to investigate the importance of hydrological inputs of the limiting nutrient P on ecosystem dynamics in an oligotrophic estuary of the Florida Everglades. Specifically, we characterized long-term variation in Taylor River water quality as well as temporal and spatial variations in aquatic, whole-ecosystem metabolism estimates. We then evaluated the contribution of seasonally changing water quality drivers to variation in aquatic ecosystem metabolism rates. When we began this study, we expected that metabolic rates would be the highest during times of the year when P concentrations were the highest because this system is P-limited.

Taylor River Metabolism

Ecosystem metabolism dynamics often differed among study ponds in Taylor River. For example, in pond 3, surface irradiance was the only significant contributor to GPP variation in the multiple regression analysis (Table 2), and the two variables were inversely correlated (Table 1). This relationship contrasted with positive correlation between irradiance and GPP averaged across all ponds and is opposite from the intuitive relationship between primary production and light availability. Similarly, while TP concentrations both upstream and downstream of our study sites were always positively correlated with GPP, this relationship was not significant for all ponds and TP was not included in the pond 3 and combined pond GPP multiple regression models. Salinity concentration, however, was a common predictor of GPP in our estuarine ponds. Models of pond R and NEP were less pond-specific and included a broader range of significant predictors than the models of GPP. For example, GPP, salinity, and upstream TP concentration were significant predictors of R in all ponds, while temperature was included in three out of the four R models. Similarly, pond NEP was frequently predicted by temperature, salinity, and upstream [TP]. The best models of pond GPP often explained much less variation than the best models of R and NEP in the same ponds. This suggests that GPP was much more spatially and temporally heterogeneous than either R or NEP. In oligotrophic Everglades ecosystems, such as the ponds in Taylor River, ecosystem productivity is highly sensitive to changes in

Table 2 Results of multiple autoregression analysis of environmental driver contributions to variability in estuarine metabolism rates. The autoregression model accounted for significant autocorrelation in the time series. Analysis was performed on weekly means of variables: *n*=number of weeks in the dataset, Temp=water temperature at 50 cm depth (degree Celsius), I_0=surface irradiance (microeinstein per square meter per second), TP 6=water column total phosphorus concentration at site TS/Ph-6 (micromolars), TP 7=water column total phosphorus at TS/Ph-7 (micromolars), P Flux 6=upstream phosphorus flux (micromoles per second), P Flux 7=downstream phosphorus flux (micromoles per second), P Ret=watershed phosphorus retention (micromoles per second), β_0=intercept of the model, r^2_{tot} = total r^2 statistic of the multiple autoregression model. Bold text indicates significance at a=0.05. Estimates of included autoregressive parameters are included in the online Supplementary Table 1

Site	GPP			R			NEP		
	Variable	Coefficient	r_{tot}^2	Variable	Coefficient	r_{tot}^2	Variable	Coefficient	r_{tot}^2
Pond 3 (*n*=51)	I_0	**−0.2202**	0.61	Temp	**10.5917**	0.80	Temp	**−12.9011**	0.82
	P Ret	0.0552		GPP	**0.5365**		TP 6	**−104.3610**	
	β_0	**204.5005**		TP 6	**164.0096**		I_0	−0.0322	
				Salinity	**4.0920**		β_0	**246.4977**	
				TP 7	**−205.3590**				
				β_0	**−129.8467**				
Pond 4 (*n*=75)	TP 6	**120.2600**	0.84	GPP	**0.9365**	0.94	Salinity	**−5.8703**	0.89
	Salinity	0.2131		Salinity	**6.1279**		TP 6	**108.8477**	
	P flux 6	−0.0001		TP 6	**−98.6709**		I_0	**0.1682**	
	β_0	−5.9737		β_0	**55.7995**		β_0	**−134.1827**	
Pond 5 (*n*=65)	Salinity	**4.4661**	0.70	Salinity	**4.7776**	0.82	Temp	**−8.3451**	0.76
	Temp	**−4.7191**		GPP	**0.5203**		P flux 6	**−0.1806**	
	TP 6	21.5845		Temp	**6.9354**		Salinity	**−3.1520**	
	β_0	**111.4480**		P flux 6	**0.1659**		TP 6	**58.7651**	
				TP 6	**−63.4286**		β_0	**108.6221**	
				β_0	−66.6672				
Combined (*n*=75)	Salinity	**4.0413**	0.77	GPP	**0.8010**	0.88	Temp	**−6.2458**	0.81
	Temp	**−3.3252**		Temp	**5.6011**		Salinity	**−4.1998**	
	β_0	**103.0369**		Salinity	**5.2138**		P flux 6	**−0.1387**	
				P flux 6	**0.1575**		TP 6	**46.9847**	
				TP 6	**−50.2415**		β_0	**87.4668**	
				β_0	**−69.2966**				

the availability of P (Gaiser et al. 2004). Thus, it is not surprising that water column total phosphorus concentration was present in nearly all our models of ecosystem metabolism. Interestingly, even though [TP] was directly related to metabolism, estimates of P flux were inversely related ecosystem metabolism in Taylor River (Table 1).

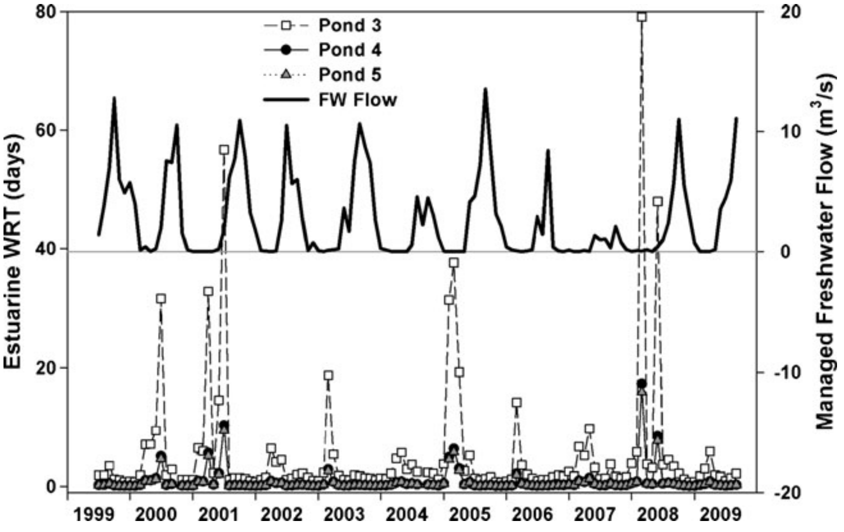

Fig. 6 Monthly estimates of estuarine water residence time in pond 3 (*open squares*), pond 4 (*black circles*), and pond 5 (*gray triangles*) from 1999 to 2009. Discharge rates (*black line*) were measured upstream in freshwater Taylor Slough near human-managed water control structures

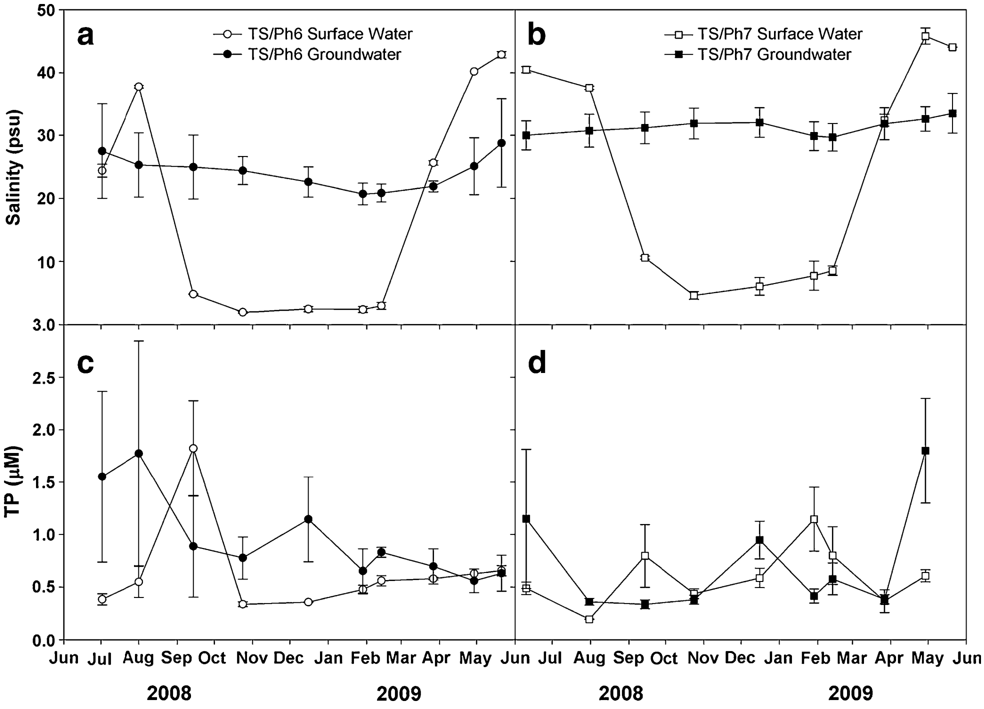

Fig. 7 Mean groundwater concentrations of salinity (practical salinity units; **a**, **b**) and TP (micromolars; **c**, **d**) measured from wells at sites TS/Ph-6 (*circles*, *left*) and TS/Ph-7 (*squares*, *right*) from June 2008 to May 2009. Groundwater means are denoted by *filled, black symbols* and surface water means are denoted by *open, white symbols*. Error bars represent ±1 SE

Given the P-depauperate conditions of the southern Everglades, these P fluxes were largely governed by variability in water discharge rather than in P concentration. Thus, periods of high P flux coincided with high rates of surface water flushing during the wet season. The stronger relationship between metabolism and [TP], as opposed to P flux, emphasizes the importance of nutrient concentrations rather than bulk nutrient load to ecosystem function in Taylor River. Furthermore, the similar omnipresence of salinity as a significant driver of ecosystem metabolism suggests that salinity can indicate the timing of P availability to the Taylor River estuary.

The specific morphological and hydrological characteristics of each pond drive some of the observed differences in pond metabolism models. For example, pond 4 lies at a unique location where the Taylor River channel turns 90° to the east before turning southwards again at pond 3 (Fig. 2). In addition, the surface water inlet and outlets are located solely in the northeastern portion of pond 4. As a result, the northeastern section of pond 4 experiences significantly more water flow than the remainder of the pond. Thus, the relative inactivity that we observed in pond 4 metabolism during much of this study may indicate that our buoy was stationed at a particularly stagnant location in the pond that only mixes with the main river channel surface water during the strongest dry season hydrological forcings. Indeed, our estimates from pond 4 showed periods of relatively low metabolic rates in November–December 2008, just before the 2009 dry season signal and during the 2009–2010 wet season. Ponds 3 and 5 were most similar both hydrologically and metabolically, in that each are situated through direct southerly flow and the metabolism of each exhibited similar temporal variability.

Although each of the ponds included in this study have different hydrodynamic and morphological characteristics, the variable influence of environmental drivers on pond production rates may reflect the varying deployment dates of instrumented buoys in each pond. For example, measurements in pond 3 began just after the large 2009 dry season productivity pulse observed in ponds 4 and 5. The 2010 dry season was much shorter than that in 2009. As a result, the window of observed metabolism in pond 3 was largely during the 2009–2010 wet season when TP and salinity were the lowest. Furthermore, this low productivity continued into the summer months when solar irradiance was the highest. Thus, during periods of a small seasonal signal, we found minimal connections between GPP and TP or salinity. In pond 5, where our buoy deployment fully captured both the 2009 and 2010 dry seasons, we observed strong, positive relationships between GPP and irradiance, TP, and salinity. In contrast, pond R and NEP appeared largely unaffected by differential buoy deployment. The regression model of pond 3 R was nearly identical to that of R in pond 5.

We observed net heterotrophy (GPP<R, NEP<0) in the open water ponds of the Taylor River estuary throughout our study period. Net heterotrophy has also been found in freshwater Everglades wetlands (Hagerthey et al. 2010) as well as other freshwater (Cole et al. 2000; Hanson et al. 2003; Sand-Jensen and Staehr 2009) and estuarine ecosystems (Flores-Verdugo et al. 1988; Smith et al. 1991; Smith and Hollibaugh 1993; Pradeep Ram et al. 2003; Duarte and Prairie 2005; Gupta et al. 2008). This heterotrophic activity must be driven by an allochthonous source of fixed carbon to subsidize aquatic ecosystem respiration. In the coastal Everglades, several researchers have investigated the potential for freshwater marsh-derived detritus to subsidize downstream estuaries. While Jaffé et al. (2001) showed that estuarine detritus contained a mix of upstream and downstream sources, more recent work has pointed toward local mangrove wetlands as the source of this organic carbon (Mead et al. 2005; Neto et al. 2006). These researchers repeatedly cited the mobility of Everglades detritus as a challenge to identifying its source and fate within the estuary. Thus, mobile wetland-produced detritus may ultimately collect in the numerous ponds within the southern Everglades ecotone where it would fuel the heterotrophy we observed.

Seasonality in the Coastal Everglades

The Greater Everglades landscape, spanning freshwater and estuarine wetlands, is characterized by very low water column P concentrations as a result of a unique combination of biogeochemical, climatic, geological, and hydrological factors (Noe et al. 2001). Consequently, Everglades ecosystems are P-limited and extremely sensitive to P inputs (Boyer et al. 1999; Noe et al. 2001; Gaiser et al. 2004). Thus, Childers (2006) proposed that ecosystem productivity in the southern Everglades ecotone should reflect availability of P. Instead of a sustained peak in ecosystem productivity in the coastal Everglades ecotone, fueled by elevated dry season P, we found that aquatic GPP showed high seasonal fluctuations (Fig. 5). Upstream [TP] was correlated to GPP in two of our three ponds (Table 1) and was a frequent predictor of pond metabolism in our multiple regression models (Table 2). Seasonal fluctuations in estuarine water column primary production have been observed in both temperate estuaries (Alpine and Cloern 1992; Mallin et al. 1993; Smith and Hollibaugh 1993) and tropical estuaries (Flores-Verdugo et al. 1988; Valiela et al. 1997; Pradeep Ram et al. 2003; Souza et al. 2009). Usually, these seasonal differences were explained by regional rainfall and river discharge patterns that supply the estuary with the limiting nutrient. In contrast to these examples, however, we observed elevated ecosystem GPP during periods of low rainfall, low river discharge, high salinity, and high [TP]. This is because the limiting nutrient, P, is not supplied to "upside-down" Everglades estuaries from a terrestrial source (Childers et al. 2006); instead, these estuaries obtain P from a combination of marine and groundwater sources (Childers 2006). However, marine P does not reach the southern Everglades because it is first sequestered by Florida Bay (see Fig. 2).

Source of Phosphorus to Taylor River

The southern Everglades and the Taylor River estuary are micro-tidal and are hydrologically uncoupled from the Gulf of Mexico (GOM) by Florida Bay; therefore, these estuarine systems are much more oligotrophic than Everglades estuaries with a direct tidal connection to P from the GOM (Childers et al. 2006). Yet, in 14 years of water quality sampling, we observed repeated seasonal increases in water column TP within Taylor River that coincided with dry season increases in water column salinity. Price et al. (2010) found that high-salinity groundwater intruding into a carbonate aquifer can mobilize carbonate-bound P from bedrock and possibly be an important source of P to the Everglades ecotone region when low surface water levels allow groundwater upwelling, such as during the southern Florida dry season. Our observations revealed that Taylor River groundwater remained saline (~30 psu) throughout our 2008–2009 sampling and that the high groundwater salinity was consistent with the extent of seawater intrusion in the Biscayne Aquifer in the region (Fitterman et al. 1999; Price et al. 2003, 2006). Zapata-Rios (2009) used a water balance approach to show that groundwater discharge to Taylor River was the greatest between May and July. This coincided with the highest rates of groundwater discharge that we observed in May 2009. Our estimates of ecosystem metabolism also showed the greatest ecosystem GPP at this time, providing evidence that saline groundwater upwelling, P supply from groundwater, and aquatic ecosystem function are tightly coupled (Price et al. 2006; Childers 2006).

Taylor River groundwater TP concentrations were variable in space and time and did not follow a seasonal pattern. Groundwater at our upstream TS/Ph-6 site revealed TP concentrations at or above 1 μM throughout much of the 2008–2009 sampling period, despite surface water TP rarely exceeding 1 μM in more than 14 years of FCE LTER water quality monitoring in Taylor River. Groundwater sampled farther downstream at TS/Ph-7 rarely exceeded 1 μM TP. Although groundwater discharge rates were higher at TS/Ph-7, closer to the coast (Zapata-Rios 2009), this did not translate into higher P concentrations in the surface water in that region. Zapata-Rios (2009) reports an average groundwater discharge rate of 5.1 mm/day at TS/Ph-6 from May–June 2009 and 18.3 mm/day at TS/Ph-7 from March–June 2009. Applying these discharge rates across a 1-m^2 area and multiplying by TP concentrations for the same time periods presented in this study (0.63 and

0.56 μM) results in estimates of average groundwater P fluxes of 3.2 and 10.2 μmol/day at TS/Ph-6 and TS/Ph-7, respectively. Total P concentration and flux estimates from TS/Ph-6 were more strongly related to observed rates of pond metabolism than identical metrics from downstream TS/Ph-7. Thus, although groundwater discharge and flux estimates at TS/Ph-6 are smaller in magnitude than those downstream at TS/Ph-7, these smaller rates, fueled by higher TP concentrations, have a greater impact on Taylor River surface water quality and aquatic ecosystem metabolism.

In addition to groundwater, P is being supplied to the Taylor River aquatic system via internal, biotic sources. Red mangrove (*R. mangle*) roots in our study system have been shown to tap into groundwater at the peat–limestone interface (about 1 m deep; Ewe et al. 2007). Davis and Childers (2007) showed that decomposition of mangrove litter increased water column TP in controlled experiments, but that this process was limited by the availability of labile carbon. Thus, groundwater P may first be "mined" by mangroves and then transferred to the aquatic system as senesced leaves where it is remineralized in ponds and creeks. Organic matter produced by phytoplankton is often highly labile (Biersmith and Benner 1998), and the addition of labile OM to oligotrophic Taylor River ponds could stimulate decomposition—so-called "priming"—of more refractory substrates, such as mangrove leaves. The primed remineralization of P from mangrove biomass would therefore be accelerated when autochthonous pond production is elevated during the dry season. Although the concept of respiratory priming originated in terrestrial ecosystems, Guenet et al. (2010) recently reviewed evidence suggesting that this effect may also apply to freshwater and marine environments. Lastly, solutes are concentrated in Taylor River during the dry season as a result of high evaporation and low precipitation rates. High estuarine water residence time during the dry season would amplify the effects of these processes by increasing the time that all of these processes are in contact with surface water, further increasing observed TP concentrations.

In an analysis of P dynamics in sediments of 48 different aquatic ecosystems, Caraco et al. (1990) found that, under oxic conditions, freshwater sediments tended to immobilize P while marine sediments tended to release P. Release of P from marine sediments has been linked to the depletion of iron—and subsequent desorption of P—as a result of sulfate reduction (Schindler 1985; Caraco et al. 1989, 1993). In addition, saline water has been shown to release P bound to calcium carbonate (Price et al. 2010). In Taylor River, the interannual oscillation from freshwater to hypersaline conditions could thus enable a corresponding pulse of P from estuarine sediments. Temporal variability in sulfate concentrations and its specific interaction with P availability should be an important topic of future research in Everglades estuaries.

It is likely that these hydrologic, biotic, and abiotic factors all contribute towards observed TP dynamics in Taylor River. These mechanisms can interact to form a positive feedback in which the appearance of elevated water column P stimulates the production of labile, autochthonous carbon, which in turn primes the remineralization of additional P from mangrove biomass. This effect would be most pronounced in the upstream reaches of Taylor River, where groundwater upwelling is the strongest, and during the dry season, when water residence times are the highest. The positive feedback loop is then stabilized by the wet season flushing of precipitation- and management-derived surface water through Taylor River. Thus, water management and restoration activities in the Everglades have a large potential to influence estuarine ecosystem function.

Conclusions

This study showed a repeated, seasonal increase in surface water P concentrations that coincided with diminished surface water discharge rates and increasing salinity concentration within the Taylor River estuary of the Florida Everglades. During the estuarine "dry" season, high aquatic ecosystem metabolism rates were consistently associated with elevated upstream total phosphorus and salinity concentrations. Pulses in aquatic metabolism rates were coupled to the timing of P supply from groundwater upwelling as well as a potential suite of hydrobiogeochemical interactions. We provide evidence that freshwater discharge has observable impacts on aquatic ecosystem function in the oligotrophic estuaries of the Florida Everglades by controlling the availability of P to the ecosystem. Future water management decisions in South Florida must include the impact of changes in water delivery on downstream estuaries.

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